Morphological diversity of the genus
Licuala (Palmae)

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Abstract

L.G. Saw[1], J. Dransfield[2] & D.M. Keith-Lucas[3] ([1]Forest Research Institute Malaysia, Kepong, 52109 Kuala Lumpur, Malaysia, Email: sawlg@frim.gov.my; [2]Royal Botanic Gardens Kew, Kew, Surrey TW9 6AB, UK; [3]School of Plant Sciences, University of Reading, Whiteknights, PO Box 221, Reading, Berkshire RG6 6AS, UK) 2003. Morphological diversity of the genus Licuala (Palmae). Telopea *10(1): 187–206.* There are about 141 described species of *Licuala*. Structurally, the genus has very consistent vegetative and fertile characters. As the genus undergoes revision, it is becoming clear that it contains great morphological variation within the strict vegetative and reproductive character constraints found in the genus. This paper describes the variation found in the genus and its significance in taxon delimitation.

Introduction

There are about 141 species of *Licuala*, distributed mainly in the Malesian region. High species diversities are centred on two main areas, one within the Sunda Shelf in Malaya and Borneo, the other centred on the Sahul Shelf on the island of New Guinea. *Licuala* is a distinct genus with well-defined characters (Uhl & Dransfield 1987). In the process of revising the genus, it has became apparent that the genus contains wide morphological variation within a rather strict set of morphological themes. It is important to understand this variation to define the taxa better. The paper was written mainly from detailed study of herbarium specimens of species found in Thailand, Malaya, Sumatra, Java, Borneo and New Guinea. The first author has also made extensive field observations on the variation of *Licuala* in Malaya (Saw 1997) and to some extent in Borneo.

Habit

The absence of any secondary vascular and mechanical tissue in palms has largely limited the growth habit of palms. As a result, palms tend to have fixed crown sizes, and aerial branching is rare (Tomlinson 1990). In general, vegetative branching is largely restricted to the base of the original trunk. The crown restriction has also produced plants displaying very simple architectural models. Palms on the whole are represented by only four (out of the total of 23) architectural models, as defined by Hallé et al. (1978). Nevertheless, there is still a surprising diversity of growth form in the family when consideration is given to the size, nature of the growth axis and basic branching patterns. These reflect the varied ecological adaptations found in the members of the family. Dransfield (1978) discussed the different growth forms found in the family and divided them into four basic categories.

1. Tree palms (palms that reach the main forest canopy).

2. Shrub palms (low palms found in the forest undergrowth).

3. Acaulescent palms (palms without a visible trunk or caudex, the true stem either being subterranean or, if aerial, very short).

4. Climbing palms (palms with narrow stems and long internodes which are not self supporting, but climb by grapnel hooks).

Licuala displays indeterminate growth and flowering is interfoliar, i.e. it has a pleonanthic habit. Following the architectural models of Hallé et al. (1978), *Licuala* manifests two models: Corner's model for solitary members and Tomlinson's model for clustering members. These models are, however, not very descriptive of the growth habits found in these palms. Some species for example can exhibit both models in different populations. *Licuala modesta* Becc. on the hill at Bukit Larut, Peninsular Malaysia, for example, expresses Tomlinson's model towards the summit of the hill but is solitary, i.e. exhibiting Corner's model, near the foot of the hill. In many clustering species, there is a transition from solitary forms in juveniles to clustered forms in adults; the architectural model thus changing. If size and the nature of clustering habit is taken into consideration, there is indeed a surprising range of growth habits in *Licuala*, which is not reflected by the definition of the tree architectural models, factors which these models do not account for. In Dransfield's categories, *Licuala* exhibits the first three groups listed above, particularly categories 2 and 3.

Members of this genus range from trees to shrubs to acaulescent palms, but none is climbing. They are small to medium palms. All are understory plants of the rainforest. The smallest amongst them, such as, *L. triphylla* Griff. or *L. kiahii* Furtado, are no more than a metre tall, while the largest are never large emergent trees but may be over 10 metres tall and can dominate the lower part of the forest canopy, e.g. *L. ramsayi* Domin of Australia (Dowe 1992).
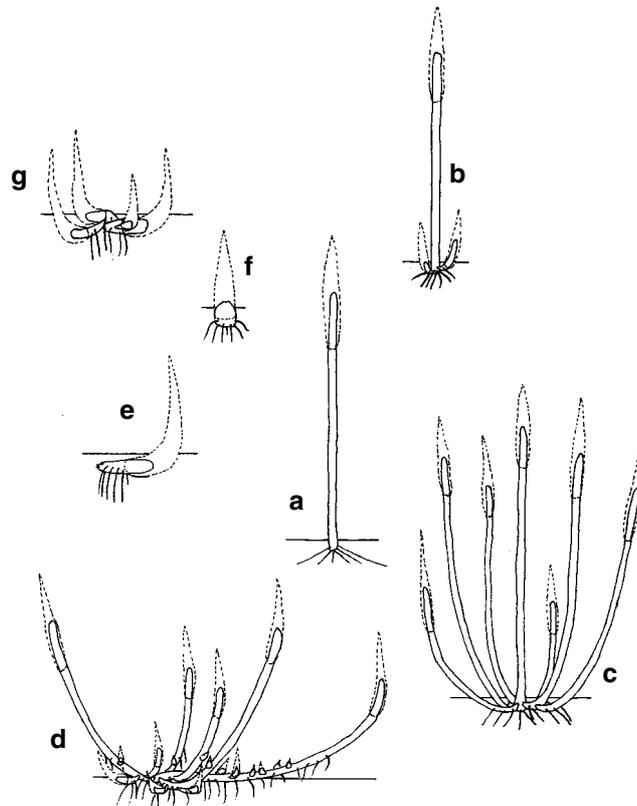
Licuala species may be solitary or clustering, with erect aerial stems ('stemmed') or acaulescent. There is, therefore, a possible combination of four basic themes in habits of *Licuala*. In general, these combinations of habits are rather taxon specific but, as discussed above, some taxa express overlapping forms. Within these basic themes, there are some degrees of variation that can be quite consistent within taxa. These habits are good field characters in determining taxa. Figure 1 gives a diagrammatic representation of the habits seen in *Licuala*.

1. Stemmed and solitary (Figure 1a)

In the simplest form, the plant is solitary and with an erect stem. In Malaya and Borneo, it is one of the commoner habits, and species with this habit include small to larger species. Smallest among them, such as *L. scortechinii* Becc. and *L. cameronensis* L.G.Saw, have stems no more than a metre tall. The larger species, such as *L. peltata* Roxb. ex Buch.-Ham., *L. longipes* Griff., *L. valida* Becc. and *L. fractiflexa* L.G.Saw are among the largest species of *Licuala* in Malaya and Borneo.

2. Stemmed, clustering with one to a few dominant shoots (Figure 1b)

Species with this habit have one to a few dominant shoots and a number of suckers at the base. Generally, the dominance of the main shoots is obvious in the field and it is only these that are fertile. Shoot dominance is probably the result of suppression of the basal suckers, as long as the dominant shoots are functioning. In some species, for example, *L. ridleyana* Becc., *L. malajana* Becc. and *L. terengganuensis* L.G.Saw, only 1–2 shoots remain dominant. In the summit population of *L. modesta* at Bukit Larut, there is a tendency for individual clumps to form clusters with a larger number of co-dominant shoots.

Fig. 1. A diagrammatic representation of the growth habits of *Licuala* species (solid line represents stem, broken line represents crown shaft). **a,** Stemmed and solitary. **b,** Stemmed, clustering with one to a few dominant shoots. **c,** Stemmed, clustered with ± equal erect shoots. **d,** Stemmed, clustered with ± decumbent shoots. **e,** Acaulescent and solitary, stem plagiotropic and **f,** with orthotropic stem. **g,** Acaulescent and clustered.

Species that are stemmed and solitary, as described above, will occasionally also produce small suckers at the base. This is suspected to be stress-related; for example, in Pasoh Forest Reserve, Malaysia, individuals of *L. longipes* that have crowns damaged by pigs, were seen to produce suckers. However, these suckers do not grow to a large size as seen in this group.

3. Stemmed, clustered with subequal erect shoots (Figure 1c)

This is an extension of the above category but instead of a distinct dominance of a few shoots, there is a cluster of subequal shoots. Here, suckering occurs early in the life of the young plant and its ramets grow at about the same rate as the mother shoot. Species in this group form large clusters. It is difficult to locate the mother shoot in older clumps. Reproductive structures are found on most of the ramets that are large enough. Only two species are known in this group, *L. spinosa* Wurmb and *L. paludosa* Griff.

4. Stemmed, clustered with about equal decumbent shoots (Figure 1d)

Very similar to category 3 but here the stems are erect to spreading and often decumbent, producing a 'colonial' habit. The stems are thin and nodes are wide apart, suggesting a rather fast growth rate. As the stem grows from an initial erect position, the stem gradually reclines onto the ground under its own weight, with its apex constantly curving up at its tip. In very old shoots, the stem may be of a considerable length, prostrate on the ground. In the former two groups with clustered habits, the suckers are formed quite close to the base of the stems. In this group, however, while there are suckers close to the base of the stem, suckers are also formed along the stems away from the base. This occurs mainly in older prostrate stems that are in contact with the ground. Adventitious roots sprout along these stems. It is not a common habit. In Malaya, it is only observed in *L. sallehana* L.G.Saw; in Kalimantan, Borneo, *L. hallieriana* Becc. has been reported to exhibit this habit. *Licuala reptans* Becc., also from Kalimantan, has been described with decumbent habit but it is solitary.

5. Acaulescent and solitary (Figures 1e & f)

Here the stem is 'unseen'. The acaulescent habit in *Licuala* is of the plagiotropic adult form as defined by Tomlinson (1990). The apical axis of the palm is oblique with unequal growth of the leaf bases (Figure 1e). This keeps the stem underground. In younger plants, the stems tend to be orthotropic (Figure 1f) but as the stem becomes more prominent, the axis becomes plagiotropic. Together with this growth habit, the nodes are also very close together, thus making very little stem height increment with every new leaf, even when the growth is orthotropic. Occasionally, as with the stemmed and solitary form, suckers may form when the plant is stressed, e.g. damaged by animals. This is another common habit in *Licuala* of Malaya. Most species with this habit are very small, e.g. *L. triphylla* Griff., *L. kiahii* Furtado, *L. tenuissima* L.G.Saw, *L. kamarudinii* L.G.Saw and *L. khoonmengii* L.G.Saw. Only one species that is considered large by *Licuala* standards has this habit, viz.: *Licuala ferruginea* Becc.

6. Acaulescent and clustered (Figure 1g)

Similar in habit to category 5 but the plant clusters. The plagiotropic growth habit is also maintained in the suckers, making the shoots of the ramets subterranean. The subsequent ramets will continue to produce further suckers. This mode of growth can result in a rather large clump of shoots from a single mother plant. Only three Malayan species have this habit, namely, *L. ahlidurii* L.G.Saw, *L. bayana* L.G.Saw and *L. lanuginosa* Ridl..

In *Raphia hookeri* G.Mann & H.Wendl. (Profizi 1985) and *Oenocarpus mapora* Karst. (De Steven 1989), suckers are reported to occur only in the young axis of the plant. Both these species are rather large clustering palms. Such suckers and in some cases bulbil formation are seen in mature reproductive stems of *Licuala*. Sucker production in *Licuala* may not be totally confined to young axes as in the case of species of *Raphia* and *Oenocarpus* mentioned above.

Tomlinson (1990) defines the colonial habit in palms, as a habit in which the palm initially has suckers that are horizontal and usually subterranean for some distance before turning erect, as distinct from the clustered habit. The axes are dimorphic as the horizontal portions bear only scale leaves and are non-flowering, whereas the erect portions bear foliage leaves and distally, inflorescence units. This definition is, of course, easily applicable to plants that show a distinct stoloniferous habit, a habit not observed in *Licuala*. The dimorphic axes, however, exist in at least the growth forms of acaulescent and clustering species and possibly also in the clustered and equal-stemmed ones. In these last two categories, the axillary suckers grow horizontally for

a very short distance from the mother shoot before forming the aerial shoots. Whether this short stem can be defined as a stolon is of course open to debate. In this instance the stem remains subterranean. True scale leaves are lacking but in the short-stemmed phase of the axillary suckers, the leaves are much reduced to be almost scale-like, the earliest-formed ones lacking laminae while the older ones have juvenile-like laminae, Dransfield (1978) reported that *L. paludosa* forms open colonies in Malesian peat swamp forest. They however do produce long stolons.

The Leaf

The plicate and usually split leaf is the most distinctive organ of the palm family and more than any other structure links palms together (Dransfield et al. 1990). The use of the characters of leaf form and the nature of the leaf splits and their relevance to the classification of palms has been the subject of much discussion (e.g. Saakov 1954, Satake 1962, and more recently Dransfield & Uhl 1986, Uhl & Dransfield 1987, Dransfield et al. 1990). The subfamily *Coryphoideae* has a wider range of leaf form than any of the six other palm subfamilies. In the subtribe *Livistoninae*, the leaves are usually palmate or costapalmate, and there are two very distinctive leaf forms which are unknown elsewhere in *Coryphoideae*, the diamond-shaped leaf of *Johannesteijsmannia* and some species of *Licuala*, and the wedge-shaped segments with 'reduplicate' margins found in almost all species of *Licuala* (Uhl & Dransfield 1987).

The leaf sheath of *Licuala* does not abscise and at maturity its original tubular nature is often no longer obvious; a ligule is absent. This corresponds to the *Trachycarpus* type of sheath, according to Tomlinson's (1962) definition of leaf sheath types, where the ventral leaf sheath tissue persists as a fibrous mat. In immature leaves, a pair of auricles enclose the younger developing leaves. The auricles in most cases are rather fragile and may disintegrate in mature leaves. In some species, the auricles are not noticeable in the crown as they disintegrate very early while in others such as *L. glabra*, they may persist for a while in the crown. However, these too soon break away. The ventral leaf sheath of *Licuala* consists of two broad categories of fibre types. They are rather constant in each species. In a number of smaller species, the ventral leaf sheath breaks up finely into a network of fine fibres consisting of mainly individual strands; examples are *L. sallehana* and *L. kamarudinii*. In most of the larger species, the ventral leaf sheath breaks up into a network of rather coarse fibres consisting of bundles of flat tape-like strands, e.g. *L. glabra* Griff., *L. paludosa*, *L. ridleyana*.

The petiole is variable in length. In very small species, it can be less than 10 cm long, but in larger species petioles can exceed 3 m long. The length in any individual often depends on the vigour of the plant and on the amount of shade received and hence the amount of etiolation. The petiole is convex abaxially, but the adaxial side is concave or channelled towards the base, flattened to slightly convex towards the apex. It is normally covered with deciduous scales on the adaxial surface, but glabrous abaxially. On older fronds, the scales may drop off leaving behind black to dark brown dot or dash-like scars on the surface. The scales do not seem to be very useful taxonomically as they are variable. The petiole will dry with distinctive colours in different shades of brown. The colours are quite useful in distinguishing species. The petioles of most species dry a light bleached or greenish brown, e.g. *L. acutifida* Mart., *L. spinosa*, *L. ferruginea* and *L. modesta*. Petioles of *L. terengganuensis, L. fractiflexa, L. bintuluensis* Becc. and *L. longipes*, however, dry a very distinctive, dark reddish brown.

The petioles are normally armed with spines along the lateral margins. Spines in palms have a number of morphological origins but functionally they serve as protective organs (Tomlinson 1962, Fisher 1981, Tomlinson 1990). The spines on the lateral margins of the petioles in *Licuala* are typified as emergences and are not

associated with any organs. This feature is very common among the fan-leafed Coryphoid palms (Tomlinson 1990). They are normally distributed along the margins of the lower part of the petiole. At the petiole base, they continue beyond but outside the leaf sheath. In *L. spinosa* and *L. peltata*, the spines are distributed along the whole length of the petiole. In *L. moyseyi* Furtado, the petiole is unarmed. Spines may be large, some to well over 1.5 cm long, but in most species they are less than 1 cm long. They are generally larger near the base of the petiole and become smaller distally. They are variously curved but generally curving towards the base; they may be regularly or irregularly sized and spaced. They can be quite variable in some species, e.g. *L. malajana*, while in others the spines can be quite distinctive, e.g. *L. paludosa* has distinctive small black spines found on the proximal half of the petiolar margins.

The leaf blades are the most conspicuous and distinctive organs of *Licuala*. They are palmate and in most species orbicular. The hastula is well developed on the adaxial surface but absent on the abaxial surface. It is usually triangular and is not useful in distinguishing taxa at any level. The blade of *Licuala* is basically induplicate as in most members of Coryphoideae. However, unique to *Licuala*, superimposed on the induplicate splits along the outer margin, are the more obvious abaxial lateral splits (Figure 2). These abaxial lateral splits divide the blade right to its insertion into compound or very rarely single-fold reduplicate segments (Dransfield et al. 1990) (e.g. in *L. bidentata* Becc. and in the Gunong Ledang population of *L. glabra* (Saw 1997)). These abaxial splits on the lateral margins of segments occur very early in the development of the leaf, while the induplicate splits on the outer margin, usual in the subfamily, occur much later (Dransfield 1970). The abaxial lateral splitting appears to be a specialised development, at least in *Licuala*. The abaxial lateral splits are unusual in being the only ones in the subfamily to reach the insertion of the blade, except in the central divisions.

Most species have segmented leaves. The number of segments in the leaf is usually variable and in most cases is not very useful in species identification. Similarly, the number of veins or costae in the segments is constant in some species, but in other species is quite variable. Segments range from single folds to many folds. Overall, segmentation is rather constant within populations but can vary between populations of the same species.
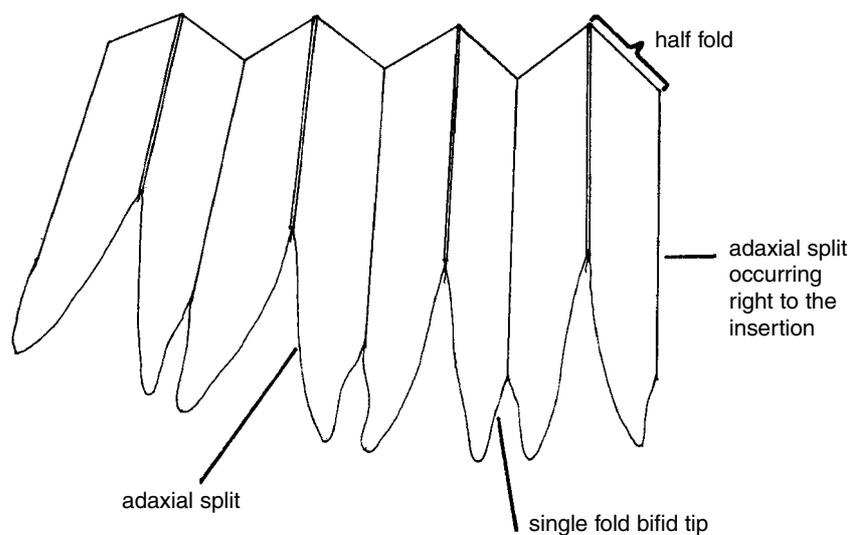

Fig. 2. Induplicate fold of *Licuala* with the abaxial splits (redrawn from Uhl & Dransfield (1987)).

Leaf forms found in *Licuala* are given in Figure 3. The eophyll of *Licuala* is simple and strap-like (Figure 3a). Its apex is truncate to rounded. This type corresponds to Tomlinson's (1960) 'Class 2' type of induplicate-leafed palms. This condition is common among the Coryphoid palms. Tomlinson (1960) further attempted to explain the phylogenetic significance of the development of the seedling series and the subsequent development of the adult leaves. In the following paragraphs, we have attempted to correlate the different leaf forms of *Licuala* with their development.

The juvenile form, lanceolate or narrowly cuneate-based and undivided, is retained in the adult leaves (neoteny) (Figure 3b) of *L. sallehana* var. *sallehana*. In *L. thoana* L.G.Saw & J.Dransfield, the juvenile-leafed form is also found in young adult reproductive individuals. However, in older individuals of this species, the blade may be segmented, generally with about two, to sometimes four, very narrow lateral segments. The mid-segment remains spathulate, and is much larger than the lateral one, very much like the juvenile-leafed form of the young adults.

If one follows the ontogeny of segmented leaves of *Licuala* species, the seedling leaves are replaced by larger and similarly shaped juvenile leaves; subsequently segmented leaves are produced. As the plant builds up its base, the older leaves become larger and the number of segments also increases. Unlike *L. thoana*, segmentation of the leaf occurs quite early, even in very young juveniles. This increment continues until the maximum number is attained for that particular species. Most species of *Licuala* in Malaya have this leaf type (Figure 3c). The lateral margin of the segments of most species is straight but in a few species, they can be curved (Figure 3i).

In most species, the central segment is prominent; it is larger than the lateral segments, while in others they are about the same size. Rarely are the mid-segments much smaller than the lateral segments (so far, only known in *L. mattanensis* Becc. var. *paucisecta* Becc. from Borneo). The central segment is very often undivided and sessile. It, however, may be petiolulate (Figure 3d). This character is not consistent in Malayan *Licuala*. It is quite common in *L. triphylla*, rare in *L. longipes*, *L. spinosa* and *L. malajana*. However, in Borneo, *L. petiolulata* consistently has a petiolulate mid-segment. In both *L. triphylla* and *L. petiolulata*, there is sometimes a further extension of the mid-segment to include one or two leaflets giving a pinnate leaf arrangement for the central 2 or 3 leaflets (Figure 3e). In describing *Licuala stenophylla* Hodel, Hodel (1997) included a form of *L. triphylla* with pinnate mid-segments (Barfod & Saw, in press). This variation, as mentioned previously, is not consistent and cannot be used as a singular character to define a taxon. The mid-segment can also be divided. In most instances, it is bifid (Figure 3f), a situation more common than normally realized. It occurs for example, in *L. glabra* var. *selangorensis*, *L. peltata* and *L. paludosa*, etc. While *L. glabra* (form found in Bukit Bauk, Terengganu, Malaysia (Saw 1997)) has a mid-segment that is normally bifid, is also sometimes further split from one of the inner sides of the bifid segment to include another segment giving a trifid segmentation. This differs from the pinnate segmentation described earlier in *L. triphylla* and *L. petiolulata*. In the Bukit Bauk population of *L. glabra*, the inner split is about the same size as the other adjacent segments of the central segmentation. In some specimens of *L. collina* L.G.Saw (ined.), the inner splits are much smaller than the adjacent segments (Figure 3h), giving it an attractive tail-like segmentation. This smaller central tail-like segmentation is again different from the central segmentation described earlier in *L. mattanensis* var. *paucisecta*. A further modification in this leaf form is the loss of the lateral segments leaving only the bifid mid-segment (Figure 3g). This unusual segmentation is also found again in some individuals of *L. collina*.

The only Malayan species with simple and orbicular leaves is *L. peltata* var. *sumawongii* L.G.Saw (Figure 3j). The other frequently cultivated species with this leaf form is *L. grandis* H. Wendl. from Vanuatu. In Borneo, at least four taxa are known to have orbicular or near orbicular fronds, *L. orbicularis* Becc., *L. cordata* Becc., *L. micholitzi* Ridl.
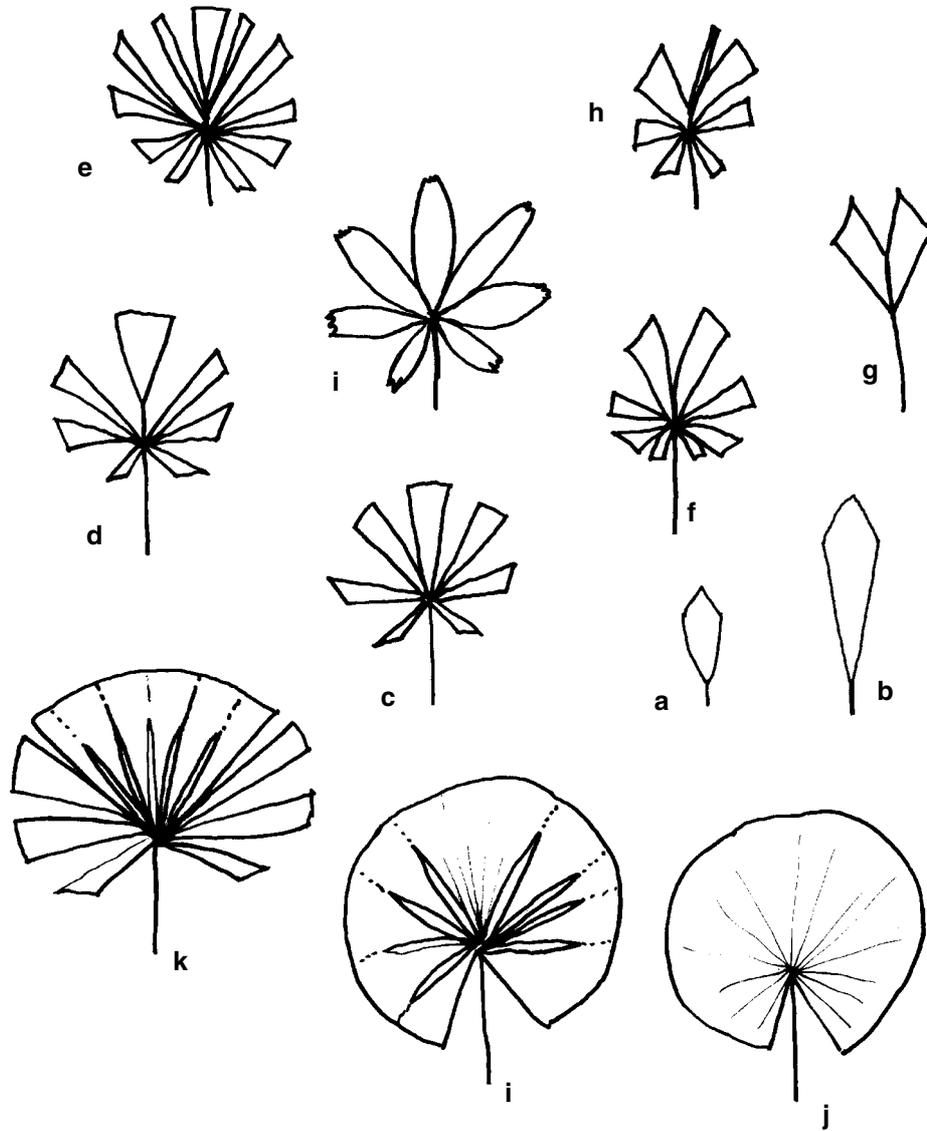
Fig. 3. Leaf types of *Licuala* species. **a,** Eophyll. **b,** Adult juvenile type or neoteny (juvenile leaf form retained in adult plants). **c.** Segmented adult leaf type. **d** ,Segmented type with petiolulate mid-segment. **e,** Segmented type with pinnate mid-segment. **f,** Segmented type with bifid mid-segment. **g,** Segmented type with bifid mid-segment with loss of lateral segments. **h,** Segmented with bifid mid-segment including a further split. **i,** Segments with curved lateral sides. **j,** Entire. **k,** Fronds with mid-segment perforated with windows. **l,** Entire leaf with windows. (See text for explanation).

var. *micholitzi* and *L. yiiana* L.G.Saw (ined.). We believe, the development of the simple leaf in this type is quite distinct from the retention of the juvenile leaf type found in *L. sallehana* var. *sallehana*. The simple leaf arises from the loss of lateral splits from two possible processes.

The suggestion for this is found in two phenomena observed in the leaves of some *Licuala* species. The first author has seen juveniles of *L. peltata* var. *sumawongii* with lateral splits that do not reach the insertion of the blade. It is known that the lateral splits occur very early in the leaf development (Dransfield 1970). Therefore, in these individuals, the incomplete splits must be part of the early development of the leaves, indicating a reversion to its ancestral form of segmented leaves as juveniles. They, however, will subsequently grow into adults with undivided leaves by the loss of the splits. In *Licuala ashtonii* L.G.Saw (ined.), a different form of splitting occurs, the margin remains entire (i.e. not broken into segments) but within the blade, splits occur from the hastula to near the edge of the frond, forming window-like splits (e.g. *P.S. Ashton* S 18263) (Figure 3l). Similar splits in *Licuala* fronds have also been observed in *L. sabahana* L.G.Saw (ined.) and the form of *L. valida* Becc. from Sepilok, Sabah (*L.G. Saw* FRI 37691 & FRI 37692) and observed on a juvenile plant of *L. ramsayi* in Singapore Botanic Gardens (first author's observation) (Figure 3k). In these last examples, however, the windows are restricted to the mid-segments, these species have segmented fronds.
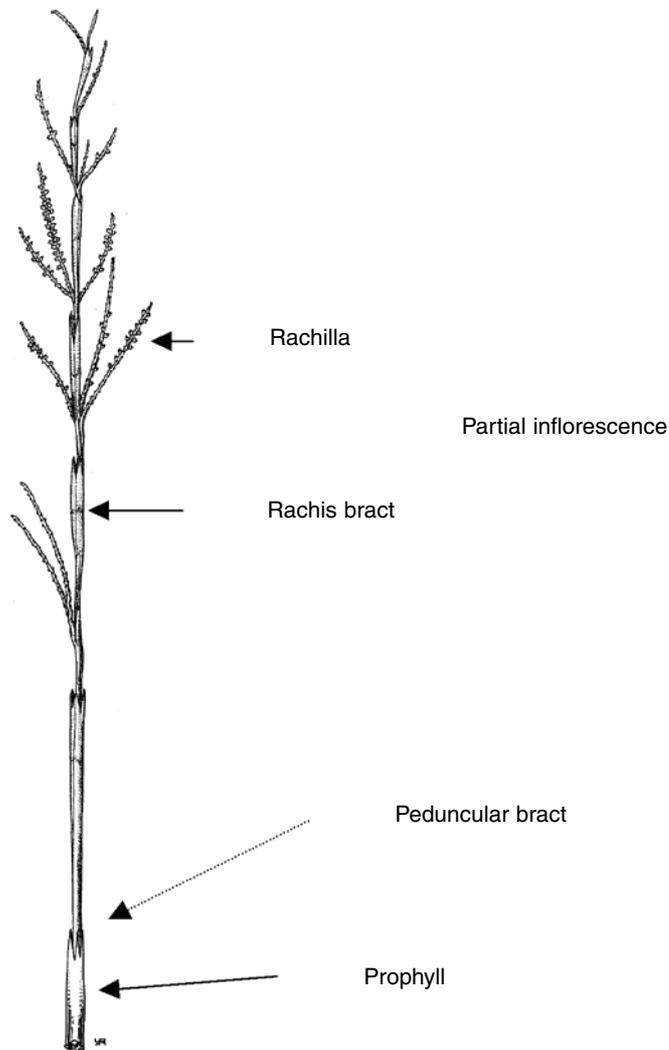
The Inflorescence

Although palm inflorescences can be quite elaborate and often massive, appearing very complicated, they are relatively easy to describe because they usually conform to very basic patterns. They are largely made up of repeating units, each unit with the same construction, and with gradual but progressive changes along any given axis (Tomlinson 1990). These have been well described and discussed by a number of authors (e.g. Tomlinson & Moore 1968, Moore & Uhl 1982, Uhl & Dransfield 1987, Tomlinson 1990).

Licuala overall shows a surprising degree of variation in its reproductive characters. Although the vegetative characters are sometimes rather variable within taxa and difficult to use, the reproductive characters are numerous and remain quite consistent in the different species. It is even possible to determine species with old infructescences. This is quite difficult with vegetative characters.

Inflorescences of *Licuala*, like those of the rest of the Coryphoid palms show a very simple construction (Uhl & Dransfield 1987). The size is variable: in small species, they may be less than 15 cm long while in large species, the inflorescence can be well over 3 m long. The inflorescence is interfoliar, consisting of a main axis and branches to two, or very rarely three orders. Figure 4 gives an example of an inflorescence of *Licuala*.

The inflorescence is displayed variously. Most species have their inflorescences displayed within the crown – that is, they are shorter than the leaves. In others, the inflorescences are much longer than the leaves, for example in *L. spinosa* and *L. paludosa*. The inflorescence is also variously positioned. This is sometimes not very obvious on herbarium specimens. The character can be quite useful in species identification, as it is quite consistent within species. Most species have spreading inflorescences. In *L. lanuginosa* and *L. ahlidurii*, the inflorescences are erect. *Licuala cameronensis* and *L. mustapana* L.G.Saw have spreading and pendulous inflorescences. The former has a very thin rachis and the inflorescence hangs over as it grows. The latter has rather long spreading inflorescences which also hang over under their own weight as they grow.

Fig.4. Inflorescence structure of *Licuala*. In this example, the species *L. egregia* lacks peduncular bract, here marked in dotted arrow. (Drawing from Saw, 1997 of *L. egregia* L.G.Saw).

The first bract of the inflorescence is a tubular, two-keeled prophyll. The prophyll is often not seen in the crown, as it usually remains hidden by the subtending foliage leaf. A number of tubular peduncular bracts may further sheath the peduncle before the first inflorescence branch occurs. In some species peduncular bracts may be absent. The number or absence of peduncular bracts appears to be quite consistent within species. However, very often this is not properly noted in herbarium specimens or

when collected, they are not collected properly. Each primary branch is subtended by a rachis bract. The rachis bracts are also tubular. In some species, the rachis bract is reduced and is not tubular, but narrowly triangular in shape, e.g. *L. scortechinii* Becc. and *L. kingiana* Becc. In most species, these bracts are cylindrical, constricted abruptly near their bases, and are rather tightly sheathing. In other species, such as *L. mirabilis* Furtado, the bracts are inflated, funnel-shaped and loosely sheathing. The mouths of the rachis bracts split obliquely and widely to one side while in others, they split only at the apex quite perpendicular to the axis of the rachis. The mouth can be fibrous, breaking open into untidy strands of fibres. In *Licuala ferruginea* Becc., for example, the bracts have this type of mouth. In most other species, the mouths are neatly irregularly split, giving an impression of being toothed.

The rachis axis is rather straight and rigid in a number of species, while in others it is flexible. In a few other species, the rachis axis is sinuous, bending at the junctions of the primary branches, e.g. *L. mirabilis.*

The first order branch complement subtended by the rachis bract is sometimes referred to as the partial inflorescence. This term is useful to describe the basic structure of the *Licuala* inflorescence. Based upon the arrangement of the partial inflorescences, four major inflorescence types are recognized (Figure 5). The simplest, corresponding to most species of Coryphoid palms is the type with a few superposed (i.e. one above another) branched partial inflorescences (Type 1 of Figure 5). In this type, the partial inflorescences can be highly branched, e.g. *L. patens* Ridl., *L. longipes* Griff. ex Mart. and *L. fractiflexa* L.G.Saw, while in others they only have a few branches, e.g. *L. ferruginea, L. malajana, L. tenuissima.* Based on Saw (1997) and Saw (in prep.), this inflorescence type is found in about 46% of the species from Malaya and Borneo (Table 1). In reducing the number of rachillae in each partial inflorescence to one (spicate), we have the Type 2 inflorescence. This inflorescence type is quite common among Malayan and Bornean *Licuala* species. A further variant of this inflorescence type is found in *L. punctulata* Burret; here it appears that the proximal two spicate partial inflorescences have merged into a single partial inflorescence giving the proximal partial inflorescence a bifurcating branch with the loss of one rachis bract (see figure 5, Type 2a). So far, this condition is only seen in this species. In both Types 1 and 2 inflorescences, there can be reduction in the number of peduncular bracts from a few to none at all. These numbers, as mentioned previously, are quite consistent within species and if properly recorded can be useful in distinguishing species.

Table 1. Comparison of inflorescence types found in Malaya and Borneo (data extracted from Saw (1997) and Saw (in prep.)).

Inflorescence type	Region		Common to both regions	Total number of species	%
	Malaya	**Borneo**			
1	20	22	4	38	46.34
2	19	12	0	32	37.80
3	1 (+1*)	6 (+2*)	0	7 (+3*)	8.54
4	1	5	0	5	7.32
Total	41	~46	4	82	100

* Overlapping inflorescence types, see text for explanation.
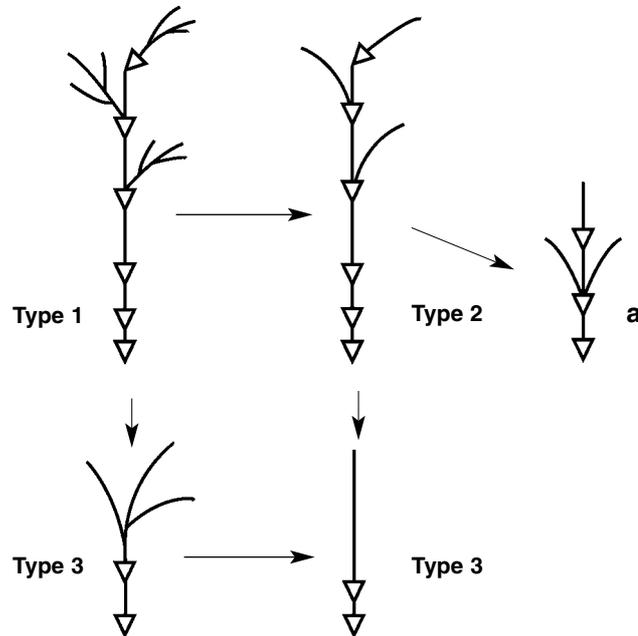
Fig. 5. Diagrammatic presentation of inflorescence types found in *Licuala*, triangles represent bracts. Possible trends of reduction of organs indicated by arrows. See text for further details.

When the inflorescence is reduced to one partial inflorescence, two inflorescence types are possible: Type 3, where the partial inflorescence is branched; and Type 4, where the inflorescence is a spike. Both Types 3 and 4 inflorescences are not very common in *Licuala*. In Malaya, only *Licuala scortechinii* has strictly a Type 3 inflorescence. There are eight other species in Borneo with this inflorescence type (Table 1). *Licuala kingiana*, *L. mattanensis* Becc. and *L. collina* L.G.Saw (ined.) (former from Malaya and the latter two from Borneo) have spicate inflorescences, i.e. Type 4 inflorescences, but sometimes these branch into two rachillae, i.e. Type 3 inflorescences. However, *Licuala spicata* Becc. and *L. elliptica* L.G.Saw (ined.) in Borneo consistently have spicate inflorescences. Although the typification of inflorescences is useful in understanding likely evolutionary processes in the genus, these types, as already obvious in the earlier discussions, are not mutually exclusive within particular species. However, in the majority of species, they are constant, making this character very useful in species identification. Species of *Licuala* in both Borneo and Malaya with Types 3 or 4 inflorescences all lack peduncular bracts. Further reduction in inflorescence bracts is seen in a number of Bornean species (e.g. *L. micholitzii* Ridl., *L. yiiana* L.G.Saw (ined.), *L. collina* L.G.Saw (ined.)) where the inflorescence bears only a prophyll and no other bract on the rachis. At least six species in Borneo have this condition.

Table 1 also indicates a trend of reduction in inflorescence parts with corresponding lower species numbers.

The rachilla takes on various forms in different species. It can be rather wiry, commonly among the smaller species. In other species, the rachilla is wiry when immature, but will become swollen and thick as the inflorescence matures. The rachillae in most species are

not ornamented. In some, they are ornamented with pits with flowers, regular ridges between the flowers, tubercles supporting flowers and short floral stalks (Figure 6). In one species, *L. whitmorei* L.G.Saw, the rachilla surface is regularly cracked when dried (Saw 1997). The rachilla on the whole may be glabrous (a rather uncommon condition, e.g. in *L. glabra*) or it may be hairy (varying in density, length and colour). Each flower is subtended by a bracteole and a floral bract, although sometimes only one of these is obvious. The rachilla characters are found to be quite useful in differentiating taxa.

We have differentiated the pedicelliform base of the flower and the floral stalk which carries the flower. The term pedicel is deliberately not used because it might cause confusion by its general usage. The floral stalk, being part of the rachilla is defined as the stalk just below the articulation with the flower (Figure 6e). The pedicelliform base, being part of the calyx, fused to the receptacle, is the part above the articulation of the flower with the rachilla. It is important to differentiate these because the stalk below the flower of some species (e.g. in some forms of *L. glabra*) consists of these two elements, while in others consists of only one element but of different origin (e.g. *L. acutifida* has a floral stalk but its calyx is not pedicelliform).

The flowers are arranged spirally all along the rachilla. In most species, the flowers are very closely packed, whereas in others they are arranged loosely on the rachilla. The flowers are strictly solitary in a number of species (Figure 7a), while in others, they are in groups near the base of the rachilla but are solitary distally. In a number of species, the cincinni are on branched floral stalks. Each cincinnus can have up to seven flowers arising from a single branched stalk, for example in *L. sallehana* (Figures 7b). In *L. tenuissima*, the flowers are also in groups but they are sessile (Figure 7c). Flowers mature about the same time in inflorescences of most species and open within a short period of each other. This is rather obvious in the herbarium specimens, as they are all about the same size and at about the same stage of development. In a number of others, common only in species that have flowers in groups, different stages of floral development are found within each cincinnus. This gives an inflorescence a more staggered period of flowering (Figure 7c).
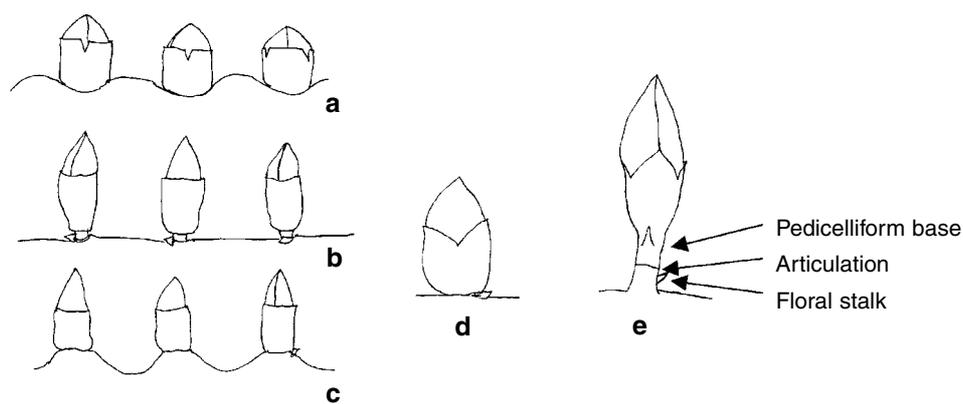
Fig. 6. Ornamentation on rachilla surfaces and floral types. **a,** Flowers in pits. **b,** Surface unornamented. **c,** Flowers on tubercles. **d,** Sessile flower. **e,** Stalked flower showing pedicelliform base, articulation and floral stalk.
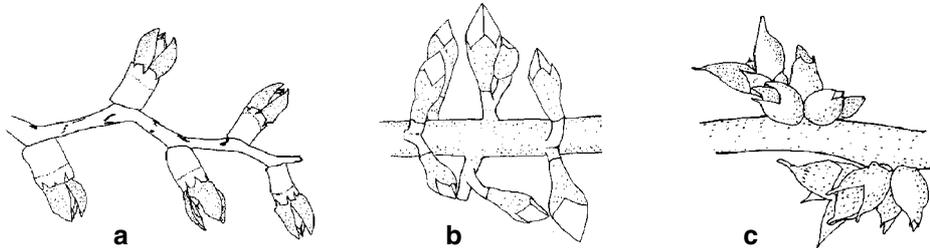
Fig. 7. Cincinni of *Licuala*. **a,** Flowers singly. **b,** Flowers in groups of 1-few on floral stalks. **c,** Flowers in groups of 3 or more, sessile.

The Flowers

Palm flowers with the basic trimerous construction are similar to those of many monocotyledonous families. Perfect (hermaphroditic) flowers which are regularly trimerous and with three separate carpels are considered to represent the ancestral condition (Tomlinson 1990). This construction is found in *Thrinacinae* and has been considered by Moore (1973), and Moore and Uhl (1982) as evidence that the *Coryphoideae* are closest to ancestral palms. These conclusions will need to be reconsidered in the light of recent phylogenetic analyses. This floral construction is also considered to be the least specialized among the palms (Uhl and Dransfield 1987). In *Livistoninae*, however, the carpels are free basally but united at the style. The fusion of the style probably represents a derived state from free carpels of the *Thrinacinae*. While the flowers of *Licuala* are of simple construction, there is a surprising array of variation in the flower, even within the strict trimerous construction, i.e. three sepals, three petals, six stamens (in two whorls of three), and three carpels.

Licuala in general has hermaphroditic flowers. Dioecy is very rare in *Licuala*, but is known in at least one, and suspected in a few other species. *Licuala gracilis* Blume from west Java has some plants with only female flowers; i.e. they have a gynoecium and staminodes but no anthers. In the same population, other individuals have what seem to be hermaphroditic flowers (collection *J. Dransfield* 1433 in Kew). One of us (JD) has observed that these individuals do not produce fruits and are functionally male plants. *Licuala hexasepala* Gagnep. from Vietnam also has a similar flower differentiation. For example, in the collections made by M. Newman 177 is female, while 179 is hermaphroditic (both numbers are in Kew). The ovary of the hermaphroditic flowers is similar to those of the female flowers. Whether the hermaphroditic flowers are also functional males as in *L. gracilis*, needs to be confirmed by field observation. There is another species with only female flowers from South China (*C.F. Wei* 123257). This new species, planted in South China Botanical Garden, was introduced from Guangxi province. It appears that a similar syndrome of dioecy has occurred in a few species of *Licuala*. We further suspect that there may be more species with this syndrome when a fuller survey of the genus is carried out.

There are two main flower tissue types found in *Licuala*. They are quite easy to recognise in dried specimens. Species with rather succulent or fleshy flowers when dried will shrink to some extent and the calyx and corolla become membranous with the calyces often loosely enclosing the corolla. These flowers also often dry dark brown

to black. The second flower type is lignified. These flowers dry various shades of brown, often light brown. On drying, the calyces continue to enclose the corolla tightly.

The calyx is sometimes stalk-like at the base, tubular, truncate, irregularly splitting or with three neat triangular lobes, glabrous or variously hairy. There are very good diagnostic characters in the calyces, particularly in the shape, striation and hairiness. They are, overall, quite constant but in some species can be quite variable and can cause confusion in the definition of taxa. *Licuala glabra*, for example, has quite variable calyces ranging from cylindrical to cyathiform to urceolate (Saw 1997). Their bases are sometimes pedicelliform and sometimes swollen. These infra-specific variations are quite constant within populations. In spite of these variations in shape, they are united in the constantly glabrous calyx with very short pointed lobes at the apex.

Striation on the calyx is normally more obvious in dried specimens than in fresh. In some species this character is very distinctive, e.g. *L. pahangensis* and *L. terengganuensis.* In species with hairy calyces, the hairs are always spreading. Although this is also a constant character in most species, there is an exception, in most of the range of *Licuala terengganuensis*, the calyx is glabrous but on Bukit Bauk, Terengganu, there are some individuals with hairy calyces together with those with usual glabrous calyces. Although there are some differences between this population and the main population outside Bukit Bauk, Saw (1997) considered them conspecific. In *L. lanuginosa* and *L. cameronensis*, the hairs are very long and shaggy. In *L. ferruginea* and related species, the hairs are distinctively ferruginous.

The corolla is usually considerably larger than the calyx, tubular at the base, and divided into three rather thick, triangular, valvate lobes. It is glabrous to variously hairy, and its adaxial surface is usually marked near the tip with the impression of the anthers. The petal shape is rather constant, i.e. triangular, this character not being very useful in defining taxa. However, *L. terengganuensis* outside the population at Bukit Bauk has corolla lobes that are strongly incurved. Most other species of *Licuala*, including the population of *L. terengganuensis* at Bukit Bauk have spreading or gradually incurving corolla lobes.

There are eight species in Malaya and *c.* 20 species in Borneo of *Licuala* with glabrous corollas. It is also interesting that all these species also have glabrous ovaries. We have found that the hairiness of the corolla to be a useful character. The hairs are all simple, but they can be orientated differently. Three types are recognized; spreading hairs (Plate 1a), spreading and appressed hairs (Plate 1b) and strictly appressed hairs (Plates 1c & d). Spreading hairs are most common amongst species with hairy corollas. There are five species in Malaya with strictly appressed hairs. The hairs appeared to be glued to the corolla surface. In some cases, when it is both densely hairy and strongly appressed, the corolla surface appears superficially glabrous. When Beccari (1921) and Kiew (1989) described *L. ridleyana* Becc. and *L. dransfieldii* Kiew (both are now considered conspecific), they had erroneously described the corollas as glabrous. The categorization of hair orientation would be rather straightforward had there been only these two types. There are, however, a few species that are intermediate between the spreading and appressed hair types. These are referred to as having corollas with appressed and spreading hairs (Plate 1b). Hair lengths and density can also be good characters. In general, similar hairs are found on both the calyx and corolla, if both are hairy.

The androecium is represented by six epipetalous stamens with somewhat distinct flattened filaments adnate to the throat of the corolla tube. The point of fusion is generally just below the base of the corolla lobes. The filaments may be free or may be united to form a staminal ring. Furtado (1940) used the nature of the androecium formation to classify the subgenera. Figure 8 gives a diagrammatic presentation of the androecium found in *Licuala*.
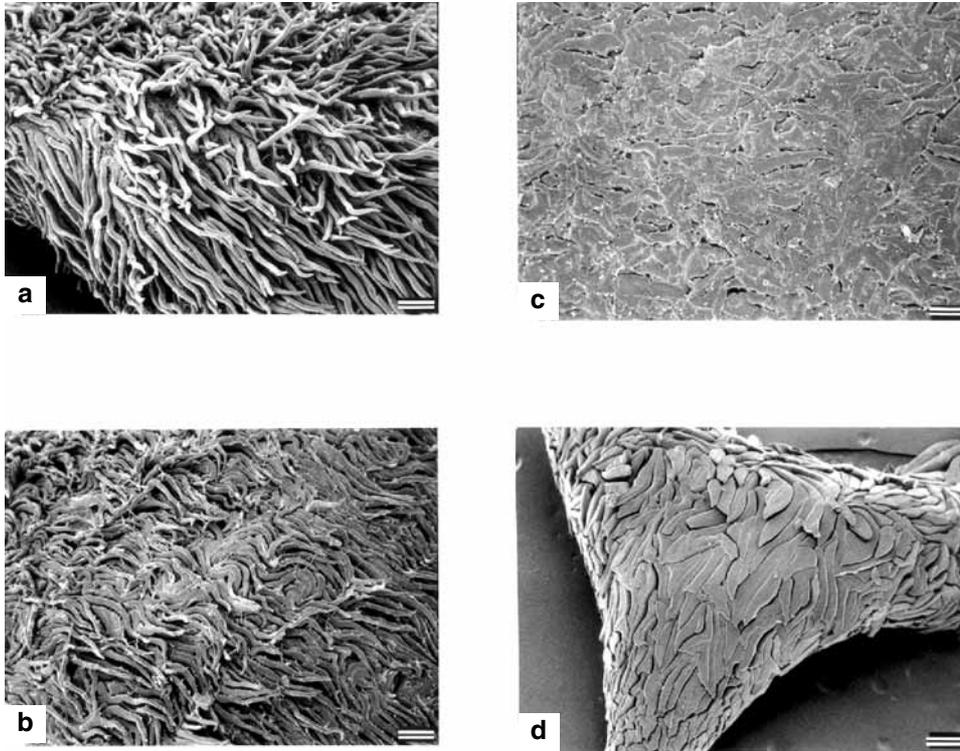
Plate 1 Corolla hair types.

a. *Licuala ahlidurii*, hairs are spreading (*L.G. Saw* FRI 39860). Scale bar = 0.1 mm

b. *Licuala fractiflexa*, hairs are appressed and spreading (*L.G. Saw* FRI 37585). Scale bar = 0.1 mm

c. *Licuala stongensis*, strictly appressed hairs (*T.C. Whitmore* FRI 12469). Scale bar = 50 mm.

d. *Licuala kingiana*, strictly appressed hairs (*R. Kiew* RK 2581). Scale bar = 0.1 mm.

In Furtado's classification, the subgenus *Licuala* includes species with stamens united at the base into a conspicuous ring adnate to the corolla throat and the staminal ring is rather uniform in height, with its filaments of about equal size (Figure 8a). It has a wide distribution, occurring in most of the range of the genus in Indo-China, Thailand, Malaya, Borneo, Philippines and Indonesia. The highest concentration of species is in Malaya and Borneo. Species with rather large flowers, about 15 mm or more long, with 6 equal free stamens adnate to the corolla tube and lacking a staminal ring are placed in subgenus *Libericula* (Figure 8b). This subgenus includes *L. peltata* Roxb. and *L. distans* Ridl. Finally, in the subgenus *Pericycla*, the staminal ring consists of three lobes, the lobes are emarginate with one filament in the notch at the apex of each lobe and one in each sinus between the lobes (Figure 8c). Most species are found in New Guinea and the islands surrounding it, east of the Wallace's line but there are two aberrant species described by Burret (1940 & 1941) with staminal rings which are slightly trilobed, which occur in South China and North Vietnam.

Two more types, representing new taxa are also included in the figure. Both of these were observed in collections made from Borneo. Figure 8d represents an androecium type where the staminal ring has filaments of two different heights alternating in two whorls. The anthers are basifixed and joined to the whole dorsum of the filament. This construction is observed in a new species collected from Brunei (*J. Dransfield*
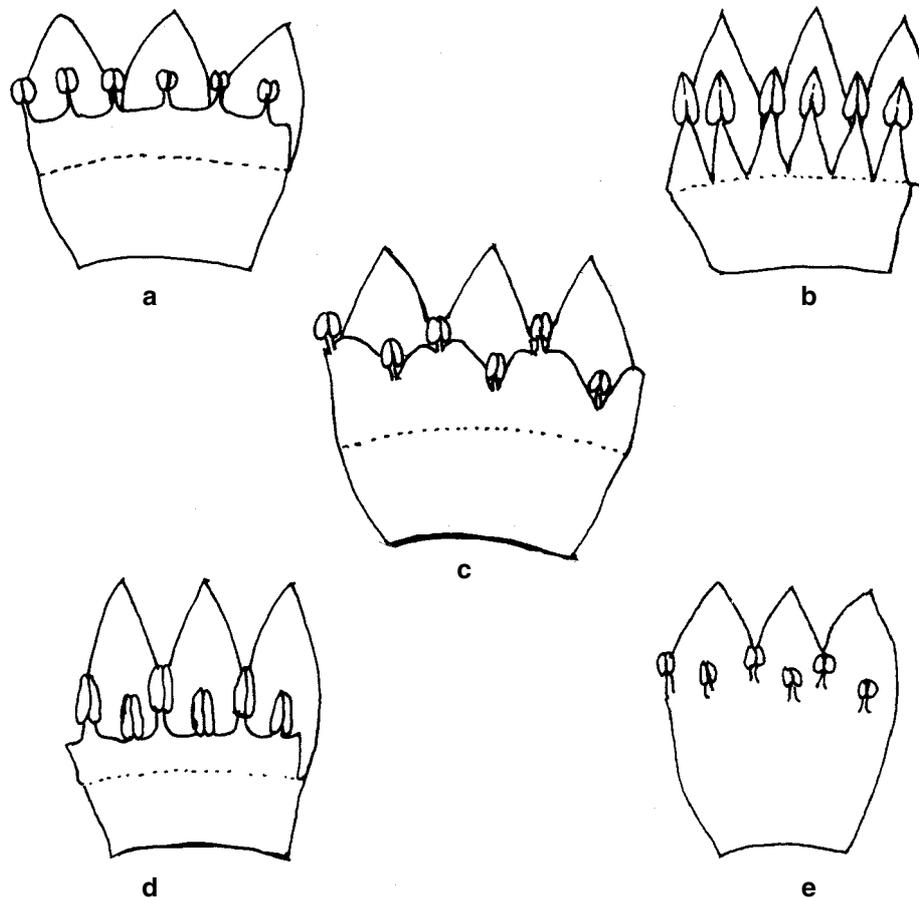
Fig. 8. A diagrammatic representation of androecium types of *Licuala* species. **a,** Regular staminal ring with equal sized filaments. **b,** Stamens free but joined at the base. **c,** Staminal ring trilobed, stamens on ridges and valleys of lobes. **d,** Staminal ring regular, filaments in two alternating lengths. **e** Filaments completely free from each other.

794); *L. bruneiana* L.G.Saw (ined.). Figure 8e represents yet another androecium type that is unlike any other we have seen. Here, the stamens are very small; the filaments are adnate to the corolla wall a short distance below the corolla lobes. What is strange about this construction is that the filaments are completely free from each other. Although the filament lacks a staminal ring in the subgenus *Libericula*, they still contact each other at the base. The flower shape on the whole is also very 'un-*Licuala*-like', i.e. its shape is ovoid and the corolla lobes split away from the calyx with a very small mouth. The species is also new and was collected by P.C. Yii (S 42003) from Bako, Sarawak (*L. flammula* (L.G.Saw (ined.)). *L. flammula* is unusual among Bornean *Licuala*, as the species appears to be dioecious, the species is currently only known by its type and the flowers of the specimen (S 42003) has female flowers, the anthers are present but appear to be empty.

Anthers can be basifixed or dorsifixed. All Malayan species of *Licuala* have dorsifixed anthers. The anthers can be either versatile or rigid. Most anthers that are dorsifixed are also versatile. When the anthers are basifixed, they are always rigid, e.g. *L. bidentata* Becc. from Borneo. There are a few species with dorsifixed anthers that are rigid too. The filament ends in a discoid apex joined to the anthers quite rigidly – so far only known from *L. fatua* Becc. and *L. hexasepala* Gagnep., both species from Indo-China. *Licuala reptans* Becc. from Borneo has inflexed anthers, and here the filament is bent twice, carrying the long, very narrowly linear pendulous anthers.

The ovary consists of three uniovulate carpels, which are fused at their apices into a single style. They are variously shaped; cylindrical, turbinate, fusiform to globular. The apex is sometimes sculptured by the impression of the anthers, giving it a truncate and channelled top. When the ovary develops with little contact with the anthers, its apex is rounded. These features appear to be constant within the species. The surface can be glabrous to hairy. A glabrous ovary is the more common situation in the genus. Out of the c. 44 species of *Licuala* found in Borneo, only two species have hairy ovaries, while the rest have glabrous ovaries (Saw, in prep.). These two are *L. triphylla* from Peninsular Malaysia and *L. pilosa* L.G.Saw (ined.), the only endemic Bornean species with a hairy ovary. Species with hairy ovaries appear to be more restricted in distribution. They are restricted to Malaya and Sumatra, though more common in Malaya. In Sumatra, the three species with hairy ovaries are also found in Malaya or are closely related to Malayan taxa, i.e. *L. longipes*, *L. ferruginea* and *L. ferruginoides*. Hairs are mostly globally distributed on the whole ovary. In some species, they may be restricted only to the upper parts. For example, *L. thoana* has an ovary with hairs in a ring around the rim of the apex of the ovary, but in closely related species, *L. ferruginea* the whole ovary is covered in hairs.

Usually only one carpel develops into a fruit, but in some species, two or even all three carpels in a flower will develop into independent drupes. Whether this character is species-specific, is still uncertain. The style is filiform or narrowly conical. The stigma is very shortly 3-lobed but sometimes it is difficult to discern the lobes.

The Fruits

The fruits are usually small and are drupaceous, usually globose or ovoid, rarely ellipsoid. Very few species are known with long ellipsoid fruits, e.g. *L. kiahii* Furtado from Malaya and *L. mattanensis* Becc. from Borneo. Immature fruits are green in most species of *Licuala* but in *L. ferruginea* and its alliance, the immature fruits are distinctively pink. Most species with green immature fruits will ripen orange to red. However, in *L. ferruginea* and its alliance, the young fruit is pink and then ripens black. In *L. densiflora* Becc., similar to *L. ferruginea*, the immature fruit is pink to red but here it matures white. Fruit surfaces or the exocarps are generally smooth but they can be shagreen (e.g. *L. tenuissima* L.G.Saw and *L khoonmengii* L.G.Saw from Malaya) to even corky warty (e.g. *L. bintuluensis* Becc. and *L. bruneiana* L.G.Saw (ined.) from Borneo). Mesocarps are usually pulpy when ripe and non-fibrous. The fruits are animal dispersed and the most likely dispersal agents are birds and small forest mammals. Most seeds are globose and some are ellipsoid, following the shape of the fruits. Endocarp surfaces are smooth in most *Licuala* species and are usually crustaceous. The endocarp usually adheres quite strongly to the seed in fresh specimens and is difficult to separate. Shrinkage of the seeds as a result of drying, for example in herbarium specimens, can result in the endocarp loosely enclosing the seed. The testa is usually very thin, brown and is strongly adherent to the seed in both fresh and dried specimens but may peel off from the seed after prolonged boiling.

In New Guinea, the fruits of some species are rather large and endocarps are rather thick and ornamented with regular longitudinal ridges, quite unlike any others (e.g. *L. beccariana* Furtado, *L. lauterbachii* and *L. crassiflora* Barfod). There are, however, other species with smooth endocarps in New Guinea. The ornamented endocarp may represent a different line of fruit types in *Licuala.* It will be very interesting to see if this condition is correlated with characters of New Guinean *Licuala* species. Ferrero (in letter to J. Dransfield, 1994) suggested that the fruits of *Licuala* with longitudinal ridges are dispersed by cassowaries.

The seed consists of a uniform endosperm, usually white and very hard when mature. Embedded in the endosperm are two structures clearly visible in longitudinal section, viz.: the chalaza that intrudes into the endosperm (as a postament) like a large inverted comma at the base of the seed and the embryo, located variously, usually about dorsal to the axis of the fruit. The embryo is straight and cylindrical, rounded distally comprising the cotyledon and flattened proximally, comprising the apical meristem and radical.

Conclusion

In conclusion, *Licuala* is shown to have rather strict morphological construction. Although vegetative characters can be useful in taxon delimitation, as often they are not. Inflorescence and floral characters are most useful.

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