

## Lanonia (Arecaceae: Palmae), a New Genus from Asia, with a Revision of the Species

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**Abstract**—A recent phylogenetic study based on molecular data indicates that *Licuala* (Arecaceae: Palmae) is not monophyletic. A highly supported group of species is resolved separately from *Licuala* and the rest of the Livistoninae, and is closely related to *Johannesteijsmannia*, requiring that the segregate group be placed in a new genus. In this study, a phylogeny based on seven gene regions resolves highly supported generic relationships of the Livistoninae. A survey of *Licuala* specimens from several herbaria indicates that, based on morphology, eight species should be recognized within this genus. A complete description of the new genus, *Lanonia*, is given. A review of morphology distinguishes synapomorphies in leaf morphology and dioecy of *Lanonia* species. All eight species are described with complete synonymy, their distributions are mapped, and lists of specimens examined are given. One species occurs in Hainan, one in Java, and six are endemic or nearly endemic to Vietnam. The following new combinations are made: *L. acaulis*, *L. calciphila*, *L. centralis*, *L. dasyantha*, *L. gracilis*, *L. hainanensis*, *L. hexasepala*, and *L. magalonii*.

**Keywords**—Dioecy, incongruence, *Licuala*, phylogenetics, Vietnam.

Despite recent phylogenetic efforts to address relationships across the palm family (Arecaceae: Palmae; e.g. Asmussen et al. 2006, Baker et al. 2009), the Trachycarpeae remains one of the most significant areas of phylogenetic ambiguity within the family due to poor resolution among genera and low support for relationships. According to the most recent family classification, subtribe Livistoninae (Coryphoideae; Trachycarpeae) comprises five genera: *Johannesteijsmannia* H. E. Moore, *Licuala* Wurmb, *Livistona* R. Br., *Pholidocarpus* Blume, and *Pritchardia* Becc. (Dransfield et al. 2005). A recent phylogenetic study of the Trachycarpeae (Bacon et al. in press) shows strong support for necessary taxonomic changes to Livistoninae genera. *Livistona* was resolved as two well-supported monophyletic groups that were not each others' sister groups and have been recognized as two distinct genera, *Livistona* and *Saribus* (Bacon and Baker 2011). *Licuala*, the largest genus of the Livistoninae, is clearly not monophyletic.

*Licuala* has been included in recent phylogenetic studies, but represented by only a single species (Asmussen et al. 2006; Baker et al. 2009; Crisp et al. 2010). Exemplar sampling within *Licuala* is inadequate since it is the largest genus of the Livistoninae and contains approximately 137 species (Govaerts and Dransfield 2005). *Licuala* are distributed from Bhutan and northeastern India throughout southeastern Asia and into the western Pacific. The two main centers of diversity are the Sunda Shelf in Malaysian Peninsula and Borneo with about 80 species, and the Sahul Shelf on the island of New Guinea with about 40 species (Saw et al. 2003). More recently, Vietnam has been found to be a third center of diversity, and 11 new species have been added to the 10 species that are currently recognized (Henderson et al. 2008).

In this study we present results from both molecular and morphological studies to show that a segregate group of *Licuala* species should be recognized at the generic level. We describe a new genus to accommodate this segregate group, and call this *Lanonia* based on the local name, la non ("hat palm"), of these plants in Vietnam, the center of diversity in the genus. We provide a multilocus phylogeny of the Livistoninae based on data from both the nuclear and plastid genomes and a taxonomic account of the new genus based on morphological data. A key as well as complete

synonymy, descriptions, lists of specimens examined, and distribution maps for all currently recognized species are given.

### MATERIALS AND METHODS

**Taxon Sampling and DNA Sequencing**—To avoid sampling bias and increase phylogenetic accuracy two species were sampled for each Livistoninae genus, not including *Lanonia*, that represented the phylogenetic diversity of the genera based on a broader study (Hillis 1998; Bacon unpubl. data). More than one accession was sampled for some *Lanonia* species and a total of 30 terminals were included in the simultaneous analysis (Kluge 1989; Nixon and Carpenter 1996; TreeBASE study number 11233). Total genomic DNA was extracted from silica-gel dried leaves following the protocol described by Alexander et al. (2007). Sequences for three plastid loci (*matK*, *ndhF*, and *trnDT*) and four nuclear loci (CISPs 4 and 5, MS, and RPB2) were generated. Single amplifications of the *matK* locus used primers *matK*-19F and *matK*-1862R, with internal sequencing for *matK*-300F, *matK*-809F, and *matK*-971R to construct contiguous sequences (Steele and Vilgalys 1994; Asmussen et al. 2006). Amplifications of CISPs 4 and 5 followed Bacon et al. (2008), MS followed Crisp et al. (2010), *ndhF* followed Cuenca and Asmussen-Lange (2007), RPB2 followed Roncal et al. (2005), and *trnDT* followed Hahn (2002). Amplified products were sequenced by the Cancer Research Center DNA Sequencing Facility at the University of Chicago. All new sequences generated in this study have been deposited in GenBank under accession numbers JF292931 to JF292988 (Appendix 1).

**Phylogenetic Analysis**—Multilocus phylogenies enabled examination of the monophyly of *Lanonia*, its relationship to other Livistoninae genera, and the relationships among *Lanonia* species. Preliminary nucleotide alignments were obtained independently for each of the seven loci using the default MUSCLE v.3.6 (Edgar 2004) settings in SeaView (Gouy et al. 2010) and manual adjustments were performed in MacClade v4.03 (Maddison and Maddison 2001) following Simmons (2004). Searches for the most parsimonious trees were conducted using 1,000 random addition tree-bisection-reconnection (TBR) searches in PAUP\* v.4.0b10 (Swofford 2001) with a maximum of ten trees held per replicate. Parsimony jackknife analyses (JK; Farris et al. 1996) were conducted using PAUP\* and 1,000 replicates were performed with 100 random addition TBR searches per replicate. jModeltest v.0.1.1 (Posada 2008) was used to select the best-fit likelihood model for each data matrix using the Akaike information criterion (Akaike 1974) without considering invariant-site models following Yang (2006). Searches for optimal maximum likelihood trees (Felsenstein 1973) and 1000 bootstrap replicates (BS; Felsenstein 1985) were conducted using the CIPRES Portal v.2.2 with the RAxML-III algorithm (Stamatakis et al. 2005; Stamatakis et al. 2008). Simultaneous analysis was performed using the GTR + I model. We mapped support values onto the parsimony strict consensus tree using TreeGraph 2 (Stöver and Müller 2010) to help minimize frequency-within-replicates (Davis et al. 1998) and undersampling-within-replicates JK and BS artifacts (Simmons and Freudenstein 2011).

For Bayesian MCMC analysis (Yang and Rannala 1997), data was partitioned by locus to allow for variation in substitution models in the BEAST package (Drummond et al. 2006; Drummond and Rambaut 2007). The analysis was run using a strict molecular clock model, a Yule pure birth speciation model, the GTR +  $\Gamma$  model of nucleotide substitution, and the default operator. The Markov chains were run for 10 million generations and repeated 10 times to test for MCMC chain convergence and to check effective sample sizes, which all exceeded 1,000. After removing an *a priori* determined 10% burn-in, BEAST log files were combined in LogCombiner v.1.5.4 to determine whether chains had reached stationarity in Tracer v1.5. Tree files were combined to estimate mean node height and the 95% highest posterior density in TreeAnnotator v.1.5.4.

**Morphological Analysis**—A survey of the morphology of specimens of both *Lanonia* and *Licuala* was carried out. Specimens were examined from the following herbaria: A, AAU, BH, F, FIPI, HN, HNU, IBSC, K, M, MO, NY, P, SYS, US, and VNM. Relevant literature was also surveyed (e.g. Saw 1997; Barfod and Saw 2002; Saw et al. 2003).

## RESULTS

**Incongruence Among Gene Trees**—Among the seven gene regions, each *Livistoninae* genus was highly-supported as monophyletic with 100% JK and BS support (Fig. 1) and 1.0

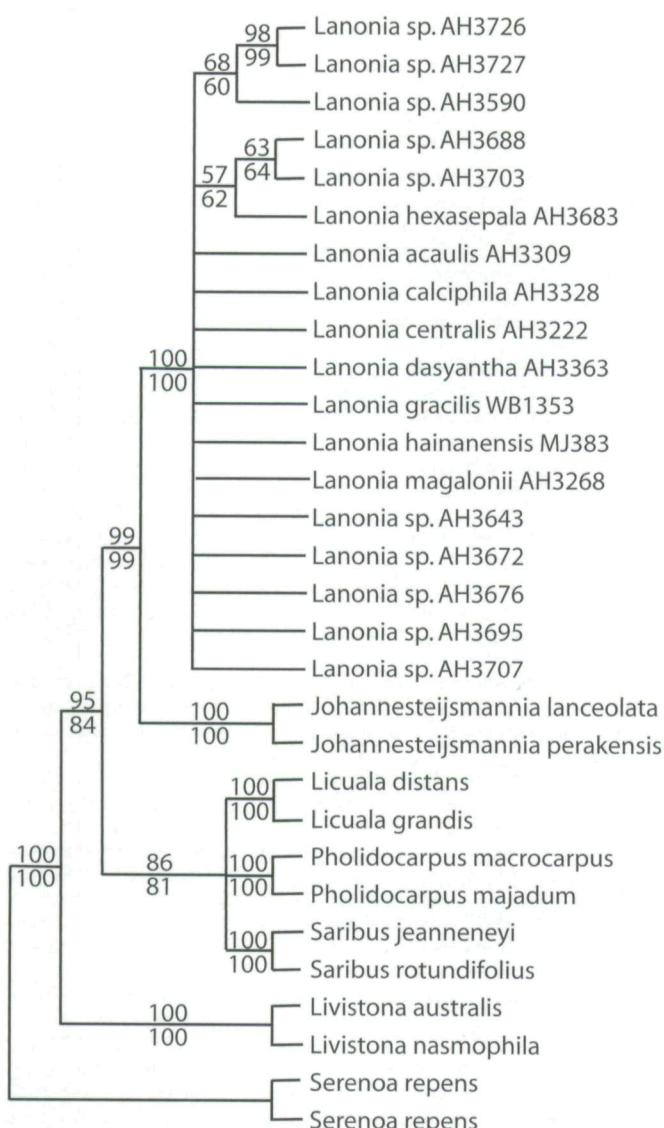


FIG. 1. The parsimony strict consensus tree with parsimony jackknife values above each branch and likelihood bootstrap values for all nucleotide characters below each branch.

posterior probability (PP; Fig. 2). The inter-generic relationships were congruent among the gene trees except for the position of *Pholidocarpus*, but the incongruences were all poorly supported (< 75% branch support). Within *Lanonia*, *L. calciphila* is resolved as sister to the rest of the genus in the *ndhF* and *RPB2* gene trees (62% and 97% JK respectively), but not in the *CISP4* gene tree (85%). The position of *Lanonia* sp. *AH3590* as sister to *Lanonia* sp. *AH3726* and *AH3727* is supported by both the *matK* (54% JK) and *RPB2* gene trees (64% JK), but not by the *CISPs 4* and *5* gene trees (85% and 63% respectively). The individuals *Lanonia* sp. *AH3676* and *AH3695* are sister in both the *ndhF* and *matK* gene trees (66% and 59% JK), but are separated by two weakly supported branches in the *MS* gene tree (60% and 50% JK). Lastly, in the *CISP5* gene tree, *L. acaulis* is resolved as sister to *L. hainanensis* (58% JK), but not in the *CISP4* or *MS* gene trees (85% and 60% JK respectively). These incongruences were maintained after resequencing of the individuals in question for the respective genes.

**Systematics Within Livistoninae and Lanonia Based on Molecular Phylogenetics**—The multilocus phylogeny resolved *Livistona* as sister to all remaining species in the subtribe (95% JK and 84% BS), a clade of *Licuala* + *Pholidocarpus* + *Saribus* (86% JK and 81% BS), and the sister relationship of *Johannesteissmannia* and *Lanonia* (99% JK and BS). Within *Lanonia* weakly supported relationships were resolved between *L. hexasepala* and *L.* sp. (AH3688 and AH3703; 57% JK and 62% BS) as well as between the *Lanonia* sp. individuals AH3590, AH3726, and AH3727 (68% JK and 60% BS).

Bayesian methods can be sensitive to missing data (e.g. Goloboff and Pol 2005) and to inflated branch-support values (e.g. Suzuki et al. 2002; Simmons et al. 2004). In the Bayesian

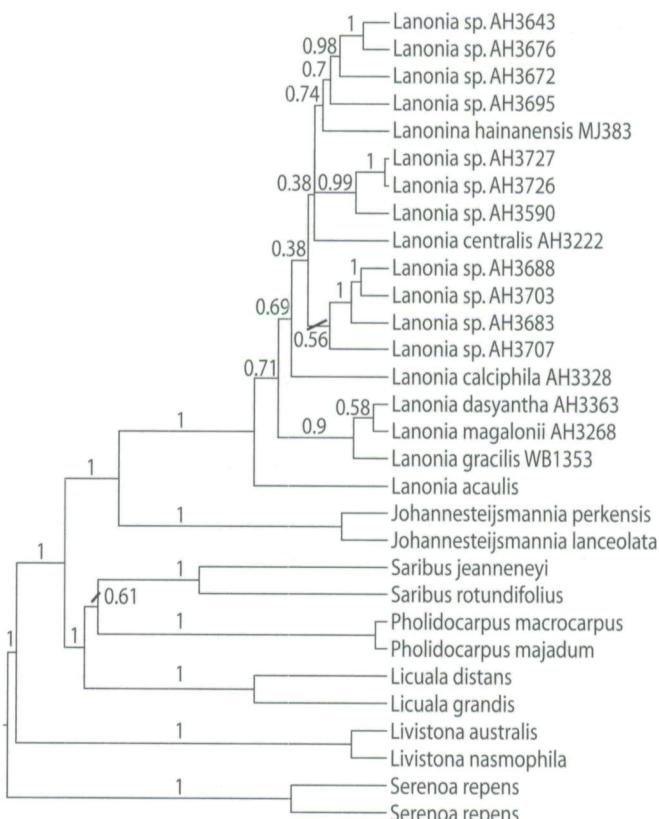


FIG. 2. The maximum clade credibility tree from BEAST analysis with posterior probabilities at each branch.

topology, many well-supported relationships not seen in the parsimony or likelihood trees were resolved (Fig. 2). Additionally, there is indication that some of the southern Vietnamese *Lanonia* lineages could be recognized as species based on the Bayesian results (*Lanonia* sp. AH3643, AH3676, AH3672, and AH3695; *Lanonia* sp. AH3727, AH3726, AH3590; *Lanonia* sp. AH3688, AH3702, AH3683, AH3707). Due to a limited number of herbarium specimens for these lineages and a limited understanding of their distributions or morphology, we await planned field and herbarium visits and subsequent sequencing efforts to further define these groups.

**Morphological Support for *Lanonia***—Based on review of pertinent herbarium material and literature, we found *Lanonia* to be distinguished by leaf synapomorphies in the central segment and a pulvinus-like structure on the abaxial surface of the costa. Floral synapomorphies of *Lanonia* include calyx and corolla that are reflexed in relation to the fruit. Staminate flowers are paired or clustered and have anthers that are dorsifixed and non-versatile. In contrast, pistillate flowers that are always solitary and the three calyx lobes split at or after anthesis to give what appears to be a 6-lobed calyx.

## DISCUSSION

**Molecular Assessment of *Lanonia* and its Sister Genus**—Incongruence between linkage groups could be due to hybridization, paralogy, selection, recombination, or incomplete lineage sorting (e.g. Doyle 1992). We suggest that hybridization is probably not responsible for these patterns because it is extremely unlikely that it would be detected among genera and across highly divergent taxa. We do not believe differential selection can account for incongruences because a majority of the phylogenetic signal is derived from non-coding genes. Evidence of paralogy was not evident by double bands in gel electrophoresis or heterozygotic chromatograms. Recombination was not detected in any of the loci using the default settings in the recombination detection program (Martin and Rybicki 2000). Incomplete lineage sorting is the likely candidate to explain the patterns of incongruence in the dataset, but despite this, each gene tree resolved all the Livistoninae genera, including *Lanonia*, as monophyletic with 100% branch-support. For future studies on the species-level relationships in *Lanonia*, coalescent methods of phylogeny reconstruction that explicitly account for lineage sorting will be used (e.g. BEST; Liu 2008).

Because gene and species trees are not necessarily synonymous, we sampled seven gene regions and as many individuals as we could to estimate species-level relationships within *Lanonia*. Our data show monophyly for Livistoninae and its genera, including *Lanonia*, *Livistona* as sister to all other Livistoninae, as well as a sister relationship between *Johannesteijsmannia* and *Lanonia* (Figs. 1, 2). The recognition of *Lanonia* is a surprising discovery but perhaps not entirely so considering *Licuala* had not been sampled with more than one species in recent phylogenetic studies (Asmussen et al. 2006; Baker et al. 2009; Crisp et al. 2010). Furthermore, a majority of the species that comprise *Lanonia* are recently described based on field work in under-collected regions of Vietnam and other areas of eastern Asia (Henderson et al. 2007, 2008). Individuals from the south of Vietnam of yet undescribed or fully sampled populations may lead to the recognition of at least two other *Lanonia* species, but we do not include them here and await future field, herbarium, and laboratory work.

## Morphological Assessment of *Lanonia* Based on Herbarium Material

**The Leaf**—The leaf is one of the most distinctive morphological features of *Lanonia*. In all species of *Licuala* s. s., the leaf has a costa (here defined as an extension of the petiole into the blade, analogous, if not homologous, with the rachis of a pinnate leaf) extending from the base to the apex of the leaf blade. Although it tapers as it extends to the apex, the costa can be clearly followed, especially on the abaxial surface, through the central leaf segment to the apex. Some variation is evident in the arrangement of the segments along the costa, and the splitting of the central segment. In some species the costa has a 'naked' basal section without segments, a condition known as petiolulate. In a few species the central segment is split, but in these the costa follows the internal margin of one of the resulting segments. Whatever the form of the leaf blade in *Licuala*, a morphological synapomorphy for the genus is that the costa is continuous from the base to the apex of the blade.

In *Lanonia*, the leaf has a different form. The costa is reduced and extends only a few centimeters from the base of the blade into the central leaf segment (Fig. 3C). Two synapomorphies for *Lanonia* are that the central segment is split as far as the apex of the costa and that on the abaxial surface of the costa, just below the apex, is a pulvinus-like structure (Fig. 3F). Although we have no evidence that this structure is a pulvinus, we prefer the term to gland until we can further explore its' anatomy. There is one, doubtful exception to this leaf morphology, discussed under *L. magalonii*.

The leaves of *Johannesteijsmannia* are different from both *Lanonia* and *Licuala*. A synapomorphy for *Johannesteijsmannia* is that the leaf blade is undivided and diamond-shaped. The costa, as in *Licuala*, is continuous from base to apex of the blade. The blade is described as subpinnately ribbed (Dransfield et al. 2008).

All species of *Lanonia* are dioecious, although they may not be strictly so. One specimen (Pételot 5395) of *L. calciphila* has two inflorescences on the same plant; one is spicate and pistillate, the other is branched and staminate. A plant of *L. dasyantha* in cultivation appeared to have both staminate and pistillate flowers on the same inflorescence. All species of *Licuala* and *Johannesteijsmannia* have hermaphrodite flowers, as far as is known (Saw et al. 2003). However, there have been some suggestions in the literature of dioecy in *Licuala* (e.g. Uhl and Dransfield 1987). Saw et al. (2003, p. 203) considered that a specimen from Sarawak (Ching S. 42003) represented a dioecious species of *Licuala*. Examination of this specimen at K shows that the leaves do not have a central bifid segment with a short costa, nor is there is a pulvinus-like structure abaxially at the costa apex. The costa continues through the central segment of the leaf as far as the apex of the segment, as in all other species of *Licuala*. The flowers of this specimen (Saw et al. 2003, Fig. 3) have a well-developed gynoecium and six stamens, but the anthers appear to be empty. Based on the empty anthers, Saw et al. (2003) believed this species to be dioecious. We do not consider this specimen to represent *Lanonia*, although it may be dioecious.

Another a morphological synapomorphy of *Lanonia* is the presence of dimorphic inflorescences, which is more obvious in some species than in others. For example, *L. calciphila* has staminate inflorescences with two to five branched partial inflorescences, each with two to four, 6–11 cm long rachillae. Pistillate inflorescences have one spicate partial inflorescence with a 13–21 cm long rachilla (Henderson 2009). On the other hand, *L. hainanensis* has several, branched staminate



FIG. 3. A. Pistillate flowers of *Lanonia acaulis* (Henderson et al. 3309) with wide rachilla, large solitary flowers, and reflexed perianth. B. Habit of *L. calciphila* (Henderson et al. 3326) with leaf with wider, split central segment. C. Detail of abaxial surface of leaf of *L. centralis* (Henderson & N. K. Ban 3428) with short costa and split central segment. D. Pistillate flowers of *L. centralis* (Henderson et al. 35654) with thin rachilla, small solitary flowers, and reflexed perianth. E. Fruits of *L. centralis*, globose, whitish at maturity, with smooth epicarp. F. Pulvinus-like structure at apex of costa, abaxial surface (*L. dasyantha*, Henderson s.n.; scale bar = 200 µm). G. Fruits of *L. dasyantha* (B. V. Thanh 229), irregularly globose, red at maturity, with warty epicarp. H. Habit of *L. hainanensis* (Guo Lixiu et al. 135), leaves with approximately equal-sized segments. I. Immature fruits of *L. hexasepala* (Henderson et al. 3684) with solitary fruits, reflexed perianth, and split calyx lobes.

and pistillate partial inflorescences but staminate inflorescences have longer and narrower rachillae while pistillate ones have shorter and wider rachillae (Henderson et al. 2007). Inflorescences of both *Licuala* and *Johannesteijsmannia* are not dimorphic, and their flowers are hermaphrodite (with the possible exceptions noted above).

Floral synapomorphies of *Lanonia* include staminate flowers that are paired or clustered (sometimes solitary) and pistillate flowers that are always solitary (Fig. 3A, D, I), as opposed to *Licuala* in which hermaphrodite flowers are solitary or clustered. Staminate flowers have anthers that are dorsifixed and non-versatile, a condition unknown in *Licuala* and *Johannesteijsmannia*. Pistillate flowers have vestigial filaments but no anthers. One of the most distinctive features of *Lanonia* is that each of the three pistillate calyx lobes splits at or after anthesis to give what appears to be a 6-lobed calyx (Fig. 3I). Both the calyx and corolla are reflexed in relation to the fruit (Fig. 3A, D, I), rather than clasping the fruit as in *Licuala* and *Johannesteijsmannia*.

We have excluded two doubtful species from *Lanonia*. *Licuala manglaensis* A. J. Hend., N. K. Ban & N. Q. Dung appears to be dioecious, but the central segment is not split and the costa extends to the apex of the blade. However, there are only two specimens of this species and more material is needed to understand leaf morphology. The second excluded species is *Licuala furcata* Becc. We have examined images of the type at FI ("Sarawak, Mte. Mattang", Apr 1866, O. Beccari 1379). The leaves appear to have the split central segment and pulvinus-like structure on the abaxial surface of the short costa, as in other species of *Lanonia*. However, the inflorescence, with its distantly spaced partial inflorescences on an extended rachis, is unlike that of *Lanonia* and more like that of *Licuala*. Furthermore, Beccari (1889, 1933) described the flowers of *Licuala furcata* as hermaphrodite and Beccari (1933, plate 9.1) illustrated a single flower. We have not examined the flowers of the type, but have examined those of one other topotypic specimen, *Ridley s. n.* at K, the leaves and inflorescences of which exactly resemble those of the type. The flowers, still in bud, resemble the flower illustrated by Beccari. They are solitary, have a well-developed style and six stamens borne on a very short staminal ring. The anthers do not appear to be dorsifixed and non-versatile, and it is not clear if pollen is present in the anthers. The fruiting calyx clearly splits into six lobes. It is possible that this species is dioecious and has vestigial anthers. Nevertheless, inclusion of this species, and *Licuala manglaensis* in *Lanonia* would introduce an element of doubt, and we prefer to await better material for morphological examination, DNA sampling, and further phylogenetic analysis before making a decision on these species. There are also several potential undescribed species of *Lanonia* known from southern Vietnam, as discussed above, but there are too few specimens of each that they are also excluded pending more material.

#### TAXONOMIC TREATMENT

***Lanonia* A. J. Hend. & C. D. Bacon, gen. nov.—TYPE:** *Lanonia acaulis* (A. J. Hend., N. K. Ban & N. Q. Dung) A. J. Hend. & C. D. Bacon. Basionym: *Licuala acaulis* A. J. Hend., N. K. Ban & N. Q. Dung

A *Licuala* differt costis brevibus corpore glanduliformi adaxiali, habitu dioecio, inflorescentiis dimorphicis, floribus

masculis aggregatis antheris dorsifixis non versatilibus, floribus pistillatis solitariis, lobis calycis ad anthese vel deinde scissi, calycem sex-partitum fingens, atque periantho fructifero reflexo.

Plants dioecious. Stems clustered or solitary, erect or sometimes creeping, or short and subterranean. Leaves costapalmate; sheaths fibrous, extended above the petioles into long auricles; petioles elongate, with widely spaced, recurved, black or brown spines along the margins, often spines absent distally; hastulas well-developed adaxially, absent abaxially; blades split to the base along abaxial ribs giving few, to many, multiple-fold segments, these with straight or slightly curved sides, with or without minute, reddish-brown scales abaxially; costas terminating at base of a split of the middle segment, with a distinct pulvinus-like structure abaxially at or near costa apices; middle segment split for half or more its length (to apex of costa) into 2 lobes, these as wide or wider than other segments, rarely the middle segment not split and then the costa continuous throughout the segment; indentations leading to adaxial folds deeper than those leading to abaxial folds, indentations deeper on lateral segments. Inflorescences unisexual and dimorphic, interfoliar, erect or curved among the leaves or sometimes becoming recurved below the leaves at or after anthesis; peduncle short, bearing a basal prophyll; rachis with 1–5 partial inflorescences (more on staminate plants, fewer on pistillate plants), these branched to 1–2 orders, subtended by broad, flattened, densely brown tomentose rachis bracts, these splitting laterally, or subtended by narrow, tubular, scarcely brown tomentose rachis bracts, these splitting apically; staminate rachillae several on each partial inflorescence, usually covered with brown hairs; floral stalks scarcely developed, solitary or borne in pairs or groups of 3, each subtended by small bracteoles; staminate flower buds globose or bullet-shaped; calyces cupular or tubular, usually gibbous, 3-lobed at the apices, often hairy; corollas split for half or more their length into 3, valvate petals, glabrous; stamens 6; filaments fused proximally into a staminal ring, this well or scarcely developed, the filaments free distally, more or less equal in length or alternately long and short; anthers rounded or oblong, dorsifixed, non-versatile; pistil vestigial; pistillate rachillae 1–several on each partial inflorescence, hairy as the staminate rachillae; floral stalks scarcely developed, solitary, each subtended by bracteoles, these sometimes ciliate; pistillate flower buds ellipsoid; calyces cupular, usually gibbous, 3-lobed at the apices with each lobe splitting again as the fruits develop and the calyx becoming 6-lobed, often hairy; corollas split for almost their entire length into 3, valvate petals, glabrous; staminal rings scarcely developed, with vestigial filaments, anthers absent; pistils tricarpellate, carpels distinct proximally, connate distally throughout stylar regions, the style rather short; locules basal in each carpel. Fruits globose or irregularly globose, with reflexed perianth, bright red or white at maturity, or ripening from pink to red to black, sometimes 2 fruits developing from one flower; epicarp warty or smooth; endocarp thin, crustaceous; endosperm homogeneous, with a prominent, regular, subbasal intrusion; embryo lateral; eophylls strap-shaped.

A genus of eight species, including *Lanonia gracilis* from Java, *L. hainanensis* from Hainan, and six species endemic to Vietnam, *L. acaulis*, *L. calciphila*, *L. centralis* (also just reaching adjacent Laos), *L. dasyantha* (also just reaching adjacent China), *L. hexasepala*, and *L. magalonii*.

KEY TO THE SPECIES OF *LANONIA*

1. Inflorescences becoming recurved below the leaves at or after anthesis; pistillate rachillae 2.5–4 mm diameter; pistillate flower buds 6–10 mm long; rachis bracts plicate ..... 2
2. Segments 5–13, mottled light and dark green; rachillae 1–7; China and northern and central Vietnam ..... *L. dasyantha*
2. Segments 22–32, green, not mottled; rachillae 9–21; central Vietnam ..... *L. acaulis*
1. Inflorescences erect or curving among the leaves; pistillate rachillae 0.5–2 mm diameter; pistillate flower buds 1.7–4 mm long; rachis bracts not plicate ..... 3
3. Fruits with smooth epicarp; partial inflorescences subtended by broad, flattened, densely brown tomentose rachis bracts, these splitting laterally; segments 8–26 ..... 4
4. Inflorescences to 30 cm long; Java ..... *L. gracilis*
4. Inflorescences 35–100 cm long; Vietnam and Hainan ..... 5
5. Fruits whitish at maturity; segments 13–26; Vietnam ..... *L. centralis*
5. Fruits orange or red at maturity; segments 12–17; Hainan ..... *L. hainanensis*
3. Fruits with warty epicarp; partial inflorescences subtended by narrow, tubular, scarcely brown tomentose rachis bracts, these splitting apically; segments 3–16 ..... 6
6. Stems, sheaths, and petioles with dense, flat, black scales; staminate flower buds 1–1.5 mm long, globose; costas 0.5–1.5 cm long ..... *L. hexasepala*
6. Stems, sheaths, and petioles without dense, flat, black scales; staminate flower buds 2.8–4.5 mm long, bullet-shaped; costas 6.0–16.0(–24.7) cm long ..... 7
7. Segments 3–4, with minute, reddish-brown scales abaxially; central Vietnam (near Da Nang City and in Thua Thien-Hue) ..... *L. magalonii*
7. Segments 5–7, without minute, reddish-brown scales abaxially; northern Vietnam (Ninh Binh, Hoa Binh, and Son La) ..... *L. calciphila*

1. *Lanonia acaulis* (A. J. Hend., N. K. Ban & N. Q. Dung)

A. J. Hend. & C. D. Bacon, comb. nov.—*Licuala acaulis* A. J. Hend., N. K. Ban & N. Q. Dung, Palms 52: 142. 2008. TYPE: VIETNAM. Da Nang City: Hoa Vang District, Ba Na-Nui Chua Nature Reserve, road to summit, 16°00'N, 108°01'E, ca. 500 m, 19 Apr 2007, A. Henderson, N. Q. Dung, N. Canh & L. V. Bo 3302 (holotype: HN! isotype: NY!).

Stems solitary, to 0.4 m tall, diameter not known, short and mostly subterranean. Leaf number not known; leaf sheaths not known; petiole length not known, the entire length with widely spaced, recurved, brown spines to 0.5 cm long, sometimes spines absent distally; blades to 108 cm wide, split into 22–32 segments, without minute, reddish-brown scales abaxially, with straight sides; costas 3.5–7.5 cm long; middle segment split almost to the base of the blade (to costa apex) into 2 lobes, these only slightly wider than the other segments, 50–59 cm long, 4–5 cm wide at the apices; segments scarcely indented at the apices; indentations leading to adaxial folds 0.3–0.7 cm deep, those leading to abaxial folds 0.1–0.2 cm deep, indentations deeper on lateral segments. Inflorescences to 50 cm long, becoming recurved below the leaves at or after anthesis; prophylls to 25 cm long; peduncles to 30 cm long; rachis 6–25 cm long with 1–2 partial inflorescences, these branched to 2 orders, subtended by broad, flattened, densely brown tomentose, plicate rachis bracts, these splitting laterally; staminate rachillae 10–21 on each partial inflorescence, 20–30 cm long, 1.5–2.5 mm diameter, densely covered with brown, felty hairs; floral stalks scarcely developed, borne in groups of 2–3, each subtended by small bracteoles; staminate flower buds 5–6 mm long, bullet-shaped; calyces ca. 2.5 mm long, tubular, gibbous, 3-lobed at the apices, glabrous or with a few, scattered, brown hairs; corollas ca. 4.5 mm long, split for two thirds their length into 3 petals, glabrous; staminal rings scarcely developed; filaments free for ca. 1.6 mm, alternately long and short; anthers ca. 0.5 mm long; pistillate rachillae 9–16 on each partial inflorescence, 8–13 cm long, 2.5–3 mm diameter, hairy as the staminate rachillae; floral stalks scarcely developed, solitary, each subtended by small bracteoles; pistillate flower buds 8–10 mm long, ellipsoid; calyces 4–4.5 mm long, cupular, briefly 6-lobed distally at anthesis (by early splitting of 3-lobed calyx), glabrous or scarcely hairy; corollas

6–8 mm long, split for about two thirds their length into 3 petals, glabrous; staminal rings scarcely developed, with vestigial filaments; pistils 3–3.5 mm long including a 1 mm long style, glabrous. Fruits not known at maturity, immature fruits globose, epicarp warty. Figure 3A.

**Distribution and Habitat**—The species is endemic to central Vietnam (Ba Na-Nui Chua Nature Reserve near Da Nang City; Fig. 4) in primary, evergreen, broad-leaved, wet forest on steep slopes at 500 m elevation.

**Local Names and Uses**—A local name is la non. No uses recorded.

**Additional Specimens Examined**—VIETNAM. Da Nang City: Hoa Vang District, Ba Na-Nui Chua Nature Reserve, road to summit, 16°00'N, 108°01'E, ca. 500 m, 20 Apr 2007, Henderson et al. 3309 (HN, NY); 4 Jun 2009, Henderson et al. 3597 (HN, NY).

2. *Lanonia calciphila* (Becc.) A. J. Hend. & C. D. Bacon, comb. nov., *Licuala calciphila* Becc., Webbia 3: 216. 1910.—TYPE: VIETNAM. “Tonkin, rive gauche de la rivière Noire a 3 km au-dessus de Phuong-Lam” [Hoa Binh: left bank of Song Da, 3 km below Phuong-Lam], 2 May 1888, B. Balansa 4361 (holotype: Pl!).

*Licuala fatua* Becc., Webbia 3: 218. 1910.—TYPE: VIETNAM. “Tonkin occidentale,” no date, Père Bon 3130 (holotype: P; isotype: FI!).

*Licuala tonkinensis* Becc., Webbia 3: 214. 1910.—TYPE: VIETNAM. “Tonkin occidentale, Vo-xa, Mt. Chua Hac” [Hoa Binh: Vo-xa, Chua Hac], 5 May 1885, Père Bon 2901 (holotype: P).

*Licuala tomentosa* Burret, Notizbl. Bot. Berlin-Dahlem 15: 98. 1940.—TYPE: VIETNAM. “Muong Thon, route du Hanoi à Hoa Binh” [Hoa Binh: Muong Thon, road from Hanoi to Hoa Binh], 19 Nov 1935, A. Pételet 5395 (holotype: P; isotypes: A! HNU! NY!).

Stems clustered, to 2 m tall, 1.5–2 cm diameter, erect or sometimes creeping. Leaves 10–17; leaf sheaths 10–15 cm long, extended above the petioles into ca. 15 cm long auricles; petioles 60–84 cm long, the proximal ca. half or less with widely spaced, recurved, brown spines to 0.6 cm long; blades to 58 cm wide, split into 5–7 segments, without minute reddish-brown scales abaxially, with straight sides; costas 6.0–10.0 cm long; middle segment split for half or

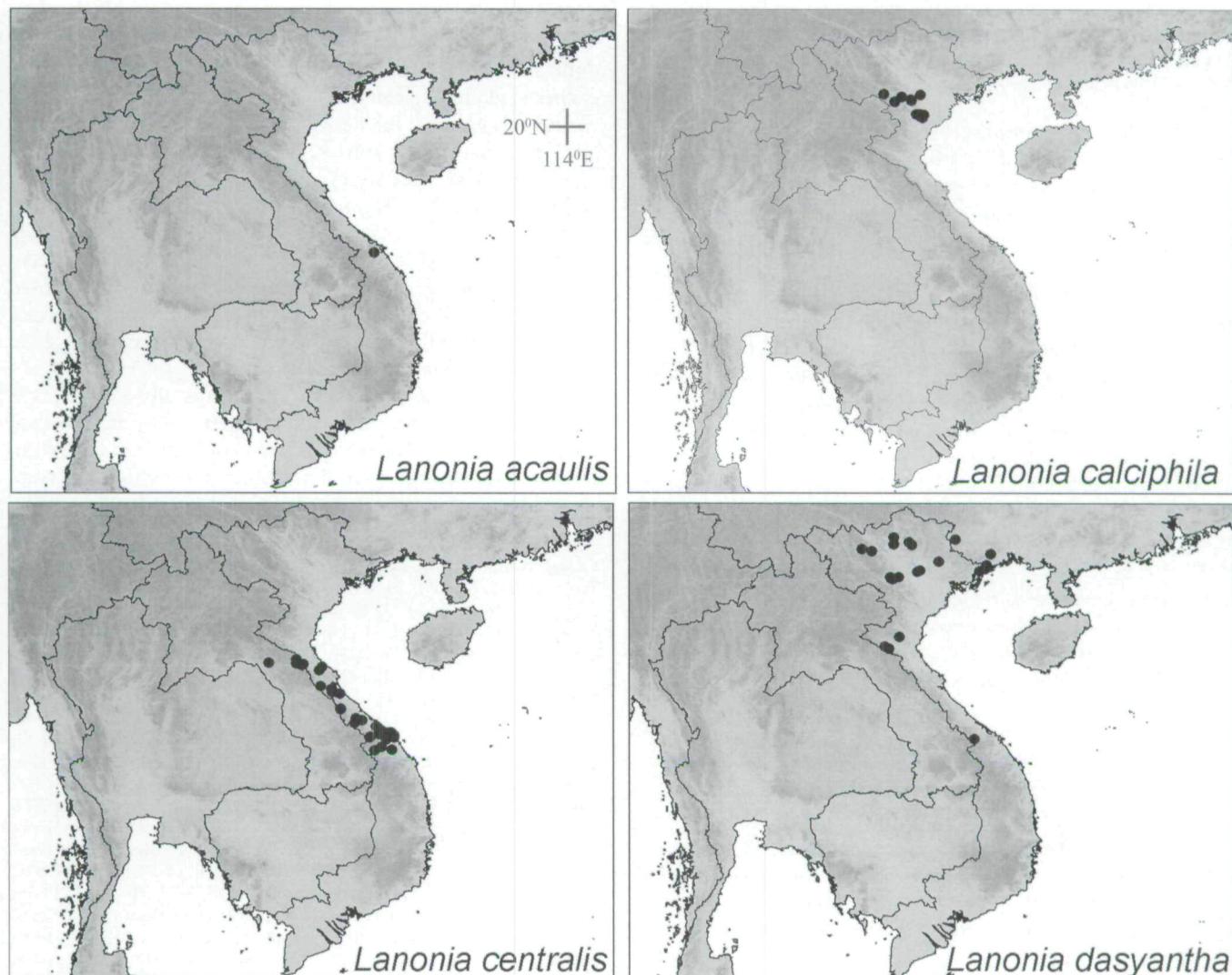


FIG. 4. Distribution maps of *Lanonia* species. Scale 1:33,000,000.

more its length (to apex of costa) into 2 lobes, these wider than the other segments, 17–28 cm long, 7–11 cm wide at the apices; indentations leading to adaxial folds 0.4 cm deep, those leading to abaxial folds 0.3 cm deep, indentations deeper on lateral segments. Inflorescences to 90 cm long, erect among the leaves; prophylls to 11 cm long; peduncles to 52 cm long; rachis to 45 cm long with 1–5 partial inflorescences (2–5 on staminate plants, 1 on pistillate plants), these branched to 1 order, subtended by narrow, tubular, scarcely brown tomentose rachis bracts, these splitting apically; staminate rachillae 2–4 on each partial inflorescence, 6–11 cm long, 1–1.5 mm diameter, moderately covered with woolly, brown hairs; floral stalks scarcely developed, solitary or borne in pairs, each subtended by small, ciliate bracteoles; staminate flower buds 2.8–4.5 mm long, bullet-shaped; calyces 2.5–3.5 mm long, cupular, gibbous, 3-lobed at the apices, ciliate, scurfy brown hairy at the bases; corollas 2.8–3.5 mm long, split for about half their length into 3 petals, glabrous; staminal rings ca. 0.5 mm long; filaments free for ca. 0.5 mm long, more or less equal in length; anthers 0.3 mm long; pistillate rachilla 1 on the single partial inflorescence, 13–21 cm long, ca. 2 mm diameter, hairy as the staminate rachillae; floral stalks scarcely developed, solitary, each subtended by ciliate bracteoles; pistillate flower buds

ellipsoid, ca. 2.5 mm long; calyces ca. 2.5 mm long, cupular, gibbous, 3-lobed at the apices with each lobe splitting again as the fruits develop and becoming 6-lobed, ciliate, brown scurfy hairy at the bases; corollas ca. 2 mm long, split for almost their entire length into 3 petals, glabrous; staminal rings scarcely developed, with vestigial filaments; pistils ca. 2 mm long including a 0.5 mm long style, glabrous. Fruits ca. 1 cm diameter, globose, bright red at maturity, sometimes 2 fruits developing from one flower, epicarp warty. Figure 3B.

**Distribution and Habitat**—The species is endemic to northern Vietnam (Ninh Binh, Hoa Binh, and Son La; Fig. 4) in primary, broad-leaved, evergreen forest on steep slopes, often in karst limestone areas, at 200–1,015 m elevation.

**Local Names and Uses**—A local name is la non. No uses recorded.

**Additional Specimens Examined**—VIETNAM. Ninh Binh: Nho Quan District, Cuc Phuong National Park, 20°15'N, 105°42'E, ca. 200 m, 3 May 2007, Henderson et al. 3326 (HN, NY), Henderson et al. 3328 (HN, NY), 20 May 2002, Averyanov et al. 1657 (HN), 8 Mar 1997, Boyce 1166 (HN, K), Boyce 1167 (HN, K), 10 Jul 1999, N. M. Cuong 248 (HN, MO), 20 Jun 1999, Alejandra 516 (HN), 2 May 1985, LX-VN 1769 (LE), 17 Oct 1996, PA 15 (HN), 11 Mar 2007, Nguyen 1372 (NY), 15 Mar 2000, P. K. Loc 10024 (HN, MO), 30 Nov 1998, Soejarto et al. 10519 (HN), 29 Jan 1975, Takhtajan et al. 2597 (K). Hoa Binh: Da Bac Distr., SW of Doan Ket Village, 20°54'N, 105°04'E, 900–1,000 m, 29 Mar 2001, HAL 358 (HN, MO); road from Hanoi

to Hoa Binh, Muong Thon, 1 Mar 1935, *Pételot* 2514 (P); Luong Son, Truong Son, 10 Jun 1983, N. L. *Tiep* 134 (HN); Mai Chau, Pa Co, 17 Dec 1999, L. X. *Phuong* 2317 (HN). Son La: Yen Chau Distr., Muong Lum Commune, Lum Village, 21°00'N, 104°29'E, 900–1,134 m, 2 Mar 2001, Harder et al. 7123 (HN, MO, NY).

**Notes**—The type locality of *Licuala fatua* was not given, and the type consists of a partial inflorescence with flowers. The partial inflorescence resembles exactly those of staminate plants of *L. calciphila*, and the drawings of the flowers given by Beccari (1933) appear to represent staminate flowers of *L. calciphila*.

The type of *Licuala tonkinensis* at P has not been seen. Beccari (1933) gave a photograph of the type, and a drawing of a pistillate flower. These appear to represent *L. calciphila*. In particular, the drawing of the pistillate flower exactly resembles those of *L. calciphila*, and the type locality of *L. tonkinensis* is within the range of *L. calciphila*. Therefore *L. tonkinensis* is treated as a synonym of *L. calciphila*.

The type specimens of *Licuala tomentosa* exactly match other specimens of *L. calciphila*. One isotype from A has two inflorescences on the same plant; one is spicate and pistillate, the other is branched and staminate.

**3. *Lononia centralis* (A. J. Hend., N. K. Ban & N. Q. Dung) A. J. Hend. & C. D. Bacon, comb. nov.**, *Licuala centralis* A. J. Hend., N. K. Ban & N. Q. Dung, Palms 52: 148. 2008.—**TYPE:** VIETNAM. Da Nang City, Hoa Vang District, Ba Na-Nui Chua Nature Reserve, road to summit, 16°00'N, 108°02'E, ca. 350 m, 19 Apr 2007, A. Henderson, N. Q. Dung, N. Canh & L. V. Bo 3299 (holotype: HN! isotype: NY!).

Stems clustered, sometimes solitary, to 5 m tall, 2–4 cm diameter, erect. Leaves 8–13; leaf sheaths 12–19 cm long, extended above the petioles into 7–14 cm long auricles; petioles 81–127 cm long, the proximal ca. quarter with widely spaced, recurved, black or brown spines to 0.5 cm long; blades 63–99 cm wide, split into 13–26 segments, with scattered minute reddish-brown scales abaxially, with straight sides; costas 2.0–5.7 cm long; middle segment split almost to the base of the blade (to apex of costa) into 2 lobes, these only slightly wider than the other segments, 40–45 cm long, 4.5–8 cm wide at the apices; indentations leading to adaxial folds to 0.5 cm deep, those leading to abaxial folds to 0.2 cm deep, indentations deeper on lateral segments. Inflorescences to 65 cm long, erect among the leaves; prophylls 15–22 cm long; peduncles 28–41 cm long; rachis 13–23 cm long, with 1–2 partial inflorescences (2 on staminate plants, 1–2 on pistillate plants), these branched to 2 orders, subtended by broad, flattened, densely brown tomentose rachis bracts, these splitting laterally; staminate rachillae 5–18 on each partial inflorescence, 6–17 cm long, ca. 1 mm diameter, moderately covered with brown, felty hairs; floral stalks scarcely developed, solitary or borne in groups of 2–3, each subtended by small bracteoles; staminate flower buds 2.7–3 mm long, bullet-shaped; calyces 1.5–2.5 mm long, shallowly lobed at the apices, glabrous or with scurfy brown hairs at their bases; corollas 2.5–3 mm long, glabrous, split to their bases into 3 petals; staminal rings 0.2 mm long; filaments free for ca. 0.5 mm, approximately equal in length; anthers ca. 0.5 mm long; pistillate rachillae 5–19 on each partial inflorescence, 10.5–19.5 cm long, to 2 mm diameter, hairy as the staminate rachillae; floral stalks scarcely developed, solitary, each subtended by small bracteoles; pistillate flower buds 2–3.5 mm long, oblong; calyces 1.5–2 mm long, cupular, 3-lobed at the apices with each lobe splitting

again as the fruits develop and becoming 6-lobed, glabrous or with scurfy brown hairs at the base; corollas 1.5–2.7 mm long, split almost to the base into 3 petals, these reflexed at and after anthesis, glabrous; staminal rings ca. 0.2 mm long at base of pistil, with vestigial filaments; pistils ca. 1 mm long including a 0.3 mm long style, glabrous. Fruits 0.6–0.8 cm diameter, globose, whitish at maturity, epicarp smooth. Figure 3C–E.

**Distribution and Habitat**—The species is known from Central Vietnam (Ha Tinh, Quang Binh, Quang Nam, Quang Tri, Thua Thien-Hue, and near Da Nang City) and adjacent Laos (Bolikhamsay; Fig. 4) in broad-leaved, evergreen, closed forest on steep slopes on shale, sandstone, or limestone rocks, and persisting in secondary forest, often occurring in great abundance, at 20–1,150 m elevation.

**Local Names and Uses**—This species is also known as la non (Vietnam). The young, unexpanded leaves are collected locally and sold in markets, and are widely used in the manufacture of the typical, conical hats worn throughout Vietnam.

**Additional Specimens Examined**—VIETNAM. Da Nang City: Hoa Vang District, Ba Na-Nui Chua Nature Reserve (“Mount Bana”), 15 Jun 1927, Clemens et al. 3356 (A, NY, P). Ha Tinh: Vu Quang National Park, road from Park Headquarters to Border Army Post, 18°20'N, 105°26'E, ca. 100 m, 17 Jul 2007, Henderson & N. K. Ban 3428 (HN, NY), 18°19'N, 105°22'E, 18 Jul 2007, Henderson & N. K. Ban 3434 (HN, NY); Huong Son Distr., Son Kim Commune, Rao Bun, 18°23'N, 105°15'E, 300–400 m, 4 May 2004, HAL 5112 (HN); Huong Son Distr., Rao An-Ngam, 18°21'N, 105°13'E, 900–1,150 m, 15 May 1998, VA 540 (HN, MO); Huong Son Distr., Nga Doi, 18°29'N, 105°13'E, 19 May 1998, VA 753 (HN, MO); Huong Son Distr., Area no. 72, 29 Apr 1998, N. T. Hiep & L. Xiem 382 (K); 2.6 km from Cat Bin to Khe Gat, 21 Jan 1990, Newman 226 (AAU, K); Can Xuyen District, Ke Go Nature Reserve, 18.156N, 105.915E, ca. 100 m, 25 Feb 2009, Henderson et al. 3480 (HN, NY). Quang Binh: Minh Hoa District, 72 km NNW of Dong Hoi, Yen Son village, 17°40'N, 105°57'E, 450–500 m, 17 Apr 1997, VH 4766 (HN, K, MO); Rung Dong San, Dong Hoi, 10 Feb 1979, L. L. Duc 15A (HN); Phong Nha Ke-Bang National Park, road near park entrance, 17°34'N, 106°18'E, ca. 20 m, 5 Apr 2007, Henderson et al. 3222 (HN, NY); Henderson et al. 3227 (HN, NY); Phong Nha-Ke Bang National Park, west branch of Ho Chi Minh trail, 17°28'N, 106°19'E, ca. 600 m, 6 Apr 2007, Henderson et al. 3229 (HN, NY); Henderson et al. 3230 (HN, NY), 7 Aug 2001, L. X. Phuong 4265 (HN). Quang Nam: Nam Giang District, Thanh My, no date, Cuong 10 (HN); Nam Giang District, Tah Bing commune, Song Tanh Nature Reserve, road 14 D to Laos, 15.660N, 107.665E, 200 m, 11 Mar 2009, Henderson et al. 3564 (HN, NY); Que Son District, Que Phong, 17 Jul 1976, LXVN 3099 (HN). Quang Tri: Da Krong District, Da Krong Nature Reserve, near Ba Long commune, 16.651N, 107.037E, ca. 500 m, 28 Feb 2009, Henderson et al. 3491 (HN, NY); Huong Hua District, Bac Huong Hu Nature Reserve, 16.938N, 106.585E, ca. 1,000 m, 3 Mar 2009, Henderson et al. 3512 (HN, NY); Massif de Dong Che, 22 May 1924, Poilane 11323 (P). Thua Thien-Hue: Bach Ma National Park, ca. 8 km from the summit, 16°13'N, 107°51'E, ca. 530 m, 13 Apr 2007, Henderson et al. 3274 (HN, NY), 11 Mar 1997, Boyce 1176 (K), 28 Apr 2003, HLF 1399 (HN), 22 Apr 2003, HLF 1286 (HN); same locality, Suoi Trai hang, 5 Feb 1990, Newman 187 (K); 8 Feb 1990, Newman 196 (K); A Luoi, 7 Sep 1980, N. K. Khoi 243 (HN); Phong Dien District, Phong Dien Nature Reserve, 16.557N, 107.232E, ca. 300 m, 5 Mar 2009, Henderson et al. 3524 (HN, NY); A Luoi District, Sao La Nature Reserve, 16.077N, 107.488E, 7 Mar 2009, Henderson et al. 3532 (HN, NY); “Col. de Nuages, près Tourane”, 17 Sep 1923, Poilane 8022 (VNM, P).

LAOS. Bolikhamsay: Pakkading District, Phou That Thon, Ban Naphong, 18°23'N, 104°22'E, 600 m, 7 Jan 1999, Evans 10 (K).

**4. *Lononia dasyantha* (Burret) A. J. Hend. & C. D. Bacon, comb. nov.**, *Licuala dasyantha* Burret, Notizbl. Bot. Gart. Berlin-Dahlem 15: 334. 1941.—**TYPE:** CHINA. Guangxi: Lungtschou, 10 Jul 1939, S. Ko 55448 (holotype: B, destroyed; isotype: SYS!).

Stems solitary or clustered, to 1.5 m tall, to 6 cm diameter, sometimes short and subterranean. Leaves 15; leaf sheaths 12–20 cm long, extended above the petioles into 6–15 cm long auricles; petioles 15–200 cm long, without spines or the proximal ca. half with widely spaced, recurved, brown spines to

1 cm long; blades 26–107 cm wide, split into 5–13 segments, mottled light and dark green, with minute reddish-brown scales abaxially, with straight or slightly curved sides; costas 5.5–17.0 cm long; middle segment deeply split (to apex of costa) into 2 lobes, these wider than the other segments, 16–58 cm long, 10–30 cm wide at the apices, rarely middle segment not split; indentations leading to adaxial folds 0.5–1 cm deep, those leading to adaxial folds 0.2–0.3 cm deep, indentations deeper on lateral segments. Inflorescences 60–70 cm long, becoming recurved below the leaves at or after anthesis; prophylls 6.5–8 cm long; peduncles 18–35 cm long; rachis 0–12 cm long, with 1, rarely 2 partial inflorescences, these branched to 1 order, subtended by broad, flattened, densely brown tomentose, plicate rachis bracts, these splitting laterally and irregularly and deeply tattering; staminate rachillae 2–7 on each partial inflorescence, 9–14 cm long, to 2 mm diameter, densely covered with brown or whitish, branched hairs; floral stalks scarcely developed, solitary or borne in pairs, each subtended by ciliate bracteoles; staminate flower buds 2–2.7 mm long, bullet-shaped; calyces 1.5–2 mm long, 3-lobed at the apices, moderately covered with brown, felty hairs; corollas 2–2.3 mm long, split for ca. half their length into 3 valvate petals, glabrous; staminal rings scarcely developed; filaments free for ca. 2 mm long, alternately long and short; anthers ca. 0.3 mm long; pistillate rachillae 1–4 on each partial inflorescence, 8–24 cm long, to 4 mm diameter, hairy as the staminate rachillae; floral stalks scarcely developed, solitary, each subtended by small, ciliate bracteoles; pistillate flower buds 6–6.2 mm long, ellipsoid; calyces 3.5–4 mm long, briefly 6-lobed at the apices at anthesis, densely covered with felty, brown hairs; corollas 4–5.5 mm long, striate, split for ca. two thirds their length into 3 petals; staminal rings ca. 1.5 mm high, with vestigial filaments; pistils ca. 4 mm long including a 1 mm long style, glabrous. Fruits 0.7–0.8 cm diameter, irregularly globose, red at maturity, epicarp warty. Figures 3F, G.

**Distribution and Habitat**—This species is known from China (Guangxi) and northern and central Vietnam (Bac Kan, Ha Giang, Lang Son, Lao Cai, Nghe An, Phu Tho, Quang Ninh, Thua Thien-Hue, Tuyen Quang, and Vinh Phuc; Fig. 4) in primary, closed, broad-leaved, evergreen forest on steep mountain slopes on granite or quartzite rocks, less often on limestone, at 100–1,000 m elevation.

**Local Names and Uses**—Local names are cay lua khua, la non, lua khua (Vietnam). No uses recorded.

**Additional Specimens Examined**—CHINA. Guangxi: Longzhou county, Longding, Li Huang 40234 (IBK); Fangchen County, Shi-Wan-Da-Shan, 11 Sep 1987, Shi Guo-Liang 15411 (K). Cultivated in South China Botanical Garden (introduced from Fangchen, Guangxi Province), 25 Apr 1992, Wei Chao Fen 123256 (K); Wei Chao Fen 123257 (K); Longzhou, Da Qing Shan, 28 May 1991, Y. Z. Wei 201491 (KUN).

VIETNAM. Bac Kan: Bang Lung, Cho Don, 30 Apr 2000, Hach 5 (HN). Ha Giang: Quang Binh district, Ngoi Sao State Forestry Company, 17 Oct 2009, N. Q. Dung 2025 (FIPI). Lang Son: Huu Lung Distr., Huu Lien Distr., Huu Lien, 21°40'N, 106°20'E, 110 m, 2 Apr 1998, Harder *et al.* 4141 (HN, K, MO, NY). Lao Cai: Van Ban Distr., Khanh Yen Ha Commune, S of Na Nheo Village, 21°59'N, 104°15'E, 1,000–1,100 m, 24 Mar 2002, HAL 2706 (HN); 900–1,000 m, 25 Mar 2002, HAL 2736 (HN); Van Ban Distr., Nam Xe Commune, Khau Co Pass, 22°02'N, 103°57'E, 1,150 m, 27 Feb 2001, Harder *et al.* 7005 (HN). Nghe An: Pu Huong Nature Reserve, 19°18'N, 105°07'E, ca. 250 m, 7 May 2007, Henderson *et al.* 3342 (HN, NY); 10 May 2007, Henderson *et al.* 3359 (HN, NY); Pu Mat National Park, road from Con Cuong to That Kem, 18°57'N, 104°48'E, ca. 100 m, 12 May 2007, Henderson *et al.* 3363 (HN, NY); Pu Mat, Phu Nhun, Khe Choang, 20 Jul 1998, N. N. Thin 299 (HN). Phu Tho: Xuan Son, Dong Son, 1 Jul 2003, L. X. Phuong 6303 (HN); 26 May 2005, L. X. Phuong 9933 (HN); Xuan Son, Thanh Son, 13 May 2004, Phuong 7895 (HN). Quang Ninh: “Tonkin, Taai Wong Mo Shan and vicinity, Shui Mei village, NE of Chuk-phai, Ha-coi”, 23 Jun–31 Aug 1939,

Tsang 29436 (C, E, K); “Tonkin, Taai Wong Mo Shan and vicinity, Shui Mei village, NE of Chuk-phai, Ha-coi”, Tsang 27250 (A, K); “Tonkin, Sai Wong Mo Shan (Sai Vong Mo Leng), Lung Wan Village, Dam-ha”, 18 May–5 Jul 1940, Tsang 29985 (K). Thua Thien-Hue: A Luoi District, Sao La Nature Reserve, 16.115N, 107.427E, 666 m, 9 Mar 2009, Henderson *et al.* 3551 (HN, NY). Tuyen Quang: Na Hang Distr., Thanh Tuong Commune, near Ban Bung Village, 22°16'N, 105°25'E, 700–750 m, 20 Mar 2001, HAL 127 (HN, MO, NY). Vinh Phuc: Me Linh, 24 Oct 2001, L. X. Phuong 4615 (HN).

**5. *Lanonia gracilis* (Blume) A. J. Hend. & C. D. Bacon, comb. nov., *Licuala gracilis* Blume in J. J. Roemer & J. A. Schultes, Syst. Veg. 7: 1303. 1830.—LECTOTYPE (here designated): Rumphia 2, t. 92. 1836.**

*Licuala flabellum* Mart., Hist. Nat. Palm. 3: 237. 1838.—TYPE: “Celebes,” no date, C. Reinwardt s. n. (holotype: M!).

Stems clustered, to 1 m tall, to 2 cm diameter, erect. Leaves ca. 40; leaf sheaths to 30 cm long, extended above the petioles into 2.5–4.5 cm long auricles; petioles to 100 cm long, the proximal half or less with widely spaced, brown spines 0.3–0.5 cm long; blades to 75 cm wide, split into 8–14 segments, with scattered, minute, reddish-brown scales abaxially, with straight sides; costas 6.5–7.5 cm long; middle segment split almost to the base of the blade (to apex of costa) into 2 lobes, these only slightly wider than the other segments, 30–41 cm long, 8.5–10 cm wide at the apices; indentations leading to adaxial folds to 0.6 cm deep, those leading to abaxial folds to 0.2 cm deep, indentations deeper on lateral segments. Inflorescences to 30 cm long, erect among the leaves; prophylls 9–10 cm long; peduncles 9–15 cm long; rachis short or absent, with 1–2 partial inflorescence, these branched to 2 orders, subtended by broad, flattened, brown tomentose rachis bracts, these splitting laterally; staminate rachillae 4–11 on each partial inflorescence, 6.5–10.5 cm long, 1.2–1.9 mm diameter, moderately covered with brown hairs; floral stalks scarcely developed, solitary or borne in groups of 2–3, each subtended by small bracteoles; staminate flower buds 3.5–4 mm long, bullet-shaped; calyces 2 mm long, 3-lobed at the apices, glabrous; corollas 3.5 mm long, split for almost all their length into 3 valvate petals, glabrous; staminal rings 0.5 mm long; filaments free for ca. 1 mm, alternately long and short; anthers 0.5 mm long; pistillate rachillae 8–9 on each partial inflorescence, 7–13.5 cm long, 1.5–2 mm diameter, hairy as the staminate rachillae; floral stalks scarcely developed, solitary, each subtended by bracteoles; pistillate flower buds 4 mm long, bullet-shaped; calyces 2.5 mm long, briefly 3-lobed at the apices, glabrous; corollas 3 mm long, split for almost all their length into 3 petals; staminal rings ca. 0.7 mm high, with vestigial filaments; pistils ca. 2.5 mm long, including a 0.5 mm long style, glabrous. Fruits 0.7–0.9 cm diameter, globose, ripening from pink to red to black at maturity, epicarp smooth.

**Distribution and Habitat**—This species is known from Indonesia, only from the summit of Mount Payung in western Java (Fig. 5) at 150 m elevation.

**Local Names and Uses**—None recorded.

**Additional Specimens Examined**—INDONESIA. Java: southwest Java, Ujungkulon Reserve, W slope of Mount Payung, 150 m, 10 Jan 1964, Kostermans 21846 (K); G. Kendeng, slopes of G. Payung, Ujung Kulon, 150 m, 15 Apr 1971, Dransfield 1433 (K). Cultivated in Kebun Raya, Bogor, Baker 1353 (K).

**Notes**—*Licuala gracilis* was included as a synonym of *L. pumila* by Beccari (1933) and this was followed by Backer and Bakhuizen van den Brink (1968). It was not until Dransfield recollected it in Ujung Kulon in 1971 that the distinctness of Blume's *L. gracilis* was recognized, and it is currently accepted as a species distinct from *L. pumila* (Govaerts and Dransfield

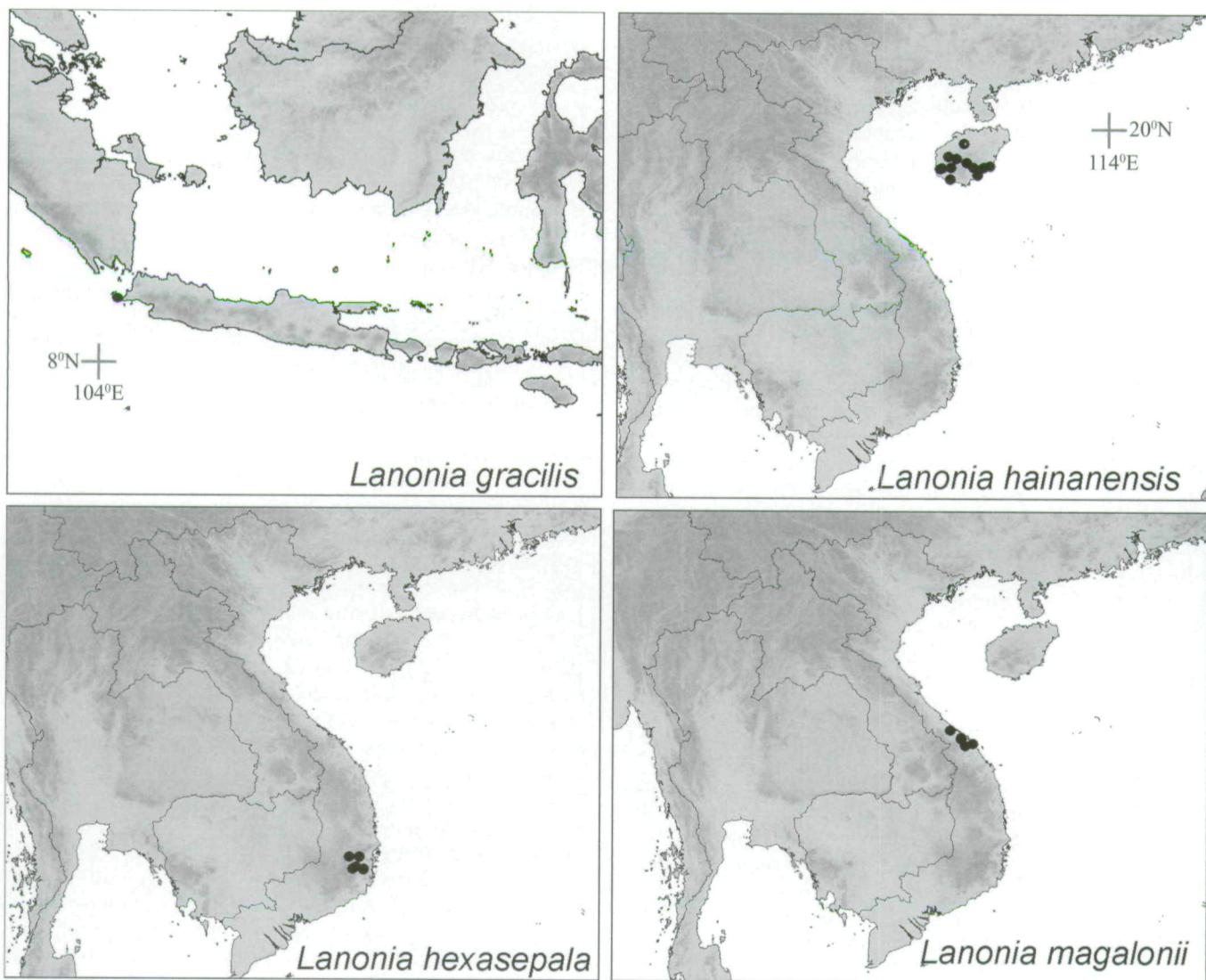


FIG. 5. Distribution maps of *Lanonia* species. Scale 1:33,000,000.

2005). Because its leaf morphology, with split central, briefly costate segment with an abaxial pulvinus-like structure, and dioecy, we here transfer it to *Lanonia*.

*Licuala flabellum* is here included tentatively as a synonym of *Lanonia gracilis*. The type at M was collected by Reinwardt and is said to come from "Celebes." John Dransfield (pers. comm.) considers that this unlikely, based on the following argument. Although Reinwardt did visit Celebes, there have been no further collections, despite rather intensive palm collecting there. In fact, *Licuala* is a rare genus in Celebes. The localities on Reinwardt's collections are notoriously vague and sometimes mistaken. The type of *L. flabellum* matches exactly that of *L. gracilis*, and it seems likely that the label locality is a mistake and in fact it was collected in Java.

6. *Lanonia hainanensis* (A. J. Hend., Guo & Barfod) A. J. Hend. & C. D. Bacon, comb. nov., *Licuala hainanensis* A. J. Hend., Guo & Barfod, Syst. Bot. 32: 718.—TYPE: CHINA. Hainan: Diaoluoshan, 18°45'N, 109°52'E, 270 m, 21 Mar 2006, Guo Lixiu, Zhou Lianxuan & A. Henderson 135 (holotype: IBSC!; isotype: NY!).

Stems clustered, to 4 m tall, 2–3 cm diameter, erect. Leaves 12–15; leaf sheaths ca. 40 cm long, extended above the peti-

oles into short auricles; petioles 50–160 cm long, the proximal ca. half with regularly spaced, recurved, brown spines to 0.5 cm long; blades to 120 cm wide, split into 12–17 segments, without or with a few, minute, reddish-brown scales abaxially, with straight sides; costas 3.0–5.7 cm long; middle segment split almost to the base of the blade (to costa apex) into 2 lobes, these only slightly wider than the others, 36–41 cm long, 7–8 cm wide at the apices; indentations leading to adaxial fold 0.7–1.3 cm deep, those leading to adaxial fold 0.2–0.3 cm deep, indentations deeper on lateral segments. Inflorescences to 100 cm long, erect among the leaves; prophylls ca. 26 cm long; peduncles ca. 50 cm long; peduncular bracts not seen; rachis ca. 50 cm long, with 2 partial inflorescences, these branched to 2 orders, subtended by broad, flattened, densely brown tomentose rachis bracts, these splitting laterally; staminate rachillae 9–16 on each partial inflorescence, 8–17 cm long, ca. 1 mm diameter, moderately covered with short, brown hairs; floral stalks scarcely developed, solitary or borne in groups of 2–4, each subtended by small bracteoles; staminate flower buds 3–3.5 mm long, bullet-shaped; calyxes ca. 2 mm long, shallowly lobed at the apices, glabrous; corollas ca. 4 mm long, glabrous, split to the base into 3 petals; staminal rings 0.8–1 mm long; filaments free for 0.6–0.8 mm,

approximately equal in length; anthers 0.5–0.6 mm long; pistillate rachillae 9–14 on each partial inflorescence, 8.5–12 cm long, ca. 2 mm diameter, hairy as the staminate rachillae; floral stalks scarcely developed, solitary, each subtended by small bracteoles; pistillate flower buds 3–3.5 mm long, oblong; calyces ca. 2 mm long, shallowly lobed at the apices, glabrous; corollas ca. 4 mm long, split to the base into 3, valvate petals, these reflexed at and after anthesis, glabrous; staminal rings with vestigial filaments; pistils 1.3–1.5 mm long including a 0.3 mm long style, glabrous. Fruits 0.7–0.9 cm diameter, globose, orange or red at maturity, epicarp smooth. Figure 3H.

**Distribution and Habitat**—This species is known from China (Hainan; Fig. 5) in lowland moist forest at 270–1,100 m elevation.

**Local Names and Uses**—Local names are ci zhou lu, chun shue, dong fang zhou lu. The leaves are used for making provisional rain coats in the forest.

**Additional Specimens Examined**—CHINA. Hainan: Qiongzhong County, 12 Oct 1956, Chen Shao Qing 10573 (IBSC); Mt. Jiangfenglin, Tian Chi, 12 May 1979, Chen 18881 (HITBC); Wanning County, Xinglong, 19 May 1979, Chen 18888 (HITBC); Ledong County, Mt. Jianfengling, 30 May 1959, Chen Zhe Lian 30277 (IBSC); 2–31 Jan 1935, Lau 5236 (A, IBSC); 14 May 1962, Zeng 13105 (HITBC); same locality, 18°44'N, 108°52'E, 850 m, 4 Dec 2000, Gilbert et al. 368 (MO); Wuzhishan City, 1,700 ft., 14 Aug 1932, Chun & Tso 43425 (IBSC, NY, US); 8 Nov 1959, Sino-German Team 1898 (IBSC); Baoting County, Dengliang 463 (IBK); Lingshui County, 16 Oct 1956, Dengliang 2608 (IBSC); Tai Pin, foot of Loi Mother mountain, Jun-Jul 1935, Gressitt 1127 (E, MO); Sanya City, 1,800 ft., Mar-Jul 1933, How 70315 (A, IBSC, NY); 15 Aug 1933, Liang 62646 (NY); Sanya City, Yeung Lam Shan, near Yeung Lam village, Yai-hsien District, 4–24 May 1935, Lau 6261 (A, IBSC); Baisha County, 23 Mar 1936, Lau 25832 (A, IBSC); Ledong County, 1 Jun 1936, Lau 26987 (A, IBSC); Danzhou, Nada, 3 Nov 1922, McClure 21539 (A, E); Hung Mo Tung, SW of Fan Ta, 25 Aug 1929, McClure & Fung 771 (NY, US); Nodoa, Lin Fa Leng, 3 Nov 1921, McClure 8060 (A, US); without locality, 4 Aug 1933, Wang 33534 (A, NY), 10 Jan 1934, Wang 36337 (NY). Cultivated plant, South China Botanical Garden, 9 Feb 2010, Jeanson 83 (NY).

**7. *Lanonia hexasepala* (Gagnep.) A. J. Hend. & C. D. Bacon, comb. nov., *Licuala hexasepala* Gagnep., Notul. Syst. (Paris) 6: 155. 1937.—LECTOTYPE (here designated): VIETNAM. “Annam, Mère et l’Enfant près de Nhatrang” [Khanh Hoa: Ninh Hoa Distr., Chu Mu], 1200 m, 4 Nov 1929, E. Poilane 5059 (holotype: P! isotype: F!).**

Stems solitary or clustered, 1.5–2 m tall, 2 cm diameter, erect, densely covered with flat, black scales. Leaves 6; leaf sheaths 7–15 cm long, densely covered with flat, black scales, extended above the petioles into 9–17 cm long auricles; petioles 16–47 cm long, scaly as the sheaths, the proximal ca. half with closely to widely spaced, recurved, black spines 0.2–0.6 cm long, these sometimes bifid; blades 20 cm wide, split into 10–14 segments, with numerous, minute reddish-brown scales abaxially, with straight sides; costas 0.5–1.5 cm long; middle segment split almost to the base of the blade (to apex of costa) into 2 lobes, these not wider than the other segments, 13–23 cm long, 2.5–3 cm wide at the apices; indentations leading to adaxial folds 1–1.5 cm deep, those leading to abaxial folds 0.4–0.6 cm deep, indentations deeper on lateral segments. Inflorescences 60 cm long, erect among the leaves; prophylls 16 cm long; peduncles not seen; rachis absent, with 1 partial inflorescence, this branched to 1 order in pistillate plants, 2 orders in staminate plants, subtended by narrow, tubular, scarcely brown tomentose rachis bracts, these splitting apically; staminate rachillae 21 on each partial inflorescence, 12–18.5 cm long, ca. 0.5 mm diameter, minutely hairy; floral stalks scarcely developed, borne in groups of 2–3, each subtended by small, ciliate bracteoles; staminate

flower buds 1–1.5 mm long, globose; calyces 0.8–1.2 mm long, cupular, gibbous, 3-lobed at the apices, sparsely hairy; corollas 0.6–1 mm long, split completely to the base into 3, valvate petals, glabrous; staminal rings short; filaments free for 0.1–0.2 mm; anthers 0.2 mm long; pistillate rachillae 10–12 on each partial inflorescence, 4–10 cm long, 0.5–0.7 mm diameter, minutely hairy; floral stalks scarcely developed, solitary, each subtended by small bracteoles; pistillate flower buds 1.5 mm long, oblong; calyces 1.5 mm long, gibbous, 3-lobed at the apices with each lobe splitting again as the fruits develop and becoming 6-lobed, minutely and sparsely hairy; corollas ca. 1 mm long, split to the base into 3 petals, these spreading horizontally as the fruits develop, glabrous; staminal rings absent, with vestigial filaments; pistils ca. 0.3 mm long including a 0.1 mm long style, glabrous. Fruits 0.6–0.7 cm diameter, globose, color not known, epicarp warty. Figure 3I.

**Distribution and Habitat**—This species is endemic to southern Vietnam (Dak Lak, Khanh Hoa, Lam Dong; Fig. 5) in primary, wet, mixed forest or cloud forest on steep, rocky slopes at 1,250–1,700 m elevation.

**Local Names and Uses**—A local name is sai. No uses recorded.

**Additional Specimens Examined**—VIETNAM. Dak Lac: Krong Bong Distr., Cu Pui Commune, from Dak Tour village to main peak of Chu Yang Sinh, 12°30'N, 108°30'E, 1,600–1,700 m, 9 May 2000, VH 6180 (HN, MO). Khanh Hoa: Khanh Vinh District, road from Nha Trang to Da Lat, 12.183N, 108.716E, 1601 m, 8 July 2010, Henderson & B. V. Thanh 3683 (HN, NY); Henderson & B. V. Thanh 3684 (HN, NY); “Province de Nha Trang, Massif du Hon Ba”, no date, Chevalier 38738 (P); “Annam, nord de Ninh Hoa près de Nha Trang, versant sud-est du massif de la Mere et L’Enfant”, 18 May 1923, Poilane 6533 (P); “Annam, nord de Ninh Hoa, près de Nha Trang”, 18 May 1923, Poilane 6542 (F, P). Lam Dong: Lac Duong Distr., Da Chay Commune, 40 km from Da Lat city, Hon Giao ridge, 12°11'N, 108°43'E, 1,600–2,000 m, 21 Apr 1997, VH 4120 (AAU, HN, K, MO); Lac Duong Distr., Bi Dup-Nui Ba National Park, new road DT 723 from Da Lat to Nha Trang, 12°10'N, 108°41'E, 1,500 m, 24 May 2007, Henderson et al. 3416 (HN); Henderson et al. 3417 (HN).

**Notes**—In the original description of this species (Gagnepain 1937), all the specimens cited were from Khanh Hoa. Gagnepain and Conrard (1937), however, included a specimen (*Magalon* 6) from near Da Nang, and used it to describe the flowers of *L. hexasepala*. This specimen was also cited by Magalon (1930) and called by him “*Licuala ternata* ou *L. triphylla* Griff.”. This Da Nang specimen is here included in *L. magalonii*. One specimen, (Chevalier 38738) appears to be a mixed collection, with only the sheet with leaves and infructescences belonging here.

**8. *Lanonia magalonii* (A. J. Hend., N. K. Ban & N. Q. Dung) A. J. Hend. & C. D. Bacon, comb. nov., *Licuala magalonii* A. J. Hend., N. K. Ban & N. Q. Dung, Palms 52: 152. 2008.—TYPE: VIETNAM. Da Nang City: Hoa Vang District, Ba Na-Nui Chua Nature Reserve, 20 Apr 2007, A. Henderson, N. Q. Dung, N. Canh & L. V. Bo 3304 (holotype: HN! isotype: NY!).**

Stems solitary or clustered, to 1.5 m tall, 2–2.5 cm diameter, sometimes short and subterranean. Leaves 6–12; leaf sheaths 14–15 cm long, extended above the petioles into ca. 10 cm long auricles; petioles 16–56 cm long, the proximal ca. half with widely spaced, recurved, brown spines to 0.2 cm long; blades 44–48 cm wide, split into 3–4 segments, with minute, reddish-brown scales abaxially, with straight sides; costas 6.3–16.0(–24.7) cm long; middle segment deeply split almost to the base of the blade (to apex of costa) into 2 lobes, these much wider than the other segments, 33–41 cm long, 13–20 cm wide at the apices (rarely the central segment not split and

then costa continuous to apex of segment); indentations leading to adaxial folds ca. 1 cm deep, those leading to abaxial folds ca. 0.2 cm deep, indentations deeper on lateral segments. Inflorescences to 54 cm long, erect or curving among the leaves; prophylls 11.5–18 cm long; peduncles 26–45 cm long; rachis 0(–14) cm long, with 1(–2) partial inflorescences, these branched to 2 orders, subtended by narrow, tubular, scarcely brown tomentose rachis bracts; these splitting apically; staminate rachillae 4–13, 10–14 cm long, 1–1.5 mm diameter, moderately covered with brown, felty hairs; floral stalks scarcely developed, borne in groups of 2–4, each subtended by ciliate bracteoles; staminate flower buds 3–3.5 mm long, bullet-shaped; calyces 1.5–2.7 mm long, gibbous, 3-lobed at the apices, glabrous; corollas 2.5–3 mm long, split for ca. two thirds their length into 3 petals, glabrous; staminal rings 0.5 mm long; filaments free for ca. 0.5 mm, approximately equal in length; anthers 0.5 mm long; pistillate rachillae 2–7 on each partial inflorescence, 4.5–15 cm long, ca. 1.5 mm diameter; floral stalks scarcely developed, solitary, each subtended by ciliate bracteoles; pistillate flower buds 2.5–3.5 mm long, oblong; calyces 1.5–2 mm long, 3-lobed at the apices with each lobe splitting again as the fruits develop and becoming 6-lobed, glabrous; corollas 2–2.5 mm long, split for 1.5 mm into 3 petals, glabrous; staminal rings vestigial; pistils ca. 1.5 mm long including a 0.2 mm long style, glabrous. Fruits 0.7–0.9 cm diameter, irregularly globose, color at maturity not known, epicarp warty.

**Distribution and Habitat**—This species is endemic to central Vietnam (near Da Nang City and in Thua Thien-Hue; Fig. 5) in primary, broad-leaved, evergreen, closed, montane forest on steep slopes on granite rocks at 1,000–1,500 m elevation.

**Local Names and Uses**—Local names are cay la ma ca, la non, la non nham. No uses recorded.

**Additional Specimens Examined**—VIETNAM. Da Nang City: Hoa Vang District, Ba Na-Nui Chua Nature Reserve, 20 Apr 2007, Henderson et al. 3305 (HN, NY), May-Jul 1927, Clemens & Clemens 4444 (NY, P), Jan-May 1927, Squires 203 (NY, US); “Mt. Bana, environs Tourane” [Da Nang City, Hoa Vang District, Ba Na-Nui Chua Nature Reserve], 24 Jan 1940, Magalon 6 (NY, P, VNM). Thua Thien-Hue: Bach Ma National Park, no date, T. P. Anh 107 (HN); 27 Oct 2004, Anon 4 (HN), 13 Apr 2007, Henderson et al. 3268 (HN, NY), 26 Apr 2003, HLF 1336 (HN), 4 May 2003, HLF 1623 (HN), 30 Jan 1990, Newman 177 (AAU, K), Newman 179 (AAU, K), 18 Apr 2003, HLF 951 (HN).

**Notes**—The first known specimen (*Magalon* 6) of this species was misidentified by Magalon (1930) as “*Licuala ternata* ou *L. triphylla* Griff.” *Licuala ternata* is now considered a synonym of *L. triphylla*, a monoecious species from Peninsular Thailand, Peninsular Malaysia, and Borneo. Gagnepain and Conrard (1937) mistakenly identified *Magalon* 6 as *Licuala hexasepala*, a species otherwise known only from the southern part of Vietnam. This specimen is also the only one examined in which the central segment is not split, and the costa is similar to other *Licuala* species and continues to the apex of the central segment. We have observed other individuals in the field with similar central segments, but possibly these are younger plants in which the leaves are not fully developed.

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APPENDIX 1. List of taxa sampled with taxonomic authorities, voucher information, and GenBank accession numbers for new sequences generated for this study.

*Lanonia hainanensis* (A. J. Hend., Guo & Barford) A. J. Hend. & C. D. Bacon—M. Jeanson 383 (NY); CISP4 JF292931, CISP5 JF292941, *matK* JF292980, MS JF292951, *ndhF* JF292961. *Lanonia hexasepala* (Gagnep.) A. J. Hend. & C. D. Bacon—A. J. Henderson et al. 3683, Vietnam (NY); CISP4 JF292932, CISP5 JF292942, *matK* JF292981, MS JF292952, RPB2 JF292968. *Lanonia* sp.1 (A. J. Hend. & C. D. Bacon ined.)—A. J. Henderson et al. 3672, Vietnam (NY); CISP4 JF292932, CISP5 JF292943, *matK* JF292982, MS JF292953, *ndhF* JF292962, *trnDT* JF292973. *Lanonia* sp.2 (A. J. Hend. & C. D. Bacon ined.)—A. J. Henderson et al. 3676, Vietnam (NY); CISP4 JF292934, CISP5 JF292944, *matK* JF292983, MS JF292954, *ndhF* JF292963, RPB2 JF292969, *trnDT* JF292974. *Lanonia* sp.3 (A. J. Hend. & C. D. Bacon ined.)—A. J. Henderson et al. 3688, Vietnam (NY); CISP4 JF292935, CISP5 JF292945, *matK* JF292984, MS JF292955, *ndhF* JF292964. *Lanonia* sp.4 (A. J. Hend. & C. D. Bacon ined.)—A. J. Henderson et al. 3695, Vietnam (NY); CISP4 JF292936, CISP5 JF292946, *matK* JF292985, MS JF292956, *ndhF* JF292965, RPB2 JF292970, *trnDT* JF292975. *Lanonia* sp.5 (A. J. Hend. & C. D. Bacon ined.)—A. J. Henderson et al. 3703, Vietnam (NY); CISP4 JF292937, CISP5 JF292947, MS JF292957, *ndhF* JF292966, RPB2 JF292971, *trnDT* JF292976. *Lanonia* sp.6 (A. J. Hend. & C. D. Bacon ined.)—A. J. Henderson et al. 3707, Vietnam (NY); CISP4 JF292938, CISP5 JF292948, *matK* JF292986, MS JF292958, *ndhF* JF292967, *trnDT* JF292977. *Lanonia* sp.7 (A. J. Hend. & C. D. Bacon ined.)—A. J. Henderson et al. 3726, Vietnam (NY); CISP4 JF292939, CISP5 JF292949, *matK* JF292987, MS JF292959, RPB2 JF292972, *trnDT* JF292978. *Lanonia* sp.8 (A. J. Hend. & C. D. Bacon ined.)—A. J. Henderson et al. 3727, Vietnam (NY); CISP4 JF292940, CISP5 JF292950 *matK* JF292988, MS JF292960, *trnDT* JF292979.

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