

A REVISION OF THE FAMILY LEEACEAE

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SUMMARY

A world wide revision of the family with a general discussion of the systematic position, the affinities within the family, the morphology of leaves, flowers, and seeds, the chromosome number, and the geographic distribution. Types of ruminant endosperm of the seed, previously unknown in the family, are illustrated and new types of pearl glands of the leaves are described. A single genus with 34 species is recognized, 32 of which occur in the Indo-Malesian area and 2 are restricted to the Afro-Madagascan area. One new species from New Guinea is described. There is a key to all species, followed by descriptions of the non-Malesian ones and full synonymy of all taxa together with distribution data. A complete revaluation of specific characters has resulted in a new concept of the species, many forms and local species no longer being maintained.

TAXONOMIC HISTORY

The *Leeaceae* were first assigned to family rank by Dumortier (1829) who removed De Candolle's tribe from the *Ampelideae* to form a new family. The type and only genus is *Leea* (1767) with *L. aequata* L. as the type species. The genus is named in honour of James Lee (1715—1795), a horticulturist who founded a nursery at Hammersmith, London, and was, together with William Malcolm, among the first to cultivate *Leea* in Europe, as early as 1767. Collections from these early cultivated specimens are preserved in the British Museum. The earliest pre-Linnean literature on the genus is by Rheede (1678/9), who was

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the first to describe and illustrate the genus under the name *Nalugu*. Rumphius (1743) described and figured two species from Amboin; these taxa are now known as *L. aculeata* and *L. aequata*.

SYSTEMATIC POSITION OF THE FAMILY

The family is placed in the *Rhamnales* in the system of Engler (1964) and is closely allied to the *Vitaceae*; in the system of Bentham and Hooker (1862) the families composing this order are classified with the *Celastrales*. Evidence from floral anatomy supports the close relationship of the families included in the *Rhamnales*. *Leeaceae* is segregated from the *Vitaceae* on account of the development of a complex staminodial tube joined to a choripetalous corolla, the locules of the ovary each having 1 ovule. Pollen evidence supports a segregation from the *Vitaceae*, but seed and embryo structures point to a close relationship to that family as does the presence of pearl glands. Airy Shaw (in Willis, 1966) suggests a distant affinity with the *Staphyleaceae*, a family previously included in the *Rhamnales*. Earlier workers have proposed a relationship to *Dilleniaceae* (Hess, 1936) on account of affinities in the wood anatomy.

AFFINITIES WITHIN THE GENUS

The genus was divided by Clarke (1881) into two series based on the colour of the flower, each series being further subdivided into sections containing one or more typical species. This classification may be summarized as follows:

Series	Sections	Typical species
<i>Rubriflorae</i> (flowers red)	<i>Edgeworthiae</i>	<i>L. alata</i>
	<i>Laetae</i>	<i>L. laeta</i>
	<i>Rubrae</i>	<i>L. rubra</i>
<i>Viridiflorae</i> (flowers green)	<i>Pycnoneurae</i>	<i>L. crispa</i>
	<i>Paucifoliolosae</i>	<i>L. macrophylla</i>
	<i>Sambucinae</i>	<i>L. sambucina</i>
	<i>Aequatae</i>	<i>L. aequata</i>

The sections erected by Clarke correspond to groups of closely related species but there are insufficient characters to form separate formal sections. The division of the genus into two series based on flower colour is also not satisfactory and more important characters are to be found in the staminodial tube. In practice there are no further characters which can be used to separate the series, and flower colour, if not noted by the collector, is often difficult to discern in the herbarium. Thus *L. trifoliata* was originally classified in the *Edgeworthiae*, but later Clarke (1899) found that it had green flowers. It is now considered to be synonymous with *L. compactiflora* (*Sambucinae*), *L. bracteata* (*Aequatae*) being a later synonym. In manuscript notes on herbarium sheets Clarke himself adds that he considered *L. wightii* (*Rubrae*) to be a form of *L. acuminata* (*Laetae*). The arrangement is unreliable and apparently never was satisfactory for the species known and described by the author.

Burtt (1935) suggested that the genus might be subdivided into types with 5-merous flowers and those with 4-merous flowers, a suggestion which at first sight appears most practicable as the Philippine taxa with mostly complex seed types would then be segregated from the rest of the genus as a distinctive group. However, this would also include

L. tetramera from the Solomon Islands, but recent collections of this species have 4- and 5-merous flowers in the same inflorescence. No formal divisions of the genus are recognized in the present work, the species being viewed as having complex multispatial relationships with each other as is also indicated by evidence from the seed types and the leaf epidermal structure.

MORPHOLOGY

Habit. Trees, shrubs, creeping or erect, or herbaceous plants with a woody base, with many species found in secondary vegetation but some are confined to the understorey of primary rain forest. In areas of seasonal drought some taxa are reported to die back to a woody base in the dry season.

Root structures. Root tubercles are common in *L. thorelii*, a species occurring in savannah vegetation. Small root swellings are also to be seen on the creeping rootstock of *L. simplicifolia*.

Leaves.

1. Leaf composition (cf. fig. 10). Formerly considerable importance was placed on the leaf composition, different species being erected for unifoliolate, simply pinnate, or multi-pinnate forms which had other vegetative and floral characters in common. In the present survey the composition of the leaves has been found to be extremely variable in most species and it is therefore frequently not a reliable character for specific distinction. The most extreme case is to be found in *L. thorelii*, where all intermediates from trifoliolate to multi-pinnate leaves may be observed on one plant. In some taxa, however, the leaf form is remarkably constant as far as is known. The widespread and frequently collected *L. aculeata* is always represented in the herbarium with simply pinnate leaves. In other taxa one leaf form may be predominant, e.g. in *L. philippinensis* simply pinnate leaves occur in the majority of collections, multi-pinnate leaves are rarely represented. In many cases it would appear that the position of the leaf in the sequence of phyllotaxis and the age of the plant may well influence leaf composition. The lower leaves are frequently less divided than the upper ones. In areas with a seasonally dry climate other factors, such as burning and seasonal die-back, also operate. The leaf composition will thus vary according to habitat and ecological conditions; apparently annually produced leaves are simple, whilst more perennial leaves are pinnate and are only produced on plants growing in more humid shrubberies. Unfortunately, these features were overlooked by earlier collectors working in these areas and contributing the majority of herbarium material of these species. Where such a range of leaf forms occurs, measurements for the unifoliolate types are given separately.

2. Leaf reduction. Reduction in the size of the lower leaflets of a pinnate leaf may be seen in scattered collections of many taxa. It may commonly be observed in *L. compactiflora* where the reduction to a trifoliolate leaf has previously been noted in the literature. In the present investigation, all states of leaf division from unifoliolate through trifoliolate to 2-pinnate have been observed in *L. crispa*. Reduction to a unifoliolate leaf form may be visualized by observing the situation in *L. magnifolia*. In the majority of collections there is a pair of structureless foliar outgrowths at the apex of the stipule and in rare cases these are developed as highly reduced leaflets.

3. Seedling development. Observations on authenticated seedling states are only known for three species: *L. aquatica*, *L. indica*, and *L. guineensis*. The first two species have been illustrated by Burger (1972) whilst *L. guineensis* is represented by a herbarium speci-

men, Tollez 203 (P), of a three months old seedling. In this specimen the first six leaves are unifoliolate, the sixth being 13 cm long by 9 cm wide, the 7th and 8th are trifoliolate. Thus, so far as is known, the usual sequence in the seedling is: unifoliolate, trifoliolate, pinnate to imperfectly bi-pinnate. Observations on herbarium material often show a similar range of variation. This range of variation of leaf form may be seen in *L. thorelii* where usually the whole plant is collected, but it can also be observed in isolated collections from other taxa. It seems certain that under certain ecological conditions precocious flowering may occur before the plant attains the mature leaf form; this occurs undoubtedly in *L. thorelii*. Many taxa have been described on the basis of the leaf form and usually the unifoliolate or trifoliolate examples are rare in the herbarium. In almost all cases there are no floral differences to be found between species based on these leaf forms and other well-known pinnate-leaved taxa. In this work these are interpreted as juvenile-leaved forms with precocious flowering. Further field observations are required on these points.

4. Leaf structures. The leaf margin is usually serrate to repand, each major serration bearing a mucilaginous gland which is particularly conspicuous in the young leaves. In most species so-called pearl glands may be found along midrib and minor veins; these are early caducous. In addition to the well-known globular pale type of *L. aequata*, some new stellate, thick types have been detected and also depressed subglobose types. In some species they are sofar only known from the stipules and young inflorescences, and in others they are completely unknown. In the latter case it seems probable that they are rapidly caducous and have been lost in drying procedures, or the material is not of a suitable age to detect them.

5. Petiolar stipules. The stipular structures originating from the highest petiole are adpressed together and form a sheath surrounding the stem apex. As the next leaf begins to grow the stipules are forced apart and remain as torn structures or soon drop off, leaving a scar on the petiole. Lateral buds, developing in the old leaf axils, are also protected by stipules, but here no leaf lamina is seen to develop. The subsequent developmental stages of these lateral shoots have not been observed. It is possible that the ancestral form of stipule is most closely approximated by the long, narrow, winged form in which the stipule extends the whole length of the petiole. This becomes reduced in length to give rise to the more persistent, short, obovate type, the shift being associated with a change of habitat from forest to secondary regrowth where the latter type predominates. The shape and form is often of diagnostic value when combined with other, floral and vegetative, features (fig. 1—4). The stipules are usually ignored by collectors and as a consequence poorly represented in the herbarium collections. Thus, nothing is known about the seasonal variation of these structures according to the age of the apex, nor of the range of possible geographical variation. Further collections with stipules are required for most taxa.

Inflorescence. The inflorescence is a leaf-opposed cyme bearing bracts at the various nodes. Usually these are small deltoid-triangular structures, but in some species they are conspicuous and well-developed. Basically the axis of the inflorescence may be viewed to branch pseudo-dichotomously up to 5 times, each main branch bearing about the same number of lateral branches, these in turn with further lateral branches, the ultimate one bearing the flowers. Such a system produces a large broad inflorescence. Condensation of this structure generally occurs by reduction of the degree of dichotomous branching and continues further by the suppression of all but the lowest main lateral branches. This gives rise to a peduncle bearing 3 branches: a condensed main axis and two lateral branches, all of similar length. Further condensation of the ultimate branches gives rise to the condensed

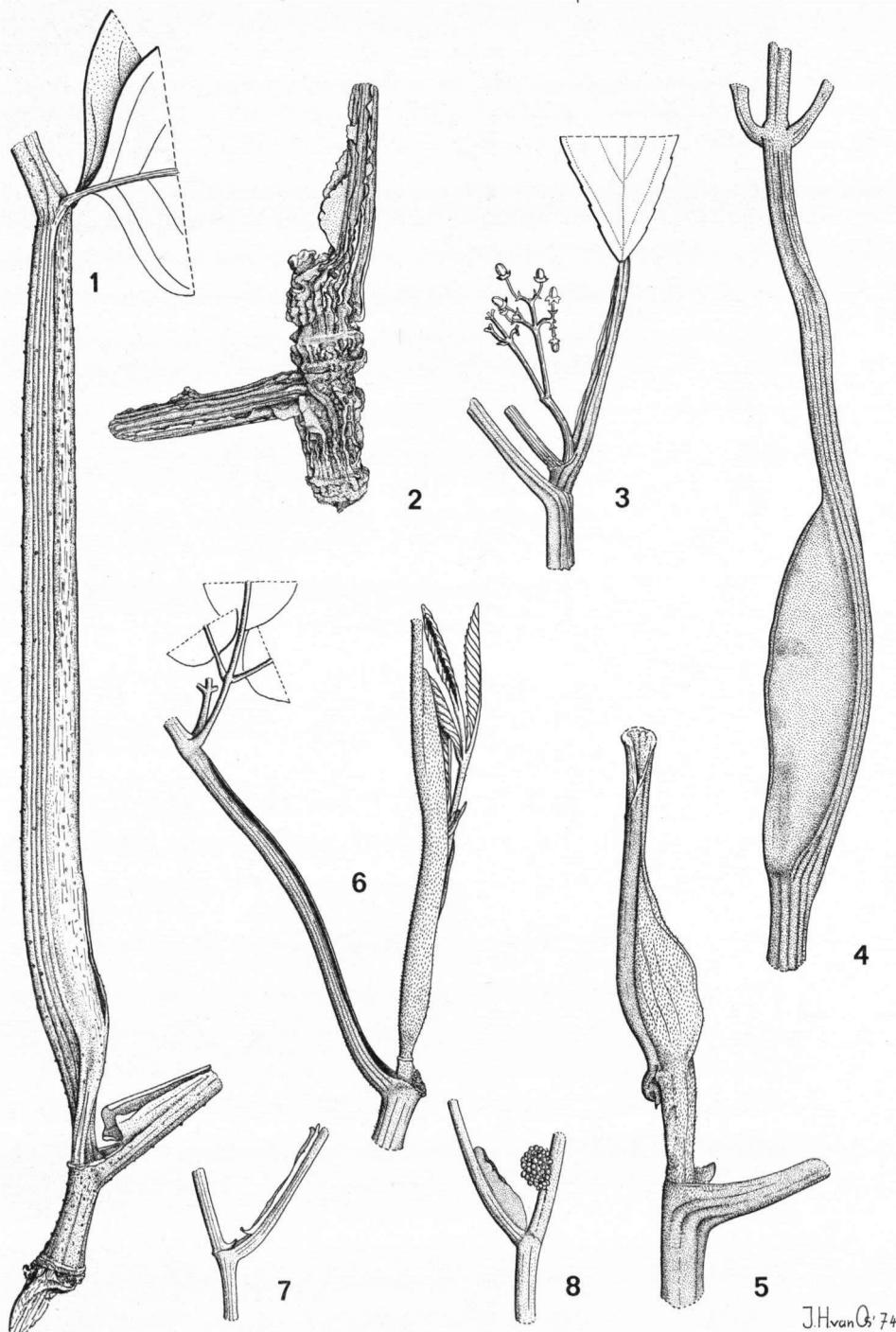
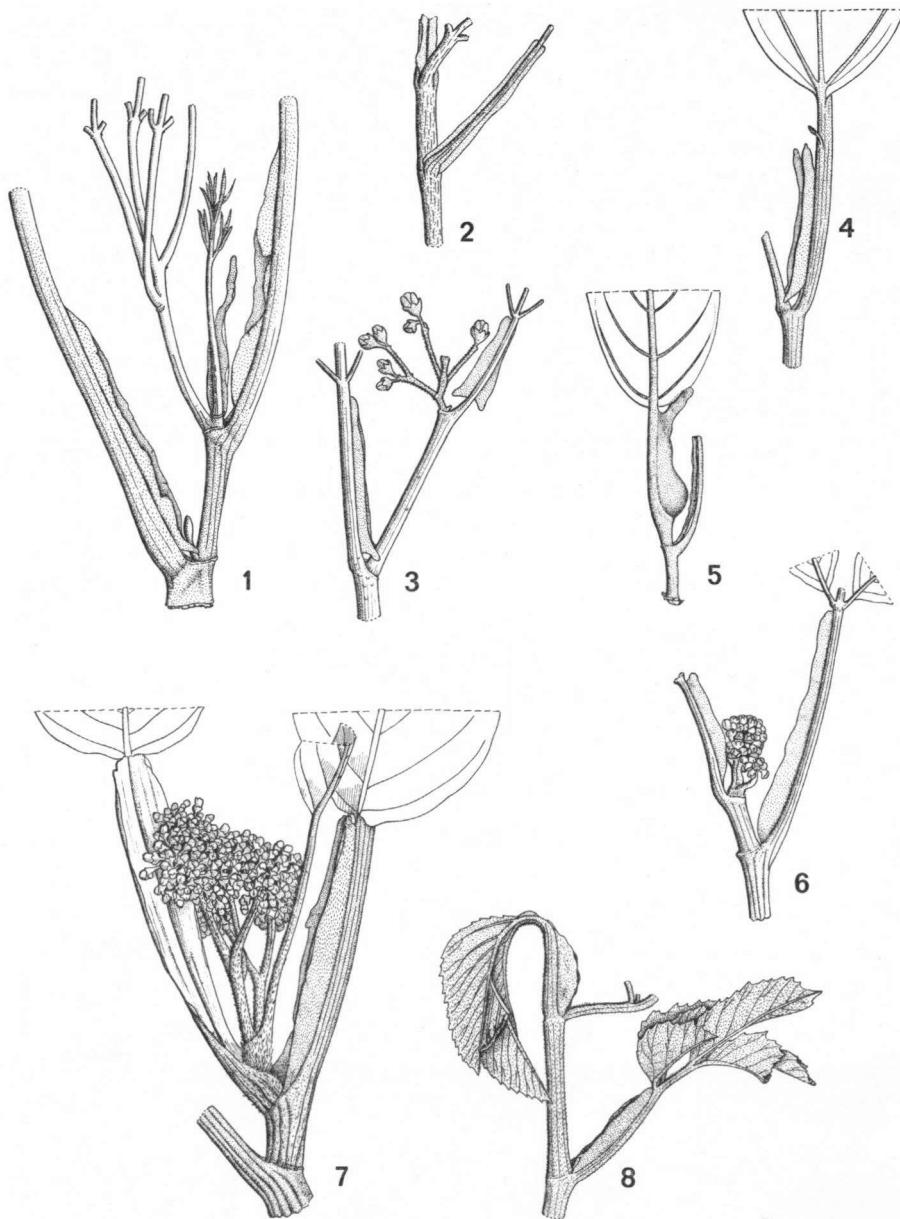


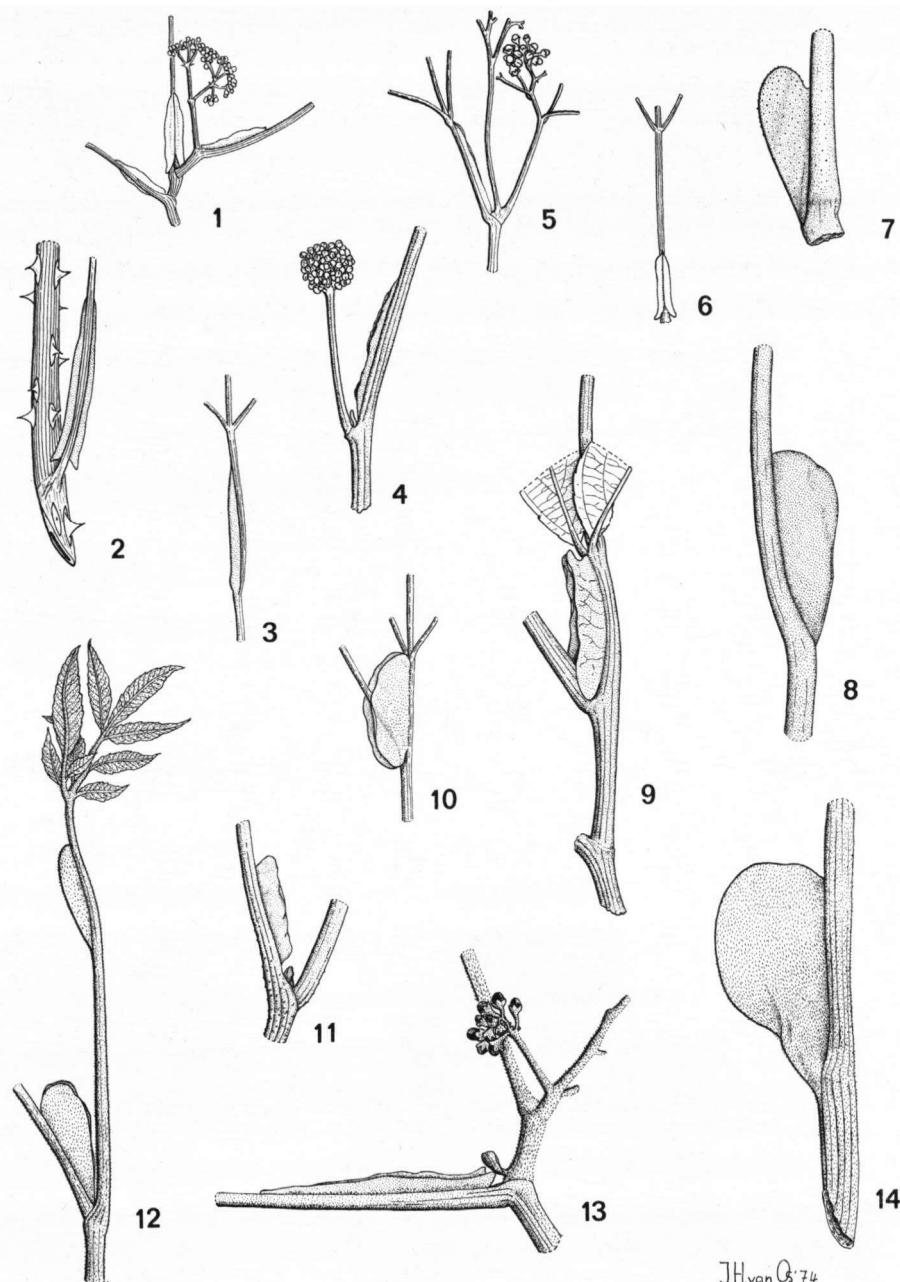
Fig. 1. Stipules of *Leea*. — 1. *L. papuana* (Pullen 5436); 2. *L. heterodoxa* (BW 3405); 3. *L. zippeliana* (van Royen & Sleumer 7270); 4. *L. coryphantha* (NGF 31590); 5. ditto (van Leeuwen 9333); 6. *L. tetramera* (NGF 31590); 7. ditto (BSIP 11244); 8. *L. simplicifolia* (Kerr 7535). All $\times \frac{1}{2}$.

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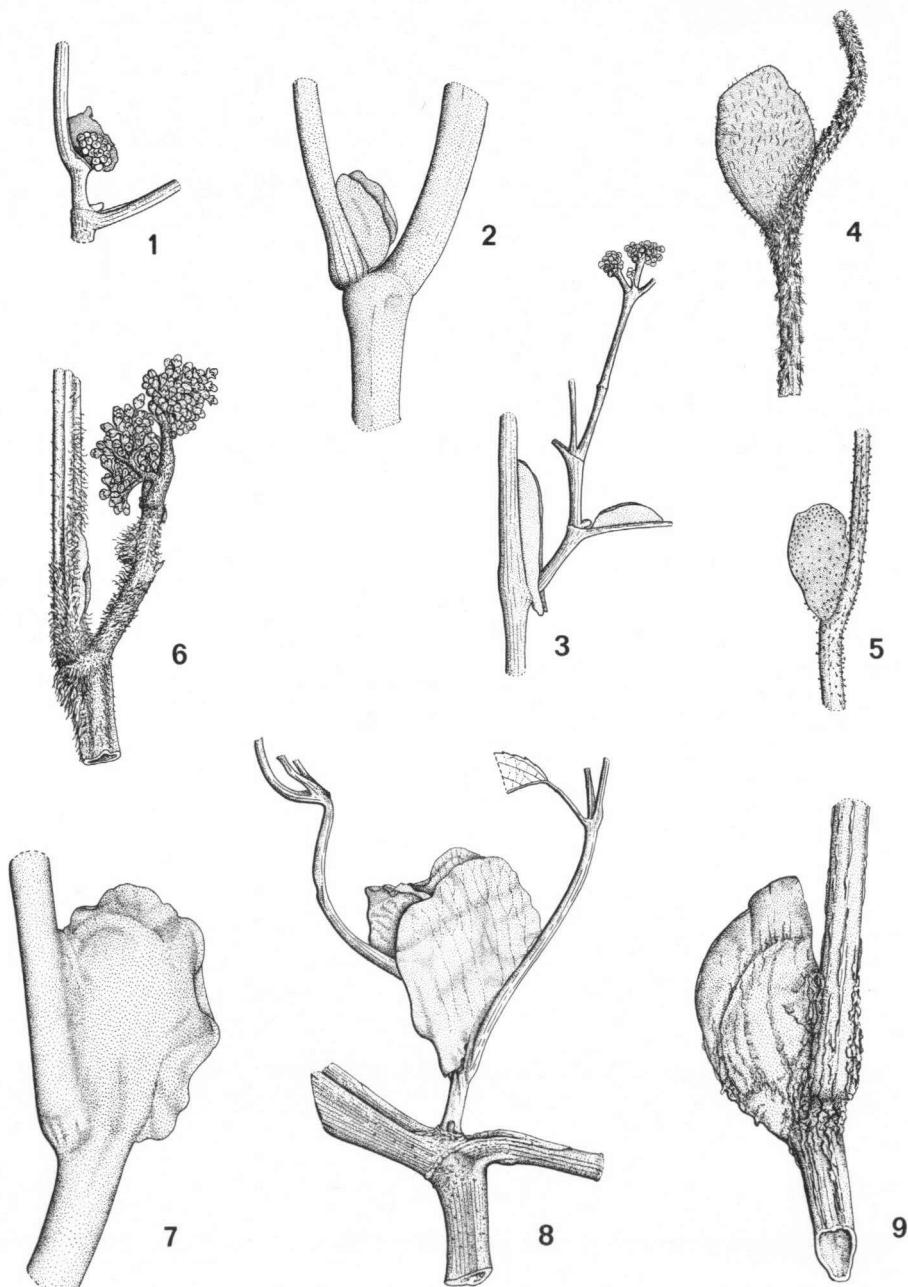
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Fig. 2. Stipules of *Leea*. — 1. *L. curtisii* (Kremppf s.n.); 2. *L. amabilis* (Hallier 2462); 3. *L. philippinensis* (PNH 21592); 4. *L. unifoliolata* (BS 33633); 5. *L. acuminatissima* (Jacobs 7803); 6. *L. quadrifida* (Loher 352); 7. *L. magnifolia* (BS 40670); 8. *L. crispa* (Kurz 107). All $\times \frac{1}{2}$.



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Fig. 3. Stipules of *Leea*. — 1. *L. thorelii* (Kerr 9004); 2. *L. angulata* (van Steenis 5333); 3. ditto (NIFS Ja 3742); 4. *L. saxatilis* (Ridley 305); 5. *L. aculeata* (Merrill 1825); 6. *L. setuligera* (Larsen 10610); 7. *L. grandifolia* (Kurz 488); 8. *L. tinctoria* (Moller & Quintas s.n.); 9. *L. alata* (Duthie 25877); 10. *L. rubra* (Kerr 21534); 11. ditto (Specht 1305); 12. *L. aquata* (Bakhuisen v. d. Brink jr. 4865); 13. *L. compactiflora* (Wang 74856); 14. *L. macrophylla* (Gamble 1966). All $\times \frac{1}{2}$.



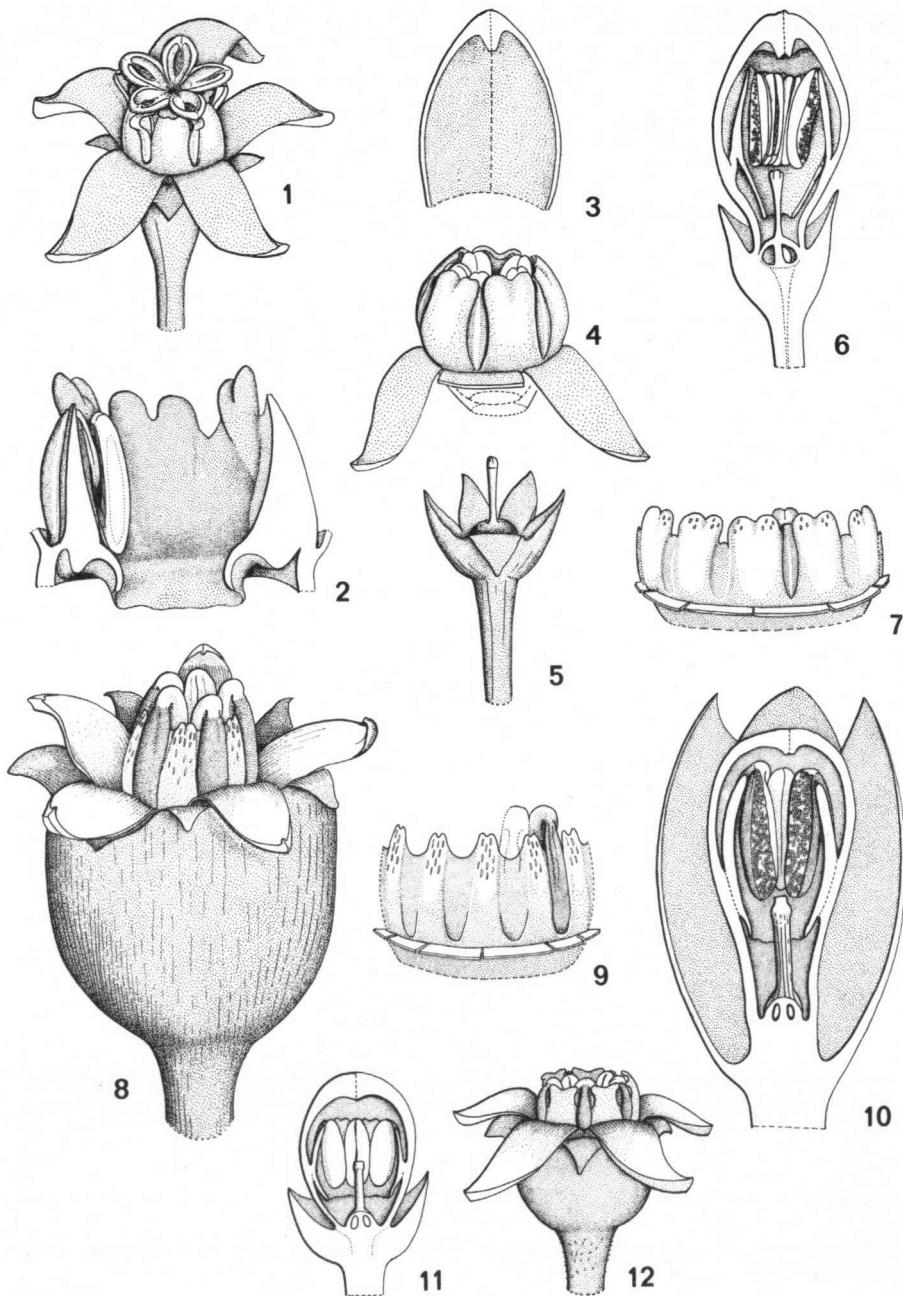
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Fig. 4. Stipules of *Leea*. — 1. *L. congesta* (Vidal 1027); 2. *L. guineensis* ('*L. negrosense*', BS 31254); 3. ditto ('*L. aurantiaca*', Haines 4755); 4. ditto ('*L. cumingii*', BS 41900); 5. ditto ('*L. papillosa*', BS. 30338); 6. *L. indica* (BSIP 5371); 7. ditto (Rutten s.n.); 8. ditto (Jacobs 7945); 9. *L. smithii* (Koorders 15876). All $\times \frac{1}{2}$.

type of axis found in *L. congesta*. If this is accompanied by reduction in the number of flowers, then an inflorescence of the type as found in *L. simplicifolia* is produced. Finally, the reduction of the peduncle gives the most extreme condensed inflorescence. The degree of reduction and condensation in any one species is exceedingly variable and has led to attempts to segregate distinct species on these characters alone. All intermediates from a highly branched inflorescence to one composed of 3 branches, with or without the peduncle strongly developed, may commonly be found in one species. Certain taxa have a typical condensed inflorescence which may vary in composition from a 3-branched system born on a peduncle to a system with condensed branches and peduncle.

Flowers. The conspicuous feature of the flowers is the presence of a tube within the whorl of stamens. This is considered to be a whorl of modified stamens and is here termed a staminodial tube. Basipetally the staminodial tube continues beyond the insertion, thus dividing the staminodial tube into an upper free part and a lower part, which is usually also free. The corolla tube itself is a composite structure composed of corolla and staminal elements (see fig. 5—7). In the descriptions the measurements of the upper and lower parts of the staminodial tube are given together with the length of the 'corolla tube + staminodial lobes', that being the length from the base of the composite corolla tube to the tip of the lobes of the upper part of the staminodial tube; the length of the free lobes of the corolla is not included but given separately. In most species the lower part of the staminodial tube appears as a short collar, but in others it extends as far as the ovary. It may also be adnate to the lower portion of the corolla tube so that it is not free. Large numbers of raphids are to be observed in the tissues of the staminodial tube and this feature may be used to differentiate the structure. Scattered raphids are commonly seen in the corolla tissue, anthers, and connective but are usually absent from the filaments. Distally from the line of insertion of the staminodial tube on the corolla tube the tissues often form a small rim, on which the filaments are inserted. This sometimes becomes swollen and sometimes fleshy. The upper part of the staminodial tube is composed of 4 or 5 lobes divided from each other by sinuses over which the filaments pass. The apex of the lobes of the staminodial tube is usually retusely notched but in extreme cases it may be deeply bifid. The filaments are inserted on the corolla tube and pass up on the outside of the staminodial tube and are attached to the anthers over the sinus of the staminodial tube. The anthers are basically dorsifixed. The connective is well developed on the dorsal side of the anthers and is purple-black in colour and conspicuously glandular. Filament-like tissue continues over the connective acropetally and basipetally beyond the point of attachment.

In most taxa the anthers in the bud and newly opened flowers are strongly syngenesious. *L. crispa* has anthers that, so far as can be ascertained, are always free. At anthesis the filaments bend outwards and backwards, the movement causes the anthers to gradually be elevated and pulled out of the staminodial tube. For the stamens to actually elevate a degree of breakage of the tissue holding the individual anthers together is required. If this is slight or non-existent then only partial movement can occur, the anthers remain together in a cylinder, and usually a number of the filaments break. The unit then moves out of the staminodial tube and soon detaches from the flower. A high degree of rupture of the tissue enables the anthers to leave the staminodial tube completely. They then sit as a star shaped plate above the tube (fig. 5.1). Complete breakage of the tissue will cause the anthers to completely reflex and appear seemingly extrose, a position illustrated by Descoings (1959). It would appear that all combinations are possible and the situation resulting in any one flower depends upon the strength and degree of breakage of the tissue joining the individual anthers. Clarke (1881) states that reflexion only occurs under dry conditions. It is not



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Fig. 5. Flower structure of *Leea*. — 1—7. *L. indica* (1. Geesink 5946, 2—7. BSIP 14885); 8—10. *L. amabilis* (Kostermans 10605); 11 & 12. *L. setuligera* (Smitinand & Sleumer 1329). 1 & 3—12 $\times 7$, 2 $\times 14.5$.

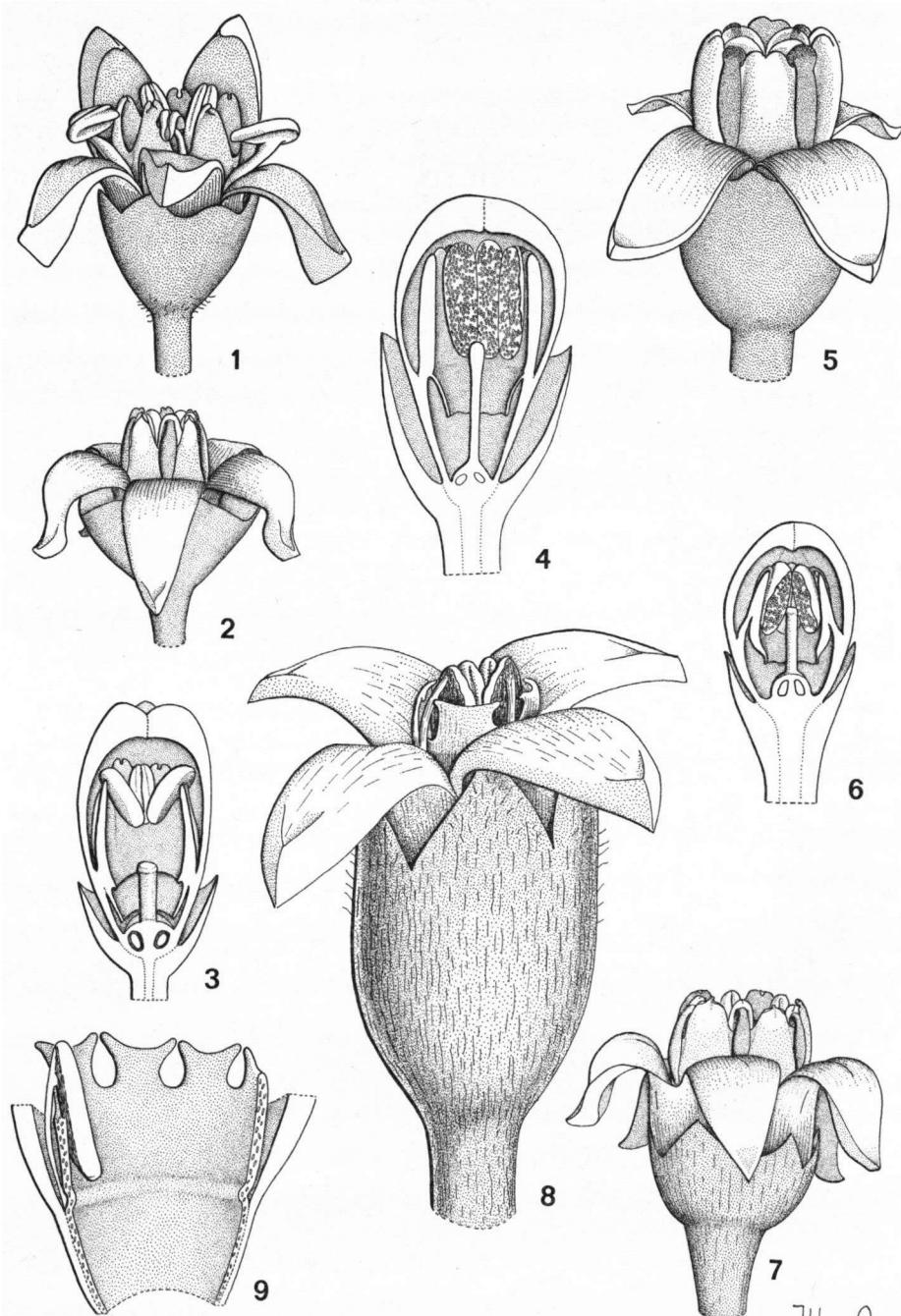
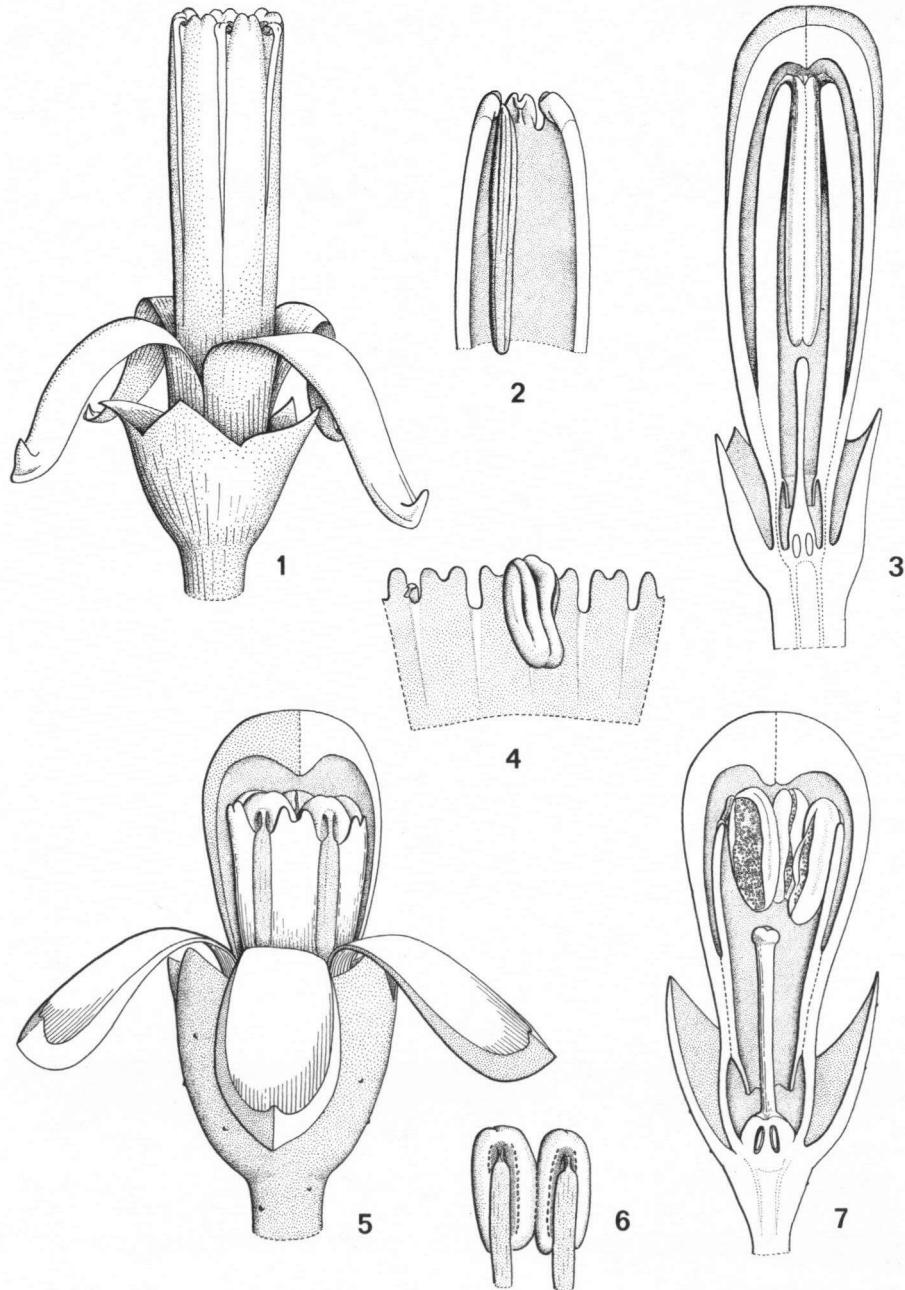


Fig. 6. Flower structure of *Leea*. — 1—3. *L. crispa* (Henry 12104); 4 & 5. *L. magnifolia* (Jacobs 7946); 6 & 7. *L. rubra* (Pullen 6703); 8 & 9. *L. papuana* (Forbes 95). All $\times 7$.

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Fig. 7. Flower structure of *Leea*. — 1—3. *L. macropus* (1. Kostermans 11199, 2 & 3. NGF 32599); 4—7. *L. krukoffiana* (NGF 37403). All $\times 7$.

known whether such reflexion is reversible and repetitive under changing climatic conditions. Clearly further field observations are required.

Flower morphology. *Leea* is separated from the *Vitaceae* by the presence of what is interpreted as a staminodial tube and the absence of a well developed 'disk'. The work of Prichard (1955) on *Rhamnaceae* and of Nair & Nambisan (1957) and Nair (1968) on *Leeaceae* shows interesting features when compared. The *Rhamnales* have a characteristic vascular pattern of the floral organs. The feature of interest is that the vascular traces to the stamens and petals have their origin in a common trace. The disk, where vascularized, is supplied by separate traces which in *Vitaceae* arise from the ovular traces. In each case there is 'excess vascular tissue'. All authors independently agree that this represents a modified obdiplostemonous condition. Nair & Nambisan (1957) have shown for *L. sambucina* that the vascular supply to the staminodial tube has an origin similar to that found in the *Vitaceae*. The question hinges on the nature of the disk in the *Vitaceae*: it could have been derived independently by reduction of structures of ancestral forms of *Rhamnales* or equally well represent a reduced staminodial tube structure. Considering current opinion, from fields of seed structure and wood anatomy, a derivation from a stock common for *Leeaceae* and *Vitaceae* is probable. Contrasting the presence or absence of a disk or staminodial tube as a criterion for family recognition has little value as available evidence suggests that the two structures are comparable, one being more reduced than the other.

POLLEN

Tarnavscchi & Petria (1968) have investigated 31 taxonomic units of *Leea*, representing 17 of the taxa accepted in the present work. The authors do not cite the collection numbers from which the samples were taken, so it is difficult to be certain of the exact identity of all of the samples. The description is taken from the original paper where further details may be found. The observations have not been checked.

Pollen grains tricolporate, (24—)30—50(—61) μm , shape suboblate to subprolate, equatorial outline variable, usually semi-angular or sub-angular; colpi generally $2/3$ or $3/4$ of the grain radius, less frequently about $1/3$ of the grain radius, exceptionally syncolpate, generally broader at the pore level, sometimes narrow. Operculi observed in the pores of the majority of species, completely detaching or only apical section detaching. Wall 2—3 μm thick, tectum reticulate.

The authors concluded that the pollen characters of the *Leeaceae* are sufficiently distinct from the *Vitaceae* to warrant separation of the two families.

SEEDS

The endosperm in the seed of *Leea* is ruminant, having basically 5 ingrowths: one along the median plane, due to the inpushing of the chalaza, two from the raphe, and one at each lateral face. The latter ingrowths leave a simple to complex pattern on the outer surface of the seed, referred to as the 'ruminant outline'. The ingrowths are produced by localized meristematic activity of the middle layers of the outer integument which causes the inner layers to be intruded; later the inner layers undergo some degree of lignification. The great development of the intruding chalazal ingrowth, to form a median plate, is apparently characteristic of *Leea*, and, so far, has not been reported from the *Vitaceae*, which have been less extensively investigated (cf. fig. 9). The present study has revealed the presence of more complicated types of ruminations than previously reported by Periasamy (1962). Extra ingrowths may be present on each lateral face. The ingrowths themselves may become much branched and reticulate, either the median plate alone, the ingrowths

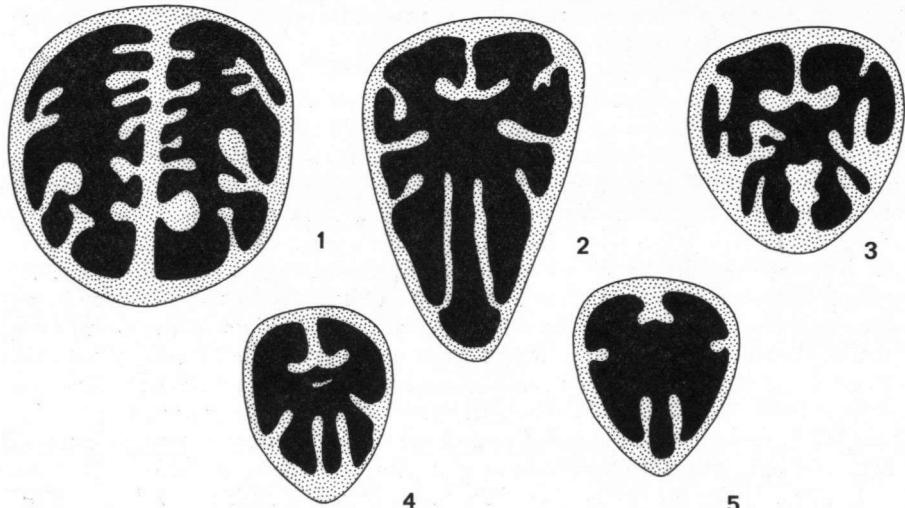


Fig. 8. Different types of ruminate endosperm found in *Leeaceae* in median T. S. — 1. *L. acuminatissima*; 2. *L. coryphantha*; 3. *L. magnifolia*; 4. *L. compactiflora*; 5. *L. indica*. All $\times 4$.

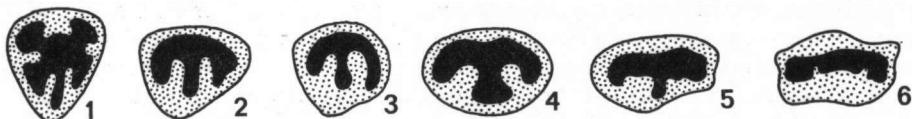


Fig. 9. Different types of ruminate endosperm found in *Vitaceae* (after Periasamy, 1962). — 1. *Leea*; 2. *Cissus*; 3. *Vitis*; 4. *Tetragastris*; 5. *Ampelocissus*; 6. *Cayratia*. All $\times 3$.

of the lateral faces alone, or both lateral face and median plate. The configurations present in median ls. are illustrated in fig. 8. Features of note are the meristematic activity of the chalaza which undergoes an expansion along the median plane towards the dorsal side of the seed. This becomes the structure termed the 'perichalaza' by Periasamy (1962). The perichalaza becomes pushed in by the ingrowths of the integument at the median plane and thus becomes broad and forked.

The endosperm develops very late in the post fertilization events, replacing the nucellus, which developed immediately after fertilization. The reserves of the endosperm are fatty and contain druses. These features are shared with the *Vitaceae*, suggesting a close relationship between the two families (Periasamy, 1962). In *Leea* the seedcoat and the innermost layer of the outer integument lack raphides which have been reported for all investigated genera of *Vitaceae*.

CHROMOSOMES

Shetty (1959) and Shetty & Raman (1960) have contributed to the knowledge of the chromosome numbers of *Vitaceae* and also have included some species of *Leea*. Counts for five taxa are to be found in the literature, and in the present work an other species has been investigated. *L. guineensis* (Mangenot, 1962) and *L. macrophylla* (incl. *L. robusta*) have counts of $2n = 24$. *L. indica* (incl. *L. sambucina*) has two counts of 24, but counts of 20 (Nair &

Nambisan, 1957) and 22 (Vatsala, 1960) have also been recorded. *L. crispa* (incl. *L. edgeworthii*) is reported to have a number of $2n = 28$. *L. aculeata* was investigated in the present work and found to have a number of $2n = 24$. However, secondary constrictions (satellites) are commonly present in this species and these, if present in other taxa, may account for the difference in numbers reported. Within the *Vitaceae* the chromosome number of $2n = 24$ is only reported for some species of *Cissus*.

GEOGRAPHIC DISTRIBUTION

The genus is centered in Malesia, extending westward to Africa and Madagascar, and eastward to Fiji. The two most common species of secondary vegetation, *L. indica* and *L. guineensis*, show the widest distribution and the greatest range of variation. These are viewed as complex species showing trends of variation of characters, in some places being temporarily isolated, appearing — and probably for a brief time maintaining themselves — as local isolates, only to merge again into the major gene pool and variation of the complex. Attempts to separate these isolates as species have always failed. Within such isolates extremes of variation are always found which cannot be separated from forms typically found in other geographically isolated populations. The lack of an obvious dispersal mechanism for the relatively large seeds (the dense concentration of raphides in the soft tissues of the berry causes considerable mechanical irritation in humans and this would suggest that the berries would not be so palatable to birds), the wide distribution of species of secondary vegetation, and the wide distribution of diverse floral types (viz. *L. tinctoria*), all give some support to the idea that the genus has had a long evolutionary history. Many individual taxa, or groups of related species with distinctive floral structures, are rare plants of the primary forest limited in distribution. There seems to have been an early divergence into these forest understorey taxa and those of secondary vegetation; the former remaining with limited distributions and forming rather distinct species whilst the latter rapidly expanded to form complex species.

Striking distributions are to be seen in *L. rubra* and *L. angulata* which extend to the Philippines, but from Borneo are only known from a few records in the extreme north or south. *L. aculeata* is exceedingly common in the Philippines and Sabah but becomes increasingly rare southward in Sarawak, Kalimantan, and Sumatra (with only two authenticated records from Java). The distribution of isolates of *L. indica* over a similar region tends to show a similar overall pattern.

L. philippinensis provides an example of extension of range to Botel Tobago I. off Taiwan. Most of the remaining species have small local distributions. In many cases the limits of distributions of the Indian taxa are still little known as are the ranges of variation of the entities composing such complex species as *L. macrophylla*. The distributions of the mainland Asiatic species are too little known for any comment to be made. In many cases single species or groups of species seem to form rather isolated components within the genus.

FOSSIL SPECIES

***Leea eo-japonica* Watari, Bot. Mag. Tokyo 64 (1951) 1, fig. 1 and 2.**

— Syntypes: Watari 64531, 64526—7, 64529, 64533.

An apparently good species described from silicified wood from the Tertiary of Japan.

Prakash & Dayal (1964) reported fossil wood resembling *Leea* from Deccan Intertrappean Beds of Mahurzan near Nagpur.

LITERATURE

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PRESENTATION OF DATA

The genus *Leea* is very homogeneous in appearance in vegetative and floral features, many species having similar ecological preferences. In many cases the species can not be separated on floral characters alone; in earlier works this has led to the recognition of many taxa based artificially on the degree of pinnation of the leaf. With fruiting material it is frequently impossible to identify the plant to species level with certainty. Vegetatively the plants are very variable, particularly in the widespread and complex species. Thus, in many cases species separation is only possible by considering several relatively small differences in the length of organs. The measurements of the floral parts are taken from mature buds just prior to opening. Drying out of the flower causes considerable changes in the appearance of the staminodial tube of open flowers and has been the cause of some confusion in the past. Terminology of the floral parts and measurements is discussed in the section on the morphology of the flowers. Collectors rarely indicate colour differences of the corolla lobes and staminodial tube, thus only a general idea of the flower colour is given to segregate red from green-white flowered species. Many attempts have been made to segregate taxa from widespread complex species such as *L. indica* and *L. guineensis*, most of these being based on vegetative features of

the leaves. With the numerous collections of these taxa now available many more intermediates can be seen and more extremes are also known, many of these being rare. It is probable that the less-collected taxa may also prove to be more variable in these characters than is known at present. Only the extremes of variation in features such as pubescence, texture, and types of margin and apex are given. The apical leaflets are usually, but by no means exclusively, larger than the lateral leaflets, but the dimensions completely intergrade. Thus the dimensions of the terminal leaflet are included in the maximum range of variation given for the leaflet length and width.

The descriptions are purposely short and essentially diagnostic whereby the differences of the species may readily be contrasted in important features. This re-assessment of characters has led to a species concept different from that held by earlier authors. In some taxa such as *L. macrophylla* it may be possible to recognize subspecific taxa when in the future more material is available and the species has been studied extensively in the field. In these cases lectotypes have been designated but this has not been done for all simple synonyms.

The species occurring exclusively outside Malesia are treated in full, the remainder will appear in Flora Malesiana and are here treated in an abbreviated manner, descriptions and full literature references being omitted. Four species so treated, *L. aquatica*, *L. guineensis*, *L. indica*, and *L. rubra*, are widespread outside Malesia. In these cases synonyms based on extra Malesian types are cited with full literature references whilst the Malesian names are treated in an abbreviated fashion.

Lists of specimens are not given and will be issued as a 'Flora Malesiana Identification List of Malesian Specimens'.

The relationships between the species is complex and uncertain and no simple linear relationships can be seen. The order of presentation attempts to place related species in close proximity, but as the relationship between groups of species is uncertain, the linear order of the groups does not reflect any natural relationship.

LEEACEAE

Leeaceae Dumort., Anal. Fam. Pl. (1829) 27, nom. cons.; Bartl., Ordin. (1830) 354; Spach, Hist. Nat. Veg. 3 (1834) 206; Horaninov, Primae Liniae Systematis Naturae (1834) 95; Miq., Fl. Ind. Bat. 1,2 (1859) 609; Gagnep., Bull. Soc. Bot. Fr. 57 (1910) 331; Fl. Gén. L.-C. 1 (1912) 934; Craib, Fl. Siam. En. 1 (1926) 316; Suesseng. in E. & P., Nat. Pfl. Fam. ed. 2, 2od (1953) 372; Dewit, Fl. Congo Belg. 9 (1960) 568; Engler, Syll. Pfl. Fam. ed. 12 (1964) 303; Wild, Fl. Zamb. 2 (1966) 492; Burger, Fam. Fl. Pl. Ethiopia (1967) 99; Descoings, Fl. Madag. Fam. 124 bis (1967) 1; Fl. Cameroun 13 (1972) 133; Airy Shaw in Willis, Dict. Fl. Pl. & Ferns, ed. 8 (1973) 643. — *Vitaceae (Ampelidaceae)* subfam. *Leeoideae* Endl., Gen. Pl. (1839) 797 (as 'Ampelideae subordo Leeaceae'); Ench. Bot. (1841) 395 (as 'Ampelideae subordo Leeaceae'); Lindl., Veg. Kingd. (1846) 440 (as 'Vitaceae subordo Leeae'); Lindley & Moore, Treasury Bot. 2 (1884) 668 (as 'Vitaceae subordo Leeae'); Gilg. in E. & P., Nat. Pfl. Fam. 3, 5 (1896) 454; Dalla Torre & Harms, Gen. Siph. 1 (1901) 303; Thonn., Blütenpfl. Afr. (1908) 368; Engler & Gilg., Syll. Pfl. Fam. ed. 8 (1919) 256. — *Vitaceae (Ampelidaceae)* tribe *Leeeae* DC., Prod. 1 (1824) 635 (as 'Ampelideae tribe Leeaceae'); Fuhlrott, Juss's und DC's Nat. Pfl. Syst. (1829) 145; Lindl., Intr. Nat. Syst. Bot. (1830) 120; G. Don, Gen. Hist. 1 (1831) 712; Meisn., Pl. Vasc. Gen. 1 (1837) 51; Boj., Hort. Maurit. (1837) 60; (all as 'Ampelideae tribe Leeaceae'); Cantley, Cat. Pl. Roy. Bot. Gard. Maurit. (1880) 5 (as 'Vitaceae tribe Leeae'); Durand, Index Gen. Phan. (1888) 71 (as 'Ampelidaceae tribe Leeae').

Trees, erect or creeping shrubs, scramblers, or herbaceous plants with a woody base; stems with rows of spines or unarmed. Leaves distichous, unifoliolate, trifoliolate, or 1- to 4-pinnate, usually imperfectly imparipinnate. Petiole or base of petiole expanded to form a stipular structure surrounding the stem apex, stipules narrowly sheathing and somewhat persistent or large, obovate, caducous. Leaflets glabrous or pubescent, hairs simple; pearl glands usually present on the undersurface, globular or stellate; margins crenate to serrate-

dentate, lobes glandular. *Inflorescence* a leaf-opposed cyme, lax or condensed by reduction of branches or peduncle or both, erect or pendulous. *Flowers* bisexual, actinomorphic, 4- or 5-merous, rarely both in the same inflorescence. *Calyx* campanulate with triangular lobes, lobes glandular at the apex. *Corolla* lobes valvate in the bud cohering by a ventrally apical keel, reflexed at maturity; basal portion choripetalous, adnate to the androecium. *Staminodial tube* inserted into the corolla at a line of attachment dividing the staminodial tube into an upper and a lower portion. Upper portion of 4 or 5 thickened lobes connate to each other by thinner tissues which form sinuses over which the filaments pass; lobes retuse, retusely apiculate to bifid at the apex. Lower portion forming a collar, usually free, sometimes extending as far as the ovary. *Filaments* flattened, non glandular, light brown, alternating with the staminodial lobes, passing upwards outside of the staminodial tube and passing over the sinuses; anthers 2-locular, introrse, usually syngenesious; connective distinct at dorsal side, purple to black, glandular, attachment to filament dorsal at 1/3 from apex, filament-like tissue continuing as a narrow strip acropetally (rather thick) and basipetally (rather thin) over the connective. *Ovary* discoid, 4—6 (—10)-locular, 1 ovule per locule; style short, entire, stigma slightly thickened. *Berry* depressed-subglobose; seeds triangular-ovate in section, endosperm ruminant. Embryo linear.

Only genus: *Leea* van Royen ex L.

LEEA

Leea van Royen ex L., Syst. Nat. ed. 12, 2 (1767) 627 & Mantissa 1 (1767) 17, 124, nom. cons.; W. Ait., Hort. Kew. 1 (1789) 283; Lamk., Encycl. Méth. 3, 2 (1792) 460; Stokes, Bot. Mater. Med. 1 (1812) 455 ('Lea'); Raf., Princip. rond. Somiol. (1814) 30 ('Leeania'); Fl. Tell. 1 (1837) 86 ('Leeania'); Roem. & Schultes, Syst. Veg. 4 (1819) 705; Roxb., Fl. Ind. ed. 1, 2 (1824) 465; DC., Prod. 1 (1824) 635; Spreng., Syst. Veg. 1 (1824) 670; Bl., Bijdr. (1825) 195; G. Don, Gen. Hist. 1 (1831) 712; Roxb., Fl. Ind. ed. 2, 1 (1832) 653; W. & A., Prod. (1834) 131; Meisn., Pl. Vasc. Gen. 1 (1836) 51; Boj., Hort. Maurit. (1837) 60; Endl., Gen. Pl. (1839) 797; Brongn., Enum. Gen. Pl. Cult. Paris (1843) 88 ('Leea'); Miq., Fl. Ind. Bat. 1, 2 (1859) 609; Benth. & Hook., Gen. Pl. 1 (1862) 388; Fl. Austr. 1 (1863) 451; Miq., Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 95; Drury, Handb. Ind. Fl. 1 (1864) 181; Baker in Oliv., Fl. Trop. Afr. (1868) 415; Brand., For. Fl. (1874) 181; Laws in Hook. f., Fl. Brit. Ind. 1 (1875) 664; Kurz, Fl. Burma 1 (1877) 278; Baker, Fl. Maurit. (1877) 54; J. Lindley & T. Moore, Treasure Bot. 2 (1884) 668; Boerl., Handl. 1 (1890) 251; Watt, Dict. Ec. Pl. India 4 (1890) 616; Baill., Hist. Pl. II (1892) 473; Trim., Handb. Fl. Ceyl. 1 (1893) 297; Engler, Pflanzenw. O. Afr. (1895) 261; King, J. As. Soc. Beng. 65, II (1896) 409; Bailey, Queensl. Fl. 1 (1899) 284; K. Schum. & Laut., Fl. Schutzgeb. (1900) 430; Dalla Torre & Harms, Gen. Siph. 1 (1901) 303; Cooke, Fl. Presid. Bomb. (1902) 326; Thonn., Blütenpfl. Afr. (1908) 368; Rechinger, Denkschr. Ak. Wiss. Wien. 89 (1914) 574; Gamble & Fisch., Fl. Presid. Madras 1 (1918) 237; Ridl., Fl. Mal. Pen. 1 (1922) 483; Hutch. & Dalz., Fl. West Trop. Afr. 1 (1928) 479; Burkhill, Dict. 2 (1935) 1326; Kanjilal & Das, Fl. Assam 1 (1936) 303; Corner, Ways. Trees 1 (1940) 97; Chittenden, Dict. Gard. 3 (1951) 1142; Suesseng. in E. & P., Nat. Pfl. Fam. ed. 2, 20d (1953) 382; Hutch. & Dalz., Fl. West Trop. Afr. ed. 2, 1 (1958) 683; Li, Woody Fl. Taiwan (1963) 524; Backer & Bakh. f., Fl. Java 2 (1965) 93; Wild, Fl. Zamb. 2, 2 (1966) 494; Dandy, Taxon 18 (1969) 468. — T y p e: *L. aquata* L. (*typus cons.*).
Nalagu Adanson, Fam. Pl. 2 (1763) 445, 581, nom. rejic.; Dennstedt, Schlüssel Hort. Ind. Malabar. (1818) 13, 27. — T y p e: Hort. Malabar. 2 (1679) 43—44, plate in Hort. Malabar. 1 (1678) 26, nom 2 (1679) 26. (is *L. crispa* L.).
Staphylea auct. non L.: Burm. f., Fl. Ind. (1768) 75, t. 23 fig. 2.
Aquilicia L., Mantissa 2 (1771) 146, 211; Lamk., Encycl. Méth. 1 (1783) 217; Cav., Dissert. 7 (1789) 371. — T y p e: *A. sambucina* L. (=*Leea indica* Merr.).
Sansovinia Scop., Intr. (1777) 228. — T y p e: *Staphylea indica* Burm. f. (=*Leea indica* Merr.).
Ottilis Gaertn., Fruct. 1 (1788) icon. tab. 57 f. 7, nom. inval; Endl., Gen. Pl. (1839) 797 pro syn. (as '*Ottilis*'). — T y p e: *O. zeylanica* Gaertn., reduced in text to *Aquilicia ottilis* Gaertn. (=*Leea ottilis* DC. =*L. indica* Merr.).
Ticorea Blanco, Fl. Filip. (1837) 85. — T y p e: *T. aculeata* Blanco (=*L. aculeata* Spreng.).
Leea series *Rubriflorae* & *Viridiflorae* Clarke J. Bot. 19 (1881) 101, 135.
Leea sections *Aequatae*, *Edgeworthiae*, *Laetae*, *Paucifoliolasae*, *Pycnoneuriae*, *Rubrae* & *Sambucinae* Clarke o.c. 63, 101, 102, 104, 135, 137, 138.

For description of the genus see family diagnosis.

Distribution: 32 species in SE. Asia, Malesia, Micronesia, Melanesia, and Australia; 2 species restricted to Africa and Madagascar.

Note. Dandy (Taxon 18, 1969: 468) has proposed to conserve *Leea* van Royen ex L. against *Nalagu* Adanson. This proposal has been accepted by the Nomenclature Committee for Spermatophyta (Taxon 19, 1970: 816).

KEY TO THE SPECIES

- | | |
|--|-----------------------------|
| 1a. Leaves unifoliolate or trifoliolate | 2 |
| b. Leaves pinnate | 17 |
| 2a. Leaves unifoliolate | 3 |
| b. Leaves trifoliolate | 10 |
| 3a. Flowers 4-merous, fruit usually 4-seeded. <i>Philippines</i> | 4 |
| b. Flowers 5-merous, fruit usually 6-seeded (sometimes less by abortion). Not in <i>Philippines</i> | 6 |
| 4a. Leaflets obovate, pair of foliar outgrowths (rarely seen as reduced leaflets) above the stipular wing | 1. <i>L. magnifolia</i> |
| b. Leaflets elliptic or ovate, foliar outgrowths absent | 5 |
| 5a. Seeds complexly ruminate. Leaflets up to 22 by 9 cm | 3. <i>L. acuminatissima</i> |
| b. Seeds simply ruminate. Leaflets usually over 22 by 9 cm | 4. <i>L. unifoliata</i> |
| 6a. Anthers free, lobes of staminodial tube deeply bifid | 25. <i>L. crispa</i> |
| b. Anthers cohering, detaching as a unit together with filaments, lobes of staminodial tube shallowly retuse | 7 |
| 7a. Calyx and corolla lobes (sometimes leaflets too) mealy pubescent; corolla thick, fleshy; anthers with thick orange-brown walls | 22. <i>L. macrophylla</i> |
| b. Calyx, corolla lobes, and leaves not mealy pubescent; corolla lobes otherwise; anther walls not so coloured | 8 |
| 8a. Corolla tube + staminodial lobes less than 3 mm long, lower free part of staminodial tube up to 0.5 mm. Fruit usually up to 10 mm diameter. <i>Thailand, Malaya, Sumatra, Java</i> | 8. <i>L. simplicifolia</i> |
| b. Corolla tube + staminodial lobes over 3 mm long, lower free part of staminodial tube over 0.5 mm. Fruit usually over 10 mm diameter. <i>New Guinea</i> | 9 |
| 9a. Corolla tube + staminodial lobes less than 4.5 mm. Leaflet base subauriculate | 9. <i>L. gonioptera</i> |
| b. Corolla tube + staminodial lobes over 4.5 mm. Leaflet base cuneate to truncate | 10. <i>L. zippelianae</i> |
| 10a. Flowers 4-merous, fruit usually 4-seeded. <i>Philippines</i> | 1. <i>L. magnifolia</i> |
| b. Flowers 5-merous, fruit usually 6-seeded (sometimes less by abortion). Not in <i>Philippines</i> | 11 |
| 11a. Petiolar stipule a narrow wing up to 10 mm broad, somewhat persistent, scar narrow | 12 |
| b. Petiolar stipule obovate, over 10 mm broad, early caducous, scar broad | 15 |
| 12a. Corolla tube + staminodial lobes usually up to 2.5 mm, staminodial tube up to 1.5 mm. Small semi-herbaceous shrubs, sometimes with creeping rootstock | 13 |
| b. Corolla tube + staminodial lobes usually over 2.5 mm, staminodial tube at least 1.5 mm. Shrubs or trees, if semi-herbaceous then over 1 m high | 14 |

- 13a. Stem, rachis, and leaflets pubescent; leaflets exceedingly heterogenous on one plant, generally up to 8 cm long. Fruit 5—7 (—9) mm diameter, deeply grooved between the segments. Semi-herbaceous, c. 1 m high 17. *L. thorellii*
- b. Stem, rachis and leaflets glabrous, leaflets not heterogeneous, usually exceeding 8 cm. Fruit c. 10 mm diameter, shallowly grooved between the segments. Undershrub with a creeping rootstock. 8. *L. simplicifolia*
- 14a. Bracts of inflorescence narrowly triangular to linear. Anthers free, not detaching as a unit together with filaments; lobes of the staminodial tube strongly bifid, sinuses deep, c. 1 mm. Leaflets 5—7 nerved at the base. Immature fruit yellow, turning purple-black 25. *L. crista*
- b. Bracts of inflorescence ovate, conspicuous. Anthers cohering, detaching as a unit together with filaments; lobes of staminodial tube shallowly retuse or cleft, sinuses shallow. Leaflets 3-nerved at base. Mature fruit orange-yellow 24. *L. compactiflora*
- 15a. Calyx and corolla lobes (sometimes leaflets too) mealy pubescent, corolla lobes thick-fleshy 22. *L. macrophylla*
- b. Calyx and leaflets not mealy pubescent, corolla lobes thin, not fleshy. 16
- 16a. Leaflets petiolate, petiolule over 10 mm. Flowers green. *Andaman Is and Nicobar Is* 23. *L. grandifolia*
- b. Leaflets usually sessile or petiolule less than 10 mm. Flowers red. *Continental India* 29. *L. alata*
- 17a. Petiolar stipule a narrow wing, up to 10 mm broad, somewhat persistent, scar usually narrow 18
- b. Petiolar stipule obovate, over 10 mm broad, early caducous, scar narrowly triangular to broad 44
- 18a. Flowers 4-merous; fruit usually 4-seeded, (if 6-seeded then fruit over 20 mm diameter) 19
- b. Flowers 5-merous; fruit usually 6-seeded. 22
- 19a. Staminodial tube over 5 mm long; fruit over 20 mm diameter, 6-seeded. *New Guinea and Solomon Is* 20
- b. Staminodial tube less than 5 mm long; fruit less than 20 mm diameter, 4-seeded. *Philippines* 21
- 20a. Lobes of staminodial tube strongly bifid. Inflorescence condensed, erect. Flowers orange-yellow. *Mainland of New Guinea* 13. *L. papuana*
- b. Lobes of staminodial tube retuse. Inflorescence lax, pendulous. Flowers white. *Solomon Is* 16. *L. tetramera*
- 21a. Staminodial tube 4—5 mm long; filaments over 2 mm; style over 2 mm long. Inflorescence generally condensed, 3-branched, peduncle usually up to 3 cm long. Young parts sometimes fulvous pubescent. Leaflets usually elliptic to elliptic-lanceolate, over 7 cm wide; ultimate venation distinct. Rumination outline simple to slightly branched 2. *L. quadrifida*
- b. Staminodial tube 2.5—4 mm; filaments up to 2 mm; style up to 2 mm long. Inflorescence generally lax and multi-branched, peduncle over 3 cm. Young parts never fulvous pubescent. Leaflets generally ovate to ovate-lanceolate and less than 7 cm wide; ultimate venation indistinct. Rumination outline complexly reticulate 6. *L. philippensis*
- 22a. Stems spiny 23
- b. Stems not spiny or information lacking 25
- 23a. Leaves 1-pinnate 20. *L. aculeata*
- b. Leaves 2- or 3-pinnate 24

- 24a. Staminodial tube over 3 mm long. Rumination outline complex. *Madagascar*
18. *L. spinea*
- b. Staminodial tube less than 3 mm long. Rumination outline simple. *Malesia*
19. *L. angulata*
- 25a. Corolla tube + staminodial lobes 6 mm or more and staminodial tube over 5.25 mm. Fruit over 20 mm diameter. *New Guinea and Solomon Is.* 26
- b. Corolla tube + staminodial lobes less than 6 mm or staminodial tube less than 5.25 mm. Fruit less than 20 mm diameter. Only *L. gonioptera*, *L. aculeata* in N.G. 29
- 26a. Leaves 3- to 4-pinnate, leaflets up to 14 by 5 cm. Flowers pink. *Mainland of New Guinea* 14. ***L. krukoffiana***
- b. Leaves 1- or 2-pinnate, leaflets mostly over 14 by 5 cm. Flowers not pink. 27
- 27a. Lobes of staminodial tube strongly bifid. Inflorescence condensed, erect. Flowers orange-yellow. *Mainland of New Guinea* 13. ***L. papuana***
- b. Lobes of staminodial tube retuse. Inflorescence lax, pendulous. Flowers white. *Bismarck Archipelago, Solomon Is.* 28
- 28a. Inflorescence usually glabrous. Corolla tube + staminodial lobes 8—11 mm, filaments 5—7 mm, anthers 3—5 mm. *Bismarck Archipelago* 15. ***L. macropus***
- b. Inflorescence usually fulvously pubescent. Corolla tube + staminodial lobes 6—8 mm, filaments 3 mm, anthers 2 mm. *Solomon Is.* 16. ***L. tetramera***
- 29a. Leaves 1-pinnate 30
- b. Leaves 2- to 4-pinnate 39
- 30a. Corolla tube + staminodial lobes usually up to 2.5 mm, (leaflets never with setaceous hairs above) staminodial tube up to 1.5 mm. Small semi-herbaceous shrubs, sometimes with creeping rootstock 31
- b. Corolla tube + staminodial lobes usually over 2.5 mm, (or if less then leaflets with setaceous hairs above) staminodial tube at least 1.5 mm. Shrubs or trees, if semi-herbaceous then over 1 m high 32
- 31a. Stem, rachis, and leaflets pubescent; leaflets exceedingly heterogeneous on one plant, generally up to 8 cm long. Fruit 5—7 (—9) mm diameter, deeply grooved between the segments. Semi-herbaceous, c. 1 m high. 17. ***L. thorelii***
- b. Stem, rachis, and leaflets glabrous; leaflets not heterogeneous, usually exceeding 8 cm. Fruit c. 10 mm diameter, shallowly grooved between the segments. Under-shrub with creeping rootstock. 8. ***L. simplicifolia***
- 32a. Bracts of inflorescence broadly ovate, somewhat foliaceous, conspicuous. Mature fruit orange-yellow. *India to China* 24. ***L. compactiflora***
- b. Bracts of inflorescence deltoid to narrowly triangular, inconspicuous. Fruit maturing red- to blue-black 33
- 33a. Flowers red to carmine in the bud (or upper surface of leaflets with setaceous hairs) 34
- b. Flowers green or white in the bud. 36
- 34a. Sinuses of staminodial tube shallow, to 0.5 mm. Upper leaf surface glabrous. *Malay Peninsula* 31. ***L. saxatilis***
- b. Sinuses of staminodial tube deep, over 1 mm. *India, Thailand, Yunnan* 35
- 35a. Leaflets always petiolate, upper surface and on nerves below with setaceous hairs. Rachis not winged 30. ***L. setuligera***
- b. Leaflets frequently sessile, usually glabrous, if pubescent then hairs not setaceous. Rachis narrowly winged 29. ***L. alata***
- 36a. Leaflets 5—7 nerved at the base, usually sparsely to densely pubescent. Lobes of staminodial tube deeply bifid, sinuses deep, c. 1 mm. Anthers free, not detaching as a unit with the filaments 25. ***L. crispa***

- b. Leaflets 3-nerved at the base, glabrous or rarely slightly pubescent. Lobes of staminodial tube shallowly retuse or cleft, sinuses shallow. Anthers cohering, detaching as a unit with the filaments. 37
- 37a. Calyx ± inflated around the corolla tube, completely enclosing the corolla in the bud. Corolla tube + staminodial lobes over 5 mm, staminodial tube over 4 mm. Fruit c. 20 mm diameter 7. *L. amabilis*
- b. Calyx not enclosing the corolla in the bud. Corolla tube + staminodial lobes less than 5 mm, staminodial tube less than 4 mm. Fruit usually less than 15 mm (rarely —20 mm) 38
- 38a. Leaflet base subauriculate. Stem smooth. Staminodial tube up to 3 mm long, lower free part up to 1.25 mm long. *New Guinea* 9. *L. gonioptera*
- b. Leaflet base rounded to cuneate. Stem spiny. Staminodial tube 3—3.5 mm long, lower free part over 1.25 mm long. Predominantly (but not exclusively) not in *New Guinea* 20. *L. aculeata*
- 39a. Corolla tube + staminodial lobes generally up to 2 (—2.5) mm, staminodial tube up to 1.5 mm. Flowers white. Fruit 5—7 (—9) mm diameter. Small herb or semi-herbaceous shrub c. 1 m high 17. *L. thorelii*
- b. Corolla tube + staminodial lobes over 2.5 mm (or if c. 2 mm then flowers red or leaflets with setaceous hairs above), staminodial tube over 1.5 mm. Fruit usually over 7 mm diameter. Shrubs or trees. 40
- 40a. Staminodial tube up to 2.25 mm long 41
- b. Staminodial tube at least 2.5 mm long 43
- 41a. Corolla tube + staminodial lobes over 3.25 mm; flowers greenish white. Fruit greyish blue. Stems and ultimate branchlets spiny. 19. *L. angulata*
- b. Corolla tube + staminodial lobes less than 3.25 mm; flowers red or pink when immature and creamish-yellow-green at maturity. Fruit red. Stems and branches not spiny 42
- 42a. Leaves membranous, above with setaceous hairs. Young flowers wine-red to carmine, sometimes becoming creamish yellow at maturity 30. *L. setuligera*
- b. Leaves chartaceous, without setaceous hairs above. Flowers and inflorescence deep red 28. *L. rubra*
- 43a. Petiole over 10 cm, petiolar stipule over 5 cm long. Stem without spines. *Malaya and Vietnam* 21. *L. curtisii*
- b. Petiole less than 10 cm, petiolar stipule up to 5 cm long. Stem spiny. *Madagascar* 18. *L. spinea*
- 44a. Flowers 4-merous; fruit usually 4-seeded. *Philippines*. 5. *L. congesta*
- b. Flowers 5-merous; fruit usually 6-seeded. 45
- 45a. Leaves 1-pinnate 46
- b. Leaves 2- to 4-pinnate 52
- 46a. Flowers red- to orange-yellow 47
- b. Flowers greenish white 48
- 47a. Leaflets sessile, rachis winged. *N. India* 29. *L. alata*
- b. Leaflets petiolulate, rachis not winged 32. *L. guineensis*
- 48a. Corolla tube + staminodial lobes over 4 mm, staminodial tube at least 2.25 mm 49
- b. Corolla tube + staminodial lobes up to 4 mm, staminodial tube up to 2.25 mm. 51
- 49a. Sinuses of staminodial tube deep, c. 1 mm. Leaflets generally over 30 cm long. Fruit c. 20 mm diameter. *New Guinea* 12. *L. coryphantha*
- b. Sinuses of staminodial tube shallow, considerably less than 1 mm. Leaflets generally, but not exclusively, up to 30 cm long 50

- 50a. Lower free part of staminodial tube 0.75—1 mm. Fruit over 20 mm diameter. Leaflets up to 12 cm wide. *New Guinea* **11. L. heterodoxa**
- b. Lower free part of staminodial tube up to 0.5 mm. Fruit up to 15 mm diameter. Leaflets over 12 cm wide. *Andaman and Nicobar Is* **23. L. grandifolia**
- 51a. Calyx and corolla lobes mealy pubescent; sinuses of staminodial tube over 1 mm, anthers with thick orange-brown walls. Leaflets generally 5-nerved at base. *India to Vietnam* **22. L. macrophylla**
- b. Calyx and corolla lobes glabrous (or calyx sparsely pubescent), not mealy; sinuses of staminodial tube less than 1 mm (or if c. 1 mm then Malayan), anther walls otherwise. Leaflets generally 3-nerved at the base **33. L. indica**
- 52a. Corolla tube + staminodial lobes over 8 mm, staminodial tube 6—7 mm. *São Tomé, Africa* **26. L. tinctoria**
- b. Corolla tube + staminodial lobes less than 8 mm, staminodial tube less than 6 mm **53**
- 53a. Corolla tube + staminodial lobes over 4 mm, staminodial tube over 3 mm. Fruit at least 20 mm diameter. *New Guinea* **54**
- b. Corolla tube + staminodial lobes less than 4 mm, staminodial tube less than 3 mm. Fruit up to 15 mm diameter **55**
- 54a. Sinuses of staminodial tube deep, c. 1 mm. Leaflets generally over 30 by 9 cm, nerves usually over 10 pairs. Stipular scar generally over 4 cm long **12. L. coryphantha**
- b. Sinuses of staminodial tube shallow, less than 0.5 mm. Leaflets generally less than 30 by 9 cm, nerves usually less than 10 pairs. Stipular scar up to 4 cm long
11. L. heterodoxa
- 55a. Calyx and corolla lobes (and sometimes leaflets too) mealy pubescent, corolla lobes thick and fleshy, anthers with thick orange-brown walls **22. L. macrophylla**
- b. Calyx and corolla lobes otherwise, anther walls thin **56**
- 56a. Inflorescence and leaflets with large, discoidal, brown pearl glands. Bracts of inflorescence large, up to 8 by 5 mm, conspicuous **27. L. aequata**
- b. Pearl glands inconspicuous or absent. Bracts smaller, inconspicuous **57**
- 57a. Petiole, rachis, and costa with crisped fluted emergences. Leaflets large, 30—40 by 10—17 cm. *Celebes* **34. L. smithii**
- b. Emergences absent. Leaflets usually (but not exclusively) smaller **58**
- 58a. Flowers greenish white **33. L. indica**
- b. Flowers red to orange-yellow **59**
- 59a. Sinuses of staminodial tube shallow **32. L. guineensis**
- b. Sinuses of staminodial tube deep **60**
- 60a. Corolla tube + staminodial lobes generally over 3 mm, staminodial tube over 2 mm. *Madagascar and Mauritius* **32. L. guineensis**
- b. Corolla tube + staminodial lobes up to 3 mm, staminodial tube less than 2 mm. *India to Australia* **28. L. rubra**

I. *Leea magnifolia* Merr. — Fig. 2:7; 6:4 & 5; 8:3.

L. magnifolia Merr., Publ. Govt. Lab. Philip. 35 (1906) 37. — T y p e: Curran FB 10279 (K, US).

L. banahaensis Elm., Leaf. Philip. Bot. 1 (1908) 318. — T y p e: Elmer 7509 (A, BO, K, L).

L. pycnantha Quisumb. & Merr., Philip. J. Sc. 37 (1928) 166. — T y p e: Ramos & Edaño BS 45743 (K, US).

L. catanduanensis Quisumb., Philip. J. Sc. 76 (1944) 203 (erroneously numbered as pt. 3, page 47). — T y p e: Ramos & Edaño BS 75429 (A).

Distribution: Philippines.

2. *Leea quadrifida* Merr. — Fig. 2:6.

L. quadrifida Merr., Philip. J. Sc. 5 (1910) Bot. 196. — Type: *Tamesis FB 13309* (n.v.).
L. agusanensis Elm., Leafl. Philip. Bot. 8 (1915) 2881. — Type: *Elmer 13500* (BM, L).
L. platyphylla Merr., Philip. J. Sc. 17 (1920) 280. — Type: *Ramos & Pascasio BS 34397* (A, K, US).

Distribution: Philippines.

Notes. In general material previously included in synonymous taxa has a tendency to have larger, more glabrous leaves and a seed with a simpler rumination outline. Material corresponding to that described as *L. quadrifida* tends to occur more commonly on ridges, particularly those bearing moss forest.

3. *Leea acuminatissima* Merr. — Fig. 2:5; 8:1.

L. acuminatissima Merr., Philip. J. Sc. 12 (1917) Bot. 281. — Type: *Ramos & Edaño BS 26260* (A, K, P, US).

Distribution: Philippines. Known only from two collections.

Note. The status of this species is uncertain and further collections are required. It may only be a precocious flowering unifoliolate form of a pinnately leaved species.

4. *Leea unifoliata* Merr. — Fig. 2:4.

L. unifoliata Merr., Philip. J. Sc. 11 (1916) Bot. 193. — Type: *Ramos BS 24873* (US).
L. longipetiolata Merr., Philip. J. Sc. 17 (1920) 282. — Type: *Ramos & Edaño BS 33633* (A, K, P, US).

Distribution: Philippines.

Note. From the collections available this species appears to be distinct from *L. acuminatissima*. However, it could well represent a precociously flowering unifoliolate form of one of the pinnately leaved species, particularly *L. quadrifida*. Further collections and field observations are required.

5. *Leea congesta* Elm. — Fig. 4:1.

L. congesta Elm., Leafl. Philip. Bot. 1 (1908) 318. — Type: *Elmer 8116* (A, K).
L. capitata Merr., Philip. J. Sc. 17 (1920) 281. — Lectotype: *Ramos & Edaño BS 19430* (US). — Syntypes: *Yates BS 25502* (n.v.); *Ramos & Edaño BS 28506* (n.v.).

Distribution: Philippines.

6. *Leea philippinensis* Merr. — Fig. 2:3.

L. philippinensis Merr., Philip. J. Sc. 1 (1906) Suppl. 89. — Type: *Ahern FB 1516* (K, US).
L. pauciflora Elm., Leafl. Philip. Bot. 8 (1919) 3103, nom. illeg., non King (1896). — *L. philippinensis* var. *pauciflora* Merr., En. Philip. 3 (1923) 13. — Type: *Elmer 18029* (A, BO, K, U).
L. nitida Merr., Philip. J. Sc. 20 (1922) 406. — Type: *Fénix BS 28428* (A, BM, K, US).

Distribution: Philippines, Taiwan: Botel Tobago (= Orchid I.).

7. *Leea amabilis* Masters — Fig. 2:2; 5:8—10.

L. amabilis Veitch [Catalogue (1882) 19, nom. nud.] ex Masters, Gard. Chron. 27 (1882) 492, fig. 77. — Type: Veitch s.n. (K).
L. amabilis Masters var. *splendens* Linden & Rodigas, Ill. Hort. 31 (1884) 59, t. 518. — Type: plate 518, from living plant forwarded by Teuscher from W. Borneo.

Distribution: Borneo.

8. *Leea simplicifolia* Zoll. & Moritzi — Fig. 1:8; 10.

L. simplicifolia Zoll. & Moritzi, Nat. Geneesk. Arch. N. I. 2 (1845) 578. — Type: Zollinger 2640 (K, P).
L. pauciflora King, J. As. Soc. Beng. 65, II (1896) 412. — Lectotype: King 1113 (K, SING). —
 Syntype: Scortechini s.n., Perak (P, SING).
L. forbesii Bak. f., J. Bot. 62 (1924) Suppl. 24. — Type: Forbes 1637 (BM, L).
L. pauciflora var. *ferruginea* Craib, Fl. Siam. En. 1 (1926) 319. — Type: Kerr 7375 (K).

Distribution: Peninsular Thailand, Malaya, Sumatra, Java.

9. *Leea gonioptera* Laut.

L. gonioptera Laut., Nova Guinea 8 (1912) 832; ditto 14 (1924) 138. — Type: von Römer 461 (L, WRSL).

Distribution: New Guinea.

Note. A little known species represented by scant herbarium material. Unifoliolate specimens can not easily be distinguished from *L. zippeliana*, differing chiefly in the tapering leaflets with subauriculate bases. Further collections are required to establish the species limits as the flowers in most of available material are immature.

10. *Leea zippeliana* Miq. — Fig. 1:3.

L. zippeliana Miq., Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 101. — Type: Zippelius s.n., July 1828, New Guinea (L, holo; U).
L. monophylla Laut., Nova Guinea 8 (1910) 302; ditto (1912) 832 pro parte; ditto 14 (1924) 137. — Lectotype: Versteeg 1339 (BO, K, L, U, WRSL). — Syntypes: Branderhorst 417 (L).
L. zippeliana var. *ornata* Laut., Bot. Jahrb. 59 (1925) 529. — Syntypes: Ledermann 8100 (B, †), Lauterbach 2186 (B, †), Hellwig 539 (B, †). — *L. micholitzii* Sanders, Catalogue (1889) 20, nom. nud.; Laut., o.c. 534, nom. nud. in nota.

Distribution: New Guinea.

11. *Leea heterodoxa* K. Schum. & Laut. — Fig. 1:2.

L. heterodoxa K. Schum. & Laut., Fl. Schutzgeb. (1900) 431, ex char.; Laut., Bot. Jahrb. 59 (1925) 530. — Type: Lauterbach 2481 (B, †).
L. gigantea K. Schum. & Laut., Fl. Schutzgeb. (1900) 433, nom. illeg., non Griff. (1864). — *L. rodatzii* Laut., Bot. Jahrb. 59 (1925) 533. — Type: Rodatz & Klink 214 (B, †, holo; iso: leaves SING, fruit WRSL).
L. tuberculata Laut., Nova Guinea 8 (1912) 832. — Type: Gjellerup 265 (L, WRSL).

Distribution: New Guinea.

Notes. From the description and key of Lauterbach I cannot see sufficient characters to separate *L. heterodoxa* from *L. tuberculata*, an opinion inferred by Lauterbach himself (Bot. Jahrb. 59, 1925, 530 in nota). No extant type material has been traced of *L. heterodoxa*. Both taxa were only known from single collections at the time of Lauterbach.

12. *Leea coryphantha* Laut. — Fig. 1:4, 5; 8:2.

L. coryphantha Laut., Nova Guinea 8 (1918) 832. — Type: Gjellerup 325 (BO, L, WRSL).

Distribution: New Guinea.

13. *Leea papuana* Merr. & Perry — Fig. 1:1; 6:8, 9.

L. papuana Merr. & Perry, J. Arn. Arb. 22 (1941) 382. — Type: Brass 7325 (A, holo; L).
L. macropus auct. non K. Schum. & Laut.: Bak. f., J. Bot. 61 (1923) Suppl. 11; ditto 62 (1924) 54.

Distribution: New Guinea.



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Fig. 10. Leaf forms of *Leea simplicifolia*. 1. Unifoliolate (*Korthals s.n.*); 2. trifoliate and simply pinnate (*Kerr 7535*); 3. multipinnate (*de Wilde 14361*). All $\times 0.35$.

14. *Leea krukoffiana* Ridsd., spec. nov. — Fig. 7:4—7.

Arbuscula usque ad 3 m alta. *Folia* 3—4-pinnata, folioli numerosis; petiolus 35 cm longus, stipulae propriae haud visae, ex cicatricibus 20 cm longis probabiliter alas angustas praebentes. Rhachis 55 cm longa. Foliola ovata usque ovato-oblonga, (7—)8—14 cm longa, (2—)3—5 cm lata, glabra, chartacea, glandulis margaritaceis globulosis sparsis, sinuato-dentata, apice acuminata, basi obtusa usque acuta, interdum inaequalia, nervis lateralibus utrinque 4—9; petioluli 2—5 mm longi. *Inflorescentiae* 10 cm longae, laxae, pubescentes; bracteae deltoideae, minutae, usque ad 2 mm longae; pedunculi 1 cm longi. *Flores* 5-meri, rosacei. *Calyx* glaberimus 4 × 4 mm, lobis 1.5 mm altis, 2—2.5 mm latis. *Corolla* tube lobi staminis inclusa 6.5—7.5 mm longa, lobis 5—6 mm longis, 2 mm latis; tubus parte staminali 5.5 mm, parte superiore libero 3.5 mm longus, lobis breviter retusis, sinu paullo depresso; parte inferiore libero 2 mm. *Filamenta* 3 mm longa; antherae 2.5 mm longae. *Ovarium* 6-loculare. *Stylus* 3 mm longus. *Fructus* ignotus.

TYPUS: Womersley & Vandenberg NGF 37403 (LAE), Kassam Pass, New Guinea, 9-12-1968.

Distribution: New Guinea.

Note. Named in honour of Dr. B. A. Krukoff for his enthusiastic support of and interest in Malesian botany.

15. *Leea macropus* K. Schum. & Laut. — Fig. 7:1—3.

L. macropus K. Schum. & Laut., Notizbl. Berl.-Dahl. 2 (1898) 130. — **Type:** *Dahl s.n.* (B, f), Ralum, New Britain 1897. — **New type:** Coode & Lake NGF 32599 (L, holo; iso in A, BO, BRI, CANB, L, LAE, SING), Tabai Rikau, New Britain, 19-12-1967.

Distribution: Bismarck Archipelago.

16. *Leea tetramera* Burtt — Fig. 1:6, 7.

L. tetramera Burtt, Kew Bull. (1935) 304. — **Type:** *Waterhouse B 78* (K, holo; L).

L. solomonensis Merr. & Perry, J. Arn. Arb. 22 (1941) 380. — **Type:** *Kajewski 2488* (A, holo; BM, BO, L).

L. suaveolens Merr. & Perry, o. c. 381. — **Type:** *Brass 3343* (A, holo; BO, L).

Distribution: Solomon Islands.

17. *Leea thorelii* Gagnep. — Fig. 3:1.

L. thorelii Gagnep., Not. Syst. 1 (1910) 230; Fl. Gén. I.-C. 1 (1912) 939; Suppl. (1950) 847; Suesseng. in E. & P., Nat. Pf. Fam. ed. 2, 202 (1953) 387. — **LECTOTYPE:** *Thorel s.n.*, Phuoc-than (P). — **Synonyms:** *Thorel s.n.*, Cay-cong (P); *Pierre 167*, Dinh Mts (P).

L. tetrasperma Gagnep., Not. Syst. 1 (1910) 230; Fl. Gén. I.-C. 1 (1912) 938, pl. 25 fig. 9—12; Craib, Fl. Siam. En. 1 (1926) 321; Gagnep., Fl. Gén. I.-C. Suppl. (1950) 846; Suesseng., Ic. — **Type:** *Thorel s.n.*, Laos (P).

Herbs to semi-herbaceous shrubs up to 1 m high, frequently with root tubercles; branches pubescent. Leaves trifoliolate to 1—3-pinnate, frequently all combinations on the same plant. Petiole 3—10 cm long; petiolar stipule a narrow wing 3—5 mm broad, 1—3 cm long; scar narrow; rachis 0—10 cm, finely pubescent, often minutely winged. Leaflets exceedingly variable on one plant, usually broadly ovate to ovate-oblong, or also orbicular to elliptic-oblong, (1—)3—8(—12) by (1—)2—5(—10) cm, sparsely pubescent, chartaceous; pearl glands globular-depressed; margin serrate or crenate to repand, often irregularly incised; apex rounded to apiculate; base rounded to cuneate, often unequal. Nerves 3—8

(—10) pairs. Petiolules 0—8 mm long, often minutely winged. *Inflorescences* up to 8 cm long, pubescent, condensed; bracts deltoid to linear, up to 3 mm long, somewhat persistent; peduncle 1—5 cm, main and ultimate branches of inflorescence condensed. *Flowers* 5-merous, white. *Calyx* pubescent, 2 by 2 mm, lobes 1 by 1 mm. *Corolla* tube + staminodial lobes 2 mm; corolla lobes 2 by 1 mm. *Staminodial tube* 1.25 mm long; upper free part 1 mm, lobes shallowly incised, sinuses shallow; lower free part 0.2 mm. *Ovary* 4—6-locular, style 1—2 mm. *Fruits* 5—8 mm diameter, blackish purple; seeds 4—6 in number, usually 4 or less by abortion, c. 3 by 3 mm, rumination outline simple, endosperm simply ruminant.

Distribution: Thailand (Northern: Nakhon Sawan; Northeastern: Khon Kaen; Eastern: Nakhon Ratchasima; Central: Chai Nat, Samut Songkhram; Southwestern: Kanchanaburi), Cambodia, Laos, S. Vietnam.

Ecology: Dry savannah woodland, bamboo forest, and grassland to 250 m alt. Often in fired areas.

18. *Leea spinea* Desc.

L. spinea Desc., Mém. Inst. Sc. Madag. Ser. B, 9 (1959) 7; Fl. Madag. Fam. 124 bis (1967) 3. — **Type:** SF (Madagascar) 3050 (P).

Trees or shrubs to 10 m high, stems and branches spiny. *Leaves* 2 (or 3)-pinnate, leaflets 11—31. Petiole up to 5 cm long; petiolar stipule a narrow wing 4—7 mm broad, 4—5 cm long; scar narrow; rachis 20—30 cm long. *Leaflets* ovate-oblong to ovate-lanceolate or elliptic-oblong to elliptic-lanceolate, (5)—8—12(—15) by (1.5)—2—3.5(—4.5) cm below sparsely pubescent, chartaceous; pearl glands not seen; margin crenate to shallowly serrulate; apex acuminate; base rounded to obtuse. Nerves 8—12 pairs, pubescent particularly in the axils. Petiolules pubescent, 3—10 mm long. *Inflorescences* up to 12 cm long, pubescent, lax; bracts broadly triangular, c. 1 by 1 mm; peduncle 3.5—5 cm long, usually bearing 3 main branches, ultimate branches compact. *Flowers* 5-merous, green. *Calyx* glabrous, 3—4 by 3—4 mm, lobes 3 by 1.5 mm. *Corolla* tube + staminodial lobes c. 4 mm; staminodial tube 3.5—4 mm; upper free part 2.5—3 mm long, lobes dentate to shallowly retuse, sinuses 0.5—0.75 mm; lower free part 1 mm. *Filaments* 1.5—1.8 mm; anthers 1.5 mm. *Ovary* 4—6-locular; style 2.5 mm. *Fruits* c. 12 mm diameter; seeds usually 6, c. 6 by 5 mm, rumination outline reticulately branched, endosperm semi-complex with an extra ingrowth on the lateral face.

Distribution: Madagascar and Comores Is.

Ecology: Dry and everwet forest to 600 m alt.

19. *Leea angulata* Korth. ex Miq. — Fig. 3:2, 3.

L. angulata Korth. ex Miq., Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 97. — **Lectotype:** *Korthals s.n.*, Krawang, Java (L). — **Synype:** Waitz s.n., Java, Kalangan (L).
[*L. horrida* T. & B., Cat. Hort. Bog. (1866) 169, nom. nud.]
L. aculeata auct. non Bl.: Kurz, J. As. Soc. Beng. 45, II (1870) 124.
L. sambucina auct. non Willd.: Bak, f. in Andrews, Monogr. Christmas I. (1900) 176.
L. sambucina Willd. var. *intermedia* Ridl., J. Str. Br. R. As. Soc. 45 (1906) 185. — **Type:** Ridley s.n., Christmas I. (n.v.).

Distribution: Nicobar Is., Peninsular Thailand, and throughout Malesia, but not yet recorded from New Guinea.

20. *Leea aculeata* Bl. ex Spreng. — Fig. 3:5.

[*Frutex aquosus mas* Rumph., Herb. Amb. 4 (1743) 102, t. 44.]

L. aculeata Bl. ex Spreng., Syst. Veg. 1 (1824) 670. — Syntypes: *Blume s.n.*, Salak & Bantam (not traced). — Lectotype: Fragment in Herb. Bl. (L, sheet no. 897.345.173).

Ticorea aculeata Blanco, Fl. Filip. (1837) 85. — *Leea aculeata* Blanco, Fl. Filip. ed. 2 (1845) 127, comb. illeg., non Bl. ex Spreng. (1824); Naves, ditto ed. 3, 1 (1877) 227, t. 306. — Type: unknown. — Topotype: Merr. Sp. Blancoanae 686 (A, K, L, P, US).

L. serrulata Miq., Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 99. — Type: *Forsten s.n.* (L, U).

L. aculeata Spreng. var. *molluccana* Miq., Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 99. — Type: *Zippelius s.n.*, Amboin (n.v.).

L. angulata auct. non Korth.: Kurz, J. As. Soc. Beng. 45, II (1876) 124; Clarke, J. Bot. 19 (1881) 105.

L. biserrata auct. non Miq.: Naves in Blanco, Fl. Filip. ed. 3 (1880) t. 306.

L. javanica auct. non Bl.: Koorders, Minah. (1898) 398.

L. sandakanensis Ridl., Kew Bull. (1931) 499; Suesseng. in E. & P., Nat. Pfl. Fam. ed. 2, 202 (1953) 386. — Syntypes: *Creagh s.n.*, Borneo, Lahut Datu, 6-4-1895, Tuilage 13-4-1895, Bulit, 11-3-1895, Sabah (K).

Distribution: Sumatra, West Java, Borneo (common in Sabah), Philippines (abundant), Celebes, Moluccas, West New Guinea (once).

Note. Unlike *L. angulata*, the spines in this species are found only on the trunk and main branches and are lacking on fertile shoots.

21. *Leea curtisii* King. — Fig. 2:1.

L. curtisii King, J. As. Soc. Beng. 65, II (1896) 416. — Type: *Curtis 2872* (SING).

[*L. stipulosa* Gagnep., Fl. Gén. I.-C., Suppl. (1950) 849, t. 106, nom. inval.]

Distribution: Malaya, N. Vietnam (Nhatrang), known only from 4 collections.

Notes. Curtis noted: 'Leaves of very young plants partly masked with silvery grey variegation down either side of the midrib'. Introduced and cultivated in Penang Botanic Gardens, but had not been traced in the last 33 years and Mr. K. G. Chang considers it unlikely that it survives.

22. *Leea macrophylla* Roxb. ex Hornem. — Fig. 3:14.

L. macrophylla Roxb. ex Hornem., Hort. Hafn. 1 (1813) 231; Roxb., Hort. Beng. (1814) 18; Fl. Ind. ed. 1, 2 (1824) 465; DC., Prodr. 1 (1824) 635; Spreng., Syst. Veg. 1 (1824) 670; G. Don, Gen. Hist. 1 (1831) 713; Roxb., Fl. Ind. ed. 2, 1 (1832) 653; Graham, Cat. Pl. Bomb. Vicinity (1839) 247; Steud., Nom. Bot. ed. 2, 2 (1840) 21, pro parte; Voigt, Hort. Sub. Calcut. (1845) 29; Wight, Ic. Pl. Ind. Or. 3 (1846) t. 1154; Dalzell & Gibson, Bomb. Fl. (1861) 41; Drury, Handb. Ind. Fl. 1 (1864) 181; Brandis, For. Fl. (1874) 102; Kurz, J. As. Soc. Beng. 44, II (1875) 178; Laws. in Hook. f., Fl. Brit. Ind. 1 (1875) 664; Clarke, J. Bot. 19 (1881) 137; Talbot, Tr. Shr. Woody Climbing. Presid. ed. 2 (1902) repr. (1949) 154; Watt, Dict. Ec. Prod. India 4 (1890) 617; Prain, Beng. Pl. (1903) repr. (1963) 240; Duthie, Fl. Up. Gangetic Pl. 1 (1903) 176; Brandis, Ind. Trees (1906) 180; Talbot, For. Fl. Bomb. Presid. & Sind 1 (1909) 326; Haines, For. Fl. Chota Nagpur (1910) 279; Craib, Aberd. Univ. Stud. 57 (1912) 43; Gagnep., Fl. Gén. I.-C. 1 (1912) 943; Gamble & Fisch., Fl. Presid. Madras 1 (1918) 239; Haines, Bot. Bihar & Orissa 1 (1925) 207; Craib, Fl. Siam. En. 1 (1926) 318; Cowan & Cowan, Trees N. Beng. (1929) 39; Kanjilal & Das, Fl. Assam 1 (1936) 305; Suesseng. in E. & P., Nat. Pfl. Fam. ed. 2, 202 (1953) 384, 387; Hundley & U Chit Ko Ko, List Tr. Shr. Herbs & Climbs. Burma (1961) 55; Suwal, Med. Pl. Nepal (1970) 132; Ic. Roxb. 4 (1970) 4, pl. 2. — Type: in Herb. Hornem. *Roxburgh s.n.*, Serampore (C).

L. integrifolia Roxb., [Hort. Beng. (1814) 85 nom. nud.]; Fl. Ind. ed. 1, 2 (1824) 472; Spreng., Syst. Veg. 1 (1824) 670, ditto 4, 2 Cur. post. (1827) 70; G. Don, Gen. Hist. 1 (1831) 712; Roxb., Fl. Ind. ed. 2, 1 (1832) 659; W. & A. Prodr. (1834) 132; Steud., Nom. Bot. ed. 2, 2 (1840) 21; Voigt, Hort. Sub. Calcut. (1845) 30; Drury, Handb. Fl. Ind. 1 (1864) 181; Laws. in Hook. f., Fl. Brit. Ind. 1 (1875) 667; Clarke, J. Bot. 19 (1881) 142; Suesseng., o.c. 358; Ic. Roxb. 4 (1972) 2, pl. 1 — Type: *Roxburgh s.n.*, Circars, ?lost (cf. Ic. no. 196, in K).

L. robusta Roxb., [Hort. Beng. (1814) 18 nom. nud.]; Fl. Ind. ed. 1, 2 (1824) 468; G. Don, Gen. Hist. 1 (1831)

- 712; Roxb., Fl. Ind. ed. 2, 1 (1832) 655; W. & A., Prodr. (1834) 132; Steud., Nom. Bot. ed. 2, 2 (1840) 21; Voigt, Hort. Sub. Calcut. (1845) 29; Drury, Handb. Fl. Ind. 1 (1864) 180; Laws. in Hook. f., Fl. Brit. Ind. 1 (1875) 667 *pro parte*; Kurz, J. As. Soc. Beng. 44, II (1875) 180; Clarke, J. Bot. 19 (1881) 164; King, J. As. Soc. Beng. 65, II (1896) 417; Cooke, Fl. Presid. Bomb. 1 (1902) 261; Talbot, Tr. Shr. Woody Climb. Bomb. Presid. ed. 2 (1902) repr. (1949) 155; Prain, Beng. Pl. (1903) repr. (1963) 239; Brandis, Ind. Trees (1906) 179; Talbot, For. Fl. Bomb. Presid. & Sind 1 (1909) 330; Haines, For. Fl. Chota Nagpur (1910) 281; Gamble & Fisch., Fl. Presid. Madras 1 (1918) 240; Haines, Bot. Bihar & Orissa 1 (1925) 209; Craib, Fl. Siam. En. 1 (1926) 320; Cowan & Cowan, Tr. N. Beng. (1929) 40; Kanjilal & Das, Fl. Assam 1 (1936) 308; Gagnep., Fl. Gén. I.-C., Suppl. (1950) 847; Suesseng., o.c. 385, 387; Santapau, Fl. Purandhar (1957) 34; Hara, Fl. E. Himal. (1966) 200; Surwal, Med. Pl. of Nepal (1970) 38; Hara, Fl. E. Himal. 2nd report (1971) 79. — T y p e: *Wallich 6826* (K).
- L. aspera* Wall. (Cat. 6825) [in Roxb., Fl. Ind. ed. 1, 2 (1824) 468, *nom. prov. in nota*] ex G. Don, Gen. Hist. 1 (1831) 713; Steud., Nom. Bot. ed. 2, 2 (1840) 21. — T y p e: *Wallich 6825* (K).
- L. simplicifolia* Griff., Not. Pl. Asiat. 4 (1854) 697, *nom. illeg.*, non Zoll. & Mor. (1845); Ic. Pl. Asiat. 4 (1854) t. 645 f. 1. — T y p e: *Griffith s.n.*, Mergui 8-1834 (K).
- L. cinerea* Laws. in Hook. f., Fl. Brit. Ind. 1 (1875) 665. — T y p e: *Wight s.n.*, Paulgautcherry (K).
- L. coriacea* Laws. in Hook. f., l.c. — T y p e: *Wight s.n.*, Paulgautcherry, India (K).
- L. diffusa* Laws. in Hook. f., o.c. 667. — T y p e: *Wallich 6825* (K).
- L. angustifolia* Laws. in Hook. f., o.c. 665; Hundley & U Chit Ko Ko, o.c. 54. — *L. parallela* Laws. var. *angustifolia* Kurz, o.c. 179. — T y p e: *McLellan s.n.*, Pegu (K).
- L. parallela* Wall. (Cat. 6828) [Steud., Nom. Bot. ed. 2, 2 (1840) 21; Voigt, Hort. Sub. Calcut. (1845) 30, all *nom. nud.*] ex Laws. in Hook. f., o.c. 666; Kurz, J. As. Soc. Beng. 44, II (1875) 178 (as var. *genuina*); Fl. Burma 1 (1877) 278; Clarke, J. Bot. 19 (1881) 139; Prain, J. As. Soc. Beng. 59, II (1890) 278; Gagnep., Fl. Gén. I.-C., Suppl. (1950) 849; Suesseng., o.c. 384, 387; Hundley & U Chit Ko Ko, l.c. — T y p e: *Wallich 6828 A & B* (K).
- L. latifolia* Wall. (Cat. 6821) ex Kurz, J. As. Soc. Beng. 44, II (1875) 178; Fl. Burma 1 (1877) 278; Clarke, J. Bot. 19 (1881) 138; King, J. As. Soc. Beng. 44, II (1896) 411; Talbot, Tr. Shr. Woody Climb. Bomb. Presid. ed. 2 (1902) repr. (1949) 155; Cooke, Fl. Bomb. Presid. 1 (1902) 260; Talbot, For. Fl. Bomb. Presid. & Sind. 1 (1909) 330; Gamble & Fisch., Fl. Presid. Madras 1 (1918) 240; Suesseng., o.c. 384. — T y p e: *Wallich 6821* (K).
- L. macrophylla* var. *oxyphylla* Kurz, J. As. Soc. Beng. 44, II (1875) 178. — S y n t y p e s: *Kurz s.n.*, Pegu; *Kurz s.n.* (not seen).
- L. talbotii* King ex Talbot, For. Fl. Bomb. Presid. & Sind 1 (1909) 329, fig. 195; Suesseng., o.c. 385. — T y p e: (not seen).
- L. venkobaranii* Gamble, Kew Bull. (1917) 26; Gamble & Fisch., Fl. Presid. Madras 1 (1918) 240; Suesseng., o.c. 385. — T y p e: *Gamble 14646* (K, CAL).
- L. pallida* Craib, Kew Bull. (1920) 302; Fl. Siam. En. 1 (1926) 319; Suesseng., o.c. 386, 387. — T y p e: *Kerr 3390* (K).
- L. sambucina* auct. non Willd.: Hosseus, Bot. Centralbl. Beih. 28 (1921) 409.
- L. parallela* Laws. var. *puberula* Craib, Fl. Siam. En. 1 (1926) 319; — T y p e: *Kerr 6153* (K).

Herbs, trees, or shrubs; young branches pubescent, often appearing mealy. Leaves unifoliolate, trifoliolate, or 1 to 3-pinnate; leaflets 1, 3, or 7—21, or numerous. Petiole to 20 cm long; petiolar stipule obovate, 2—6 by 1—4 cm, scar broad, similarly long; rachis (0—)10—15(—40) cm long, sparsely to densely hairy. Leaflets: unifoliolate specimens broadly ovate, 20—65 by 15—60 cm, margin serrate, apex acuminate, base cordate; pinnate specimens variable, ovate to ovate-lanceolate, or elliptic to elliptic-lanceolate, (8—) 14—26(—35) by (2—)4—8(—14) cm, upper surface glabrous to sparsely hairy, often drying blue-green in glabrous forms or dark brown-black in hairy forms, lower surface sparsely to densely hairy, sometimes with short mealy pubescence, chartaceous to subcoriaceous, margins sinuate to repand or serrate, apex acuminate, base rounded to sub-cordate, sometimes cuneate. Nerves (4—)8—14 pairs, pubescent or hairy. Petiolules 0—25 mm, pubescent to hairy. Inflorescences 12—45 (—60) cm long, broad, multi-branched, main and ultimate branches somewhat lax, finely mealy pubescent; bracts deltoid to narrowly triangular to 6 mm long; peduncle up to 25 cm long. Flowers 5-merous, greenish-white. Calyx 1.5—3 by 2.5—4 mm, mealy pubescent; lobes 0.25—1 by 1.5—3 mm. Corolla tube + staminodial lobes 3—4 mm; corolla lobes 2—4 by 1—2 mm, greyish pubescent to papillose, thick.

Staminodial tube 1.5—2 mm long; upper free part 1.25—1.75 mm, lobes slightly retuse or shallowly cleft, sinuses 1.25—1.75 mm deep; lower free part 0.2—0.5 mm. *Filaments* 1.25—1.75 mm; anthers 1.5—2 mm, anther walls thick, orange-brown, sometimes dark brown. *Ovary* 6-locular; style 1—1.5 mm. *Fruits* 10—15 mm diameter, seeds c. 4 by 3 mm, usually 6, rumination outline simple, endosperm simply ruminate.

Distribution: India (Bombay, Central Prov., Mysore, Madras, Orissa, Bihar, Bengal, United Prov., Sikkim, Khasia, Assam), Bhutan, Nepal, Bangladesh, Gt. Cocos I., Burma (Upper and Lower), Thailand (Northern: Chiang Mai; Central: Phra Nakhon; South-western: Kanchanaburi, Ratchaburi), Cambodia, Laos.

Ecology: Open vegetation, dry forest and teak forest, particularly forest borders and regrowths to 2250 m alt.

Notes. Previous authors have recognized some 3 to 4 basic entities, further geographic isolates of these being described as species in local floras. These entities were:

- Entity 1. Large unifoliolate leaves, sometimes trifoliolate (incl. *L. macrophylla* *sensu stricto*).
- 2. Leaves large, trifoliolate or 1-pinnate (incl. *L. cinerea*, *L. coriacea*, *L. latifolia*).
- 3. Leaves 1- or 2-pinnate, leaflets ovate-lanceolate (incl. *L. parellela*).
- 4. Leaves 2- or 3-pinnate, leaflets with scattered hairs above, upper epidermis with wax deposits (incl. *L. robusta*).

Examination of type material and classical Indian collections at Kew indicates that the flower structure is essentially the same in all cases. Differences in such features as the degree of indentation of the lobes of the staminodial tube, as reported in the literature, could not be confirmed; those which exist are clearly due to age: the staminodial tube in older open flowers withers and thus appears less indented than in the bud. Features such as papillose hairs on the calyx and corolla, the thick corolla lobes, and the characteristic orange-brown walls of the stamens are common to all entities. Mealy pubescent leaves are common in entity 1, frequent in entity 2, rare in entity 3, and not observed in entity 4. In the material at present available no good characters exist to separate the entities, earlier workers depended on degree of leaf pinnation. Entity 4 appears to be the most distinct and is characterized by the presence of hairs and microscopically by wax deposits on the upper leaf surface. In their distributions the entities overlap completely and too little is known of the ecology to ascertain if there is an ecological separation within sympatric ranges. Further collections and field observations are required, particularly on the incidence of different leaf forms. The group of entities is best viewed as a complex species with a variety of forms, probably ecological, which require further field investigation.

23. *Leea grandifolia* Kurz — Fig. 3:7.

L. grandifolia Kurz, J. Bot. 13 (1875) 325; J. As. Soc. Beng. 45, II (1876) 124; Clarke, J. Bot. 19 (1881) 138; Prain, J. As. Soc. Beng. 60, II (1891) 167; King, J. As. Soc. Beng. 65, II (1896) 411; Suesseng. in E. & P., Nat. Pfl. Fam. ed. 2, 20d (1953) 384. — Type: Kurz s.n., Katachal, Nicobar Is. (BO, K).

Trees or treelets, up to 7 m high. *Leaves* 1-pinnate, rarely trifoliolate, leaflets (3)5—7. Petiole c. 12 cm long; petiolar stipule half obovate, c. 3.5 by 1.2 cm, scar broad, 4 cm long; rachis 14—18 cm long. *Leaflets* broadly ovate to ovate or broadly elliptic to elliptic, (15)—20—30 by 12—16(—23) cm, glabrous, (sub) coriaceous: pearl glands not seen; margin shallowly serrulate; apex acute to shortly acuminate; base rounded to obtuse. Nerves 8—12 pairs. Petiolules up to 2.5 cm long. *Inflorescences* 6—8 cm long, glabrous; bracts deltoid to triangular, early caducous; peduncle 2—3 cm long, main and ultimate branches short.

Flowers 5-merous, greenish-white. *Calyx* 2 by 4 mm, glabrous; lobes 1 by 2 mm. *Corolla* tube + staminodial lobes 4.5 mm; corolla lobes 3 by 1.5 mm. *Staminodial tube* 2.25 mm long; upper free part 2 mm, lobes shallowly cleft at the apex, sinuses 0.5 mm; lower free part 0.25 mm. *Filaments* 1.5 mm; anthers 1.5 mm. *Ovary* 6-locular; style 2.5 mm. *Fruits* (*ex descr.*) 5—12 mm diameter, black.

Distribution: Andaman & Nicobar Is.

Ecology: Secondary lowland vegetation, particularly in the coastal belt.

24. *Leea compactiflora* Kurz — Fig. 3:13; 8:4.

- L. compactiflora* Kurz, J. As. Soc. Beng. 42, II (1873) 65, ditto, 44, II (1875) 179; Fl. Burma 1 (1877) 279; Clarke, J. Bot. 19 (1881) 138; Gage, Rec. Bot. Surv. Ind. 3 (1904) 37; Suesseng. in E. & P. Nat. Pf. Fam. ed. 2, 20d (1953) 385, 387. — *Type:* Kurz s.n., Martaban (*n. v.*).
L. trifoliata Laws. in Hook. f., Fl. Brit. Ind. 1 (1875) 666; Clarke, o.c. 101; J. Linn. Soc. Bot. 25 (1899) 13; Kanjilal & Das, Fl. Assam 1 (1936) 305; Suesseng., o.c. 383. — *LECTOTYPE:* Jenkins s.n., Assam (K). — *Synonyms:* Booth s.n., Bhutan (K), Griffith s.n., Mishmi Hills (K).
L. robusta auct. non Roxb.: Laws. in Hook. f., o.c. 667 *pro parte*.
L. bracteata Clarke, J. Bot. 19 (1881) 164; J. Linn. Soc. Bot. 25 (1889) 13; Duthie, Fl. Up. Gangetic Plain 1 (1903) 176; Brandis, Ind. Trees (1906) 180; Gagnep., Fl. Gén. I.-C. 1 (1912) 942; Cowan & Cowan, Trees N. Beng. (1929) 40; Kanjilal & Das, Fl. Assam 1 (1936) 308; Gagnep., Fl. Gén. I.-C., Suppl. (1950) 851; Suesseng., o.c. 385. — *LECTOTYPE:* Hook. f. & Thoms. 169 (K). — *Synonyms:* from Sikkim & Khasia: Clarke 11824, 12517, 17726; Griffith 1283; Hook. f. & Thoms. 170, 1638, s.n. 11-7-1850, s.n. 22-7-50, Treutler 336; from Oudh Terai: Thoms. s.n. (all at K).

Small shrubs, sometimes with creeping rootstock, or trees up to 10 m high. *Leaves* (trifoliate or) 1- or 2-pinnate, basal pair of leaflets often highly reduced; leaflets (3—) 7—15. Petiole (2—) 12—20 cm long; petiolar stipule a narrow wing (2—) 5—8 by 0.2—0.5 cm, scar narrow, similarly long; rachis (2—) 12—20 cm long. *Leaflets* elliptic to elliptic-lanceolate or ovate to ovate-lanceolate (5—) 10—25(—30) by (2.5—) 5—11(—13) cm, (glabrous—) ferruginously hairy, (sub)coriaceous, pearl glands not seen; margin serrulate; apex acuminate; base truncate to obtuse; nerves 8—15 pairs, usually hairy. Petiolules 2—20 mm, usually hairy. *Inflorescences* (3—) 8—15 cm long, short and compact, pubescent; bracts broadly ovate, to 2 by 0.5 cm, conspicuous; peduncle (1—) 3—5 (—10) cm long, ultimate branches short. *Flowers* 5-merous, greenish white. *Calyx* c. 3 by 3 mm, (glabrous—) pubescent; lobes 2 by 2 mm. *Corolla* tube + staminodial lobes 3—3.5 mm; corolla lobes 3 by 2 mm. *Staminodial tube* 2—2.5 mm; upper free part 1.5—2 mm, lobes shallowly retuse or cleft, sinuses shallow; lower free part 0.25—0.5 mm. *Filaments* 1—1.4 mm; anthers 1.75—2 mm. *Ovary* (2—) 4—6-locular; style 2—3 mm. *Fruits* 7—10 mm diameter, orange-yellow; seeds usually 6, often less by abortion, c. 3 by 3 mm, rumination outline simple, endosperm simply ruminate.

Distribution: India (Sikkim, Assam, Khasia, Manipur), Bhutan, W. Bengal, S. Burma, Laos, N. Vietnam, China (Yunnan).

Ecology: Woodland on shaded ravines and hillsides; sometimes dying back to a woody base in drier localities; up to 2000 m alt.

25. *Leea crispa* van Royen ex L. — Fig. 2:8; 6:1—3.

- [*Nalugu* Rheede, Hort. Malabar. 2 (1679) 43—44, plate in Hort. Malabar. 1 (1678) 26, *non* 2 (1679) 26].
L. crispa van Royen ex L., Syst. Nat. ed. 12, 2 (1767) 627 & Mantissa 1 (1767) 124; W. Ait., Hort. Kew. 1 (1789) 283; Lamk., Encycl. Meth. 3, 2 (1792) 460; Salisb., Prod. (1796) 318; Jaume St.-Hilaire, Expos. Fam. Nat. 1 (1805) 344; Hornem., Hort. Hafn. 1 (1813) 213; Roem. & Schultes, Syst. Veg. 4 (1819) 706;

- Spreng.*, Syst. Veg. I (1824) 670; DC., Prodr. I (1824) 635; Roxb., Fl. Ind. ed. I, 2 (1824) 467; G. Don, Gen. Hist. I (1831) 713; Roxb., Fl. Ind. ed. 2, I (1832) 655; Steud., Nom. Bot. ed. 2, 2 (1840) 21; Voigt, Hort. Sub. Calcut. (1845) 29; Drury, Handb. Ind. Fl. I (1864) 181; Laws. in Hook. f., Fl. Brit. Ind. I (1875) 655; King, J. As. Soc. Beng. 44, II (1875) 179; Fl. Burma I (1877) 280; Clarke, J. Bot. 19 (1881) 135; Watt, Dict. Ec. Prod. India 4 (1890) 616; Talbot, Tr. Shr. Woody Climbing. Bomb. Presid. (1894) ed. 2 (1902) repr. (1949) 154; Cooke, Fl. Presid. Bombay I (1902) 259; Prain, Beng. Pl. (1903) repr. (1903) 239; Brandis, Ind. Trees (1906) 180; Talbot, For. Fl. Bomb. Presid. & Sind I (1909) 327; Gagnep., Fl. Gén. I.-C. I (1912) 936, pl. 25 f. 1—8; Gamble & Fisch., Fl. Presid. Madras I (1918) 240; Haines, Bot. Bihar & Orissa I (1925) 208; Craib, Fl. Siam. En. I (1926) 317; Cowan & Cowan, Trees N. Beng. (1929) 39; Kanjilal & Das, Fl. Assam I (1936) 305; Suesseng. in E. & P., Nat. Pfl. Fam. ed. 2, 20d (1953) 383, 387; Kihara, Fl. Pl. & Ferns Nepal Himalaya (1955) 177; Hundley & U Chit Ko Ko, List Tr. Shr. Herbs & Climbing. Burma (1961) 55; Hara, Fl. E. Himal. (1966) 200. — T y p e: *Herb. Linn. ex Van Royen* (LINN.). *L. pinnata* Andrews, Bot. Rep. 5 (1804) t. 355; Spreng., Syst. Veg. I (1824) 670. — T y p e: Andrews' plate 355.
- L. herbacea* Hamilton, Trans. Linn. Soc. 14 (1823) 228; Steud., Nom. Bot. ed. 2, 2 (1840) 21; Clarke, J. Bot. 19 (1881) 137; J. Linn. Soc. Bot. 25 (1899) 13; Prain, Beng. Pl. (1903) repr. (1903) 239; Brandis, Ind. Trees (1906) 180; Haines, For. Fl. Chota Nagpur (1910) 280; Gamble & Fisch., Fl. Presid. Madras I (1918) 240; Craib, Fl. Siam. En. I (1926) 317; Cowan & Cowan, Trees N. Beng. (1929) 40; Gagnep., Fl. Gén. I.-C., Suppl. (1950) 848; Suesseng., o.c. 384, 387; Hundley & U Chit Ko Ko, I.c.; Hara, Fl. E. Himal. (1966) 200; Fl. E. Himal. 2nd Rep. (1971) 78. — T y p e: *Wallich* 6829 (leg. Hamilton) (K).
- L. aspera* Edgeworth, Trans. Linn. Soc. 20 (1846) 36, nom. illeg., non Wall. ex G. Don (1831); Brandis, For. Fl. (1874) 102; Laws. in Hook. f., Fl. Brit. Ind. I (1875) 665; Kurz, J. As. Soc. Beng. 44, II (1875) 179; Fl. Burma (1877) 280; Clarke, J. Bot. 19 (1881) 136; Watt, Dict. Ec. Prod. India 4 (1890) 616; Talbot, Tr. Shr. Woody Climbing. Bomb. Presid. ed. 2 (1902) repr. (1949) 154; Duthie, Fl. Up. Gang. Pl. I (1903) 176; Prain, Beng. Pl. (1903) repr. (1903) 239; Brandis, Ind. Trees (1906) 180; Talbot, For. Fl. Bomb. Presid. & Sind I (1909) 327; Haines, For. Fl. Chota Nagpur (1910) 280; Kanjilal, For. Fl. Siwalik & Jaunsar (1911) 112; Bamber, Pl. of Punjab (1916) 109; Gamble & Fisch., Fl. Presid. Madras I (1918) 240; Haines, Bot. Bihar & Orissa I (1925) 208; Osmaston, For. Fl. Kumaon (1927) 122; Kanjilal & Das, Fl. Assam (1936) 306; Suesseng. o.c. 383; Hundley & U Chit Ko Ko, I.c. — *L. edgeworthii* Santapau, Rec. Bot. Surv. Ind. 16 (1953) 54; Fl. Panjab (1957) 34; Banerji, Rec. Bot. Surv. Ind. 19, 2 (1965) 33. — L e c t o t y p e: *Edgeworth* 318 (K). — S y n t y p e: *Royle s.n.*, NW. India (K).
- L. pumila* Kurz, J. As. Soc. Beng. 41, II (1872) 302; ditto 44, II (1875) 179; Laws. in Hook. f., Fl. Brit. Ind. I (1875) 606; Kurz, Fl. Burma I (1877) 278; Williams, Bull. Herb. Boiss. II, 5 (1905) 217; Suesseng. o.c. 383, pro parte; Hundley & U Chit Ko Ko, List Tr. Shr. Herb. & Climbing. Burma (1961) 155. — T y p e: Kurz 107 (K).

Semi-herbaceous shrubs to trees, up to 8 m high; stems often fluted and crisply winged. *Leaves* (unifoliolate, trifoliolate, or) 1- or 2-pinnate; leaflets (3)5—7(—15). Petiole 1—4 cm; petiolar stipule a narrow wing 1.5—4 by 0.5 cm, scar narrow, 1—3 cm long; rachis (0—)4—12(—25) cm, often crisply winged. *Leaflets* broadly ovate to ovate-oblong, less frequently broadly elliptic to elliptic-oblong, (4—)10—18(—28) by (2—)5—12 (—16) cm, chartaceous to subcoriaceous, above glabrous or sparsely hairy, below glabrous to densely hairy; pearl glands globular, sparse; margins deeply crenate to serrate; apex acuminate; base rounded to cordate, 5—7-nerved. Nerves 8—16 pairs. Petiolules 5—15 (—25) mm long, often winged. *Inflorescences* 2—12 cm long, glabrous or pubescent; bracts ovate to linear-lanceolate, up to 6 mm long; peduncle 0—6 cm, often fluted or crisply winged, ultimate branches short, fine. *Flowers* 5-merous, greenish white. *Calyx* 2 by 3 mm, glabrous to pubescent, lobes 0.5 by 1.5 mm. *Corolla* tube + staminodial lobes 3—4 mm; corolla lobes 2.5—3 by 1—1.5 mm. *Staminodial tube* 2—2.5 mm long; upper free part 1.5—2 mm, lobes deeply bifid, sinuses deep, c. 1 mm; lower free part 0.5 mm. *Stamens* free; filaments 1.25 mm; anthers 1 mm, attached to the filaments by a conspicuous boss. *Ovary* 4—8-locular; style 1—2 mm. *Fruits* c. 12 mm diameter, purple black; seeds usually 6, c. 5 by 3 mm, rumination outline simple, endosperm simply ruminate.

Distribution: India (Bombay, Central Prov., Mysore, Madras, Orissa, Bengal, Bihar, United Prov., Punjab, W. Himalayas, Sikkim, Khasia, Assam, Manipur), Bhutan, Nepal,

Bangladesh, Burma (Lower, Upper, & Northern), Thailand (Northern: Chiang Mai, Nakhon Sawan, Mae Hong Son; Southwestern: Kanchanaburi), Cambodia, Laos, N. & S. Vietnam, China (Yunnan).

Ecology: Evergreen, deciduous, and lower montane forests to 2250 m alt; also in grass-land plains where it often dies back annually.

26. *Leea tinctoria* Baker — Fig. 3:8.

L. tinctoria Baker in Oliv., Fl. Trop. Afr. 1 (1868) 416; Clarke, J. Bot. 19 (1881) 167; Ficalho, Pl. Ut. Afr. Port. (1884) 123; Planch. in Henriq., Bol. Soc. Brot. 10 (1893) 109; Gilg in E. & P., Nat. Pfl. Fam. 3, 5 (1896) 456; Hiern, Cat. Afr. Pl. Welw. 1 (1896) 165; Gilg & Brand, Bot. Jahrb. 44 (1912) 549, fig. 18 L—P; Chev., Sudania 2 (1914) 45, 48, 54; Henriq., Sudania 27 (1917) 190; Engler in Engler & Drude, Veg. Erd. 9, 3, 2 (1921) 342; Exell, Cat. Vasc. Pl. S. Tomé (1944) 142; Suesseng. in E. & P., Nat. Pfl. Fam. ed. 2, 20d (1953) 388, fig. 100 L—P. — **LECTOTYPE:** Welwitsch 1502 (BM, LISU). — **Synonym:** Ackermann s.n., s.l. (K).

Shrubs or small trees to 4 m high. *Leaves* 1- or 2-pinnate, to c. 75 cm long. Petiole to 17 cm; petiolar stipule half-obovate, c. 5 by 1.5 cm, scar broad, c. 5 cm long; rachis to 45 cm long. *Leaflets* ovate to ovate-oblong or elliptic-oblong (5)—10—15(—20) by (2.5)—4—6(—10) cm, glabrous; margin dentate-serrate to crenate; apex acuminate, base rounded to cuneate. Nerves 5—12 pairs. Petiolules 5—15 mm. *Inflorescences* to 15 cm, compact, rusty tomentose, bracts deltoid, up to 2 mm long; peduncle to 8 cm, ultimate branches short. *Flowers* 5-merous, calyx red, corolla orange, staminal tube white. *Calyx* 5 by 5 mm, pubescent; lobes 1 by 2 mm. *Corolla tube* + staminodial lobes 10 mm; corolla lobes 7 by 2.5 mm. *Staminodial tube* 6—7 mm; upper free part 4 mm, lobes slightly cleft at the apex, sinuses 3 mm; lower free part 3 mm. *Filaments* 3 mm; anthers 2 mm. *Ovary* 4—6-locular; style 8—11 mm. *Fruits* 6—8 mm diameter; seeds usually 6, 3 by 2 mm, rumination outline simple, endosperm simply ruminant.

Distribution: São Tomé I. (situated in the Gulf of Guinea, Atlantic Ocean).

Ecology: Lowland forest, particularly streamsides, up to 1500 m.

Note. An endemic species not recorded from other islands of the chain. No closely allied species in Africa or mainland Asia.

27. *Leea aequata* L. — Fig. 3:12.

[*Frutex aquosus femina* Rumph., Herb. Amb. 4 (1743) 103, t. 45].

L. aequata L., Syst. Nat. ed. 12, 2 (1767) 627 & Mantissa 1 (1767) 124. — **Type:** *Herb. Linn.* 1118: 1 (LINN.).

L. hirta Roxb. ex Hornem., Hort. Hafn. 1 (1813) 231. — *L. scabra* Roxb. ex Roemer & Schultes, Syst. Veg. 4 (1819) 814 in obs. — **Type:** *Wallich* s.n., Bengal, in Herb. Hornem. (C), (no. 665 ex Herb. Banks).

L. hirsuta Bl. ex Spreng., Syst. Veg. 1 (1824) 670. — **Type:** *Blume* s.n., Buitenzorg, Java (L).

L. ancolona Miq., Fl. Ind. Bat. 1, 2 (1859) 611. — **Type:** *Junghuhn* s.n., Tobing, Sumatra (U).

L. kurzii Clarke, J. Bot. 19 (1881) 165. — **Type:** *Kurz* s.n., Waterhouse Cove, Andaman Is. (K).

L. hispida Gagnep., Not. Syst. 1 (1910) 229. — **Type:** *Thorel* 2130, Laos (P).

Distribution: India (Bombay, Mysore, Madras, Central Prov., Orissa, Bihar, Bengal, United Prov., Sikkim, Assam), Bhutan, Nepal, Bangladesh, Andaman Is., Upper & Lower Burma, Thailand (Northern: Mae Hong Son, Nakhon Sawan; Eastern: Nakhon Ratchasima; Southwestern: Kanchanaburi; Peninsular: Krabi, Surat Thani), Cambodia, Laos, N. & S. Vietnam, and throughout Malesia, except New Guinea.

28. *Leea rubra* Bl. ex Spreng. — Fig. 3:10, 11; 6:6, 7.

- L. rubra* Bl. ex Spreng., Syst. Veg. 1 (1824) 670. — T y p e: *Blume s.n.*, s.l. (L.).
L. polyphylla Miq., Fl. Ind. Bat. 1, 2 (1859) 610. — *L. rubra* var. *polyphylla* Miq., Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 97. — T y p e: *Junguhuhn s.n.*, Antjol, Java (L, U).
L. rubra var. *apiifolia* Zipp. ex Miq., l.c. — T y p e: *Zippelius s.n.*, Timor (L, U).
L. sanguinea auct. non Wall.: Kurz, J. As. Soc. Beng. 42, II (1873) 66, *pro parte*.
L. coccinea auct. non Planch.: Kurz, ditto 44, II (1875) 179.
L. brunoniania Clarke, J. Bot. 19 (1881) 166. — L e c t o t y p e: *Schultz* 627, Port Darwin, Australia (K). — S y n t y p e: *R. Brown* 5272, N. Australia (K).
L. linearifolia Clarke, J. Bot. 19 (1881) 165. — T y p e: *Lebeuf* 214 (K).
[*L. rubra* forma *celebica* Koord., Minah. (1898) 398, nom. nud., name without description for a Koorders collection from Ratatotok, Celebes.]

Distribution: India (Assam, Khasia, Bengal), Bangladesh, Burma, Thailand (Northern: Chiang Mai, Nakhon Sawan; Central: Phra Nakhon, Pathum Thani; Southeastern: Prachin Buri; Peninsular: Phuket), Cambodia, Laos, N. & S. Vietnam, throughout Malesia but in the Philippines only in Palawan, N. Australia.

29. *Leea alata* Edgeworth — Fig. 3:9.

- L. alata* Edgeworth, Trans. Linn. Soc. 20 (1846) 36; Brand., For. Fl. (1874) 102; Laws. in Hook. f., Fl. Brit. Ind. 1 (1875) 665; Clarke, J. Bot. 19 (1881) 101; Duthie, Fl. Up. Gangetic Plain 1 (1903) 175; Prain, Beng. Pl. (1903) repr. (1963) 239; Brandis, Ind. Trees (1906) 179; Haines, Fl. Chota Nagpur (1910) 279; Kanjilal, For. Fl. Siwalik & Jaunsar (1911) 112; Haines, Bot. Bihar & Orissa 1 (1925) 207; Osmaston, For. Fl. Kumaon (1927) 121; Kanjilal & Das, Fl. Assam 1 (1936) 303; Suesseng. in E. & P., Nat. Pfl. Fam. ed. 2, 202 (1953) 383. — L e c t o t y p e: *Edgeworth* 319 (K). — S y n t y p e: *Royle* s.n., NW. India (K).
L. rubra auct. non Bl.: Royle, Ill. Bot. Himal. Mount. (1835) 145.

Herbaceous to woody shrubs up to 3 m high, branches often ribbed. Leaves 1-pinnate, rarely trifoliolate, leaflets (3)5—9. Petiole 4—8 cm long; petiolar stipule oblong, 3—4 by 1 cm, scar broad, of similar length; rachis 5—15 cm, narrowly winged. Leaflets elliptic-oblong to elliptic-lanceolate, (10—)15—25(—36) by (2—)4—7(—8) cm, glabrous or rarely minutely pubescent, chartaceous to subcoriaceous, pearl glands stellate, infrequent; margins dentate-serrate; apex acute, base rounded, unequal. Nerves 8—12 pairs. Petiolules 0—3(—10) mm. Inflorescences 10—25 cm long, glabrous or minutely pubescent, compact; bracts deltoid, up to 2 mm long, inconspicuous; peduncle 4—20 cm long, ultimate branches short, somewhat condensed. Flowers 5-merous, red. Calyx 2—2.5 by 1.5—2 mm, glabrous; lobes 1 by 1 mm. Corolla tube + staminodial lobes 3 mm; corolla lobes 2.5 by 1 mm. Staminodial tube 2 mm long; upper free part 1.75 mm, lobes shallowly retuse, sinuses deep, 1.5—1.75 mm; lower free part 0.25 mm. Filaments 1 mm; anthers 1.25 mm. Ovary 6-locular; style 1 mm. Fruits 5—10 mm diameter, seeds usually 6, c. 3 by 2 mm, rumination outline simple, endosperm simply ruminate.

Distribution: India (Punjab, United Prov., Central Prov., Orissa, Bihar, Bengal, Assam, Khasia, Sikkim), ?Nepal, Bhutan.

Ecology: Dry woodland and hill forest. Usually dying back in the dry season to a woody base.

30. *Leea setuligera* Clarke — Fig. 3:6; 5:11 & 12.

- L. setuligera* Clarke, J. Bot. 19 (1881) 105; Cooke, Fl. Presid. Bomb. 1 (1902) 261; Suesseng. in E. & P., Nat. Pfl. Fam. ed. 2, 202 (1953) 383; Santapau, Rec. Bot. Surv. Ind. 16 (1953) 56. — T y p e: *Stocks* s.n., Concan (K).
L. mastersii Clarke, o.c. 142; Gagnep., Fl. Gén. I.-C., Suppl. (1950) 854; Suesseng., o.c. 385, 387. — T y p e: *Masters* (400), Assam (K).

L. mastersii var. *siamensis* Craib, Fl. Siam. En. 1 (1926) 319; Gagnep., Fl. Gén. I.-C., Suppl. (1950) 854.
Type: Kerr 5485 (K).

L. tenuifolia Craib, Kew Bull. (1926) 359; Fl. Siam. En. 1 (1926) 321; Gagnep., o.c. 852; Suesseng., o.c. 385, 387. — Type: Kerr 9114 (K).

Small shrubs up to 2 m high. Leaves 2- or 3-pinnate, leaflets numerous. Petiole 8—20 cm long; petiolar stipule a narrow wing 2—5 by 3—1 cm, scar narrow, of similar length; rachis 8—20 cm long. Leaflets (broadly) ovate to ovate-oblong, less frequently elliptic to elliptic-oblong, (2)—6—12(—25) by (1)—2—5(—11) cm, above setaceous hairy, below with setaceous hairs on the nerves, membranous to chartaceous, sometimes wine coloured below, pearl glands angular, sparse; margin serrate; apex acuminate; base acute to rounded, rarely subcordate or unequal. Nerves 6—12 pairs. Petiolules c. 5 mm long. Inflorescences 5—15 cm long, condensed or lax, pubescent; bracts narrowly triangular, inconspicuous; peduncle up to 8 cm long, ultimate branches short and condensed or long and multi-branched. Flowers 5-merous wine red to carmine in the bud, creamish-yellow when open. Calyx 1.5 by 2.5 mm, pubescent; lobes 1 by 1 mm. Corolla tube + staminodial lobes 2—2.75 mm long; corolla lobes 2—2.25 by 1.25—1.5 mm. Staminodial tube 1.5—1.8 mm long; upper free part 1—1.5(—2) mm, lobes notched or cleft, sinuses deep, 1—1.25 mm; lower free part 0.2—0.3 mm. Filaments 0.75—1.25 mm; anthers 1—1.25 mm. Ovary 4—6-locular; style 1 mm. Fruits 7—10 mm diameter; seeds 4—6 in number, c. 5 by 4 mm, rumination outline simple, endosperm simply ruminant.

Distribution: India (Concan, Assam), Thailand (Northern: Chiang Mai, Mae Hong Son; Eastern: Nakhon Ratchasima), China (Yunnan). Known only from 7 collections.

Ecology: Undershrubs in deciduous forest.

Note. Very similar to *L. guineensis* in general appearance, and possibly frequently overlooked and confused with that species. Probably most closely related to the little known *L. saxatilis* from Malaya.

31. *Leea saxatilis* Ridl. — Fig. 3:4.

L. saxatilis Ridl., J. Str. Br. R. As. Soc. 75 (1917) 26. — Lectotype: Ridley 305 (SING). — Syntype: Ridley 8260 (SING).

Distribution: Malaya.

Note. A rarely collected species most probably related to *L. setuligera* Clarke; further collections and field observations required.

32. *Leea guineensis* G. Don — Fig. 4:2—5.

L. guineensis G. Don, Gen. Hist. 1 (1831) 712; Hook. f., Niger Fl. (1849) 268; Clarke, J. Bot. 19 (1881) 166; Engler, Pflanzenw. O. Afr. vol. C (1895) 261; Hiern, Cat. Welw. Pl. 1 (1896) 164; De Wild., Ét. Fl. Bas-et Moy.-Congo 1 (1904) 163, 286; Miss. Laur. 1 (1905) 150; Palacky, Cat. Pl. Madag. 5 (1907) 51; T. & H. Dur., Syll. Fl. Congo. (1909) 109; De Wild., Comp. Kasai (1910) 347; Ét. Fl. Bas-et Moy.-Congo 3 (1910) 226; Ann. Mus. Congo Bot. V, 3 (1910) 226, Ét. Fl. Bang. Ub. (1911) 230, 343; Ann. Soc. Sc. Brux. 38, 2 (1914) 19; Bull. Jard. Bot. État. Brux. 4 (1914) 157; Mildbr., Wiss. Ergeb. Deutsch. Zentr. Afr. Exp. 1907—1908, 2 (1914) 494, 681; De Wild., Bull. Jard. Bot. État. Brux. 5 (1919) 340; Miss. de Briey au Mayumbe (1920) 186, 252; Pl. Bequaert 1 (1922) 373; Exell, J. Bot. 66, Suppl. Polypet. (1928) 83; Hutch. & Dalz., Fl. W. Tr. Afr. 1 (1928) 479, Appendix (1937) 304; Staner & Boutique, Mat. Pl. Med. Indig. Congo Belge (1937) 118; Gossweiler & Mendonça, Cart. Fitogeogr. Angola (1939) 90; Robyns, Fl. Sperm. Parc Nat. Albert 1 (1948) 361; Andrews, Fl. Pl. Engl.-Egypt. Sudan 2 (1952) 312, fig. 111; Suesseng. in E. & P., Nat. Pl. Fam. ed. 2, 202 (1953) 388; Exell & Mendonça, Conspl. Fl. Angola 2, 1 (1954) 71; Lawalree, Rés. Sc. Exp. Hydr. Lac Tanganyika 4, 2 (1955) 79; Keay in Hutch. & Dalz., Fl. W. Tr. Afr. ed. 2, 1 (1958) 683; Descoings, Mém. l'Inst. Sc. Madag. (1959) sér. B (1960) 18; De Wit, Fl. Congo Belg. 9 (1960) 569, fig. 14; Irvine, Woody Pl. Ghana (1961) 487; White, For. Fl. N.

- Rhod. (1962) 231; H. Wild in Fl. Zambes. 2, 2 (1966) 494, t. 99; Descoings, Fl. Madag. fam. 124 bis (1967) 6; Fl. Cameroun 13 (1972) 134. — T y p e: G. Don s.n. (BM).
- L. sambucina* auct. non Willd.: Schum. & Thon., Beskr. Guin. Pl. (1827) 154; Baker in Fl. Tr. Afr. 1 (1868) 415; Fl. Maurit. (1877) 54; Cantley, Cat. Roy. Bot. Gard. Maurit. (1880) 5; Hoffm., Linnaea 43 (1881) 124; Cordemoy, Fl. Réunion (1894) 412; Dur. & Schinz, Ét. Fl. l'État Ind. Congo 1 (1896) 96; Acad. Roy. Belg. 53 (1896) 16; De Wild. & Dur., Ann. Mus. Congo Bot. II, 1 (1899) 16; ditto 2 (1900) 13; Pl. Gilettiae 1 (1900) 19; De Wild., Bull. Herb. Boiss. II, 1 (1900) 9; De Wild. & Dur., Ann. Mus. Congo Bot. III, 1 (1901) 50; Volkens, Bot. Jahrb. 31 (1902) 468; De Wild., Pl. Laur. (1903) 41; Pl. Ut. ou Int. Congo 2 (1906) 129; Matsumura & Hayata, J. Coll. Sc. Univ. Tokyo 22 (1906) 93; Palacky, Cat. Pl. Madag. 5 (1907) 51; Hayata, Ic. Pl. Form. 1 (1911) 150.
- L. maculata* Desf., Cat. Pl. Hort. Reg. Paris, ed. 3, Addit. (1832) 406. — T y p e: ? *Herb. Desf.* (not found,? lost).
- L. arborea* Telf. ex W. & A., Prodr. (1834) 132 in obs. — T y p e: *Wallich* 6824L (K).
- L. arborea* Sieber ex Boj., Hort. Maurit. (1837) 61, nom. illeg., non Telf. ex W. & A. (1834); Voigt, Hort. Sub. Calcut. (1845) 30. — *L. sambucina* Willd. var. *arborea* Miq., Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 99; Clarke, Ic. — T y p e: *Sieber* 321 (L).
- L. manillensis* Walp., Nov. Act. Ac. Caes. Leop. -Car. 19 (1843) Suppl. 1. — T y p e: *Meyen* s.n., Manila, Philippines (K. P.).
- L. aurantiaca* Zoll. & Mor., Nat. Geneesk. Arch. N. I. 2 (1851) 577. — T y p e: *Zollinger* 2297 (K, P).
- L. coccinea* Planch., Hort. Donat. (1854) 6; Hook. f., Bot. Mag. 88 (1862) t. 5299. — [*L. lucida* Linden ex Planch., Hort. Donat. (1854) 6, pro syn.; Linden Catalogue no. 8 (1853) 10, no 10 (1855) 16, no 11 (1856) 14, nom. nud.] — T y p e: not traced.
- L. punctata* Desf. ex Planch., Hort. Donat. (1854) 6, nom. nud. in nota. — T y p e: not traced.
- L. cuspidifera* Baker, J. Linn. Soc. 22 (1855) 461. — *L. guineensis* var. *cuspidifera* Desc., Mém. Inst. Sc. Madag. (1959) sér. B, 9 (1960) 16; Fl. Madag. fam. 124 bis (1967) 10. — T y p e: *Baron* 4785 (K).
- L. javanica* auct. non Bl.: Miq., Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 100.
- [*L. speciosa* Sieb. ex Miq., Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 99, nom. nud. in nota.]
- L. laeta* Wall. [Cat. 6831; Steud., Nom. Bot. ed. 2, 2 (1840) 21; all nom. nud.] ex Kurz, J. As. Soc. Beng. 42, II (1873) 65. — T y p e: *Wallich* 6831 (K).
- L. sanguinea* Wall. [Cat. 6824; Boj., Hort. Maurit. (1837) 61; all nom. nud.] ex Kurz, J. As. Soc. Beng. 42, II (1873) 66, pro parte. — T y p e: *Wallich* 6824M (K).
- L. acuminata* Wall. [Cat. 6830; Steud., Nom. Bot. ed. 2, 2 (1840) 21; Kurz, Rep. Veg. And. Isl. (1870) 34; all nom. nud.] ex Clarke, J. Bot. 19 (1881) 141. — T y p e: *Wallich* 6830 (K).
- L. cumingii* Clarke, J. Bot. 19 (1881) 166. — T y p e: *Cuming* 1379 (K).
- L. pumila* auct. non Kurz: Clarke, J. Bot. 19 (1881) 102; Suesseng., o.c. 383, pro parte.
- L. wightii* Clarke, J. Bot. 19 (1881) 105; Jackson in Index Kew. 2 (1895) 48 ("*L. wrightii*"); Brandis, Ind. Trees (1906) 179; Gamble & Fisch., Fl. Presid. Madras 1 (1918) 239; Suesseng., o.c. 383. — *L. staphylea* auct. non Roxb.: Wight, Illustr. Ind. Bot. 1 (1845) t. 58; Ic. Pl. Asiati. 1 (1854) t. 78. — Lectotypus: *Wight* 523, Courtallum anno 1835 (K). — Syntypes: *Wight* 523, Malabar anno 1836 (K).
- L. parva* Elm., Leafl. Philip. Bot. 1 (1908) 317. — T y p e: *Elmer* 6175 (A, K).
- L. negrosense* Elm., Leafl. Philip. Bot. 2 (1908) 494. — T y p e: *Elmer* 10174 (BO, K, L, US).
- L. palawanensis* Elm., Leafl. Philip. Bot. 5 (1913) 1851. — T y p e: *Elmer* 13256 (BO).
- L. euphlebia* Merr., Philip. J. Sc. 9 (1915) Bot. 453. — T y p e: *Vanoverberg* 444 (A, K, L).
- L. parvifoliola* Merr., Philip. J. Sc. 11 (1916) Bot. 145. — T y p e: *Tarrosa* FB 14241 (n.v.).
- L. papillosa* Merr., Philip. J. Sc. 13 (1918) Bot. 307. — T y p e: *Ramos* BS 30338 (US).
- L. luzonensis* Elm., Leafl. Philip. Bot. 8 (1919) 3104. — T y p e: *Elmer* 17766 (A, BO, G, K, L, P, U).
- L. robusta* auct. non Roxb.: Ridl., Fl. Mal. Pen. 1 (1922) 486; Craib, Fl. Siam. En. 1 (1926) 320.
- L. dentata* Craib, Kew Bull. (1926) 357; Fl. Siam. En. 1 (1926) 317; Gagnep., Fl. Gén. I.-C., Suppl. (1950) 846; Suesseng., o.c. 386, 387. — T y p e: *Kerr* 3294 (K).
- L. schomburgkii* Craib, Kew Bull. (1926) 358; Fl. Siam. En. 1 (1926) 321; Gagnep., Fl. Gén. I.-C., Suppl. (1950) 855; Suesseng., o.c. 387. — T y p e: *Schomburgk* 256 (K, P).
- L. brunoniania* auct. non Clarke: Laut., Bot. Jahrb. 63 (1930) 277; Kanehira, Bot. Mag. Tokyo 45 (1931) 295; Fl. Micronesia (1933) 208; J. Dep. Agr. Kyushu Imp. Univ. 4 (1936) 362. — *L. pallidifolia* Kanehira, Bot. Mag. Tokyo 49 (1935) 354; Suesseng., o.c. 388. — T y p e: *Kanehira* 2026 (P, US).
- L. bulusanensis* Elm., Leafl. Philip. Bot. 10 (1939) 3801. — T y p e: *Elmer* 17089 (A, BO, K, L, U).
- L. guineensis* forma *longifoliolata* Desc., Mém. l'Inst. Sc. Madag. (1959) sér. B, 9 (1960) 23; Fl. Madag. fam. 124 bis (1967) 8. — T y p e: *Perrier* 6190 (P).
- L. guineensis* forma *monticola* Desc., o.c. (1960) 26; o.c. (1967) 8. — T y p e: *Perrier* 6173 (P).
- L. guineensis* forma *spiculata* Desc., o.c. (1960) 27; o.c. (1967) 10. — T y p e: *Leandri* 875 (P).
- L. guineensis* forma *truncata* Desc., o.c. (1960) 27; o.c. (1967) 10. — T y p e: *Humbert* & *Capuron* 21923 (P).
- L. guineensis* forma *comoriensis* Desc., o.c. (1960) 29; o.c. (1967) 11. — T y p e: *Boivin* 3261 (P).
- L. guineensis* forma *orientalis* Desc., o.c. (1960) 31; o.c. (1967) 12. — T y p e: *SF* (*Madagascar*) 2488 (P).

Distribution: Africa: West Tropical (incl. Gulf of Guinea Is. to São Tomé), Central and East Tropical Madagascar, Bourbon, Mauritius; Asia: India (Bombay, Madras northwards to United Prov., eastwards to Sikkim and Assam), Andaman Is., Burma, Thailand, Cambodia, Laos; southwards becoming very rare: Peninsular Thailand, Malaya, Sumatra, Java, Lesser Sunda Is. (apparently absent from Borneo), Philippines (abundant throughout), Taiwan, Micronesia (Palau), N. Celebes, New Guinea (rare in this area).

Notes. In the present circumscription the species shows a wide range of variability, both geographically and ecologically. It is undoubtedly a complex species composed of overlapping entities which cannot be satisfactorily delimited from each other, these entities sometimes having different ecological preferences. Previous workers, particularly in the Philippines, have created many small segregate species which can no longer be maintained as with increased material available all degrees of intermediates are found to exist. Most of these taxa were separated only by minor vegetative differences. The conclusion, that there is but one variable species in Asia and Malesia, independently concurs with that reached by Gagnepain (1910) in his essay on the classification of the Asiatic species of *Leea*, and that of Banerjee & Babu on the conspecific nature of *L. aurantiaca* and *L. acuminata*. Comparison of the African and Asiatic material of '*L. guineensis*' and '*L. manillensis* sensu lato' showed that no clear-cut differences could be found in herbarium material other than vague suggestions from the field notes that the colour of the staminodial tube might be different in living material; morphological characters of the leaves and flowers completely overlap.

Within the total gene pool area of the species certain regions of gene pool instability may be envisaged to occur, these being physically expressed by populations with a wide range of morphological variants, mostly in the leaf form and vestiture. Such extremely variable populations occur in Madagascar and in the Philippines. These areas may be considered to have been populated by groups of isolates from a parent gene pool. Subsequent proliferation and expansion of these isolates resulted in a number of quasi stable forms, mostly characterized by leaflet vestiture and -dimensions, but occasionally modification of the staminodial tube also occurs. This latter feature is seen in the Madagascan forms where the sinuses of the staminodial tube are deep in comparison to the populations of mainland Africa. This structural modification within a species is paralleled in the *L. indica* complex by the form previously described as *L. gigantea*. In Madagascar there are also wide ranges of leaf forms which have been discussed by Descoings (1959). The geographic location of these forms suggest that the parent gene pool had already become isolated from the Asiatic populations prior to the expansion into Madagascar, and that continued isolation did not produce morphological diversification in the population of continental Africa.

Within the Asiatic component of the gene pool there are clearly two ecological forms, one of shaded forest occurring in Malaya, Sumatra, and Java, the other of secondary vegetation occurring in mainland Asia and in the Philippines. Within the latter area a vast range of forms is encountered and here the taxon appears to replace *L. indica* as a member of secondary vegetation.

Several morphological trends are apparent but none is clearly demarcated from the parent stock. Of these the entity '*L. manillensis*' commonly occurs from Taiwan to the Philippines. It is characterized by small leaf dimensions and usually by the presence of hairy domatia. However, all degrees of intermediates are to be found between this entity and '*L. negrosense*' with leaflets which are larger, somewhat hairy, and coriaceous, or glabrous to sparsely pubescent. The most distinctive entity has woolly-hairy stems and setaceous to hispid hairs on the upper leaf surface; this may be a semi-stable form within the Philippines, but again intermediates exist with the parent population. Previously this

entity was given specific rank as *L. cumingii*'. There is a parallel form from the Solomon Islands in the *L. indica* complex. The Indian material shows a less wide range of variation, but in the area Thailand to Vietnam a further morphological leaf form occurs which may well be an expression of an 'edge of range effect'. The inter-relationships of these different leaf forms can only be further resolved by ecological and population studies.

33. *Leea indica* (Burm. f.) Merr. — Fig. 4:6—8; 5:1—7; 8:5.

- Staphylea indica* Burm. f., Fl. Ind. (1768) 75, t. 23 fig. 2. — *Aquilia sambucina* L., Mant. 2 (1771) 211 nom. illeg.; Cavanilles, Dissert. 7 (1789) 372, t. 218. — *Leea sambucifolia* Salisb., Prod. (1796) 317, nom. illeg. — *Leea sambucina* Willd., Sp. Pl. 1 (1798) 1177, nom. illeg. — *L. staphylea* Roxb. [Hort. Beng. (1814) 18, nom. nud.] Fl. Ind. ed. 1, 2 (1824) 471, nom. illeg. — *L. indica* Merr., Philip. J. Sc. 14 (1919) 245. — T y p e: Burm. f., t. 23 fig. 2, description.
- Aquilia otilis* Gaertn., Fruct. 1 (1788) 275. — [*Otillia zeylanica* Gaertn., o.c. t. 57, nomen.] — *Leea otilis* DC., Prod. 1 (1824) 636; Moon, Cat. Ceyl. (1824) 18. — T y p e: *Herb.* Gaertn. (n.v.).
- L. robusta* Bl., Bijdr. (1825) 198, nom. illeg., non Roxb. ex Hornem. (1813). — *L. sundaica* Miq., Fl. Ind. Bat. 1, 2 (1859) 610. — T y p e: *Blume s.n.*, Megamendong, Java (BO; L holo).
- L. gigantea* Griff., Not. Pl. Asiat. 4 (1854) 697; Id. Pl. Asiat. 4 (1854) t. 645 fig. 2; Kurz, J. As. Soc. Beng. 42, II (1873) 65; ditto 44, II (1875) 178; Fl. Burma 1 (1877) 280; Clarke, J. Bot. 19 (1881) 140; King, J. As. Soc. Beng. 65, II (1896) 412; Brandis, Ind. Trees (1906) 179; Ridl., Fl. Mal. Pen. 1 (1922) 484, fig. 48; Craib, Fl. Siam. En. 1 (1926) 317; Suesseng., in E. & P., Nat. Pfl. Fam. ed. 2, 2od (1953) 384, 385; Hundley & U Chit Ko Ko, List Tr. Shr. Herb. Climb. Burma (1961) 55. — T y p e: *Griffith s.n.*, Oct. 1834, Moulmein, Burma (K).
- L. viridiflora* Planch., Hort. Donat. (1854) 6; Suesseng. in E. & P., Nat. Pfl. Fam. ed. 2, 2od (1953) 384. — T y p e: *Hügel s.n.*, Malabar (n.v.).
- L. sumatrana* Miq., Fl. Ind. Bat. 1, 2 (1859) 611; Sum. (1861) repr. (1862) 200. — *L. sambucina* Willd. var. *sumatrana* Miq., Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 99. — T y p e: *Junghuhn s.n.*, near Padang, Sumatra (BO, L, U).
- L. biserriata* Miq., Sum. (1861) repr. (1862) 518. — *L. sambucina* Willd. var. *biserriata* Miq., Ann. Mus. Lugd.-Bat. 1 (1863) 99. — T y p e: *Teysmann s.n.*, Banka (L, U).
- L. fuliginosa* Miq., Sum. (1861) repr. (1862) 202, 518. — *L. sundaica* Miq. var. *fuliginosa* Miq., Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 96. — T y p e: *Teysmann* (3910) s.n., near Moeraradocewa, Palembang, Sumatra (BO, L, U).
- L. palembanica* Miq., Sum. (1861) repr. (1862) 203, 519. — T y p e: *Teysmann s.n.*, Palembang, Sumatra (BO, L, U).
- L. pubescens* Zipp. ex Miq., Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 97. — T y p e: *Zippelius s.n.*, Timor (K, L).
- L. sambucina* Willd. var. *heterophylla* Zipp. ex Miq., Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 99. — T y p e: *Zippelius s.n.*, New Guinea (L).
- L. sambucina* Willd. var. *robusta* Miq., l.c. — T y p e: *Blume s.n.*, Java (L).
- L. sambucina* Willd. var. *simplex* Miq., l.c.; Suesseng. o.c. 384. — T y p e: *Zippelius* (35a), New Guinea (L).
- L. sundaica* Miq. var. *pilosiuscula* Spanoghe ex Miq., l.c. — T y p e: *Spanoghe s.n.*, Timor (L).
- L. sundaica* Miq. var. *subsessilis* Miq., l.c.; Laut., Bot. Jahrb. 59 (1925) 534. — T y p e: *Zippelius s.n.*, New Guinea (L).
- [*L. divaricata* T. & B., Cat. Hort. Bog. (1866) 388, nom. nud.]
- L. celebica* Clarke, J. Bot. 19 (1881) 166; Suesseng., o.c. 384. — T y p e: *Riedel s.n.*, N. Celebes (K).
- L. sambucina* Willd. var. *occidentalis* Clarke, o.c. 140. — S y n t y p e s: *Wallich* 6824 A, B, D, H (K).
- L. umbraculifera* Clarke, J. Bot. 19 (1881) 141; Brandis, Ind. Trees (1906) 179; Cowan & Cowan, Trees N. Beng. (1929) 40; Kanjilal & Das, Fl. Assam 1 (1936) 306; Suesseng., o.c. 384; Hara, Fl. E. Himal. (1966) 200; ditto 2nd Rep. (1971) 79. — S y n t y p e s: *Hook. f. & Thoms. s.n.*, Clarke 24804, Sikkim; *Booth s.n.*, Bhutan; *Hook. f. & Thoms. s.n.* 15-6-1850, Clarke 17815, 40681, Khasia; *Jenkins s.n.*, *Wallich* 6830, Assam (all at K).
- L. brunonianum* auct. non Clarke: Engl., Bot. Jahrb. 7 (1886) 460; K. Schum., Bot. Jahrb. 9 (1888) 208; K. Schum. & Laut., Fl. Schutzgeb. (1900) 430; Laut., Bot. Jahrb. 59 (1925) 530.
- L. naumannii* Engl., Bot. Jahrb. 7 (1886) 466. — T y p e: *Naumann s.n.*, New Hannover 24-7-1875 (B, †).
- L. javanica* auct. non Bl.: King, J. As. Soc. Beng. 65, II (1896) 418.
- L. roehrsiana* Sanders [Catalogue (1899) 21, nom. nud.] ex Masters, Gard. Chron. III, 23 (1898) 242, fig. 92; Bonstedt in Parey's Blumengart. (1931) 895. — *L. sambucina* Willd. var. *roehrsiana* Chittenden, Dict. Gard. 3 (1951) 1143. — T y p e: Gard. Chron. III, 23 (1898) fig. 92.
- L. novoguineensis* Val., Bull. Dépt. Agr. Ind. Néerl. 10 (1907) 31. — T y p e: *Koch s.n.*, 1903, Etna Bay, New Guinea (BO, L, holo).

- L. ramosii* Merr., Philip. J. Sc. 17 (1920) 282. — T y p e: *Ramos & Pascasio BS.* 34945 (P).
L. gracilis Laut., Bot. Jahrb. 59 (1925) 532. — T y p e: *Ledermann* 12550 (WRSL).
L. expansa Craib, Kew Bull. (1926) 358; Fl. Siam. En. 1 (1926) 317; Gagnep., Fl. Gén. I.-C., Suppl. (1950) 852; Suesseng., o.c. 386, 387. — T y p e: *Kerr* 9236 (K).
L. longifoliola Merr., Lingnan Sc. J. 14 (1935) 33, fig. 11; Gagnep., Fl. Gén. I.-C., Suppl. (1950) 853; Suesseng., o.c. 387. — T y p e: *Lau* 556, Hunan (A, BM, K, US).

Distribution: Ceylon, India (Bombay, Madras northwards to Punjab, Sikkim, Assam), Nepal, Bangladesh, Andaman and Nicobar Is., Burma, Thailand, Cambodia, Laos, N. & S. Vietnam, Hainan, China (Yunnan, Kwangsi), throughout Malesia, N. Australia, Solomon Is., Santa Cruz Is., New Hebrides (Espiritu Santo), Fiji (Vanau Levu, Ovalau, Viti Levu, Kandavu, Moala), ?Tonga Is.

Notes. Many attempts have been made to segregate this common widespread species into smaller taxonomic units, particularly by Miquel who studied plants from the area where the greatest morphological diversity occurs. The majority of these segregates have been established on leaflet characters. One entity, somewhat distinctive in flower by the deep sinuses of the staminodial tube, occurs from Burma to Malaya together with the normal of *L. indica*, overlapping in vegetative and other characters. It was considered to be specifically distinct by Griffith, who described it as *L. gigantea*. The situation closely parallels that found in the Madagascan material of *L. guineensis* where the same deep sinuses occur. In *L. guineensis* this character occurs allopatrically in an insularly isolated population whilst in '*L. gigantea*' the character occurs sympatrically within the range of *L. indica*.

The remainder of the material shows rather interesting trends, particularly in leaf vestiture and dimensions. Within the area from India across to China and southwards to Java the leaflets tend to be more or less glabrous and apparently have a trend to increase in size, culminating in large leaflet forms in Java. In the herbarium, leaflets of all size classes may be found on plants from Java, whilst, as far as can be ascertained, large leaflet forms do not occur in India. This trend is particularly apparent in the terminal leaflets. Eastwards across the Lesser Sunda Islands leaf pubescence tends to increase, culminating in very pubescent forms in New Guinea and the Bismarck Archipelago. The Solomon Islands have been very intensively collected and are relatively over-represented in the collections compared to other areas, but here all but two collections are more or less glabrous. Further eastwards to Fiji both pubescent and glabrous forms occur, but there is a decrease in the leaf size so that the glabrous form cannot be separated from the material from India or Ceylon.

Two specimens from the Solomon Islands, BSIP 5371 (Rob Roy I.) and NGF 16378 (Bougainville), are unusual in having very large leaves (*c.* 25 by 12 cm) which are hairy on the nerves, whilst the remainder of the Solomon Islands material is glabrous. Furthermore the stem, rachises, stipules, and inflorescences are covered with bristle-like hairs, a feature somewhat paralleling the condition found in '*L. cumingii*' of the *L. guineensis* complex.

However, although certain general trends in leaf dimension and vestiture can be recognized, random exceptions occur in all areas and no absolute trends can be delimited. So within New Guinea occasional glabrous-leaved specimens occur which cannot be separated from material from normal populations in Malaya. The problem is to obtain uniform comparable samples from the widespread populations of a species common in populated areas and frequently subjected to cutting and coppicing.

34. *Leea smithii* Koorders — Fig. 4:9.

- L. smithii* Koorders, Minah. (1898) 398, 622. — [*L. boerlageana* Koorders, Minah. (1898) 68, *nomen.*] — *Lectotype:* Koorders 15876 (BO, K, L). — *Synonym:* Koorders 15888 (BO, L).

Distribution: NE. Celebes.

Note. In absence of flowers the taxonomic status and position remains in doubt. The fluted stems and the structure of the epidermis and cuticle are very distinctive. However, there is a possibility that the taxon represents an extreme of variation of *L. indica*.

DUBIOUS SPECIES

1. (*Leea erecta* Voll. & Brade, Rodriguesia 1 (1935) 59, *nom. nud.*) An invalid horticultural name entered in a seed list.
2. *Leea humilis* Hassk., Cat. Hort. Bog. (1844) 169, *descr. in nota*; Miq., Fl. Ind. Bat. 1, 2 (1859) 611.
Probably *L. aquatica*.
3. *Leea javanica* Bl. ex Spreng., Syst. Veg. 1 (1824) 670; Bl., Bijdr. (1825) 197; Spreng., Syst. Veg. 4, 2 (1827) Cur. post. 70; G. Don, Gen. Hist. 1 (1831) 712; Steud., Nom. Bot. ed. 2, 2 (1840) 21; Hassk., Cat. Hort. Bog. (1844) 168; Miq., Fl. Ind. Bat. 1, 2 (1859) 610. — Type: Blume s.n., Meggamedung (not traced).

Blume's description reads: 'L: caule tereti punctato-scabro, foliis bipinnatis, foliolis infimis saepe geminis, oblongis acute serrulatis glabris'.

No authentic specimen of this species has been traced, a situation which was also reported by Koorders & Valeton (Bijdr. Booms. 9, 1903: 13). From the description it can be seen that the taxon has bipinnate leaves with glabrous leaflets. Thus, if it is a *Leea*, by elimination of other possibilities, the description must apply to either *L. guineensis* G. Don (*L. aurantiaca* Zoll. & Mor.) or *L. indica* (Burm. f.) Merr. It has variously been interpreted as one or the other by most authors except Koorders who, in earlier years, in part identified plants of *L. aculeata* Bl. ex Spreng. with this taxon. This clearly is an error as the leaves in that species are always 1-pinnate. King, Ridley, and Backer & Bakh. f. interpreted this to have green flowers and thus representing a form of *L. indica*. On the other hand, Miquel and Merrill considered that it represented a red flowering taxon. This latter view would seem more probable, as Blume also described two forms of *L. indica* under *L. sambucina* Willd. and *L. robusta* Bl., the remaining possible entity of this species likely to be distinguished would be *L. sundaica* Miq., but this has pubescent leaves. If it can be shown conclusively that it represents a red flowered species then clearly this name will take priority over *L. guineensis*.

EXCLUDED SPECIES

1. [*Leea cordata* Wall., Cat. 6819; Steud., Nom. Bot. ed. 2, 2 (1840) 21; Kurz, J. As. Soc. Beng. 42, II (1873) 66, *in nota*; all *nom. nud.*] = *Vitis* sp. — *V. aff. pallida* W. & A. or *aff. repanda* W. & A. (*Vitaceae*) fide Laws. in Hook. f., Fl. Brit. Ind. 1 (1875) 668; Suesseng. in E. & P., Nat. Pfl. Fam. ed. 2, 20d (1953) 390.
2. *Leea dielsii* Léveillé, Feddes Repert. 8 (1910) 58; Fl. Kouy-Tcheou (1914) 25. — Type: Cavalerie 1027 (*n.v.*) = *Ampelopsis chaffanjoni* (Léveillé) Rehder (*Vitaceae*); fide Rehder, J. Arn. Arb. 15 (1934) 25.
3. [*Leea laevis* Heyne ex Wall., Cat. 1258, *nom. nud.*; Hook. & Jackson, Index Kew. 2 (1895) 48, *pro syn.* of *Heynea trijuga* Roxb.] = *Trichilia connaroides* (W. & A.) Bentv. (*Meliaceae*); fide Bentv., Acta Bot. Neerl. 11 (1962) 13.
4. [*Leea odontophylla* Wall., Cat. 6820, *nom. nud.*] = *Ampelopsis latifolius* (Wall.) Planch. (*Vitaceae*); fide Laws. in Hook. f., Fl. Brit. Ind. 1 (1875) 668; Suesseng. in E. & P., Nat. Pfl. Fam. ed. 2, 20d (1953) 390.

5. *Leea spinosa* Spreng., Syst. Veg. 1 (1825) 670 = *Aralia chinensis* L. (Araliaceae). Merrill, Int. Rumph. (1917) 347, has pointed out that Sprengel apparently intended only to transfer to *Leea* the plant depicted by Rumphius, Herb. Amb. 4 (1743) t. 44. Linnaeus, Syst. Nat. ed. 10 (1759) 967, included this plate in the synonymy of *Aralia chinensis*, following the interpretation of Stickman, Herb. Amb. (1754) 16; Linn., Amoen. Acad. 4 (1759) 127. Unfortunately, Sprengel's good intentions went astray as he effectively renamed *Aralia chinensis* L., Sp. Pl. (1753) 273, and not the plant from Ambon.
6. *Leea theifera* Léveillé, Feddes Repert. 8 (1910) 58; Fl. Kouy-Tcheou (1914) 25. — Type: Cavalerie 243 (n. v.) = *Ampelopsis cantoniensis* (Hook. & Arn.) Planch. (Vitaceae); fide Rehder, J. Arn. Arb. 15 (1934) 26.

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