

# Towards a monophyletic *Licania*: a new generic classification of the polyphyletic Neotropical genus *Licania* (Chrysobalanaceae)

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**Summary.** *Licania*, currently the most species-rich genus of Chrysobalanaceae, is confined to the Neotropics, and is highly polyphyletic in molecular phylogenetic analyses. These studies show that the three subgenera of *Licania*, as well as sections within them, are not supported as monophyletic. Here we re-delimit the genus using a molecular phylogenetic analysis as a framework. We recognise the following eight genera: core *Licania*, *Moquilea*, *Leptobalanus*, *Hymenopus*, *Microdesmia*, *Parinariopsis*, *Geobalanus*; and *Cordillera* gen. nov. is described to accommodate *Licania platycalyx*. New combinations, as well as a description of each genus and a key to the species are provided, in addition to a key for all the Neotropical genera of the family, including those presented here. Chrysobalanaceae now comprise sixteen Neotropical genera and the redefined *Licania*, with c. 100 species, is then the second largest genus in the family after *Hirtella* (107 species).

**Key Words.** *Cordillera*, *Geobalanus*, *Hymenopus*, *Leptobalanus*, Malpighiales, *Microdesmia*, *Moquilea*, Neotropical flora, *Parinariopsis*.

## Introduction

*Licania* Aubl. (Aublet 1775), as currently delimited, with over 214 species endemic to the Neotropics (Prance & Sothers 2003a; Sothers *et al.* 2014), is the largest genus of Chrysobalanaceae. Its distribution spans the southern USA, Mexico, Central America, the Caribbean and tropical South America. Although at the alpha-taxonomic level the genus, and family as a whole is considered well known, recent molecular studies have highlighted the polyphyly of *Licania* (Bardon *et al.* 2016; Sothers 2010; Sothers *et al.* 2014). Prance & White (1988) divided *Licania* into five subgenera, *Afrolicania*, *Angelesia*, *Licania*, *Moquilea* and *Parinariopsis*. Recently the African and Malesian subgenera, *Afrolicania* and *Angelesia*, respectively, have been re-instated at generic rank (Prance & Sothers 2003a; Sothers & Prance 2014, respectively), rendering *Licania* entirely Neotropical. This paper addresses the polyphyly of the remaining three subgenera.

*Licania* and its subgenera have a complex taxonomic history. Ever since Aublet (1775) described *Licania* and *Moquilea*, among other Neotropical genera of Chrysobalanaceae such as *Acioa* and *Couepia*, in his *Histoire des Plantes de la Guyane*, taxonomists have disagreed over their circumscription. Aublet (1775)

distinguished *Licania* from *Moquilea* by the length of the stamens in relation to the corolla: exerted in *Moquilea* vs included in *Licania*. He placed *Couepia* near *Moquilea*, presumably based on the exerted stamens and their number, despite differences in the position of the ovary on the receptacle (basal in *Moquilea* and *Licania* vs at the mouth in *Couepia* and *Acioa*). After his death in 1778, Aublet's herbarium was dispersed and as a result, during the 19th century, confusion prevailed over the delimitation of *Licania* and *Moquilea*. Subsequent taxonomists either accepted *Licania* and *Moquilea* as separate genera (Martius & Zuccarini 1827; Zuccarini 1832; Meisner 1837a & b; Bentham 1840; Endlicher 1840, 1842; Hooker 1865, 1867; Fritsch 1888), or considered *Moquilea* as a synonym of *Licania* (Grisebach 1857; Baillon 1869; Eichler 1878; Fritsch 1889); or treated *Couepia* as a synonym of *Moquilea* (Martius & Zuccarini 1827; Walpers 1843; Mueller 1857). Others accepted all four genera cited above (Jussieu 1789; Brown 1818; Candolle 1825; Lindley 1836; Fritsch 1888). Grisebach (1857) was the first to merge *Moquilea* into *Licania*.

Bentham (1840) accepted *Moquilea*, *Licania* and *Couepia* as distinct genera (he did not see *Acioa* and therefore did not consider it). He delimited *Licania* as

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displaying the following characters: 4 – 5-dentate or shortly pentafid calyx, apetalous or with 4 – 5 petals, fewer than 15 fertile stamens, and ovary at the base of the receptacle; he divided the genus into five sections: *Batheogyne*, *Leptobalanus*, *Microdesmia*, *Eulicania*, and *Hymenopus*. Bentham defined *Moquilea* as having a pentafid calyx, with petals present, more than 30 fertile stamens, and ovary at the base of the receptacle, characters which overlapped with those of *Licania*. Hooker (1867) accepted both *Licania* and *Moquilea* as genera but redefined Bentham's sections of *Licania*: *Licania* with two sections (*Eulicania* and *Hymenopus*) and *Moquilea* with three (*Eumoquilea*, *Leptobalanus* and *Microdesmia*). Thus, both *Licania* and *Moquilea* included apetalous and petalous taxa. Fritsch (1888) recognised the four genera of Aublet (*Acioa*, *Couepia*, *Licania* and *Moquilea*) but later merged *Moquilea* with *Licania* (Fritsch 1889), following Grisebach (1857). This concept of *Moquilea* as a synonym of *Licania* was followed in most subsequent classifications (Hallier 1903; Prance 1963, 1972a, 1989; Prance & White 1988; Prance & Sothers 2003a) and in the 20th century only Hutchinson (1964) treated *Licania* and *Moquilea* as separate genera.

When Prance & White (1988) divided *Licania* into five subgenera, *Licania*, *Moquilea*, *Parinariopsis*, *Afrolicania* and *Angelesia*, this was based largely on characters of the ovary (unilocular and at or near the base of the receptacle) and other characters such as stamen exertion; subgenus *Licania* was subdivided into five sections (sects. *Hirsuta*, *Hymenopus*, *Cymosa*, *Pulverulenta*, *Licania*) and subgenus *Moquilea* into three (sects. *Moquilea*, *Leptobalanus*, *Microdesmia*). Molecular phylogenetic analyses retrieved species in *Licania* subgen. *Moquilea* as sister to core *Couepia* (Bardon *et al.* 2013; Sothers 2010; Sothers *et al.* 2014) and further indicated that the sections of subgen. *Licania* and subgen. *Moquilea* were not supported as monophyletic (Sothers unpublished data; Bardon *et al.* 2013). These results paved the way for a reassessment of the monophyly of *Licania*.

Here we propose a new generic classification for *Licania* s.l. based on molecular phylogenetic evidence supported by morphological characters. We divide the genus into eight genera, five of the eight sections in subgen. *Licania* and subgen. *Moquilea* are recognised as genera: *Moquilea*, *Leptobalanus*, *Microdesmia*, *Hymenopus* and *Licania*; the taxa in subgen. *Licania* sect. *Hirsuta* are incorporated into genus *Hymenopus*, and subgen. *Licania* sects. *Cymosa* and *Pulverulenta* remain in core *Licania* and are not recognised as sections; subgen. *Parinariopsis* is upgraded to generic rank, *Geobalanus* is re-instated at generic rank from the synonymy of subgen. *Moquilea* to accommodate three species previously in sect. *Moquilea* (*L. michauxii*, *L. riverae* and *L. retifolia*). A new genus, *Cordillera*, is

described to accommodate *Licania platycalyx*, which was previously transferred to *Licania* from *Couepia* (Sothers *et al.* 2014: 193).

## Materials and Methods

Methodology for DNA extraction, sequencing and matrix alignment, and phylogenetic analyses follows that of Sothers *et al.* (2014). We include the taxa and markers of Sothers (2010) (85 taxa, 4524 bp, two plastid and two nuclear markers) with additional taxa and one additional marker added since that study (184 taxa, 5348 bp, 3 plastid and 2 nuclear). Results for the phylogenetic analyses are presented in Fig. 1 (combined strict consensus tree with bootstrap support); Appendix 1 includes the taxa used for the molecular phylogenetic analyses presented here, and the markers used; the ITS and *Xdh* datasets are missing several taxa.

## Results

Fig. 1 is a strict consensus tree of the combined dataset of the five markers, three plastid (*matK*, *ndhF* and *rbcL*) and two nuclear (ITS rDNA and *Xdh*). The type species for seven of the eight sections of *Licania* subgen. *Licania* and subgen. *Moquilea* have been included in the analysis presented here (Table 1). Further comments on the recognition and relationships among the genera are included under each genus in the section on taxonomy.

Species of *Licania* s.l. were retrieved in four major clades: 1) a large clade composed of species in subgen. *Licania* sect. *Licania*, sect. *Cymosa* and sect. *Pulverulenta* (= genus *Licania* s.s.), with moderate support and sister to *Hirtella*; 2) a large clade, which includes *Gaulettia*, sister to *L. arborea* (= genus *Microdesmia*) and *L. platycalyx* (= genus *Cordillera*) and with species from subgen. *Licania* sect. *Hymenopus* retrieved in two subclades (= genus *Hymenopus*): one also including *L. latifolia* (previously in subgen. *Licania* sect. *Hirsuta*) and *L. amapaensis* (previously subgen. *Moquilea* sect. *Microdesmia*), sister to *Afrolicania*, and the other subclade including the type of sect. *Hymenopus* (*L. divaricata*) sister to *L. licaniiflora* (= genus *Parinariopsis*), with moderate support; 3) a highly supported clade of species from subgen. *Moquilea* sect. *Leptobalanus* (= genus *Leptobalanus*) sister to *Gaulettia*; and 4) species in subgen. *Moquilea* sect. *Moquilea* retrieved in two lineages sister to *Couepia* (= genus *Moquilea*).

*Licania michauxii* and *L. riverae* (= genus *Geobalanus*), previously of subgen. *Moquilea* sect. *Moquilea*, are retrieved in a fifth clade together with the Paleotropical genera *Grangeria* and *Parastemon*, distantly related to *Licania* s.l. but without support.

Analyses for the ITS, *Xdh* and plastid datasets displayed similar results to the combined analysis presented here. Our results are also broadly supported by other phylogenetic analyses (Bardon *et al.* 2016; Sothers *et al.* 2014; Sothers 2010).

## Discussion

This study presents a new classification for *Licania* s.l. given its rampant polyphyly as evidenced in phylogenetic studies involving the Chrysobalanaceae (Bardon *et al.* 2013; Sothers 2010; Sothers *et al.* 2014; Yakandawala *et al.* 2010). Moreover, morphological characters that were previously held as central to the taxonomy of subgenera and sections, do not support the previous classification. Table 1 outlines the taxonomic changes made here as compared with the previously accepted delimitation of *Licania* s.l. and Table 2 summarises the key morphological characters for the genera treated here.

The unexpected revelation of a close relationship between *Couepia* and *Licania* subgen. *Moquilea* uncovered by molecular phylogenetic studies (Sothers 2010; Sothers *et al.* 2014), highlighted the need to re-evaluate the monophyly of *Licania* s.l. Within Chrysobalanaceae, genera have often been defined by suites of overlapping characters. Among these characters, however, the position of the ovary on the receptacle has been emphasised as pre-eminent and is generally constant within genera. *Couepia* and *Licania* were separated mainly because of the differing position of the ovary, despite sharing other characters. In *Licania* s.l. the ovary was typically at, or near, the base of the receptacle, except in *Licania* subgen. *Parinariopsis* (= genus *Parinariopsis*) and *Licania platycalyx* (= genus *Cordillera*), which were unique within *Licania* s.l. because of the ovary positioned laterally rather than at the base of the receptacle. Outside *Licania* s.l., only in *Parinari* and *Hirtella* does the ovary occur in two different positions within the same genus, on the wall or at the mouth of the receptacle. Despite this, the pantropical genus *Parinari* is highly supported in phylogenetic analyses, as are the Neotropical *Hirtella*.

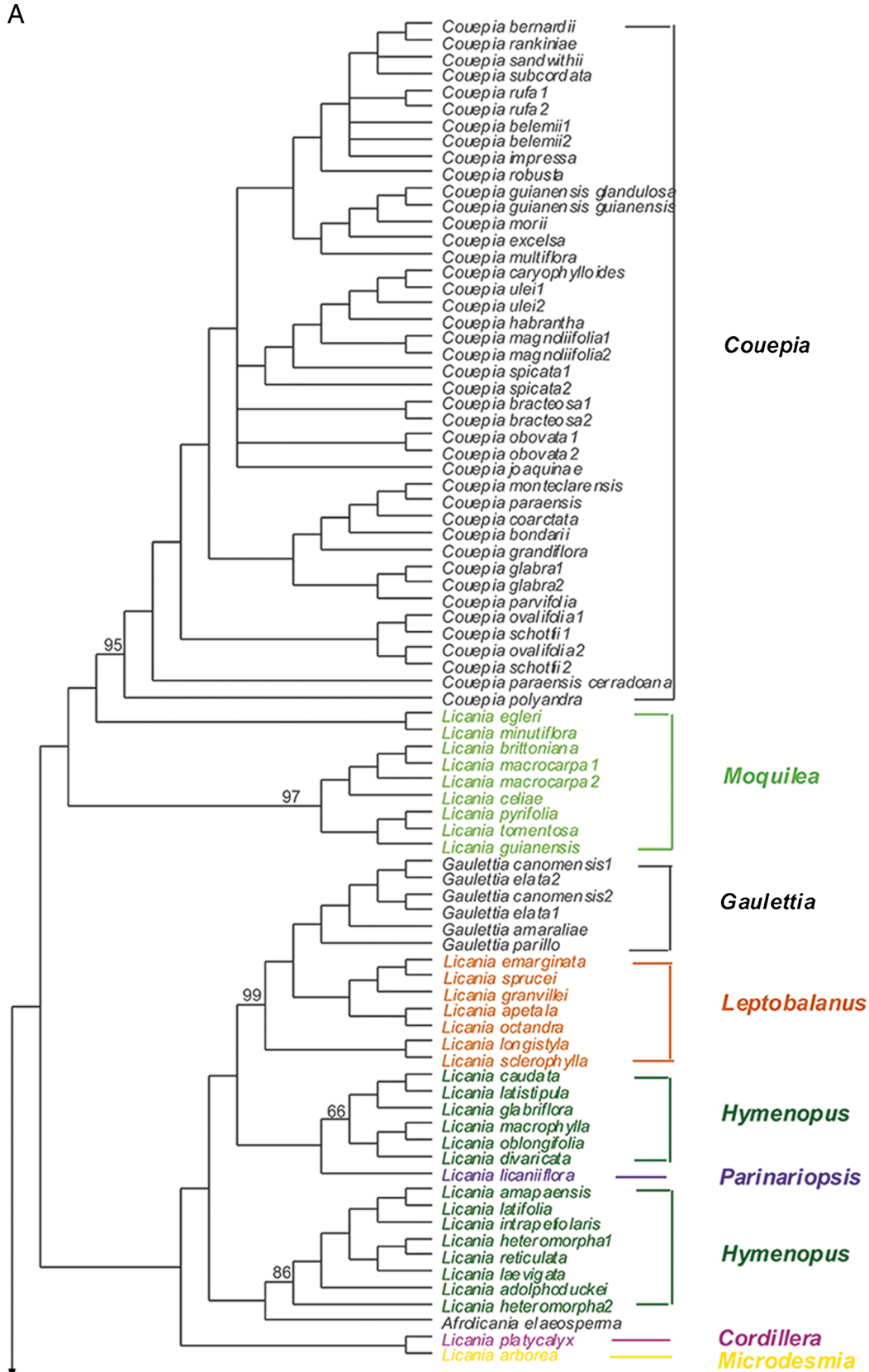
The redelimitation of the former subgen. *Licania* and subgen. *Moquilea* into six segregate genera follows a major split among taxa with petals (genera *Moquilea*, *Hymenopus*, *Microdesmia*, *Geobalanus*) and apetalous taxa (genera *Leptobalanus* and *Licania*). In previous classifications (Prance & White 1988; Prance & Sothers 2003a), both subgen. *Moquilea* and subgen. *Licania* included sections with and without petals. Thus, subgen. *Moquilea* comprised sects *Moquilea*, *Microdesmia* (with petals) and *Leptobalanus* (apetalous); subgen. *Licania* consisted of apetalous sects. *Licania*, *Cymosa* and *Pulverulenta*, sect. *Hirsuta* with petals, and sect. *Hymenopus* with both apetalous

and petalous taxa (Table 1). Apetaly is present in only one other genus, the monospecific *Afrolicania*, endemic to and widespread in West and western Central Africa; its presence in the large clade of Neotropical taxa of Chrysobalanaceae (c. 400 spp.) means that this clade is not exclusively Neotropical as stated by Sothers *et al.* (2014). Our new classification indicates that apetaly has arisen more than once in Chrysobalanaceae.

Other characters that had been used to separate species into subgenera and sections of *Licania* s.l. include number of stamens, their length relative to the calyx (far-exserted vs equal or included), presence of stomatal cavities on the lower surface of the leaf and leaf pilosity. Generally, the delimitation of sections as defined by Prance & White (1988) and Prance & Sothers (2003a) are retrieved as well-supported clades in the phylogeny presented here, but not as sections of *Licania* s.l. Thus, the generic status conferred on *Moquilea* and *Licania* by Aublet (1775), as well as Bentham's (1840) suggestion that his sections of *Licania* (e.g. *Leptobalanus*, *Microdesmia*, *Hymenopus*) were worthy of generic status, hold true.

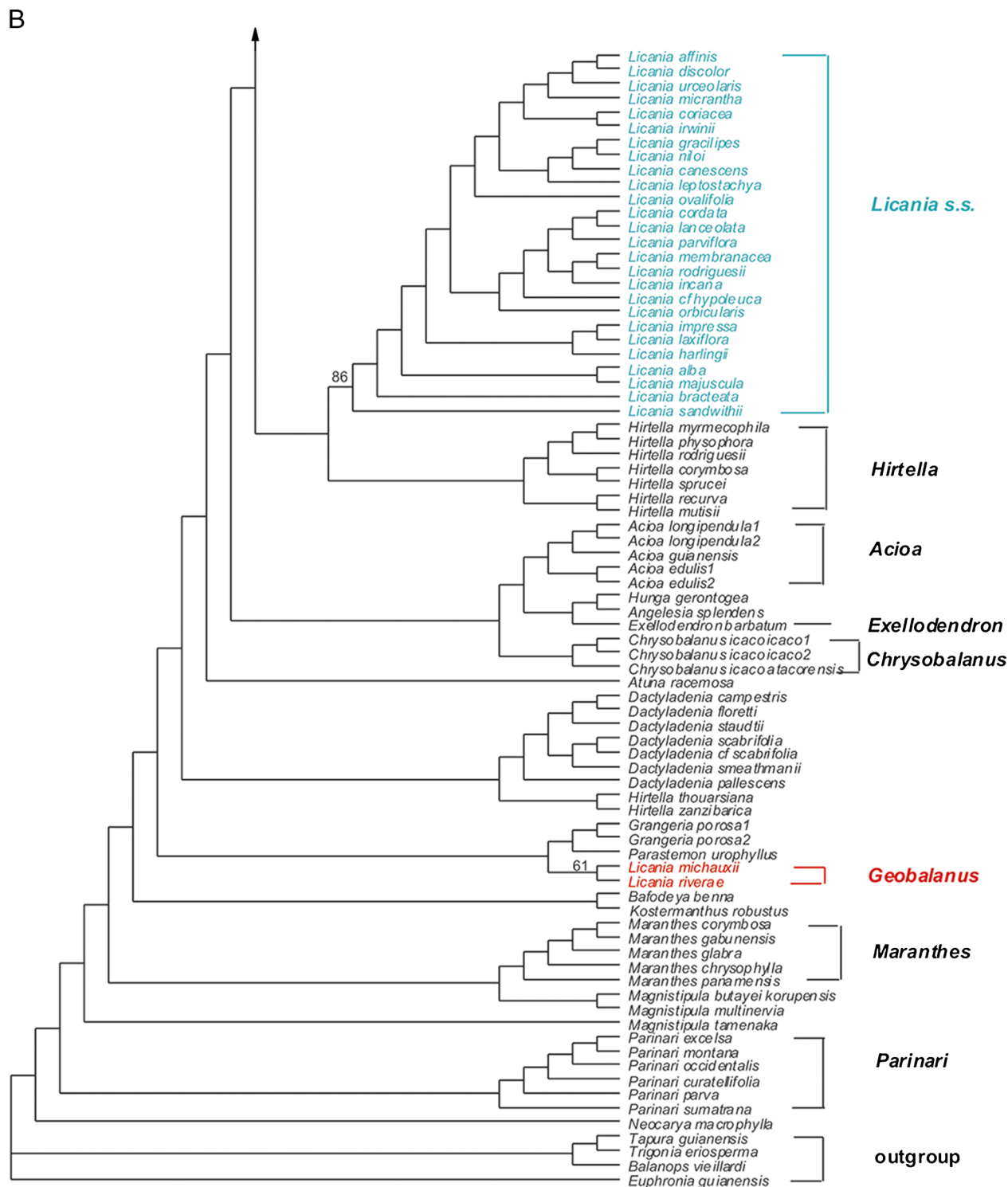
We took a conservative approach with respect to accepting genera, particularly where the placement of species is not well-supported by either morphology or phylogenetic results. This is the case for *Hymenopus* as defined here, for which two separate (but closely placed) clades are retrieved, but no morphological characters have been found to circumscribe them as separate genera. Our data do not refute or support species of *Hymenopus* as a single genus. Similarly in *Moquilea*, two species (*M. egleri* and *M. minutiflora*) are retrieved in a separate clade, but we keep them within the concept of *Moquilea* for now. Further changes may be needed if these now separate clades do not form a single clade with more morphological and molecular studies, but at present giving these distinct generic recognition seems unwarranted. Other genera that are here weakly supported in the phylogenetic analyses are *Parinariopsis*, *Cordillera*, *Microdesmia* and *Geobalanus*, but delimitation of these genera is well-supported by morphological and geographic evidence.

In the molecular phylogeny presented here, the segregate genera of *Licania* s.l. are variously allied to *Couepia*, *Gaulettia* and *Hirtella*. *Chrysobalanus* is distantly related to these genera even though there have been suggestions of merging it with *Licania* (Gómez de la Maza 1887; Morales 1887; Chappill 1992). Relationships among *Geobalanus*, *Microdesmia* and *Moquilea* remain unclear but they appear to be phylogenetically distinct. Prance (pers. obs.) regarded sect. *Microdesmia* (of subgen. *Moquilea*) as artificial; and a much reduced *Microdesmia* is maintained as a genus here, albeit further sampling is needed. The two species display a unique geographic disjunction and suggest ecological niche adaptation. *Geobalanus* displays few morpholog-



**Fig. 1.** Strict consensus tree of the combined analysis (plastid, ITS and *Xdh*), highlighting clades with taxa of *Licania* s.l. and the new generic names; bootstrap support is shown above branches. Clades of all other Neotropical genera and the outgroup are also cited.





**Fig. 1.** (continued)

ical characters to distinguish it from *Moquilea*, *Microdesmia* and *Chrysobalanus*, although *Microdesmia* has deeply reticulate leaves often with stomatal cavities, characters that are lacking in *Geobalanus*, *Moquilea* and *Chrysobalanus*.

Despite the generally well-supported molecular results for *Licania* s.l. and its segregates, the morphological characters that distinguish the eight genera discussed here are comparatively few and not well studied. Characters that merit further investigation

**Table 1.** Taxonomic representation of the progression of changes from the previous classification of *Licania* s.l., sensu Prance & White (1988) and Prance & Sothers (2003a), and the current classification presented here. Species in bold have been sequenced and are included in Fig. 1.

genus LICANIA subgen. LICANIA					genus LICANIA subgen. MOQUILEA		
Leaf lower surface glabrous, hirsute, pulverulent, lanate or with stomatal cavities. Petals present or absent. Stamens 3 – 8 (– 11), unilateral or inserted in a complete circle; filaments shorter than or equalling calyx lobes.					Leaf lower surface glabrous, lanate, or with stomatal cavities. Petals present or absent. Stamens 8 – 50, inserted in a complete circle; filaments usually far exceeding, rarely equalling calyx lobes.		
sect. Hirsuta	sect. HYMENOPUS	sect. Cymosa	sect. Pulverulenta	sect. LICANIA	sect. MOQUILEA	sect. LEPTOBALANUS	sect. MICRODESMIA
T: <i>L. latifolia</i>	T: <i>L. divaricata</i>	T: <i>L. hypoleuca</i>	T: <i>L. coriacea</i>	T: <i>L. incana</i>	T: <i>L. guianensis</i>	T: <i>L. apetala</i>	T: <i>L. rigida</i>
Leaf lower surface hirsute at least on venation, not tomentose	Leaf lower surface entirely glabrous	Leaf lower surface pulverulent-farinaceous, lanate, or with stomatal cavities	Leaf lower surface pulverulent-furfuraceous	Leaf lower surface lanate or with stomatal cavities	Leaf lower surface glabrous or lanate	Leaf lower surface glabrous, lanate or with stomatal cavities	Leaf lower surface glabrous, lanate or with stomatal cavities
Flowers borne on primary branches of inflorescence, never in cymes	Flowers borne on primary branches of inflorescence or in small cymes on slender peduncles	Flowers borne in small cymes on short secondary branches of inflorescence	Flowers borne on primary inflorescence	Flowers borne on primary branches of inflorescence	Inflorescence panicle of cymes	Inflorescence panicle or panicle of cymes	Inflorescence racemose panicles or tem & axil panicles or spikes or racemes
Petals present	Petals present or absent*	Petals absent	Petals absent	Petals absent	Petals present	Petals absent	Petals present
genus HYMENOPUS		genus LICANIA			genus MOQUILEA	genus LEPTOBALANUS	genus MICRODESMIA genus HYMENOPUS genus MOQUILEA
Petals present		Petals absent			Petals present	Petals absent	Petals present
Stamens 3 – 10, unilateral or inserted in a complete circle or ¼ circle		Stamens (2) 3 – 8 (– 11), unilateral or inserted in a complete circle			Stamens 14 – 90, inserted in a complete circle Stamens 14 – 17, inserted in a complete circle	Stamens (7) 8 – 14 (– 22), inserted in a complete circle	Stamens 8 – 14, unilateral or inserted in a complete circle
Filaments shorter than or equalling calyx lobes, rarely exserted		Filaments shorter than or equalling calyx lobes			Filaments far exceeding calyx lobes Filaments exserted	Filaments far-exceeding calyx lobes, less often equal	Filaments equalling calyx lobes
T: <i>Hymenopus divaricatus</i>		T: <i>Licania incana</i>			T: <i>Moquilea guianensis</i>	T: <i>Leptobalanus apetalus</i>	T: <i>Microdesmia rigida</i>
<b>Hymenopus</b> <i>H. latifolius</i> <i>H. costaricensis</i> <i>H. hirsutus</i> <i>H. hispidus</i> <i>H. krukovii</i> <i>H. lasserii</i>	<b>Hymenopus</b> <i>H. divaricatus</i> =T <i>H. adolphoduckei</i> <i>H. caudatus</i> <i>H. glabriflorus</i> <i>H. heteromorphus</i> <i>H. intrapetalus</i> <i>H. laevigatus</i> <i>H. latistipulus</i> <i>H. macrophyllus</i> <i>H. oblongifolius</i> <i>H. reticulatus</i> <i>H. arachicarpus</i> <i>H. arachnoideus</i> <i>H. conferruminatus</i> <i>H. miltonii</i> <i>H. minutiflorus</i> <i>H. occultans</i> <i>H. operculipetalus</i> <i>H. pakaramensis</i> <i>H. prismatocarpus</i> <i>H. sothersiae</i>	<b>Licania</b> <i>L. gracilipes</i> <i>L. hypoleuca</i> <i>L. impressa</i> <i>L. membranacea</i> <i>L. arianae</i> <i>L. cuprea</i> <i>L. cymosa</i> <i>L. dealbata</i> <i>L. densiflora</i> <i>L. pallida</i> <i>L. furfuracea</i> <i>L. elliptica</i> <i>L. parvifructa</i> <i>L. piresii</i> <i>L. santosii</i> <i>L. ternatensis</i>	<b>Licania</b> <i>L. affinis</i> <i>L. canescens</i> <i>L. coriacea</i> <i>L. niloi</i> <i>L. orbicularis</i> <i>L. urceolaris</i> <i>L. boyanii</i> <i>L. buxifolia</i> <i>L. cuyabensis</i> <i>L. davillifolia</i> <i>L. elliptica</i> <i>L. glauca</i> <i>L. teixeirae</i>	<b>Licania</b> <i>L. incana</i> =T <i>L. alba</i> <i>L. bracteata</i> <i>L. cordata</i> <i>L. discolor</i> <i>L. harlingii</i> <i>L. lanceolata</i> <i>L. laxiflora</i> <i>L. leptostachya</i> <i>L. majuscula</i> <i>L. micrantha</i> <i>L. ovalifolia</i> <i>L. parviflora</i> <i>L. rodriguesii</i> <i>L. sandwithii</i> <i>L. apiculata</i> <i>L. apiknae</i> <i>L. aracaensis</i> <i>L. bahiensis</i> <i>L. belemii</i> <i>L. bellingtonii</i> <i>L. blackii</i> <i>L. caldasiana</i> <i>L. cidii</i> <i>L. compacta</i> <i>L. condoriensis</i> <i>L. coupiifolia</i> <i>L. crassivenia</i> <i>L. cruegeriana</i> <i>L. ferreirae</i> <i>L. foldatsii</i> <i>L. hebantha</i> <i>L. hitchcockii</i> <i>L. hoehnei</i> <i>L. indurata</i> <i>L. jimenezii</i> <i>L. kunthiana</i> <i>L. lamentanda</i> <i>L. maxima</i> <i>L. microphylla</i> <i>L. mollis</i> <i>L. montecagudensis</i> <i>L. naviculistipula</i> <i>L. nelsonii</i> <i>L. nitida</i> <i>L. paraensis</i> <i>L. pittieri</i> <i>L. pruinoso</i> <i>L. riedelii</i> <i>L. robusta</i> <i>L. roiratensis</i> <i>L. rufescens</i> <i>L. savannarum</i> <i>L. spicata</i> <i>L. stewardii</i> <i>L. steyermarkii</i> <i>L. stricta</i> <i>L. subrotundata</i> <i>L. tepuiensis</i> <i>L. tocantina</i> <i>L. triandra</i> <i>L. trigonioides</i> <i>L. vaupesiana</i> <i>L. velutina</i>	<b>Moquilea</b> <i>M. guianensis</i> = T <i>M. brittoniana</i> <i>M. celiae</i> <i>M. egleri</i> <i>M. macrocarpa</i> <i>M. minutiflora</i> <i>M. pyrifolia</i> <i>M. tomentosa</i> <i>M. angustata</i> <i>M. aneae</i> <i>M. belloii</i> <i>M. boliviensis</i> <i>M. cabrerae</i> <i>M. cariae</i> <i>M. ceciophora</i> <i>M. chiriquiensis</i> <i>M. comiculata</i> <i>M. dodsonii</i> <i>M. durifolia</i> <i>M. espinae</i> <i>M. fasciculata</i> <i>M. filomenoi</i> <i>M. fritschii</i> <i>M. gentryi</i> <i>M. gonzalezii</i> <i>M. grandibracteata</i> <i>M. guatemalensis</i> <i>M. hedbergii</i> <i>M. imbaimadaensis</i> <i>M. jaramilloi</i> <i>M. kallunkiae</i> <i>M. klugii</i> <i>M. leucosepala</i> <i>M. longicuspudata</i> <i>M. longipedicellata</i> <i>M. longipetala</i> <i>M. maranbensis</i> <i>M. maritima</i> <i>M. megalophylla</i> <i>M. montana</i> <i>M. palcazuensis</i> <i>M. platypus</i> <i>M. salzmännii</i> <i>M. tachirensis</i> <i>M. unguiculata</i> <i>M. vasquezii</i> <i>M. veneralensis</i>	<b>Leptobalanus</b> <i>L. apetalus</i> =T <i>L. emarginatus</i> <i>L. granvillei</i> <i>L. longistylus</i> <i>L. octandrus</i> <i>L. sclerophyllus</i> <i>L. sprucei</i> <i>L. albiflorus</i> <i>L. bullatus</i> <i>L. calvescens</i> <i>L. cardiophyllus</i> <i>L. cuatrecasasii</i> <i>L. cuspidatus</i> <i>L. diegogomezii</i> <i>L. foveolatus</i> <i>L. fuchsii</i> <i>L. gardneri</i> <i>L. humilis</i> <i>L. jefensis</i> <i>L. josecamosii</i> <i>L. latus</i> <i>L. maguirei</i> <i>L. mexicanus</i> <i>L. morii</i> <i>L. parvifolius</i> <i>L. persaudii</i> <i>L. sparsipilis</i> <i>L. stevensii</i> <i>L. turbinatus</i> <i>L. undulatus</i> <i>L. wurdackii</i>	<b>Microdesmia</b> <i>M. rigida</i> =T <i>M. arborea</i> <b>Hymenopus</b> <i>H. amapaensis</i> *** <b>Moquilea</b> <i>M. araneosa</i> ** <i>M. chocoensis</i> ** <i>M. salicifolia</i> ** <i>M. silvatica</i> ** <i>M. subarachnophylla</i> ** <i>M. tambopatensis</i> ** <i>M. velata</i> **

+Previously in synonymy of *Moquilea*, now re-established genus; \*Previously in *Licania* sect. *Hymenopus*, transferred to *Licania* s.s.; \*\*Previously in *Licania* sect. *Microdesmia*, transferred to *Moquilea*; \*\*\*Previously in *Moquilea* sect. *Microdesmia*, transferred to *Hymenopus*

**Table 2.** Selected key morphological characters of genera previously in *Licania* s.l. treated here.

Genera Characters	<i>Conditillera</i>	<i>Parinariopsis</i>	<i>Microdesmia</i>	<i>Crobatanus</i>	<i>Hymenopus</i>	<i>Leptobalanus</i>	<i>Moquilea</i>	<i>Licania</i>
Number species	1	1	2	3	28	31	54	100
Leaf pilosity undersurface	sparse appressed pubescence	lanate	glabrous	glabrous, lanate	glabrous, hirsute	glabrous, lanate	glabrous, lanate	glabrous, lanate, tomentose, pulverulent
Stomatal cavities	absent	absent	present	absent	absent	present in some species	absent	present in some species
Inflorescence	panicle	panicle	racemose panicle	panicle, cymose panicle	racemose panicle, panicle	racemose panicle, panicle of cymes, panicle	racemose panicle, panicle, raceme	racemose panicle, panicle, spike
Petals	5	5	5	5	4 or 5	0	4 or 5	0
Stamen number	c. 54	(16) 18 – 25	8 – 14	14 – 17	3 – 10	(7) 8 – 10 (14) ( <i>L. cadavescens</i> = 22)	11 – 60 (90)	(2) 3 – 7 (8 – 11)
Stamen arrangement	complete circle	complete circle	complete circle or unilateral	complete circle	complete circle, $\frac{3}{4}$ circle, unilateral	complete circle	complete circle	unilateral or complete circle
Filaments fused/free	connate at base	almost free to base	connate for $\frac{1}{2}$ length	connate at base	free, connate at base or to $\frac{1}{2}$ length	free or connate at base	free or connate at base	free, less often connate at base or to $\frac{1}{2}$ length
Filaments included/exserted	exserted	slightly exserted	equal	exserted	included, equal or rarely exserted	(far-) exserted, rarely equal	(far-) exserted or rarely included	included or equal length
Ovary	lateral	lateral	basal	basal	basal	basal	basal	basal

include leaf pilosity, presence of stomatal cavities, inflorescence type, sessile vs pedicellate flowers, receptacle morphology, stamen disposition, degree of fusion of the stamens, and fruit characters. Future work should focus on a greater understanding of the morphological differences between the apetalous genera *Leptobalanus* and *Licania*, and more taxon sampling within *Moquilea*, including taxa formerly in sect. *Microdesmia*. Relationships among the two clades of *Hymenopus* should also be resolved. Additional sampling may support further changes, but there is strong support for the phylogenetic framework presented here: *Moquilea* is sister to *Couepia*, core *Licania* appears in a separate lineage from *Leptobalanus*, *Microdesmia* and *Hymenopus*, as well as from the monospecific *Cordillera* and *Parinariopsis*, and *Geobalanus*.

### Taxonomy

Below we present our concept of the genera derived from *Licania* s.l., based on molecular phylogenetic

analyses supported by morphological evidence. All species and names previously in *Licania* s.l. cited in Prance & Sothers (2003a) are included here, in addition to five others described since then: *Licania condoriensis* Prance (2013: 72), *L. palcazuensis* Prance (2014: 2), *L. apiknae* Prance (2014: 4), *L. monteagudensis* Prance (2014: 6), and *L. arachicarpa* N. Zamora (2013: 1). A key to the Neotropical genera of Chrysobalanaceae, together with brief generic descriptions, keys to species, new combinations, synonymy, geographic distribution, and habitat where known are included. Genera are presented in order of increasing number of species, beginning with the monospecific genera *Cordillera*, gen. nov., and *Parinariopsis*, followed by *Microdesmia* (2 spp.), *Geobalanus* (3 spp.), *Hymenopus* (28 spp.), *Leptobalanus* (31 spp.), *Moquilea* (54 spp.) and *Licania* s.s. (c. 100 spp.). For species descriptions of all except five recently described species, see Prance & Sothers (2003a, b). All specimens cited have been seen by either the first and/or second authors, apart from specimens of *L. arachicarpa*.

### Key to Neotropical genera<sup>1</sup>

1. Ovary bilocular
  2. Stamens exerted, 20 – 60, in a complete circle; ovary at mouth of receptacle . . . . . **Maranthes**
  2. Stamens 6 – 9, unilateral; ovary at side of receptacle or at mouth
    3. Leaves with reticulate venation or with stomatal cavities, lanate (never glabrous); epicarp verrucose . . . . . **Parinari**
    3. Leaves not reticulate, venation indistinct, without stomatal cavities, leaf undersurface glabrous or with whitish pubescence; epicarp smooth . . . . . **Exellodendron**
1. Ovary unilocular
  4. Ovary at base of receptacle
    5. Petals absent, stamens 2 – 14 (– 22)
      6. Stamens exerted, always in a complete circle, (7 –) 8 – 10 (14 – 22) . . . . . **VI. Leptobalanus**
      6. Stamens included, unilateral or less frequently in a complete circle, (2 –) 3 – 7 (11). . . . . **VIII. Licania**
    5. Petals present, stamens 3 – 90
      7. Stamens included, 3 – 10, leaf undersurface smooth, glabrous or hirsute. . . . . **V. Hymenopus**
      7. Stamens exerted (or less often equalling), 11 – 90 (– 300), if only 8 – 14 then leaves deeply reticulate or with stomatal cavities
        8. Stamens equalling calyx in length, 8 – 14, leaves deeply reticulate or with stomatal cavities . . . . . **III. Microdesmia**
        8. Stamens far exerted, 11 – 90, leaves not deeply reticulate, without stomatal cavities
          9. Filaments partially fused in groups, pubescent; fruit longitudinally ridged . . . . . **Chrysobalanus**
          9. Filaments free almost to base, glabrous; fruit not longitudinally ridged
            10. Inflorescence of cymose or compact panicles 1 – 5 cm long; stamens 14 – 17. . . . . **IV. Geobalanus**
            10. Inflorescence racemose, panicles or racemose panicles, usually exceeding 5 cm in length; stamens 11 – 90 . . . . . **VII. Moquilea**
    4. Ovary at mouth of receptacle or laterally on wall of receptacle

<sup>1</sup> Roman numerals refer to genera treated here.



11. Receptacle flattened, almost solid; Andean, montane ..... **I. Cordillera**
11. Receptacle short or cylindrical, hollow with a distinct cavity; lowland or rarely montane
12. Stamens united into a ligule for at least ½ their length, or inflorescence flagelliflorous ..... **Acioa**
12. Stamens free almost to base, inflorescence not flagelliflorous
13. Stamens 3 – 9, unilateral; leaves glabrous or hispid, without stomatal cavities; bracteoles often glandular ..... **Hirtella**
13. Stamens 12 – 300, unilateral or in a complete circle; leaves glabrous or pubescent, but not hispid, or with stomatal cavities; bracteoles not glandular
14. Stamens exerted barely beyond calyx; ovary inserted laterally in mid receptacle; bracteoles enclosing flower buds. .... **II. Parinariopsis**
14. Stamens far exerted; ovary inserted at mouth of receptacle; bracteoles usually not enclosing flower bud except in some *Couepia*
15. Leaves lanate pubescent, or hairs only between reticulations or within stomatal cavities; deeply reticulate and usually with stomatal cavities ..... **Gaulettia**
15. Leaves lanate, tomentose, hirsute or glabrous, without stomatal cavities
16. Calyx lobes with 2 glands on exterior ..... **Acioa edulis**
16. Calyx lobes without glands on exterior
17. Stamens c. 17; fruit small with bony endocarp ..... **Hirtella recurva**
17. Stamens 20 – 300; fruit with hard woody endocarp ..... **Couepia**

**I. Cordillera** Sothers & Prance gen. nov. Type: *Couepia platycalyx* Cuatrec.

<http://www.ipni.org/urn:lsid:ipni.org:names:77156115-1>

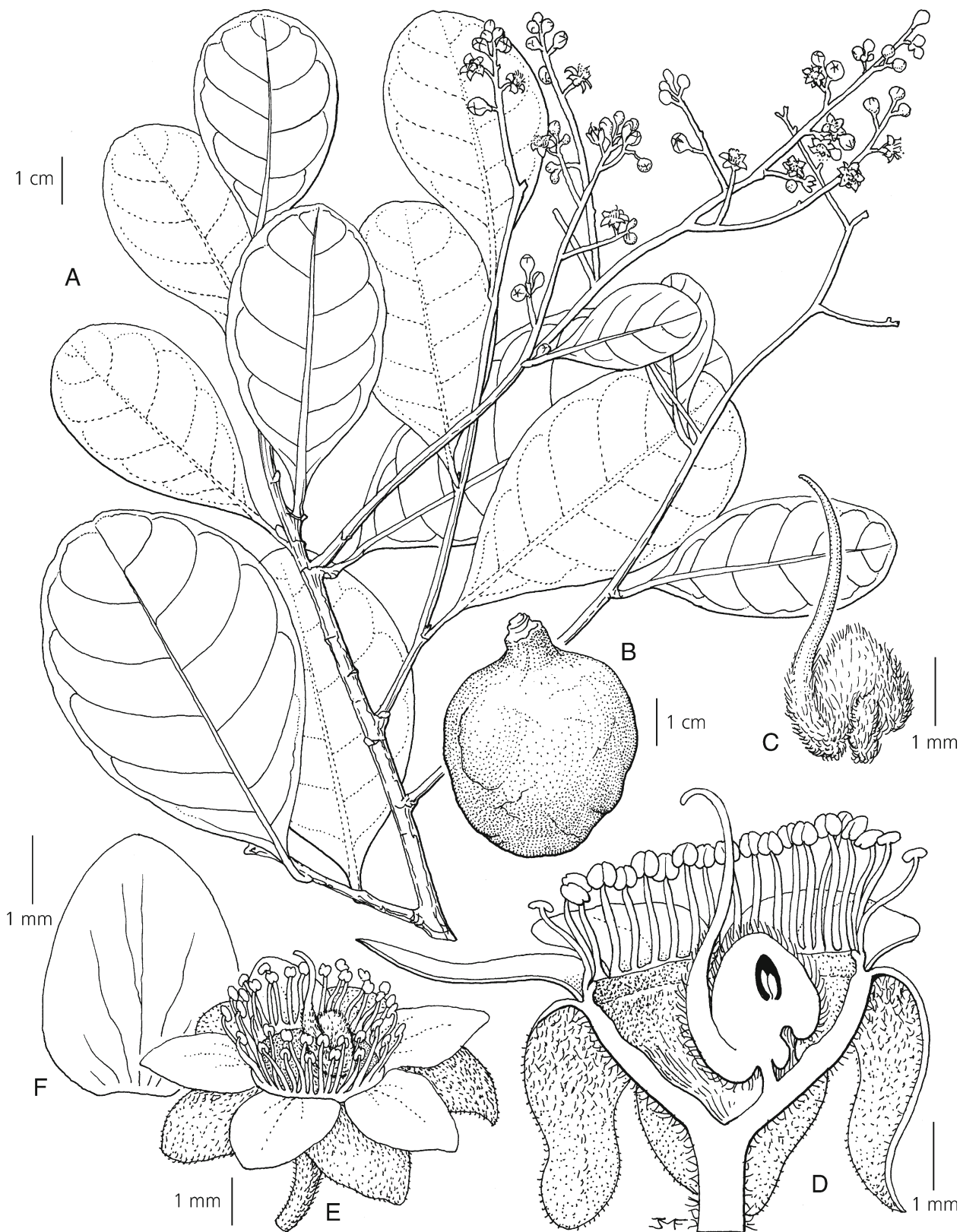
*Trees.* Leaves with caducous stipules; petioles 7.8 mm long, glabrous, terete; lamina obovate to obovate-orbicular, 8.5 – 12 × 7.9 cm, rounded at base and apex, glabrous above, with very sparse short appressed pubescence beneath; primary veins 10 – 12 pairs, prominent beneath. *Inflorescences* terminal little-branched panicles; rachis and branches with a few minute appressed hairs. Bracts and bracteoles to 1.5 mm long, caducous. Receptacle broadly turbinate, flattened, oblique, almost solid, 3 mm long, appressed pubescent on exterior, with dense deflexed hairs at throat within, filling the very small cavity; pedicels to 1.5 mm long. Calyx lobes rounded. Petals 5, unequal in length, glabrous, white. Stamens c. 54, inserted in a complete circle; filaments glabrous, exerted, connate at base. *Ovary* villous, on wall of receptacle. Style pubescent at base. *Fruit* ovoid, 8 × 5.5 cm; epicarp glabrous, smooth or with a few large scars or sparse lenticels; mesocarp thin, fleshy; endocarp thin, bony, glabrous within. Fig. 2.

**RECOGNITION.** *Cordillera* shares affinities with both *Couepia* and *Licania*; it has a greater number of stamens (c. 54) as in *Couepia* (10 – over 300), but the ovary is positioned at the side of the receptacle, differing from both *Licania* s.s. (at the base) and *Couepia* (at the mouth). It also differs from *Couepia* by the turbinate and almost solid receptacle (vs hollow in *Couepia*). It has petals, unlike *Licania* s.s.

**DISTRIBUTION.** A monospecific genus restricted to the Neotropics, from Costa Rica and Panama to northern South America, in Colombia, Ecuador and Venezuela. Occurs in higher altitude Andean and Central American forests, from 1000 – 2700 m, and has been recorded as low as 250 m.

**ETYMOLOGY.** The epithet *Cordillera* alludes to the locality where José Cuatrecasas collected the type specimen, in the Cordillera Oriental, as cited on the label. This name is appropriate since it also highlights the distribution and habitat of the genus: high altitudes along the Andes mountain range.

**NOTES.** The generic position of *Cordillera platycalyx* has always been problematic. Cuatrecasas (1950) stated that it was ‘an extraordinary member of *Couepia* and of the Chrysobalanoideae’, and Prance (1972a) was uncertain of its affinities to *Couepia* because of the ovary and fruit; he saw only the type and one other specimen so maintained the species in *Couepia*. Sothers *et al.* (2014: 193) transferred *Couepia platycalyx* to *Licania* but stated that its inclusion in *Licania* was tentative, primarily to effect the monophyly of *Couepia*. Here we provide further evidence from molecular phylogenetic analyses and incorporating more sampling of *Licania* that do not place *Cordillera platycalyx* in a clade with *Licania* s.s. *Cordillera platycalyx* shares a similar receptacle morphology to *Licania* but differs in the position of the ovary, which is on the wall of the receptacle rather than at its base. *Parinariopsis licaniiflora* also has a laterally inserted ovary, but not on the wall of the receptacle, and differs from *Cordillera platycalyx* in other characters, such as the number of stamens (54 in *Cordillera*; 18 – 25 in *Parinariopsis*), the receptacle



**Fig. 2.** *Cordillera platycalyx*. A habit; B fruit; C style and ovary; D half flower; E flower; F petal. A, C – F drawn from G. Herrera 5375; B drawn from O. Vargas 175. DRAWN BY J. M. FOTHERGILL.

which is almost solid in *Cordillera* (a character found elsewhere only in *Maranthes*), and in fruit characters. In addition, the two genera are separated geographically and altitudinally; *Cordillera platycalyx* is restricted to the highlands of western Amazonia, the Andes and southern Central America, whereas *P. licaniiflora* has an eastern Amazonian and Guianan distribution, occurring in lowland areas. *Cordillera* also differs from *Couepia* and *Licania* s.l. by the leafless flowering branches, an unusual character in Chrysobalanaceae.

***Cordillera platycalyx* (Cuatrec.) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:77156116-1>

*Couepia platycalyx* Cuatrec., *Fieldiana*, Bot. 27: 66 (Cuatrecasas 1950); *Licania platycalyx* (Cuatrec.) Sothers & Prance (Sothers *et al.* 2014: 193). Type: Colombia, Cundinamarca, Cordillera Oriental, Dintel, entre Facatativa y La Vega, *Cuatrecasas & Pérez-Arbeláez* 15336 (holotype F; isotypes COL, US).

**DISTRIBUTION AND HABITAT.** Costa Rica and Panama to northern South America, in Colombia, Ecuador and Venezuela. Occurs in higher altitude Andean and Central American forests, from 1000 – 2700 m, and has been recorded as low as 250 m.

**II. *Parinariopsis* (Huber) Sothers & Prance stat. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:77156120-1>

*Licania* subg. *Parinariopsis* Huber, *Bol. Mus. Goeldi Hist. Nat. Ethnogr.* 5: 368 (1909). Type: *Licania parinarioides* Huber.

*Moquilea* subg. *Microbalanus* Blume (1856 [1852]: 92). Type: *Moquilea parviflora* Blume (= *Licania obtusifolia* Fritsch).

*Trees.* Leaf lower surface deeply reticulate and lanate. Petiole usually with two large glands. Inflorescence panicles. Bracts and bracteoles large (3 – 6 mm) and enclosing groups of flowers. Petals 5. Stamens 16 (18) – 25, inserted in a complete circle; filaments almost free, slightly exceeding calyx lobes, hirsutulous. Ovary villous, inserted at side of receptacle. Fruit oblong, 6 – 8 × 3 – 4.5 cm, stipitate when young, becoming sessile by expansion of the stipe; epicarp conspicuously lenticellate; endocarp glabrous within. Fig. 3F.

**DISTRIBUTION.** Guianas, Venezuela, Colombia, Peru and Amazonian Brazil (Acre, Amazonas, Pará).

**NOTES.** *Parinariopsis*, a monospecific genus, was previously included as a subgenus of *Licania*. Huber (1909) described it under *Licania* but noted it as distinct from other *Licania*. The position of *Parinariopsis* lacks support but it is morphologically distinct from all other genera included in that clade, composed of genera with morphologically diverse features. It differs from core *Licania*, *Moquilea*, *Leptobalanus*, *Geobalanus*, *Microdesmia* and *Hymenopus* by the ovary inserted at the side of the receptacle (vs at the base) and from most species of *Licania* s.l. by the pair of bracts enclosing the flower buds, a feature common in *Parinari* and a few species of *Couepia*; it differs from *Cordillera* by the hollow receptacle (vs almost solid in *Cordillera*). In addition, *Parinariopsis* and *Cordillera* are allopatric; *Parinariopsis* is a species from the eastern Amazon region and the Guianas in lowland rainforest, whereas *Cordillera* is found in northwestern Andean South America, extending into Central America, in higher elevation forests.

***Parinariopsis licaniiflora* (Sagot) Sothers & Prance stat. & comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:77156118-1>

*Moquilea licaniiflora* Sagot, *Ann. Sci. Nat., Bot.*, Ser. VI, 15: 308 (1883), as *licaniaeflora*; *Licania bracteosa* Fritsch (1889: 54), *nom. superfl. illegit.*; *Licania licaniiflora* (Sagot) S. F. Blake (1917: 66). Type: French Guiana, Rio Oiapoque, *J. Martin* s.n. (lectotype P, fide Prance 1972a: 91; isolectotype K).

*Moquilea parviflora* Blume (1856 [1852]: 92); *Licania obtusifolia* Fritsch (1889: 53); *Licania parviflora* (Blume) Lemée (1952: 23), *nom. illegit., non L. parviflora* Benth. (Bentham 1840), **synon. nov.** Type: French Guiana, *Hort. Bot. Paris* s.n. (not traced; PCU missing, n.v.).

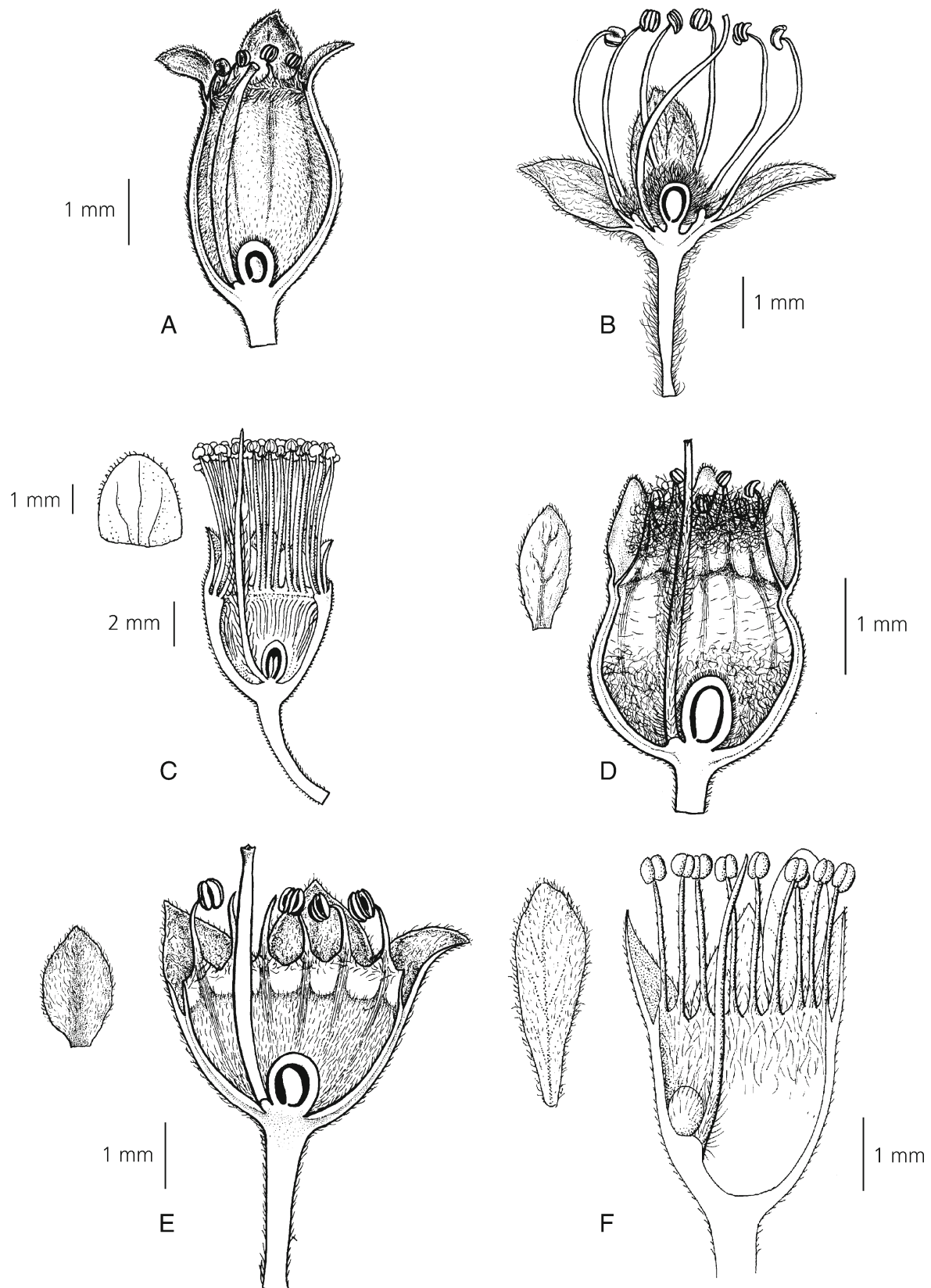
*Licania parinarioides* Huber (1909: 368). Type: Brazil, Pará, rio Mapuera, *A. Ducke* s.n. (holotype MG 8961; isotypes F, RB 15180).

*Licania parinarioides* var. *latifolia* Maguire (Cowan 1952: 397). Type: Brazil, Pará, Cameté, *A. Ducke* s.n. (holotype US; isotypes BM, MG 16299, RB).

*Licania capinensis* Huber (1910: 71). Type: Brazil, Pará, Capim, *J. E. Huber* s.n. (holotype MG 946; isotype BM).

*Licania huberiana* Maguire (Cowan 1952: 398). Type: Brazil, Pará, Belém, rio Guamá, *A. Ducke* s.n. (holotype US; isotypes P, RB 18809, S).

*Licania obovatifolia* Maguire (Cowan 1952: 398). Type: Brazil, Amazonas, rio Negro, Paduari, *R. L. Fróes* 22566 (holotype NY, isotypes COL, IAN, SP).



**Fig. 3.** Transverse section of selected flowers of the segregates of *Licania* sensu lato. **A** *Licania kunthiana*; **B** *Leptobalanus sclerophyllus*; **C** *Moquilea longicuspidata*; **D** *Hymenopus macrophyllus*; **E** *Geobalanus oblongifolius*; **F** *Parinariopsis licaniflora*. ADAPTED FROM THE ARTWORK OF J. DYER (**A, B, D, E**), J. M. FOTHERGILL (**C**) AND R. WISE (**F**).



*Licania wilson-brownei* Maguire (Cowan 1952: 399). Type: Guyana, Iramaipong, Kanuku Mts, *G. Wilson-Browne* 482 (F. D. 5888) (holotype NY; isotypes K, US).

**DISTRIBUTION AND HABITAT.** Widespread in the Guianas, Venezuela, Colombia, Peru and Amazonian Brazil (Acre, Amazonas, Pará). Open forest at river margins, savanna margins and in secondary forest.

**NOTES.** We have been unable to locate a type specimen for *Moquilea parviflora*, renamed as *Licania obtusifolia* by Fritsch (1889). It was described from very poor material and Prance (1972a: 194) placed it among imperfectly known species. We have placed it in synonymy because the brief description fits that of *Parinariopsis licaniiiflora* well, but a further search for the type would be worthwhile.

### III. *Microdesmia* (Benth.) Sothers & Prance stat. nov.

<http://www.ipni.org/urn:lsid:ipni.org:names:77156124-1>

*Licania* sect. *Microdesmia* Benth., *J. Bot. (Hooker)* 2: 212 (Bentham 1840). Type: *Licania rigida* Benth.

*Trees.* Leaf lower surface lanate and deeply reticulate; stomatal cavities present. Petiole with two glands. Bracteoles small, persistent. Inflorescence racemose panicles. Bracts and bracteoles persistent, 1.5 – 2.5 mm long. Petals 5. Stamens

8 – 14, inserted in a complete circle, equalling calyx lobes; filaments connate for half their length, densely pubescent. Ovary villous to densely villous, at base of receptacle. Fruit ovoid, 4 – 5.5 cm long; epicarp smooth, glabrous; endocarp puberulous or glabrous within.

**DISTRIBUTION.** Two species, *Microdesmia arborea* widely distributed from Mexico and Central America to northwestern South America (Venezuela, Colombia, Bolivia, Peru, Ecuador) and in Brazil in the state of Acre, and *M. rigida* restricted to northeastern Brazil.

**NOTES.** *Licania* sect. *Microdesmia* was treated as artificial by Prance (pers. obs.) and of the 11 species listed in Prance & Sothers (2003a), one is transferred here to *Hymenopus*, seven to *Moquilea* and only two species remain in *Microdesmia*, *M. rigida* and *M. arborea*. These two species have deeply reticulate lower leaf surfaces with stomatal cavities and are allopatric. Both species produce a seed oil extracted for use in paints, soaps, candles and as grease; their wood is durable and used for building and construction purposes. As a result they have been cultivated and moved around by indigenous and local people for their useful products, especially the oil. Both species occur in dry habitats (caatinga, gallery, scrub, dry plains). The combination of deeply reticulate leaf venation and stomatal cavities in species occurring in drier habitats as seen in *M. arborea* and *M. rigida* suggest that this genus has a similar adaptation to *Gaulettia* (Sothers *et al.* 2014), a genus mostly restricted to white sand habitats.

### Key to species of *Microdesmia*

1. Stamens 8 – 12; pubescence of inflorescence light grey; Mexico and Central America to western and central South America . . . . . 1. **M. arborea**
1. Stamens c. 14; pubescence of inflorescence ferruginous; restricted to northeastern Brazil. . . . . 2. **M. rigida**

### 1. *Microdesmia arborea* (Seem.) Sothers & Prance comb. nov.

<http://www.ipni.org/urn:lsid:ipni.org:names:77156125-1>

*Licania arborea* Seem., *Bot. Voy. Herald* 3: 118, t. 25 (Seemann 1853). Type: Panama, *H. Cuming* 1109 (holotype BM; isotypes E, K, MO; phototype US).

*Licania seleriana* Loes. (Loesener 1911: 55). Type: Mexico, Oaxaca, S. Bartolo Yauhtepec, *G. E. Seler* 1660 (lectotype GH, fide Prance & Sothers 2003a: 91; isolectotype US).

*Licania retusa* Pilg. (Pilger 1914: 137). Type: Brazil, Acre, *E. Ule* 9568 (holotype B, destroyed; lectotype designated here, K; isotypes L, RB, U).

*Licania bullatifolia* Cuatrec. (Cuatrecasas 1950: 63). Type: Colombia, Putumayo, *J. Cuatrecasas* 10865 (holotype F; isotypes COL, NY, P, US).

**DISTRIBUTION AND HABITAT.** From Mexico through Central America to Bolivia, Colombia, Peru, Ecuador, Venezuela and northern Brazil. Certainly native in Mexico and Central America and N South America, possibly introduced further south into Ecuador, Peru and Brazil for the oil bearing seeds. Dry plains, slopes and scrub forest.

### 2. *Microdesmia rigida* (Benth.) Sothers & Prance comb. nov.

<http://www.ipni.org/urn:lsid:ipni.org:names:77156126-1>

*Licania rigida* Benth., *J. Bot. (Hooker)* 2: 220 (Bentham 1840). Type: Brazil, Ceará, *G. Gardner* 1592 (holotype K; isotypes BM, F, G, GH, NY, OXF, P, US, W).

*Pleragina umbrosissima* Arruda ex H. Kost. (Koster 1816: 500), *nom. inval.*, fide G. T. Prance 1966: 134.



**DISTRIBUTION AND HABITAT.** Native to northeastern Brazil, cultivated in Puerto Rico, Trinidad and Florida, and perhaps naturalised elsewhere in the Neotropics. Dry forest and gallery forest.

**IV. *Geobalanus* *Small* (1913: 80).** Type: *Geobalanus oblongifolius* (Michx.) Small.

*Suffrutex* with underground stems or small trees. *Leaves* glabrous or lanate. Petioles glandular or eglandular. *Inflorescences* panicles or cymose panicles. Bracts and bracteoles minute, persistent or caducous. Petals 5, not clawed (vs clawed in *Chrysobalanus*). Stamens 14 – 17, filaments exceeding to far-exceeding calyx lobes, in a complete circle, connate at base or to  $\frac{1}{3}$ , glabrous. *Ovary* glabrous or sparsely villous, at base of receptacle. *Fruit* ovoid, to 3 cm long; epicarp smooth, glabrous; endocarp hard, fibrous, pubescent within. Fig. 3E.

**DISTRIBUTION.** Three species distributed from southeastern United States, to Mexico, El Salvador and Costa Rica.

**NOTES.** *Geobalanus* differs from *Licania* and *Leptobalanus* by the presence of petals (vs apetalous in the other two genera). It is distinguished from *Hymenopus* by the more numerous stamens and the filaments exceeding the calyx lobes (vs 3 – 10 stamens and included in *Hymenopus*). It differs from *Chrysobalanus* by the stamens (slightly united in *Chrysobalanus* vs markedly united at the base in *Geobalanus*), the inflorescence and the unridged fruit in *Geobalanus* (vs ridged in *Chrysobalanus*). The three species of *Geobalanus* occupy distinct habitats: *G. oblongifolius* is found in pine barrens, sand dunes and oak scrubland; *G. retifolius* in gallery and non-flooded forests and *G. riverae* is found in transition forests, between humid and dry forests, from 600 – 900 m. The position of *Geobalanus* in the phylogenetic tree presented here lacks support, appearing as an early diverging genus sister to *Parastemon* and *Grangeria*, both paleotropical genera. However, other phylogenetic analyses place *G. oblongifolius* (as *L. michauxii*) sister to *Licania* s.l., *Couepia*, *Hirtella*, and *Gaulettia* (Bardon *et al.* 2016), genera to which it holds greater affinities.

### Key to species of *Geobalanus*

1. Leaves oblong-elliptic; filaments connate for  $\frac{1}{3}$  of length . . . . . **3. *G. riverae***
1. Leaves lanceolate to oblong-lanceolate; filaments connate only at base. . . . . **2**
  2. Tree; inflorescence short and dense with rachis glabrous; petioles 4 – 6 mm long; Mexico and El Salvador . . . . . **2. *G. retifolius***
  2. Suffrutex; inflorescence lax with rachis puberulous; petioles 1 – 3 mm long; SE USA. . . . . **1. *G. oblongifolius***

**1. *Geobalanus oblongifolius* (Michx.) Small (1913: 81, 200).** *Chrysobalanus oblongifolius* Michx. (Michaux 1803: 283); *Chrysobalanus incanus* Raf. (Rafinesque 1836: 26); *Licania michauxii* Prance (1970: 526). Type: U.S.A., Georgia, A. Michaux s.n. (holotype P). *Chrysobalanus retusus* Raf. (Rafinesque 1836: 26). Type: U.S.A., L. W. Nuttall (in *Herb. Collins*) s.n. (holotype BM). *Geobalanus pallidus* Small (1913: 81, 200); *Chrysobalanus pallidus* (Small) L. B. Sm. (Smith 1946: 136). Type: Florida: J. K. Small & J. J. Carter 711 (lectotype NY, fide Prance 1972a: 42).

**DISTRIBUTION AND HABITAT.** SE United States. Pine barrens, sand dunes and oak scrubland.

**2. *Geobalanus retifolius* (S. F. Blake) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:77156130-1>

*Licania retifolia* S. F. Blake, *Contr. Gray Herb.* 52: 66 (1917). Type: Mexico, Guerrero, Cerro de los Cayones, E. Langlassé 992 (holotype GH; isotypes K, P, US).

**DISTRIBUTION AND HABITAT.** Southwestern Mexico and El Salvador. Gallery and non-flooded forests; rare.

**3. *Geobalanus riverae* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:77156131-1>

*Licania riverae* Prance, *Kew Bull.* 50: 711 (1995). Type: Costa Rica, Guanacaste, P. N. Rincón de La Vieja, San Jorge, G. Rivera E. 1296 (holotype K; isotypes INB, MO).

**DISTRIBUTION AND HABITAT.** Costa Rica. Transition between humid and dry forest, 600 – 900 m.

**V. *Hymenopus* (Benth.) Sothers & Prance stat. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:77156133-1>

*Licania* sect. *Hymenopus* Benth., *J. Bot. (Hooker)* 2: 212 (Bentham 1840). Type: *Licania divaricata* Benth.

*Licania* sect. *Hirsuta* Prance (1967: 226), **synon. nov.** Type: *Licania latifolia* Benth.

*Trees.* Leaf lower surface glabrous or hirsute, never tomentose, pulverulent, farinaceous nor with stomatal cavities. Petiole with pair of glands present or not. *Inflorescences* terminal and subterminal panicles or racemose panicles. Bracts and bracteoles small, persistent to subsistent. Petals 4 – 5. Stamens 3 – 10, unilateral, in  $\frac{3}{4}$  of a circle or in a complete circle, equal or shorter than calyx; filaments glabrous, free, connate either at base only, to  $\frac{1}{2}$  length or fully connate (only in *H. conferruminatus*). *Ovary* villous, tomentose, pilose or velutinous; at base of receptacle. *Fruit* globose, ovoid, ellipsoid, pyriform, to 9 × 8 cm, epicarp costate, smooth, glabrous, lenticellate, or pilose; endocarp glabrous or sparsely puberulous within. Fig. 3D.

**DISTRIBUTION.** Twenty-eight species from Central America (Costa Rica and Panama), Trinidad and Tobago, to northern South America (Colombia, Peru, Ecuador, Bolivia, Venezuela, the Guianas, and in Brazil mainly in the Amazonian region. Absent from Mexico.

**NOTES.** The genus *Hymenopus* includes species formerly in *Licania* sect. *Hymenopus* and sect. *Hirsuta* of subgen. *Licania*, and one species formerly in subgen. *Moquilea* sect. *Microdesmia*; the apetalous species previously in sect. *Hymenopus* are transferred to *Licania* s.s.; these taxa also have unilateral stamens, a predominant character in *Licania* s.s. *Hymenopus* differs from *Licania* by the presence of petals and by the mostly glabrous or hirsute leaves. They share the ovary at the base of the receptacle and reduced number of stamens. Taxa of *Hymenopus* sequenced here are retrieved in two subclades that do not appear to have any clear morphological synapomorphies to distinguish them. Our analyses do not refute or support the two clades of *Hymenopus* as distinct from each other. We have chosen to maintain all the taxa as a single genus. Further work may prove that there is more than one distinct genus within our concept of *Hymenopus*.

### Key to species of *Hymenopus*

1. Leaf lower surface sparsely hirsute along venation or hispid at least on midrib
  2. Inflorescence and flowers sparsely hirsutulous; leaf lamina appearing deeply rugose above; primary veins and venation deeply impressed on upper surface
    3. Primary veins 13 – 17; petioles 10 – 16 mm; stamens 10. . . . . **2. H. amapaensis**
    3. Primary veins 7 – 10; petioles 6 – 10 mm; stamens 3 or 7 – 9
      4. Leaf oblong, apex acuminate; Brazil (Amazonia). . . . . **11. H. hirsutus**
      4. Leaf ovate to ovate-elliptic, apex rounded to obtuse; Central America . . . . . **7. H. costaricensis**
  2. Inflorescence and flowers densely pubescent; leaf lamina not rugose, primary veins plane or impressed and venation more or less plane on upper surface
    5. Young stems, leaf midrib, and lower inflorescence branches hispid; Venezuela (Amazonas) . . . . . **12. H. hispidus**
    5. Young stems puberulous; leaf midrib hirsute; inflorescence and exterior of flowers with short grey pubescence or densely ferruginous-tomentose
      6. Inflorescence and exterior of flowers with a short grey pubescence; Trinidad and Amazonian Venezuela, Guianas, Brazil . . . . . **10. H. heteromorphus**
      6. Inflorescence and exterior of flowers densely ferruginous-tomentose
        7. Leaf chartaceous, apex acuminate; Bolivia and Amazonia (Brazil, Ecuador, Peru) . . . . . **14. H. krukovii**
        7. Leaf thick-coriaceous, apex rounded to apiculate
          8. Primary leaf veins 6 – 9, prominent above; petioles 3 – 4 mm long; Guyana, Venezuela. . . . . **16. H. lasseri**
          8. Primary leaf veins 12 – 20, slightly impressed above; petioles 7 – 15 mm long; Guyana and Amazonia. . . . . **17. H. latifolius**
  1. Leaf lower surface glabrous
    9. Flowers in small cymules on short distinct secondary branches of inflorescence at least 1 mm long
      10. Leaves with a finely pointed acumen 15 – 30 mm long; flowers c. 1 mm long; ovary and style pubescent; Colombia (Valle) . . . . . **21. H. minutiflorus**
      10. Leaves rounded or acute to broadly acuminate, the acumen 2 – 10 mm long; flowers 2 – 5 mm long; ovary and style glabrous or pubescent
        11. Inflorescence compact and triangular, to 8 cm long; rachis and branches glabrous, the rachis not lenticellate; peduncles 2 – 4 mm long; exterior of flowers glabrous; stamens 5; Costa Rica . . . . . **24. H. operculipetalus**
        11. Inflorescence lax and spreading, over 8 cm long; rachis and branches sparsely puberulous to tomentellous; peduncles sessile to c. 1 mm long; exterior of flowers puberulous, tomentellous or tomentose; stamens 5 – 7

12. Flowers 4 – 5 mm long, inflorescence rachis 2–3 mm thick; leaves thickly coriaceous; Venezuela. . . . . **25. H. pakaraimensis**
12. Flowers 1.5 – 3 mm long; inflorescence rachis 1 mm thick; leaves chartaceous or thinly coriaceous
13. Leaf apex rounded; reticulation intricate; Trinidad and Amazonian Venezuela, Guianas, Brazil. . . . . **10. H. heteromorphus**
13. Leaf apex acuminate; reticulation lax; Amazonia
14. Petioles 7 – 12 mm long, with 2 glands near junction of lamina; inflorescence rachis lenticellate; stamens 6 – 7; endocarp longitudinally striate; Amazonia . . . **27. H. reticulatus**
14. Petioles 4 – 6 mm long, eglandular; inflorescence rachis not lenticellate; stamens 5; endocarp not striate; Brazil (C Amazonia) . . . . . **1. H. adolphoduckei**
9. Flowers borne mainly on primary branches of inflorescence or on secondary branches, but not in pedunculate cymules
15. Leaves narrowly oblong with nearly parallel sides; stamens usually slightly exceeding calyx lobes; mouth of receptacle filled by a dense lanate mass; petals slightly unguiculate
16. Receptacle narrowly urceolate, densely arachnoid-pubescent; flowers in dense glomerules on primary branches; Guyana and western Amazonia . . . . . **4. H. arachnoideus**
16. Receptacle campanulate, puberulous; flowers not densely glomerulate
17. Flowers 1.5 – 2 mm long; leaves to 17 cm long, usually smaller; stipules to 5 mm, caducous; Brazil (Amazonia) . . . . . **22. H. oblongifolius**
17. Flowers 2.5 – 3 mm long; leaves usually exceeding 16 cm in length (to 40 cm); stipules to 15 mm, subsistent; Guianas, Venezuela, eastern Brazilian Amazonia. . . . . **19. H. macrophyllus**
15. Leaves ovate to oblong-lanceolate, but sides converging; stamens shorter than calyx lobes; mouth of receptacle with short deflexed hairs only; petals with broad simple bases
18. Exterior of flowers and rachis and branches of inflorescence glabrous or sparsely hirsutulous; filaments connate for at least ½ length
19. Leaf apex caudate to cuspidate
20. Leaves elliptic, coriaceous, the apex caudate; petioles 5 – 7 mm long; French Guiana, Brazil (Amazonia), Colombia, Peru. . . . . **5. H. caudatus**
20. Leaves narrowly oblong, chartaceous, the apex cuspidate; petioles 1 – 3 mm long; Brazil (Mato Grosso) . . . . . **20. H. miltonii**
19. Leaf apex acute to acuminate
21. Stipules large and foliaceous, caducous; exterior of flowers glabrous; French Guiana, Venezuela . . . . . **18. H. latistipulus**
21. Stipules small, lanceolate, persistent; exterior of flowers hirsutulous
22. Leaves 20 – 31 × 6.5 – 11.5 cm, primary veins and midrib slightly impressed above; petioles 10 – 13 mm; Brazil (Rondônia) . . . . . **6. H. conferruminatus**
22. Leaves up to 27 × 10 cm usually much smaller, primary veins and midrib plane or impressed above; petioles 2 – 9 mm
23. Leaves 9 – 27 cm long, thick-coriaceous, the apex abruptly short-acuminate; primary veins plane above; Guianas, Brazil (Pará) . . . . . **8. H. divaricatus**
23. Leaves 7 – 11 cm long, membranous, the apex with a well-developed acumen 5 – 9 mm long; primary veins slightly impressed above; Costa Rica, Venezuela, Brazil (Pará) . . . . . **9. H. glabriflorus**
18. Exterior of flowers and usually rachis and branches of inflorescence densely puberulous to tomentose; pubescence completely covering exterior of calyx; filaments free to base
24. Midrib broad towards base, 2 – 3.5 mm thick; leaves very thick-coriaceous; stipules to 15 mm long, subsistent; anthers deltoid or nearly so; Amazonia . . . . . **13. H. intrapetiolaris**
24. Midrib narrower towards base, 1 – 2 mm thick; leaves membranous to coriaceous; stipules to 8 mm long, persistent to caducous; anthers reniform
25. Calyx lobes and petals 4; stamens 3 . . . . . **3. H. arachicarpus**
25. Calyx lobes and petals 5; stamens 5 – 7
26. Leaf apex long acuminate, base cuneate, petioles eglandular, leaf base confluent into petiole
27. Leaves 9 – 18 × 4.2 – 7 cm; flowers brown pubescent; Guianas, Brazil (Amazonia) . . . . . **15. H. laevigatus**
27. Leaves 4 – 5 × 2.5 – 3.8 cm; flowers grey pubescent; Brazil (Amazonia) . . . **23. H. occultans**
26. Leaf apex retuse to bluntly acuminate, base subcordate, rounded, subcuneate; petioles usually glandular, leaf base not confluent; Trinidad and Amazonia

28. Stipules 5 – 6 mm long, caducous; primary veins prominulous above; petioles 8 – 13 mm, with 2 prominent raised glands; Brazil (C Amazonia) . . . . . **28. H. sothersiae**
28. Stipules 1 – 3.5 mm long, persistent or caducous; primary veins plane or slightly impressed above; petioles 3 – 12 mm, eglandular or with 2 ± sessile glands
29. Primary veins plane above, secondary venation plane or only slightly raised; petioles usually glandular, endocarp usually smooth, not angular (ridged in var. *glabrus*); Amazonia . . . . . **10. H. heteromorphus**
29. Primary veins slightly impressed above, secondary venation prominently reticulate; petioles eglandular; endocarp angular but not ridged; Venezuela, Brazil (C Amazonia) . . . . . **26. H. prismatocarpus**

**1. *Hymenopus adolphoduckei* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:77156951-1>

*Licania adolphoduckei* Prance, *Novon* 11: 325 (2001).  
Type: Brazil, Amazonas, Reserva Florestal Ducke, Manaus – Itacoatiara road, km 26, P. A. C. L. Assunção 502 (holotype INPA; isotype K).

**DISTRIBUTION AND HABITAT.** Brazil, central Amazonia. Beside rivers and streams in forest, on sandy soil.

**2. *Hymenopus amapaensis* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:77156952-1>

*Licania amapaensis* Prance, *Fl. Neotrop. Monogr.* 9: 174 (1972a). Type: Brazil, Amapá, rio Araguari, Serra do Navio, J. M. Pires, W. A. Rodrigues & G. C. Irvine 51198 (holotype NY; isotypes IAN, INPA, K, MG).

**DISTRIBUTION AND HABITAT.** Northern Brazil and French Guiana. Non-flooded forest.

**3. *Hymenopus arachicarpus* (N. Zamora) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:77156953-1>

*Licania arachicarpa* N. Zamora, *Phytoneuron* 26: 1 (2013). Type: Costa Rica, Heredia, Sarapiquí, Finca La Selva, the OTS Field Station on the Rio Viejo just E of its junction with the Rio Sarapiquí, about 100 m, B. Hammel 11149 (holotype CR; isotypes CAS, LSCR, MO, NY).

**DISTRIBUTION AND HABITAT.** Costa Rica (Osa Peninsula). Tropical wet forest formations.

**4. *Hymenopus arachnoideus* (Fanshawe & Maguire) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:77156954-1>

*Licania arachnoidea* Fanshawe & Maguire, *Bull. Torrey Bot. Club* 75: 318 (Maguire 1948a). Type: Guyana, Bartica-Potaro road, D. B. Fanshawe 1495 (F.D.4231) (holotype NY; isotypes IAN, K).

**DISTRIBUTION AND HABITAT.** Guyana, Amazonian Brazil and western Amazonia in Colombia, Ecuador and Peru. Non-flooded forest.

**5. *Hymenopus caudatus* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:77156955-1>

*Licania caudata* Prance, *Fl. Neotrop. Monogr.* 9: 100 (1972a). Type: Brazil, Amazonas, Manaus, D. Coelho INPA 3946 (holotype NY; isotypes IAN, INPA, MG, RB).

**DISTRIBUTION AND HABITAT.** Widespread in Amazonia (Guianas, Colombia, Ecuador, Peru, Brazil). Flooded as well as non-flooded forest.

**6. *Hymenopus conferruminatus* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:77156956-1>

*Licania conferruminata* Prance, *Kew Bull.* 49: 362 (1994). Type: Brazil, Rondônia, Ji-Paraná, 45 km from town on line 56, C. A. Cid Ferreira 9032 (holotype INPA; isotypes CAS, K, MO).

**DISTRIBUTION AND HABITAT.** Brazil; known only from the type collection. Forest on terra firme.

**7. *Hymenopus costaricensis* (Standl. & Steyerl.) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:77156957-1>

*Licania costaricensis* Standl. & Steyerl., *Publ. Field Mus. Nat. Hist., Bot. Ser.* 22: 335 (Standley & Steyermark)



1940). Type: Costa Rica, Alajuela, San Carlos, Vila Guesada, *Au. Smith* 1779 (holotype F; isotypes MO, NY, US; phototype K).

**DISTRIBUTION AND HABITAT.** Costa Rica and Panama. Collected in hill pastures in the Alajuela province of Costa Rica and in lowland forest in Panama.

**8. *Hymenopus divaricatus* (Benth.) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:77156958-1>

*Licania divaricata* Benth., *J. Bot. (Hooker)* 2: 221 (Bentham 1840); *Licania heteromorpha* Benth. var. *divaricata* (Benth.) Fritsch (1889: 45). Type: Guyana, *R. & R. Schomburgk* 463 (holotype K; isotypes BM, CGE, G, L, NY, OXF, P, W).

**DISTRIBUTION AND HABITAT.** Guianas and northern Brazil. Forest on terra firme and savanna margins.

**9. *Hymenopus glabriflorus* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:77156959-1>

*Licania glabriflora* Prance, *Fl. Neotrop. Monogr.* 9: 104 (1972a). Type: Venezuela, Bolívar, Sierra Imataca, Río Reforma, *J. A. Steyermark* 87907 (holotype NY).

**DISTRIBUTION AND HABITAT.** Costa Rica, Colombia, Venezuela, Guianas and Brazil (Amapá, Pará). Terra firme forest.

**10. *Hymenopus heteromorphus* (Benth.) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:77156960-1>

*Licania heteromorpha* Benth., *J. Bot. (Hooker)* 2: 221 (Bentham 1840). Type: Guyana, *R. & R. Schomburgk* 873 (holotype K; isotypes BM, F, GH, L, NY, OXF, P, US, W).

*Licania guianensis* Klotzsch in M. R. Schomb. (Schomburgk 1848: 1199), *nom. nud.*

**DISTRIBUTION AND HABITAT.** Central and South America. A variable and widespread species which we divide into five varieties. For distribution see under each variety.

**10a. *Hymenopus heteromorphus* var. *heteromorphus***

*Licania benthamii* Hook. f. (Hooker 1867: 12). Type: Venezuela, Amazonas, Vasiva and Pacimoni, *R. Spruce* 3278 (lectotype K, fide Prance 1972a: 106; isolectotypes BM, BR, C, CGE, GH, GOET, LD, LE, NY, OXF, P, RB, TCD).

*Licania biglandulosa* Griseb. ex Urb. (Urban 1908: 354). Type: Trinidad, *H. Cruieger* 105 (lectotype GOET, fide Prance & Sothers 2003a: 114; isolectotype K).

**DISTRIBUTION AND HABITAT.** Trinidad to Colombia and Peru, the Guianas, Venezuela, Brazil and Bolivia. Commonest in periodically flooded forest, but occurring elsewhere.

**10b. *Hymenopus heteromorphus* var. *glabrus* (Mart. ex Hook. f.) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:77156962-1>

*Licania glabra* Mart. ex Hook. f., *Fl. Bras.* 14 (2): 10 (Hooker 1867); *Licania heteromorpha* var. *glabra* (Mart. ex Hook. f.) Prance (1972a: 108). Type: Venezuela, Amazonas, Río Guainia, mouth of Río Casiquiare, *R. Spruce* 3503 (lectotype K, fide Prance 1972a: 108; isolectotypes NY, TCD, P).

*Licania costata* Spruce ex Hook. f. (Hooker 1867: 10), *nom. nud. in synonym.*

**DISTRIBUTION AND HABITAT.** Colombia, Venezuela, Guyana, French Guiana, Brazil, Bolivia and Peru. Riverine forest mainly in W Amazonia, but scattered throughout the basin.

**10c. *Hymenopus heteromorphus* var. *subcordatus* (Fritsch) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:77156963-1>

*Licania heteromorpha* var. *subcordata* Fritsch, *Ann. K. K. Naturhist. Hofmus.* 4: 45 (1889); *Licania subcordata* Fritsch (1894: 18). Type: Brazil, Amazonas, *J. E. Pohl* 4402 (lectotype W, fide Prance 1972a: 108).

**DISTRIBUTION AND HABITAT.** Amazonian Venezuela and Brazil. Riverine forest.

**10d. *Hymenopus heteromorphus* var. *perplexans* (Sandwith) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:77156964-1>

*Licania heteromorpha* var. *perplexans* Sandwith, *Bull. Misc. Inform., Kew* 1931: 371 (1931). Type: Guyana, Roraimas, *R. & R. Schomburgk* 824 (holotype K; isotypes NY, W).



**DISTRIBUTION AND HABITAT.** Guyana. Forest.

**10e. *Hymenopus heteromorphus* var. *revolutus*** (Prance) Sothers & Prance **comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:77156968-1>

*Licania heteromorpha* var. *revoluta* Prance, *Acta Amazon.* 13 (1): 24 (1983). Type: Brazil, Amazonas, 20 km NW of Manaus, Tarumã, B. W. & S. P. Nelson 1058 (holotype INPA; isotypes K, NY, RB).

**DISTRIBUTION AND HABITAT.** Brazil; known only from the type collection. Forest on terra firme, clay soil.

**11. *Hymenopus hirsutus*** (Prance) Sothers & Prance **comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:77156974-1>

*Licania hirsuta* Prance, *Fl. Neotrop. Monogr.* 9: 92 (1972a). Type: Brazil, Amazonas, rio Tefé, R. L. Fróes 26137 (holotype NY; isotypes IAN, NY).

**DISTRIBUTION AND HABITAT.** French Guiana, Peru and Brazilian Amazonia. Flooded or non-flooded forest.

**12. *Hymenopus hispidus*** (Prance) Sothers & Prance **comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:77156975-1>

*Licania hispida* Prance, *Fl. Neotrop. Monogr.* 9S: 37 (1989). Type: Venezuela, Amazonas, Dept. Río Negro, Cerro Aratitoye, J. A. Steyermark, P. E. Berry & F. Delascio 130185 (holotype NY; isotype MO).

**DISTRIBUTION AND HABITAT.** Venezuela; known only from the type. Forest at base of high bluffs of an igneous rock mountain.

**13. *Hymenopus intrapetiolaris*** (Spruce ex Hook. f.) Sothers & Prance **comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:77156976-1>

*Licania intrapetiolaris* Spruce ex Hook. f., *Fl. Bras.* 14 (2): 11 (Hooker 1867). Type: Venezuela, Amazonas, Río Guainia, R. Spruce 3539 (lectotype K, fide Prance 1972a: 105; isolectotypes BM, BR CGE, E, LE, NY, OXF, P, TCD, W).

*Licania heteromorpha* var. *grandifolia* Benoist (1919: 513). Type: French Guiana: Cayenne, J. Martin s.n. (syntype K).

*Licania intrapetiolaris* var. *brevis* J. F. Macbr. (Macbride 1934: 369). Type: Peru: Mishuyacu, near Iquitos, G. Klug 612 (holotype F).

**DISTRIBUTION AND HABITAT.** Guianas, N Brazil and Amazonian Colombia, Peru and Venezuela. Lowland forest in open places.

**14. *Hymenopus krukovii*** (Standl.) Sothers & Prance **comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:77156977-1>

*Licania krukovii* Standl., *Field Mus. Nat. Hist., Bot. Ser.* 17 (3): 256 (Standley 1937). Type: Brazil, Amazonas, near mouth of rio Embira, B. A. Krukoff 5070 (holotype F; isotypes A, BM, K, LE, M, MICH, MO, NY, S, US).

**DISTRIBUTION AND HABITAT.** Western Amazonia in Bolivia, Ecuador, Peru, Brazil. Forest on high ground, and upland in Bolivia.

**15. *Hymenopus laevigatus*** (Prance) Sothers & Prance **comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:77156981-1>

*Licania laevigata* Prance, *Fl. Neotrop. Monogr.* 9S: 41 (1989). Type: Brazil, Amazonas, Manaus-Caracará Rd., km 45, M. F. Silva & L. Coelho 80 (holotype INPA35442; isotype NY).

**DISTRIBUTION AND HABITAT.** Venezuela, Guianas, Brazil and Peru. Terra firme forest.

**16. *Hymenopus lasserii*** (Maguire) Sothers & Prance **comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:77156982-1>

*Licania lasserii* Maguire, *Fieldiana, Bot.* 28: 253 (1952). Type: Venezuela, Bolívar, Kavanayen, T. Lasser 1730 (holotype NY; isotype F).

**DISTRIBUTION AND HABITAT.** Colombia, Guyana and adjacent Venezuela. Open forest on slopes, and savanna and river margins.

**17. *Hymenopus latifolius*** (Benth. ex Hook. f.) Sothers & Prance **comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:77156992-1>

*Licania latifolia* Benth. ex Hook. f., *Fl. Bras.* 14 (2): 11 (Hooker 1867). Type: Brazil, Pará, Óbidos,

*R. Spruce* 457 (lectotype K, fide Prance 1972a: 96; isolectotypes CGE, NY, OXF, P).

*Licania obovata* Benth. ex Hook. f. (Hooker 1867: 11). Type: Brazil, Amazonas, Manaus, *R. Spruce* 1569 (lectotype K, fide Prance 1972a: 95; isolectotypes BM, C, CGE, E, GH, GOET, K, LD, LE, M, NY, OXF, P, TCD).

**DISTRIBUTION AND HABITAT.** Guianas, Venezuela and Amazonian Ecuador, Peru and Brazil. Non-flooded forest.

**18. *Hymenopus latistipulus* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:77156996-1>

*Licania latistipula* Prance, *Fl. Neotrop. Monogr.* 9: 103 (1972a). Type: Venezuela, Delta Amacuro, east of Río Grande, ENE of El Palmar, near boundary of Bolívar State, *L. Marciano-Berti* 346 (holotype VEN; isotype VEN).

**DISTRIBUTION AND HABITAT.** French Guiana and Venezuela. Forest on high ground.

**19. *Hymenopus macrophyllus* (Benth.) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:77157006-1>

*Licania macrophylla* Benth., *Hooker's J. Bot. Kew Gard. Misc.* 2: 240 (Bentham 1850). Type: Brazil, Pará, near Belém, *R. Spruce* 139 (lectotype K, fide Prance 1972a: 100; isolectotypes CGE, NY, OXF, P, W s.n., probable isotype).

**DISTRIBUTION AND HABITAT.** Guianas, Venezuela, Peru and Amazonian Brazil. Periodically flooded forest.

**20. *Hymenopus miltonii* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472813-2>

*Licania miltonii* Prance, *Acta Amazon.* 13 (1): 24 (1983). Type: Brazil, Mato Grosso, Aripuanã, BR-164, Núcleo Juína, *M. G. Silva & A. Pinheiro* 4296 (holotype MG; isotype NY).

**DISTRIBUTION AND HABITAT.** C & W Brazil (Mato Grosso, Acre). Forest on terra firme, clay soil.

**21. *Hymenopus minutiflorus* (Cuatrec.) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472814-2>

*Licania minutiflora* Cuatrec., *Fieldiana, Bot.* 27: 64 (Cuatrecasas 1950), non *L. minutiflora* (Sagot) Fritsch (1889); *Licania minuscula* Cuatrec. (Cuatrecasas 1951: 113). Type: Colombia, Chocó, *J. Cuatrecasas* 21546 (holotype F; isotypes COL, P).

**DISTRIBUTION AND HABITAT.** Colombia; known only from the original collections. Gallery forest.

**22. *Hymenopus oblongifolius* (Standl.) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472815-2>

*Licania oblongifolia* Standl., *Field Mus. Nat. Hist., Bot. Ser.* 17 (3): 257 (Standley 1937). Type: Brazil, Amazonas, Humaitá, *B. A. Krukoff* 6812 (holotype F; isotypes A, B, BM, BR, K, LE, MICH, MO, NY, RB, S, US).

**DISTRIBUTION AND HABITAT.** Amazonia: Venezuela, Peru and Brazil (Amazonas, Pará). Non-flooded forest.

**23. *Hymenopus occultans* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472816-2>

*Licania occultans* Prance, *Fl. Neotrop. Monogr.* 9S: 42 (1989). Type: Brazil, Amazonas, Manaus-Itacoatiara Rd., km 31, *W. C. Steward & J. F. Ramos* P17669 (holotype INPA; isotypes MO, NY).

**DISTRIBUTION AND HABITAT.** Central Amazonia and French Guiana. Forest on terra firme.

**24. *Hymenopus operculipetalus* (Standl. & L. O. Williams) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472817-2>

*Licania operculipetala* Standl. & L. O. Williams, *Ceiba* 3: 46 (Standley & Williams 1952). Type: Costa Rica, Puntarenas, Palmar, S of Osa, *P. H. Allen* 6030 (holotype EAP, *n.v.*; isotypes GH, US; phototype K).

**DISTRIBUTION AND HABITAT.** Known only from Costa Rica. Forested hills.

**25. *Hymenopus pakaraimensis* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472818-2>

*Licania pakaraimensis* Prance, *Brittonia* 28: 218 (1976).  
Type: Venezuela, Bolívar, Sierra Pakaraima, headwaters of Río Paragua, J. A. Steyermark 107357 (holotype NY; isotypes MO, VEN).

**DISTRIBUTION AND HABITAT.** Venezuela; known only from the type collection. Submontane forest at 1400 m.

**26. *Hymenopus prismatocarpus*** (Spruce ex Hook. f.) Sothers & Prance **comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472819-2>

*Licania prismatocarpa* Spruce ex Hook. f., *Fl. Bras.* 14 (2): 19 (Hooker 1867). Type: Venezuela, Amazonas, San Carlos, Río Negro, R. Spruce 3490 (lectotype K, fide Prance 1972a: 106; isoelectotypes BM, BR, CGE, GH, LD, LE, NY, OXF, P, TCD, W).

**DISTRIBUTION AND HABITAT.** Central Amazonian Brazil and Venezuela. Forest on terra firme.

**27. *Hymenopus reticulatus*** (Prance) Sothers & Prance **comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472820-2>

*Licania reticulata* Prance, *Fl. Neotrop. Monogr.* 9: 97 (1972a). Type: Brazil, Amazonas, Manaus, Parque 10, F. Mello & L. Coelho s.n. (holotype NY; isotypes IAN, INPA 4141, MG).

**DISTRIBUTION AND HABITAT.** French Guiana, western (Colombia, Ecuador, Peru) and Brazilian Amazonia. Non-flooded and periodically flooded forest.

**28. *Hymenopus sothersiae*** (Prance) Sothers & Prance **comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472821-2>

*Licania sothersiae* Prance, *Novon* 11: 328 (2001). Type: Brazil, Amazonas, Manaus, Reserva Florestal Ducke, J. E. L. S. Ribeiro 1142 (holotype INPA; isotype K).

**DISTRIBUTION AND HABITAT.** Brazil, central Amazonia. Forest on terra firme.

**VI. *Leptobalanus*** (Benth.) Sothers & Prance **stat. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472823-2>

*Licania* sect. *Leptobalanus* Benth., *J. Bot. (Hooker)* 2: 212 (Bentham 1840). Type: *Licania apetala* (E. Mey.) Fritsch.

*Licania* sect. *Batheogyne* Benth. (Bentham 1840: 212). Type: *L. turbinata* Benth.

*Trees.* Leaf lower surface glabrous, tomentose or lanate, stomatal cavities present or absent. Petiole with or without glands. *Inflorescence* panicle, racemose panicle or panicle of cymes. Bracteoles small. Petals absent. Stamens (7 –) 8 – 10 (12 – 14) (19 in *L. joseramosii*; 22 in *L. calvescens*), filaments usually far exceeding calyx lobes (equalling or shorter in *L. emarginatus*), in a complete circle; filaments free or less often slightly connate at base, glabrous. *Ovary* villous or bearing some form of pilosity, or in some species glabrous above and densely villous or tomentose at base only, rarely entirely glabrous (*L. undulatus*); inserted at base of receptacle. *Fruit* globose to ellipsoid, 5.5 × 2 – 2.5 cm; epicarp smooth, lenticellate or pubescent; endocarp pubescent or rarely glabrous (*L. granvillei* and *L. sparsipilis*). Fig. 3B.

**DISTRIBUTION.** Thirty-one species, from Mexico, Central America and the Caribbean through to northern South America, the Guianas, Peru, Ecuador, Bolivia and SE Brazil.

**NOTES.** *Leptobalanus* includes species previously in *Licania* sect. *Leptobalanus*. The genus is apetalous as in core *Licania*, but differs by the mostly far-exserted to exerted stamens (vs included in *Licania*) and the slightly more numerous stamens (vs 3 – 8 in *Licania*), although there is an overlap with some species of *Licania* displaying 8 – 11 stamens. *Leptobalanus* shares a similar number of stamens with *Hymenopus* but differs by the absence of petals (vs presence of petals in *Hymenopus*) and the exerted stamens (vs included in *Hymenopus*). In *Leptobalanus* the stamens are in a complete circle (vs mostly unilateral in *Licania*). In molecular phylogenetic analyses *Leptobalanus* is retrieved in a clade with *Microdesmia*, *Afrolicania*, *Parinariopsis*, *Cordillera*, *Gaulettia* and *Hymenopus*.

**Key to species of *Leptobalanus*** (key does not include *L. mexicanus* as it is imperfectly known)

1. Leaf lower surface glabrous or lanate, the venation not prominent, stomatal cavities absent; stamens 8 – 14 (–22) (19 in *L. joseramosii*; 22 in *L. calvescens*)
2. Stamens exerted well beyond calyx lobes
  3. Most flowers borne in small groups or cymules on distinct secondary branches (peduncles) of inflorescence; peduncles over 2 mm long
  4. Rachis of inflorescence densely yellow-villous-tomentose; Amazonia (Brazil, Colombia, Venezuela) . . . . . **31. *L. wurdackii***

4. Rachis of inflorescence grey-puberulous
  5. Inflorescence short and compact, 3 – 5 cm long; flowers 4 – 5 mm long; leaves ovate; NE Brazil . . . . . **29. *L. turbinatus***
  5. Inflorescence longer and spreading, 6 – 20 cm long; flowers 2 – 3.5 mm long; leaves oblong to elliptic
    6. Flowers 3.5 – 5 mm long; petioles deeply canaliculate; with 2 prominent glands at lamina base; rachis arachnoid-pubescent when young; Amazonia. . . . . **17. *L. latus***
    6. Flowers 2 – 3 mm long; petioles terete to shallowly canaliculate; lamina base eglandular; rachis puberulous; Guianas, Brazil to S Amazonia . . . . . **2. *L. apetalus***
3. Flowers borne on primary branches of inflorescence; peduncles usually sessile
  7. Leaf apex predominantly obtuse to rounded
    8. Rachis of inflorescence densely villous-tomentose; flowers c. 4 mm long; NW Amazonia (Colombia, Brazil, Venezuela). . . . . **31. *L. wurdackii***
    8. Rachis of inflorescence grey-puberulous; flowers 3 mm long; Guianas, Brazil (Amazonia) . . . . . **23. *L. parvifolius***
  7. Leaf apex distinctly acuminate (rarely only bluntly acuminate in *L. jefensis*)
    9. Flowers 4 – 5 mm long; receptacle cupuliform (except in *L. diegogomezii*)
      10. Leaves with hispid pubescence on venation otherwise glabrous; receptacle campanulate; leaf base subcordate; Costa Rica . . . . . **8. *L. diegogomezii***
      10. Leaves glabrous or with short waxy lanate-pulverulent pubescence beneath; receptacle urceolate; leaf base usually rounded to subcuneate
        11. Leaves glabrous beneath, inflorescence grey-villous-tomentose; Brazil (Mato Grosso). . . . . **19. *L. maguirei***
        11. Leaves with short persistent waxy lanate-pulverulent pubescence beneath; inflorescence brown-puberulous to tomentellous when mature; Amazonian Colombia, Peru, Brazil. . . . . **17. *L. latus***
    9. Flowers 2 – 3.5 mm long; receptacle urceolate or campanulate
      12. Stipules persistent on young branches; petioles densely tomentose when young, 2.5 – 3.5 mm thick; upper portion of ovary glabrous; central Brazil . . . . . **12. *L. gardneri***
      12. Stipules usually caducous; petioles sparsely lanate-pubescent, puberulous, or glabrous, to 2 mm thick; upper portion of ovary pubescent
        13. Inflorescence sparsely hirsutulous or yellow-arachnoid-tomentose; flower exterior yellow-brown-tomentose; petioles 2 – 3 mm long, canaliculate
          14. Inflorescence sparsely hirsutulous; leaf apex finely acuminate, the acumen 5 – 10 mm long; northern Colombia . . . . . **7. *L. cuspidatus***
          14. Inflorescence arachnoid-tomentose; leaf apex acute or bluntly acuminate, the acumen 3 – 5 mm long; Panama . . . . . **15. *L. jefensis***
        13. Inflorescence puberulous to tomentose; flower exterior grey-tomentose; petioles 3 – 11 mm long, terete or shallowly canaliculate towards base
          15. Leaf bases subcordate; Panama . . . . . **21. *L. morii***
          15. Leaf bases cuneate or subcuneate to rounded
            16. Leaf lower surface rufous-brown-pubescent, with deeply reticulate venation; petioles 8 – 11 mm long; leaf apex acuminate or cuspidate; inflorescence brown-tomentellous or tomentellous
              17. Leaf apex acuminate, the acumen 5 – 10 mm; stamens 7 – 8; Costa Rica. . . . . **28. *L. stevensii***
              17. Leaf apex cuspidate, the acumen 10 – 15 mm long; stamens 10 – 12; Colombia . . . . . **6. *L. cuatrecasii***
            16. Leaf lower surface glabrous or rarely white-arachnoid-pubescent, venation smooth, not deeply reticulate; petioles 3 – 8 mm long (9 – 11 in *L. undulatus*); leaf apex acuminate; inflorescence brown or grey-puberulous to tomentose
              18. Rachis and branches of inflorescence tomentose; petioles usually bearing 2 distinct glands; Central America . . . . . **26. *L. sparsipilis***
              18. Rachis and branches of inflorescence puberulous; petioles eglandular
                19. Leaves oblong lanceolate, margins undulate; Colombia (Caquetá). . . . . **30. *L. undulatus***
                19. Leaves elliptic to oblong, margins entire

20. Leaves bullate; stamens 8; Peru . . . . . **3. L. bullatus**
20. Leaves not bullate; stamens 14
21. Inflorescence and flower exterior sparsely puberulous; leaves thickly coriaceous, the apex finely attenuate with acumen 10 – 25 mm long; Guianas, N Amazonian Brazil . . . **13. L. granvillei**
21. Inflorescence usually densely grey-puberulous; leaves chartaceous, the apex acuminate with acumen 3 – 15 mm long; Colombia, Peru, Venezuela to southern Brazil . . . **2. L. apetalus**
2. Stamens not or scarcely exceeding calyx lobes
22. Leaf lower surface lanate; flowers sessile on primary branches of inflorescence; stamens c. 22; Colombia (Valle) . . . . . **4. L. calvescens**
22. Leaf lower surface glabrous; flowers in groups on distinct secondary branches of inflorescence; stamens 10 – 19; Amazonia
23. Stamens c. 19; leaves 15 – 20 cm long, with long acumen 11 – 19 mm long; flowers c. 5 mm long; Brazil (N Amazonia) . . . . . **16. L. joseramosii**
23. Stamens 10 – 11; leaves 3 – 8.5 cm long, with acumen 0 – 6 mm long; flowers 2 – 3 mm long; Peru, Venezuela, Amazonian Brazil . . . . . **9. L. emarginatus**
1. Leaf lower surface with stomatal cavities or very deeply cut reticulation resembling stomatal cavities, lanate-pubescent in mouth of cavities; stamens 8 – 13
24. Inflorescence with secondary branches; flowers on distinct secondary branches of inflorescence that are at least 2 mm long
25. Flowers in small distinct groups or in cymules on short secondary branches (peduncles); leaf upper surface smooth, the base rounded to cuneate
26. Inflorescence 15 – 22 cm long, ferruginous-arachnoid; leaf lower surface brown when dry; Guyana . . . . . **24. L. persaudii**
26. Inflorescence 6 – 8 cm long, grey-arachnoid or puberulous; leaf lower surface grey when dry; Guianas, Brazil (northern Amazonia) . . . . . **27. L. sprucei**
25. Flowers more or less clustered in large groups on primary and secondary branches of inflorescence, but without distinct peduncles; leaf upper surface usually papillose, the base often cordate; Brazil (Amazonia and south) . . . . . **25. L. sclerophyllus**
24. Inflorescence with primary branches only; flowers on primary branches of inflorescence, sessile or rarely with short peduncles not exceeding 1 mm in length
27. Pedicels 2 mm long (in bud), to 4 mm in flower; Guianas . . . . . **1. L. albiflorus**
27. Pedicels not exceeding 2 mm, often shorter
28. Leaf reticulation extremely prominent on upper surface; fruit exterior appressed-sordid-yellow-velutinous
29. Leaves deeply cordate; Colombia, Venezuela . . . . . **5. L. cardiophyllus**
29. Leaves rounded to subcuneate at base
30. Petioles 5 – 13 mm long; flowers c. 3 mm long, borne on slender branchlets 0.5 – 1 mm thick; receptacle campanulate; flowers and inflorescence grey-tomentose; Panama, Venezuela, Guianas, western and central Amazonia (Brazil, Ecuador, Peru) . . . . . **18. L. longistylus**
30. Petioles 15 – 20 mm long; flowers c. 4 mm long, borne on branchlets c. 2 mm thick; receptacle cupuliform; flowers and inflorescence brown-tomentose; Colombia (Pacific) . . . . . **11. L. fuchsii**
28. Leaf reticulation prominulous on upper surface; fruit exterior glabrous or brown-tomentose
31. Young branches densely tomentellous, with a thick corky bark; central Brazil . . . . . **14. L. humilis**
31. Young branches glabrous or nearly so, the bark thin
32. Flowers 3.5 – 5 mm long; leaf apex mucronate; Guyana . . . . . **10. L. foveolatus**
32. Flowers 2 – 3 mm long; leaf apex rounded to acuminate
33. Leaf apex finely acuminate, leaves narrowly oblong; Central America . . . . . **15. L. jefensis**
33. Leaf apex acute to bluntly acuminate, leaves ovate to oblong; Brazil (Amazonia), Venezuela, Guianas . . . . . **22. L. octandrus**

**1. Leptobalanus albiflorus** (Fanshawe & Maguire)  
Sothers & Prance **comb. nov.**

*Licania albiflora* Fanshawe & Maguire, *Bull. Torrey Bot. Club*  
75: 318 (Maguire 1948a). Type: Guyana, Madray-  
Bubu trail, Essequibo-Demerara Region, *D. B.*  
*Fanshawe* 1678 (*F.D.* 4414) (holotype NY; isotype K).

<http://www.ipni.org/urn:lsid:ipni.org:names:60472825-2>



**DISTRIBUTION AND HABITAT.** Guianas, rare but widespread. Primary forest.

**2. *Leptobalanus apetalus* (E. Mey.) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472826-2>

*Hirtella apetalus* E. Mey., *Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur.* 12: 803 (Meyer 1825); *Licania apetalus* (E. Mey.) Fritsch (1889: 54). Type: Suriname, Meyer s.n. (holotype GOET; isotype M).

**2a. *Leptobalanus apetalus* (E. Mey.) Sothers & Prance var. *apetalus*.** Type: Suriname, Meyer s.n. (holotype GOET; isotype M).

*Licania pendula* Benth. (Bentham 1840: 218); *Moquilea pendula* (Benth.) Hook. f. (Hooker 1867: 22); *Licania apetalus* var. *pendula* (Benth.) Fritsch (1889: 55). Type: Brazil, lagoons of rio Negro, R. & R. Schomburgk 906 (holotype K; isotypes BM, CGE, E, F, GH, LE, NY, OXF, P, TCD, US, W).

*Licania floribunda* Benth. (Bentham 1840: 219); *Moquilea floribunda* (Benth.) Hook. f. (Hooker 1867: 21). Type: Guyana, without locality, R. & R. Schomburgk 897 (holotype K; isotypes BM, CGE, E, F, GH, L, OXF, P, US, W).

*Moquilea orinocensis* Rusby (1920: 27). Type: Venezuela: Punta Piedra Is., H. H. Rusby & R. W. Squires 426 (holotype NY; isotypes F, K, M, MO, Z).

*Licania dahlgrenii* Standl. (Standley 1937: 255). Type: Brazil, Piauí, Pedro Segundo, B. E. Dahlgren 876 (holotype F; isotypes P, S, US).

*Licania hylaea* Cuatrec. (Cuatrecasas 1956: 198). Type: Colombia, Amazonas, Río Apaporis between Río Kananari and Pacoa, H. García-Barriga 14100 (holotype US; isotypes COL, NY).

**DISTRIBUTION AND HABITAT.** Throughout the Guianas, Venezuela, Bolivia, Ecuador, Peru, Colombia, and in Amazonian, northeastern, central and southeastern Brazil. Gallery forest, periodically flooded forest, river margins, savanna margins, and open river beaches on sandy soil.

**2b. *Leptobalanus apetalus* var. *apertus* (Benth.) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472827-2>

*Licania aperta* Benth., *J. Bot. (Hooker)* 2: 218 (Bentham 1840); *Licania apetalus* var. *aperta* (Benth.) Prance (1972a: 68). Type: Guyana, R. & R. Schomburgk 593 (holotype K; isotypes BM, BR, CGE, E, GH, L, NY, OXF, P).

*Licania pubiflora* Benth. (Bentham 1840: 219). Type: Guyana, R. & R. Schomburgk 136 (holotype K; isotypes BM, CGE, NY, OXF, P, TCD).

*Licania caracasana* Klotzsch ex Hook. f. (Hooker 1867: 25), *nom. nud. in synon.*

*Licania affinis* Kuntze (1891: 217), *nom. illegit., non* Fritsch (1889).

*Licania kuntzeana* Urb. (Urban 1908: 353); *Moquilea kuntzeana* (Urb.) R. O. Williams (1932: 314). Type: Trinidad-Tobago, Trinidad, C. E. O. Kuntze 1014 (lectotype K, fide Prance & Sothers 2003a: 70; isolectotype US).

**DISTRIBUTION AND HABITAT.** Trinidad, Venezuela, Guianas and in Amazonian Bolivia, Colombia, Ecuador, Peru, and Brazil. Riverine forest, riverbanks and fresh water beaches, and savanna margins.

**3. *Leptobalanus bullatus* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472828-2>

*Licania bullata* Prance, *Kew Bull.* 50: 143 (1995). Type: Peru, Huánuco, Prov. Pachitea, region of Pucallpa, Sira Mts, B. Wallnöfer 13-41088 (holotype K; isotype W).

**DISTRIBUTION AND HABITAT.** Peru. Lower montane forest around 800 m.

**4. *Leptobalanus calvescens* (Cuatrec.) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472829-2>

*Licania calvescens* Cuatrec., *Fieldiana, Bot.* 27: 64 (Cuatrecasas 1950). Type: Colombia, Valle, Río Yurumanguí, Veneral, J. Cuatrecasas 15835 (holotype F; isotype COL).

**DISTRIBUTION AND HABITAT.** Colombia (Chocó and Valle). Pacific coastal forests.

**5. *Leptobalanus cardiophyllus* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472830-2>

*Licania cardiophylla* Prance, *Kew Bull.* 47: 637 (1992). Type: Venezuela, Amazonas, Dept. Atabapo, Caño Yagua, Cucurital de Yagua, G. Davidse, O. Huber & S. S. Tillett 17437 (holotype MYF; isotypes K, MO, NY).

**DISTRIBUTION AND HABITAT.** Venezuela and Colombia. Gallery forest.

**6. *Leptobalanus cuatrecasii* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472831-2>

*Licania cuatrecasii* Prance, *Acta Amazon.* 8 (4): 577 (1978). Type: Colombia, Valle, Alto Yunda, Río Anchicayá, S. Hilty 0-1 (holotype US; isotype NY).

**DISTRIBUTION AND HABITAT.** Known only from Colombia (Valle) and Ecuador. Upland and lowland forest.

**7. *Leptobalanus cuspidatus* (Rusby) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472832-2>

*Moquilea cuspidata* Rusby, *Descr. S. Amer. Pl.* 27 (1920); *Licania cuspidata* (Rusby) Prance (1972a: 72). Type: Colombia, Magdalena, Santa Marta, near Las Partidas, H. H. Smith 1773 (holotype NY; isotypes A, BM, BR, F, GH, K, MICH, P, US).

**DISTRIBUTION AND HABITAT.** Colombia; known only from the type collection. Montane forest.

**8. *Leptobalanus diegogomezii* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472833-2>

*Licania diegogomezii* Prance, *Kew Bull.* 50: 717 (1995). Type: Costa Rica, Puntarenas, Res. Forestal Golfo Dulce, 10 km from Chacarita, R. Aguilar 898 (holotype MO; phototype K).

**DISTRIBUTION AND HABITAT.** Costa Rica; known only from two collections. Lowland forest, 100 m.

**9. *Leptobalanus emarginatus* (Spruce ex Hook. f.) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472834-2>

*Licania emarginata* Spruce ex Hook. f., *Fl. Bras.* 14 (2): 15 (Hooker 1867). Type: Brazil, Amazonas, rio Uaupés, near Panurú, R. Spruce 2699 (lectotype K, fide Prance 1972a: 74; isolectotypes BM, BR, CGE, F, GH, GOET, LD, LE, NY, OXF, P, RB, W).

*Licania petrensis* Prance (1995: 713). Type: Venezuela, Amazonas, Dept. Atures, Puerto Ayacucho-El Burro, Km 48, A. Gröger 690 (holotype VEN; isotype K).

**DISTRIBUTION AND HABITAT.** Venezuelan Guayana and Amazonian Brazil and Peru. Non-flooded forest, especially on granitic outcrops.

**10. *Leptobalanus foveolatus* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472835-2>

*Licania foveolata* Prance, *Fl. Neotrop. Monogr.* 9: 80 (1972a). Type: Guyana, Upper Mazaruni R., Aga Creek, R. Boyan 28 (F.D. 7852) (holotype K; isotypes NY, U).

**DISTRIBUTION AND HABITAT.** Collected only in Guyana. Riverine forest.

**11. *Leptobalanus fuchsii* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472836-2>

*Licania fuchsii* Prance, *Fl. Neotrop. Monogr.* 9: 79 (1972a). Type: Colombia, Chocó, Río Baudó, 13.5 km above mouth, H. P. Fuchs 22036 (holotype NY; isotypes K, MO, US).

**DISTRIBUTION AND HABITAT.** Colombia. Pacific coastal forest.

**12. *Leptobalanus gardneri* (Hook. f.) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472848-2>

*Moquilea gardneri* Hook. f., *Fl. Bras.* 14 (2): 21 (Hooker 1867); *Licania gardneri* (Hook. f.) Fritsch (1889: 56). Type: Brazil, Minas Gerais, near São Romão, G. Gardner 4539 (holotype K; isotypes BM, GH).

*Licania mattogrossensis* Pilg. (Pilger 1923: 540); *Moquilea mattogrossensis* (Pilg.) Malme (1930: 11). Type: Brazil, Mato Grosso, Coxim, F. C. Hoehne 4262 (holotype B, destroyed; lectotype R, fide Prance & Sothers 2003a: 74; phototype NY).

**DISTRIBUTION AND HABITAT.** Bolivia, and in C, NE, SE and N Brazil. Riverine forest bordering cerrado, and in cerrado itself.

**13. *Leptobalanus granvillei* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472849-2>

*Licania granvillei* Prance, *Proc. Kon. Ned. Akad. Wetensch.* C. 89: 114 (1986). Type: French Guiana, Saül, Monts La Fumée, S. A. Mori & B. M. Boom 14764 (holotype NY; isotypes CAY, P).

**DISTRIBUTION AND HABITAT.** From Panama, Ecuador and Colombia to French Guiana, Guyana, Venezuela and Brazil (Amazonas). Upland forest on terra firme and along riverbanks.

**14. *Leptobalanus humilis*** (Cham. & Schltld.) Sothers & Prance **comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472850-2>

*Licania humilis* Cham. & Schltld., *Linnaea* 2: 549 (Chamisso & Schlechtendal 1827); *Moquilea humilis* (Cham. & Schltld.) Hook. f. (Hooker 1867: 26); *Chrysobalanus humilis* (Cham. & Schltld.) Kuntze (1893: 76). Type: Brazil, Minas Gerais, F. Sellow s.n. (holotype LE; isotype BR; isotype fragments F, M, P). *Chrysobalanus sublanatus* Kuntze (1893: 76). Type: Brazil, Mato Grosso, C. E. O. Kuntze s.n. (holotype NY). *Licania ulei* Taub. (Taubert 1896: 428). Type: Brazil, Minas Gerais, rio Paranaíba, E. Ule 3187 (holotype B, destroyed; lectotype designated here, HBG; isotype R).

**DISTRIBUTION AND HABITAT.** Bolivia and Brazil. In cerrados.

**15. *Leptobalanus jefensis*** (Prance) Sothers & Prance **comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472851-2>

*Licania jefensis* Prance, *Brittonia* 28: 215 (1976). Type: Panama, Summit of Cerro Jefe, J. D. Dwyer et al. 5047 (holotype NY; isotype MO).

**DISTRIBUTION AND HABITAT.** Known only from Costa Rica and Panama. Cloud forests.

**16. *Leptobalanus joseramosii*** (Prance) Sothers & Prance **comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472852-2>

*Licania joseramosii* Prance, *Acta Amazon.* 8 (4): 581 (1978). Type: Brazil, Amazonas, Manaus-Caracará Rd., Km 130, O. P. Monteiro & J. F. Ramos 29 (holotype INPA 54340; isotype NY).

**DISTRIBUTION AND HABITAT.** Brazil; known only from the type collection. White sand forest or campina.

**17. *Leptobalanus latus*** (J. F. Macbr.) Sothers & Prance **comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472853-2>

*Licania lata* J. F. Macbr., *Candollea* 5: 369 (Macbride 1934). Type: Peru, Loreto, Mishuyacu, near Iquitos, G. Klug 560 (holotype F; isotype NY).

**DISTRIBUTION AND HABITAT.** Guianas, Venezuela, C & W Amazonia (Colombia, Ecuador, Peru and Brazil). Non-flooded forest and secondary scrub on sandy soil.

**18. *Leptobalanus longistylus*** (Hook. f.) Sothers & Prance **comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472856-2>

*Moquilea longistyla* Hook. f., *Fl. Bras.* 14 (2): 24 (Hooker 1867); *Licania longistyla* (Hook. f.) Fritsch (1889: 56). Type: Venezuela, Amazonas, Río Orinoco below Esmeralda, R. Spruce 3232 (lectotype K, fide Prance 1972a: 78; isolectotypes BM, BR, E, GH, LE, NY, OXF, P, TCD, W).

**DISTRIBUTION AND HABITAT.** Panama, Venezuela, Guianas, and W & C Amazonia in Colombia, Ecuador, Peru, and in C and N Brazil. Periodically flooded forest.

**19. *Leptobalanus maguirei*** (Prance) Sothers & Prance **comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472857-2>

*Licania maguirei* Prance, *Fl. Neotrop. Monogr.* 9: 70 (1972a). Type: Brazil, Mato Grosso, rio Juruena, Brasília to Acre Highway, B. Maguire, J. M. Pires, C. Maguire & N. T. da Silva 56470 (holotype NY).

**DISTRIBUTION AND HABITAT.** Brazil (known only from Mato Grosso and Mato Grosso do Sul). Riverine forest.

**20. *Leptobalanus mexicanus*** (Lundell) Sothers & Prance **comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472858-2>

*Licania mexicana* Lundell, *Wrightia* 5: 40 (1974). Type: Mexico, Sinaloa, between Rancho Del Piño and Chele, C. L. Lundell 13023 (holotype LL; isotypes CAS, MICH).

**DISTRIBUTION AND HABITAT.** Known only from the type. Habitat unknown.

**21. *Leptobalanus morii* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472869-2>

*Licania morii* Prance, *Brittonia* 28: 215 (1976). Type: Panama, El Llano-Cartí Rd, 12 km from Inter American Hwy, S. A. Mori & J. A. Kallunki 4665 (holotype NY; isotype MO).

**DISTRIBUTION AND HABITAT.** Panama; known only from the type collection. Moist forest at 350 m.

**22. *Leptobalanus octandrus* (Hoffmanns. ex Roem. & Schult.) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:604728702>

*Hirtella octandra* Hoffmanns. ex Roem. & Schult., *Syst. Veg.* ed. 9, 5: 274 (Roemer & Schultes 1819); *Licania turiuva* Cham. & Schldtl. (Chamisso & Schlechtendal 1827: 550), *nom. superfl. illegit.*; *Moquilea turiuva* (Cham. & Schldtl.) Hook. f. (Hooker 1867: 25), *nom. superfl. illegit.*; *Licania octandra* (Hoffmanns. ex Roem. & Schult.) Kuntze (1891: 217). Type: Brazil, Pará, F. W. Sieber s.n. (holotype B, Herb. Willdenow 4851; phototype NY).

**22a. *Leptobalanus octandrus* subsp. *octandrus***

*Licania bothynophylla* Mart. (Martius 1841: 15); *Moquilea bothynophylla* (Mart.) Hook. f., (Hooker 1867: 26). Type: Brazil, Rio de Janeiro, Campos Bravos, C. F. P. Martius 449 (holotype M; isotypes BR, F, GH, K, LE, M, NY, P, W).

*Moquilea utilis* Hook. f. (Hooker 1867: 24); *Licania utilis* (Hook. f.) Fritsch (1889: 56). Type: Brazil, Pará, Santarém, R. Spruce 877 (lectotype K, fide Prance 1972a: 83; isoelectotypes LD, NY, P).

*Licania sellowiana* Klotzsch ex Hook. f. (Hooker 1867: 26), *nom. nud. in synonym.*

*Licania hookeri* var. *obtusata* Huber (1909: 368). Type: Brazil, Pará, Faro, A. Ducke MG 8371 (holotype MG; isotypes BM, G).

*Licania takutuensis* Standl. (Smith 1939: 182). Type: Guyana, W extremity of Kanuku Mts, A. C. Smith 3302 (holotype F; isotypes A, IAN, K, LE, NY, P, S, US).

**DISTRIBUTION AND HABITAT.** Widely distributed from N Venezuela through the Guianas, Peru, Colombia, Bolivia and E & C Amazonia to Northeast, East-central & Southeast Brazil. Forest, both on flooded and non-flooded ground but especially in open riverine habitats and at savanna margins, and in the gallery forest of the Planalto of central Brazil.

**22b. *Leptobalanus octandrus* subsp. *pallidus* (Hook. f.) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472871-2>

*Moquilea pallida* Hook. f., *Fl. Bras.* 14 (2): 25 (Hooker 1867); *Licania hookeri* Fritsch (1889: 56); *Licania pallida* (Hook. f.) Kuntze (1891: 217) *nom. illegit.*, *non L. pallida* Spruce ex Sagot (1883: 306); *Licania octandra* subsp. *pallida* (Hook. f.) Prance (1972a: 84). Type: Venezuela, Amazonas, Río Casiquiari, Vasiva or Pacimoni, R. Spruce 3302 (lectotype K, fide Prance 1972a: 84; isoelectotypes BM, BR, CGE, E, GH, GOET, LD, LE, P, OXF, RB, TCD).

*Licania egensis* Fritsch (1889: 58). Type: Brazil, Amazonas, Tefé, E. Poeppig 2531 (lectotype W, fide Prance 1972a: 84; isoelectotypes G, LE).

*Licania stenocarpha* Standl. (Standley 1937: 258). Type: Brazil, Amazonas, São Paulo de Olivença, B. A. Krukoff 8553 (holotype NY; isotypes A, BM, BR, F, K, MO, P, S, US).

**DISTRIBUTION AND HABITAT.** Amazonia: Guyana, Venezuela, Bolivia, Colombia, Ecuador, Peru and Brazil. Non-flooded forest.

**22c. *Leptobalanus octandrus* subsp. *grandifolius* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472872-2>

*Licania octandra* subsp. *grandifolia* Prance, *Acta Amazon.* 4 (1): 18 (1974). Type: Brazil, Amazonas, Rio Javari, behind Estirão do Equador, E. Lleras, W. C. Steward, J. C. Ongley et al. P17270 (holotype INPA; isotypes K, MO, NY, P).

**DISTRIBUTION AND HABITAT.** Colombia, Peru and Brazil. Forest on terra firme, especially on sandy soils.

**23. *Leptobalanus parvifolius* (Huber) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472873-2>

*Licania parvifolia* Huber, *Bol. Mus. Paraense Hist. Nat.* 5: 367 (1909). Type: Brazil, Pará, rio Mapuera [infra Taboleiro Grande], A. Ducke s.n. (holotype MG 8979; isotypes F, G, RB).

*Licania arachnites* Standl. (Smith 1939: 181). Type: Guyana, Essequibo R., near Onoro Creek, A. C. Smith 2696 (holotype F; isotypes A, IAN, K, MAD, MO, NY, P, U, US).



**DISTRIBUTION AND HABITAT.** Guyana, Venezuela, Bolivia and the southern part of Amazonian Brazil. Open riverine localities, especially river banks and islands.

**24. *Leptobalanus persaudii*** (Fanshawe & Maguire) Sothers & Prance **comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472874-2>

*Licania persaudii* Fanshawe & Maguire, *Bull. Torrey Bot. Club* 75: 375 (Maguire 1948b). Type: Guyana, Hope, A. C. Persaud 95 (lectotype NY, fide Prance 1972a: 75; isolectotypes F, K, US).

**DISTRIBUTION AND HABITAT.** Confined to the Guianas. Primary forests.

**25. *Leptobalanus sclerophyllus*** (Hook. f.) Sothers & Prance **comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472875-2>

*Moquilea sclerophylla* Hook. f., *Fl. Bras.* 14 (2): 23, t. 7 (Hooker 1867); *Moquilea sclerophylla* var. *pohliana* Hook. f. (Hooker 1867: 24), *nom. inval.*; *Licania sclerophylla* (Hook. f.) Fritsch (1889: 56). Type: Brazil, Minas Gerais, C. F. P. Martius 1467 (lectotype M, fide Prance 1972a: 77; isolectotype BR).

*Moquilea sclerophylla* var. *myristicoides* Hook. f. (Hooker 1867: 24); *Licania myristicoides* Benth. (Hooker 1867: 24), *nom. inval. in synon.*; *Licania sclerophylla* var. *myristicoides* (Hook. f.) Fritsch (1889: 56). Type: Brazil, Pará, Santarém, R. Spruce 987 (lectotype K, fide Prance & Sothers 2003a: 84; isolectotypes NY, P).

*Moquilea sclerophylla* var. *scabra* Hook. f. (Hooker 1867: 24); *Licania scabra* Benth. ex Hook. f. (Hooker 1867: 24), *nom. inval. in synon.*; *Licania sclerophylla* var. *scabra* (Hook. f.) Fritsch (1889: 56). Type: Brazil, Pará, Santarém, R. Spruce 840 (lectotype K, fide Prance & Sothers 2003a: 84; isolectotypes NY, P).

*Licania aspera* Standl. (Standley 1937: 254). Type: Brazil, Pará, R. C. Monteiro da Costa 279 (holotype F; isotypes IAN, US).

**DISTRIBUTION AND HABITAT.** Bolivia, Colombia, Peru, eastern and southern Amazonia and the planalto of central Brazil. Non-flooded forest, riverine forest or cerrado.

**NOTE.** The collection Martius 1467b is the type of *Swartzia lomatosus* Mart. and has been erroneously cited as the type of *Leptobalanus sclerophyllus*.

**26. *Leptobalanus sparsipilis*** (S. F. Blake) Sothers & Prance **comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472876-2>

*Licania sparsipilis* S. F. Blake, *Contr. Gray Herb.* 52: 67 (1917). Type: Belize, Sittee R., M. E. Peck 858 (holotype GH; isotypes K, NY).

**DISTRIBUTION AND HABITAT.** From southern Mexico to Colombia. Forest on low wet ground.

**27. *Leptobalanus sprucei*** (Hook. f.) Sothers & Prance **comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472877-2>

*Moquilea sprucei* Hook. f., *Fl. Bras.* 14 (2): 22 (Hooker 1867); *Licania sprucei* (Hook. f.) Fritsch (1889: 55). Type: Brazil, Amazonas, Manaus, R. Spruce 1801 (lectotype K, fide Prance 1972a: 76; isolectotypes BM, CGE, E, GH, GOET, LD, LE, M, NY, P, RB, TCD, W).

**DISTRIBUTION AND HABITAT.** Guianas, Venezuela and in the Amazon region of Brazil. Primary forest on non-flooded ground and secondary forest.

**28. *Leptobalanus stevensii*** (Prance) Sothers & Prance **comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472878-2>

*Licania stevensii* Prance, *Kew Bull.* 47: 637 (1992). Type: Costa Rica, Limón, 2 km S of Río Colorado, W. D. Stevens, G. Herrera & O. M. Montiel 25100 (holotype K; isotype MO).

**DISTRIBUTION AND HABITAT.** Costa Rica. Lowland evergreen forest, often on slopes.

**29. *Leptobalanus turbinatus*** (Benth.) Sothers & Prance **comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472885-2>

*Licania turbinata* Benth., *J. Bot. (Hooker)* 2: 218 (Bentham 1840). *Moquilea turbinata* (Benth.) Hook. f. (Hooker 1867: 23). Type: Brazil, Pernambuco, G. Gardner 1149 (holotype K; isotypes BM, CGE, E, GH, NY, OXF, P, S, SP, US, W).

**DISTRIBUTION AND HABITAT.** NE Brazil (Bahia and Pernambuco). Coastal forest and restinga forest.

**30. *Leptobalanus undulatus*** (Prance) Sothers & Prance **comb. nov.**



<http://www.ipni.org/urn:lsid:ipni.org:names:60472886-2>

*Licania undulata* Prance, *Kew Bull.* 50: 715 (1995).  
Type: Colombia, Caquetá, Araracuara region,  
Quebrada El Engaño, D. Restrepo & A. Matapí  
542 (holotype MO; phototype K).

**DISTRIBUTION AND HABITAT.** Colombia; known only from the type collection. Habitat unknown.

**31. *Leptobalanus wurdackii* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472887-2>

*Licania wurdackii* Prance, *Fl. Neotrop. Monogr.* 9: 63 (1972a). Type: Venezuela, Amazonas, Río Atabapo, Caño Guasariapuna, 1 km above San Fernando, B. Maguire, J. J. Wurdack & G. S. Bunting 36238 (holotype NY; isotypes K, P).

**DISTRIBUTION AND HABITAT.** Amazonian regions of Venezuela, Colombia and Brazil (Amazonas). Riverine forest and river banks.

**VII. *Moquilea* Aubl., *Hist. Pl. Guiane* 1: 521, t. 208 (Aublet 1775).**

*Dahuronia* Scop. (Scopoli 1777: 219), *nom. superfl. illegit*; *Licania* subg. *Moquilea* (Aubl.) Prance (1967: 224); *Licania* sect. *Moquilea* (Aubl.) Prance (1970: 527). Type: *Moquilea guianensis* Aubl.

*Trees.* Leaf lower surface glabrous or lanate, never with stomatal cavities. Petiole with or without glands. *Inflorescence* panicles, racemes or racemose panicles. Bracteoles small. Petals 4–5. Stamens 11–60 (–90), in 1–several rows (as in *Couepia*), inserted in a complete circle; filaments glabrous, usually far exceeding calyx lobes, less frequently only slightly exceeding or rarely equalling the calyx lobes, free or slightly united at base. *Ovary* lanate, tomentose or pilose, inserted at base of receptacle. *Fruit* globose to ellipsoid, to 11–15 × 10 cm, epicarp glabrous, smooth, lenticellate, crustaceous or pubescent; endocarp glabrous or sparsely pubescent within. Fig. 3C.

**DISTRIBUTION.** A genus with 54 species distributed from Mexico, Central America (Panama, Nicaragua, Costa Rica), the Leeward and Windward Islands, and throughout South America (Guianas, Venezuela, Colombia, Ecuador, Peru, Bolivia, Brazil).

**NOTES.** Bentham (1840) maintained *Moquilea* as a distinct genus and stated that it had similar flowers to *Chrysobalanus* (all fertile stamens and in a complete circle), differing mostly in the inflorescence type. *Moquilea* shares several morphological characters with *Couepia*, such as number of stamens, exserted stamens, and leaf pilosity, but differs in the placement of the ovary. *Moquilea* is retrieved as sister to *Couepia* in all our analyses (combined, plastid, ITS and *Xdh*) and in a separate lineage from *Licania* s.s., *Leptobalanus*, *Hymenopus* and *Chrysobalanus*. It appears in two lineages (*M. egléri* and *M. minutiflora* distinct from the rest of *Moquilea*) but morphologically they are not distinguishable and so we have maintained them as *Moquilea* pending further analyses.

### Key to species of *Moquilea*

1. Stamens exserted beyond calyx lobes, 12–90
2. Leaf lower surface with an appressed lanate-arachnoid pubescence
  3. Inflorescence of fasciculate, short, dense-flowered racemes; primary veins impressed above; Panama . . . . . **18. *M. fasciculata***
  3. Inflorescence of lax, branched, racemose panicles or cymose panicles, or a raceme with long pedicels; primary veins usually prominulous or plane above
    4. Inflorescence a few flowered (3–4) raceme; pedicels 5–7 mm long, thin; leaves long-cuspidate with thin acumen 15–25 mm long; Ecuador . . . . . **32. *M. longicuspidata***
    4. Inflorescence of lax branched racemose panicles or cymose panicles; pedicels sessile or rarely to 5 mm long, thick; leaves acuminate
      5. Primary leaf veins 8–15 pairs, the lamina usually oblong-lanceolate
        6. Leaves 4–11 × 1.1–4 cm, oblong-lanceolate
          7. Inflorescence of once-branched racemose panicles; stamens c. 25; receptacle sessile . . . . . **5. *M. boliviensis***
          7. Inflorescence of much-branched panicles with many short branches bearing 1–3 flowers; stamens 12–14; receptacle shortly pedicellate. . . . . **41. *M. palcazuensis***
        6. Leaves 15–20 × 5.5–8.3 cm, oblong
          8. Petioles 13–15 mm long, slightly winged; lamina coriaceous; Venezuela . . . **8. *M. cariae***
          8. Petioles 5–8 mm long, not winged; lamina chartaceous, leaf apex cuspidate, acumen 5–10 mm; Ecuador. . . . . **10. *M. celiae***

5. Primary leaf veins 16 – 29 pairs, the lamina oblong to elliptic
  9. Inflorescence ramiflorous, borne on young woody twigs well below shoot apex
    10. Flowers (calyx and receptacle) 6 – 7 mm long, young leaf lower surface with shaggy dense ferruginous pubescence; leaves 27 – 47 cm long; Colombia, Ecuador
      11. Leaves elliptic, 22 – 26 cm broad; petioles 20 – 25 mm long; stipules 10 – 12 mm long; Colombia (Valle). . . . . **21. M. gentryi**
      11. Leaves oblong, 9 – 10.5 cm broad; petioles 14 – 15 mm long; stipules 5 – 7 mm long; Ecuador (Napo). . . . . **26. M. hedbergii**
    10. Flowers (calyx and receptacle) 2 – 5.5 mm long, leaf lower surface with compact appressed pubescence or with caducous pubescence, becoming glabrous when mature; leaves 16 – 33 cm long
      12. Leaf lower surface glabrous when mature, with a lanate caducous pubescence on youngest leaves; flowers c. 2 mm long; Colombia (Valle, 0 – 50 m) . . . . . **53. M. velata**
      12. Leaf lower surface with a compact persistent grey-lanate or brown pubescence; flowers 3 – 5.5 mm long
        13. Leaf lower surface ferruginous to brown-tomentose, secondary venation not conspicuously reticulate
          14. Stamens 13 – 15; stipules linear, 4 – 7.5 cm long; petioles canaliculate; Costa Rica . . . . . **4. M. belloii**
          14. Stamens 25 – 30; stipules triangular-lanceolate, 3 – 7 mm long; petioles terete; Colombia, Ecuador, Peru. . . . . **35. M. macrocarpa**
        13. Leaf lower surface grey-tomentellous, conspicuously reticulate with parallel secondary venation; leaves thickly coriaceous
          15. Inflorescence 15 – 30 cm long, much-branched, flowers densely packed, bracteoles caducous; Colombia, Ecuador. . . . . **15. M. durifolia**
          15. Inflorescence 8 – 15 cm long, unbranched or with a few branches; bracteoles persistent, membranous; Ecuador . . . **23. M. grandibracteata**
  9. Inflorescence terminal or axillary, but on leafy shoot apex
    16. Flowers 1.5 – 2 mm long; leaves 12 – 19 × 3 – 6 cm, brown-pubescent beneath, without conspicuously reticulate venation; Colombia . . . . . **54. M. veneralensis**
    16. Flowers 3 – 5 mm long; leaves 15 – 35 × 6 – 13 cm, grey-pubescent beneath, often with conspicuously reticulate parallel tertiary venation
      17. Inflorescence and flowers with light-brown-tomentellous pubescence, leaves gradually tapering from mid-point to acuminate apex; centre primary veins far apart (18 – 22 mm), the secondary venation obscure; Colombia (Chocó) . . . . . **37. M. maritima**
      17. Inflorescence and flowers with ferruginous pubescence; leaves tapering from well above midpoint, centre primary veins 5 – 15 mm apart, with conspicuous parallel secondary venation
        18. Leaves 6 – 9.5 × 2 – 3 cm; petioles 4 – 5 mm long; Venezuela (Lara) . . **40. M. montana**
        18. Leaves 12 – 46 × 3 – 26 cm; petioles 6 – 15 mm long
          19. Leaf bases subcordate, with 2 stalked glands near junction of petiole; Costa Rica . . . . . **13. M. corniculata**
          19. Leaf bases rounded to subcuneate, without stalked glands
            20. Leaves oblong-lanceolate 20 – 37 cm long, primary veins impressed above
              21. Primary leaf veins 21 – 24 pairs; petioles 6 – 8 mm long, terete; secondary venation conspicuously reticulate with parallel secondary veins; bracts 25 – 35 mm, persistent; Peru (San Martín, Pasco). . . . . **19. M. filomenoi**
              21. Primary leaf veins 34 – 40 pairs; petioles 11 – 15 mm long, canaliculate; secondary venation inconspicuous and covered by lanate pubescence, bracts caducous; Peru . . . **52. M. vasquezii**
            20. Leaves oblong, 12 – 18 cm long; primary veins plane to prominulous above
              22. Leaf apex cuspidate; petioles 6 – 8 mm long; flowers sessile; Ecuador . . . . . **10. M. celiae**
              22. Leaf apex acuminate; petioles 10 – 12 mm long; flowers on pedicels 0.5 mm long; Colombia (Antióquia). . . . **7. M. cabreræ**

2. Leaf lower surface glabrous when mature (sometimes lanate when young)
23. Exterior of flowers and inflorescence glabrous or sparsely puberulous
24. Leaf broadly acuminate, the acumen 4 – 8 mm long; flowers 2.5 – 3 mm long; pedicels 2 – 5 mm long; Brazil (Bahia) . . . . . **45. *M. salzmannii***
24. Leaf with well-developed finely pointed acumen 8 – 12 mm long; flowers 4 – 4.5 mm long; pedicels 1 – 3 mm long
25. Inflorescence and exterior of flowers puberulous; petioles 10 – 12 mm long; leaves elliptic, 5.5 – 9 cm broad; Peru (Loreto) . . . . . **30. *M. klugii***
25. Inflorescence and exterior of flowers glabrescent; petioles 5 – 7 (– 9) mm long; leaves oblong to oblong-elliptic, 2 – 5.5 cm broad; Guianas, Peruvian Amazonia . . . . . **25. *M. guianensis***
23. Exterior of flowers and usually inflorescence densely tomentose
26. Petals unguiculate
27. Flowers 5 – 6 mm long; pedicels 2 – 2.5 mm long; ovary pilose; Brazil (Amazonia) . . . **51. *M. unguiculata***
27. Flowers 3 mm long; pedicels 0 – 0.25 mm long; ovary glabrescent; Amazonia (Brazil, Bolivia, Peru) . . . . . **34. *M. longipetala***
26. Petals not clawed
28. Leaves 30 – 40 × 20 – 25 cm . . . . . **38. *M. megalophylla***
28. Leaves smaller, 2 – 15 (30) × 1.5 – 10 (14)
29. Leaf veins and midrib impressed on upper surface
30. Petioles 10 – 13 mm long; leaves 10 – 14 × 2.5 – 5.2 cm; primary veins 11 – 17 pairs; stamens 17; western Amazonia. . . . . **1. *M. angustata***
30. Petioles 5 – 7 mm long; leaves 14 – 25 × 4.5 – 8 cm; primary veins 18 – 22 pairs; stamens 12 – 14; Brazil (Pará) . . . . . **2. *M. annae***
29. Leaf veins plane or prominulous on upper surface
31. Leaves with a farinaceous pubescence when young
32. Inflorescence racemose or little-branched; petioles 4 – 6 mm long . . **50. *M. tomentosa***
32. Inflorescence much-branched; petioles 8 – 16 mm long . . . . . **43. *M. pyrifolia***
31. Leaves glabrous when young
33. Inflorescence with flowers borne in cymules on short tertiary branches . . . . . **48. *M. tachirensis***
33. Inflorescence not in cymules
34. Pedicels 3 – 7 mm long; leaves with finely pointed acumen 1.5 – 2.5 mm long . . . . . **33. *M. longipedicellata***
34. Pedicels 0.5 – 2.5 mm long; leaf acumen rather blunt or cuspidate, less than 10 mm long
35. Petioles 16 – 22 mm long
36. Petioles terete, thick, leaf apex rounded; stamens c. 22. . . **28. *M. jaramilloi***
36. Petioles canaliculated, thin; leaf apex acuminate; stamens c. 14 . . . . . **9. *M. cecidiophora***
35. Petioles 2 – 15 mm
37. Stamens 25 – 30
38. Inflorescence a much-branched panicle . . . . . **14. *M. dodsonii***
38. Inflorescence a racemose panicle
39. Leaves 21 – 26 cm long; primary veins 15 – 19 pairs; petioles c. 10 mm long . . . . . **17. *M. espiniae***
39. Leaves 6 – 14 cm long; primary veins 8 – 11 pairs; petioles 4 – 6 mm long . . . . . **31. *M. leucosepala***
37. Stamens 11 – 23
40. Leaves oblong-lanceolate, 13 – 22 cm long. . . . **42. *M. platypus***
40. Leaves elliptic to oblong, usually smaller (15 – 18.5 in *M. maranhensis*; 10 – 21 in *M. guatemalensis*)
41. Leaf base subcordate; stamens 16 – 33
42. Leaves 15 – 18.5 cm long . . . . . **36. *M. maranhensis***
42. Leaves 8 – 15.5 cm long. . . . . **6. *M. brittoniana***
41. Leaf base rounded to cuneate; stamens 11 – 21
43. Leaves 2 – 4 × 1.1 – 2.7 cm. . . . . **27. *M. imbaimadaensis***
43. Leaves 4.5 – 16 × over 2 cm broad Brazil, Colombia, Peru

44. Flowers 4 – 5 mm long; stipules linear 5 – 7 mm . . . . . **22. M. gonzalezii**
44. Flowers 2 – 3.5 mm long; stipules to 2 mm long
45. Petioles 2 – 5 mm long; leaves obovate to elliptic
46. Inflorescence once-branched; leaves obovate to elliptic, 4.5 – 9 cm long . . . . . **16. M. egleri**
46. Inflorescence twice-branched; leaves elliptic, 10 – 21 cm long. **24. M. guatemalensis**
45. Petioles 6 – 14 mm long; leaves oblong to oblong-elliptic
47. Leaf apex cuspidate; stamens 11 – 12 . . . . . **29. M. kallunkiae**
47. Leaf apex acuminate; stamens 16 – 21
48. Inflorescence rachis and branches sparsely grey-pubescent. **20. M. fritschii**
48. Inflorescence rachis and branches brown or yellow-brown tomentose
49. Inflorescence little-branched; flowers 3 – 4 mm; ovary and petioles glabrous . . . . . **11. M. chiriquiensis**
49. Inflorescence much-branched; flowers 2 – 3 mm; ovary pubescent; petioles tomentose . . . . . **39. M. minutiflora**
1. Stamens equalling or shorter than calyx lobes, 10 – 17 (– 25 in *L. salicifolia* and *L. silvatica*)
50. Leaves 15 – 36 cm long; stipules 12 – 22 mm long; inflorescence borne on woody defoliated stalks . . **53. M. velata**
50. Leaves less than 14 cm long; stipules 2 – 10 mm long; flowers in terminal or axillary inflorescences on young branchlets
51. Inflorescence of unbranched subspikes or racemes
52. Flowers c. 1.5 mm long, borne in clusters along rachis, the rachis 4 – 15 mm long; Colombia (Boyacá) . . . . . **47. M. subarachnophylla**
52. Flowers c. 2.5 mm long, not clustered, the rachis 2 – 4 mm long; Peru (Madre de Dios) . . . . . **49. M. tambopatensis**
51. Inflorescence of panicles, or a panicle of cymules
53. Leaf lower surface densely lanate-pubescent
54. Leaf apex with a well-developed acumen 3 – 5 mm long; stamens c. 25; exterior of receptacle ferruginous; Colombia (Antióquia) . . . . . **44. M. salicifolia**
54. Leaf apex obtuse to broadly acuminate, the acumen not exceeding 1 mm; stamens c. 15; exterior of receptacle brown; Brazil (Goiás) . . . . . **3. M. araneosa**
53. Leaf lower surface glabrous
55. Leaf acumen 3 – 7 mm long; leaves 5 – 10 cm long; stamens c. 25; flowers sessile on primary branches of inflorescence, densely brown-tomentose; eastern Brazil . . . . . **46. M. silvatica**
55. Leaf acumen 10 – 15 mm long; leaves 7.5 – 14 cm long; stamens 12 – 14; flowers predominantly on short secondary branches of inflorescence, short grey-tomentose; Colombia (Valle) . . . . . **12. M. chocoensis**

**1. *Moquilea angustata* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472888-2>

*Licania angustata* Prance, *Fl. Neotrop. Monogr.* 9: 53 (1972a).

Type: Brazil, Amazonas, Mun. de São Paulo de Olivença, near Palmares, B. A. Krukoff 8445 (holotype NY; isotypes A, BM, BR, F, K, LA, LE, MO, P, S, US).

**DISTRIBUTION AND HABITAT.** Western Amazonia: Ecuador, Peru and Brazil. Lowland non-flooded forests.

**2. *Moquilea anneae* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472889-2>

*Licania anneae* Prance, *Brittonia* 31: 250 (1979c). Type: Brazil, Pará, Cuiabá-Santarém Hwy., km 1305, vicinity of Igarapé José Preto, G. T. Prance, A. S. Silva, M. J. Balick et al. 25652 (holotype MG; isotypes AAU, FHO, K, MO, NY, P, RB, U, US).

**DISTRIBUTION AND HABITAT.** Brazil; known only from the type collection. Disturbed forest beside road on marginally flooded and non-flooded areas.

**3. *Moquilea araneosa* (Taub.) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472890-2>

*Licania araneosa* Taub., *Bot. Jahrb. Syst.* 21: 428 (Taubert 1896). Type: Brazil, Goiás, Serra Dourada, E. Ule 2885 (holotype B, destroyed; lectotype HBG, fide Prance 1972a; isolectotypes P, R, fragment F).

**DISTRIBUTION AND HABITAT.** Brazil (planalto central). Cerrado and gallery forest.

**4. *Moquilea belloi* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472891-2>

*Licania belloi* Prance, *Kew Bull.* 50: 709 (1995). Type: Costa Rica, Alajuela, Reserva Biológica Monteverde, Río Peñas Blancas, E. Bello 1321 (holotype K; isotypes CR, MO).

**DISTRIBUTION AND HABITAT.** Costa Rica and Nicaragua. Lowland and premontane moist tropical forest, 0–800 m.

**5. *Moquilea boliviensis* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472892-2>

*Licania boliviensis* Prance, *Fl. Neotrop. Monogr.* 9: 43 (1972a). Type: Bolivia, Dept. La Paz, Larecaja Province, 10 km S of Mapiri, B. A. Krukoff 111233 (holotype NY; isotypes A, F, K, LA, MICH, MO, S, US).

**DISTRIBUTION AND HABITAT.** Bolivia. Terra firme forest.

**6. *Moquilea brittoniana* (Fritsch) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60473137-2>

*Licania brittoniana* Fritsch, *Oesterr. Bot. Z.* 42: 6 (1892), as *britteniana*. Type: Bolivia, Río Beni, near junction with Madre de Dios, H. H. Rusby 2442 (holotype NY; isotypes BM, E, F, GH, K, MICH, P, US).

*Licania pallida* Britton, *Bull. Torrey Bot. Club* 17: 9 (1890), non *L. pallida* Spruce ex Sagot (1883: 306).

*Moquilea elata* Pilg. (Pilger 1914: 136); *Licania elata* (Pilg.) Pilg. ex L. O. Williams (1936: 174). Type: Brazil, Acre, Seringal São Francisco, E. Ule 9446 (holotype B, lost; lectotype MG 14292, fide Prance & Sothers 2003a: 63; isolectotype K).

**DISTRIBUTION AND HABITAT.** W Amazonia in Bolivia, Colombia, Ecuador, Peru and Brazil. Non-flooded and periodically flooded forest.

**7. *Moquilea cabreræ* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472893-2>

*Licania cabreræ* Prance, *Brittonia* 28: 210–212 (1976). Type: Colombia, Antioquia, Estación Experimental Florestal, Piedras Blancas, I. Cabrera R. 94 (holotype COL).

**DISTRIBUTION AND HABITAT.** Colombia. Montane and cloud forests, at 2200–2550 m.

**8. *Moquilea cariae* (Cardozo) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472898-2>

*Licania cariae* Cardozo, *Ernstia n.s.* 1: 143 (1992), as *carii*. Type: Venezuela, Aragua, Parque Nacional Henri Pittier, A. Cardozo & D. Hidalgo 1666 (holotype MY).

**DISTRIBUTION AND HABITAT.** Venezuela; known only from the type location. Cloud forest.

**9. *Moquilea cecidiophora* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472899-2>

*Licania cecidiophora* Prance, *Biotropica* 10: 85 (1978). Type: Peru, Amazonas, E of Chávez Valdivia Military Post, E. Ancuash 752 (holotype NY; isotypes F, MO).

**DISTRIBUTION AND HABITAT.** Peru. Rainforest on terra firme.

**10. *Moquilea celiae* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472900-2>



*Licania celiae* Prance, *Mem. New York Bot. Gard.* 64: 198 (1990). Type: Ecuador, Napo, Parque Nacional Yasuní, C. E. Cerón & F. Hurtado 3843 (holotype K; isotypes AAU, F, GB, MO, NY).

**DISTRIBUTION AND HABITAT.** Ecuador and Peru. Lowland rainforest and premontane wet forest to 800 m.

**11. *Moquilea chiriquiensis* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472902-2>

*Licania chiriquiensis* Prance, *Brittonia* 29: 154 (1977). Type: Panama: Chiriquí, Cerro Colorado, S. A. Mori & R. L. Dressler 7778 (holotype NY; isotype MO).

**DISTRIBUTION AND HABITAT.** Panama. Cloud forest over 1200 m.

**12. *Moquilea chochoensis* (Cuatrec.) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472903-2>

*Licania chochoensis* Cuatrec., *Fieldiana, Bot.* 27: 65 (Cuatrecasas 1950). Type: Colombia, Chocó, Río San Juan, Quebrada del Taparal, J. Cuatrecasas 21455 (holotype F; isotype P).

**DISTRIBUTION AND HABITAT.** Confined to Colombia. Pacific coastal forests.

**13. *Moquilea corniculata* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472904-2>

*Licania corniculata* Prance, *Kew Bull.* 50: 141 (1995). Type: Costa Rica, Puntarenas, Cantón de Osa, Rancho Quemado, J. Marín 458 (holotype K; isotypes CR, MO).

**DISTRIBUTION AND HABITAT.** Costa Rica (Puntarenas and Osa Peninsula). Lowland rainforest.

**14. *Moquilea dodsonii* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472905-2>

*Licania dodsonii* Prance, *Fl. Neotrop. Monogr.* 9S: 27 (1989). Type: Ecuador, Esmeraldas, Mun. de Lita, Lita-San Lorenzo km 19, P. Acevedo R. & D. C. Daly 1657 (holotype NY; isotype K).

**DISTRIBUTION AND HABITAT.** Panama and Ecuador. Tropical rainforest.

**15. *Moquilea durifolia* (Cuatrec.) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472906-2>

*Licania durifolia* Cuatrec., *Fieldiana, Bot.* 27: 61 (Cuatrecasas 1950). Type: Colombia, Valle, Cordillera Occidental, Monte de La Guarida, J. Cuatrecasas 22251 (holotype F; isotypes COL, MAD, P).

**DISTRIBUTION AND HABITAT.** Colombia, Ecuador and Peru. Montane and cloud forests, 500 – 2000 m.

**16. *Moquilea egleri* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472909-2>

*Licania egleri* Prance, *Fl. Neotrop. Monogr.* 9: 56 (1972a). Type: Brazil, Pará, Tapajós, rio Cururu, W. A. Egler 887 (holotype NY; isotypes IAN, MG 23789).

**DISTRIBUTION AND HABITAT.** Amazonian Brazil and northern limits of the planalto of central Brazil and in Bolivia, Colombia, Peru and Venezuela. Open non-flooded forest, beside rivers and in tall cerrado (cerradão).

**17. *Moquilea espinae* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472908-2>

*Licania espinae* Prance, *Kew Bull.* 47: 633 (1992). Type: Colombia, Chocó, Bahía Solano Mun., Corregimiento El Valle between El Valle and Cabañas Punta Roca, J. Espina, F. Garcia & S. Pino 2879 (holotype CHOCO; isotype MO).

**DISTRIBUTION AND HABITAT.** Colombia; known only from the type collection. Rainforest.

**18. *Moquilea fasciculata* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472910-2>

*Licania fasciculata* Prance, *Acta Amazon.* 8 (4): 579 (1978). Type: Panama, Colón, Zona de Santa Rita, M. D. Correa A. & R. L. Dressler 1815 (holotype MO; isotype NY).

**DISTRIBUTION AND HABITAT.** Panama. Forests.

**19. *Moquilea filomenoi* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472912-2>

*Licania filomenoi* Prance, *Fl. Neotrop. Monogr.* 9S: 20 (1989). Type: Peru, Prov. Mariscal Cáceres, San Martín, 12 km W of Tocache Nuevo, Río Tocache, 500 m, A. H. Gentry *et al.* 25665 (holotype NY; isotypes F, MO).

**DISTRIBUTION AND HABITAT.** Peru (San Martín and Pasco). Mature flatland forest on lateritic soil.

**20. *Moquilea fritschii* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472913-2>

*Licania fritschii* Prance, *Fl. Neotrop. Monogr.* 9: 59 (1972a). Type: Brazil, Pará, Belém, Reserva Mocambo, J. M. Pires & N. T. da Silva 6731 (holotype NY; isotypes IAN, UB).

**DISTRIBUTION AND HABITAT.** Amazonian Brazil. Periodically flooded forest.

**21. *Moquilea gentryi* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472914-2>

*Licania gentryi* Prance, *Fl. Neotrop. Monogr.* 9S: 24 (1989). Type: Colombia, Valle, Bajo Calima, 15 km N of Buenaventura, A. H. Gentry *et al.* 40355 (holotype MO; isotype NY).

**DISTRIBUTION AND HABITAT.** Colombia. Lowland rainforest.

**22. *Moquilea gonzalezii* (Miranda) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472915-2>

*Licania gonzalezii* Miranda, *Bol. Soc. Bot. México* 29: 36 (1965). Type: Mexico, Nayarit, J. G. Ortega 41 (holotype MEXU; isotype US).

**DISTRIBUTION AND HABITAT.** Southwestern Mexico. Gallery forest, 780 – 800 m alt.

**23. *Moquilea grandibracteata* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472916-2>

*Licania grandibracteata* Prance, *Fl. Neotrop. Monogr.* 9S: 22 (1989). Type: Ecuador, Pichincha, Reserva Forestal ENDESA, J. Jaramillo 7413 (holotype NY; isotypes MO, QCA).

**DISTRIBUTION AND HABITAT.** Ecuador, known only from the Andean foothills. Primary forest.

**24. *Moquilea guatemalensis* (Lundell) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472917-2>

*Licania guatemalensis* Lundell, *Wrightia* 5: 39 (1974). Type: Guatemala, Izabal, between Seja and Fronteras on Petén-Guatemala road, E. Contreras 10742 (holotype LL; isotypes P, US).

**DISTRIBUTION AND HABITAT.** Guatemala; known only from the type collection. High forest.

**25. *Moquilea guianensis* Aubl. (Aublet 1775: 521).**

*Licania guianensis* (Aubl.) Griseb. (Grisebach 1857: 198). Type: French Guiana, J. B. C. F. Aublet s.n. (holotype BM; phototype BR).

**DISTRIBUTION AND HABITAT.** Guianas, Venezuela, the Amazon delta, W Amazonia, Ecuador, Peru and in Brazil. Riverine, terra firme and premontane forests.

**26. *Moquilea hedbergii* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472919-2>

*Licania hedbergii* Prance, *Opera Bot.* 121: 279 (1993). Type: Ecuador, Napo, El Chaco Cantón, Tres Cruces, between Ríos Santa Rosa and El Salado, W. Palacios 6261 (holotype K; isotypes MO, QCNE).

**DISTRIBUTION AND HABITAT.** Ecuador; known only from the type collection. Lower montane moist forest, 1600 m.

**27. *Moquilea imbaimadaiensis* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472921-2>

*Licania imbaimadaiensis* Prance, *Kew Bull.* 47: 635 (1992). Type: Guyana, Cuyuni-Mazaruni region, Imbaimadai, L. J. Gillespie 2695 (holotype K; isotype US).

**DISTRIBUTION AND HABITAT.** Guyana; known only from the type collection. Low sclerophyllous forest adjacent to rapids on conglomerate.

**28. *Moquilea jaramilloi* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472922-2>

*Licania jaramilloi* Prance, *Kew Bull.* 47: 249 (1992). Type: Colombia, Amazonas, Quebrada El Sol, trib. of Río Caquetá, *R. Jaramillo & P. A. Palacios* 7940 (holotype COL).

**DISTRIBUTION AND HABITAT.** Colombia; known only from the type collection. River margin.

**29. *Moquilea kallunkiae* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472924-2>

*Licania kallunkiae* Prance, *Acta Amazon.* 8 (4): 583 (1978). Type: Panama, Colón, Santa Rita Rd., *S. A. Mori & J. A. Kallunki* 5052 (holotype NY; isotypes BM, CAS, K, MO).

**DISTRIBUTION AND HABITAT.** Costa Rica and Panama. Wet forest.

**30. *Moquilea klugii* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472925-2>

*Licania klugii* Prance, *Fl. Neotrop. Monogr.* 9: 47 (1972a). Type: Peru, Loreto, Río Putumayo, Flórida, *G. Klug* 2221 (holotype NY; isotypes BM, F, GH, K, US).

**DISTRIBUTION AND HABITAT.** Amazonian Peru. Riverine forest.

**31. *Moquilea leucosepala* (Griseb.) R. O. Williams (1932: 315)**

*Licania leucosepala* Griseb. (Grisebach 1857: 198). Type: Leeward Is., Guadeloupe, without locality, *E. P. Duchassaing* s.n. (holotype GOET; isotypes K, P).

**DISTRIBUTION AND HABITAT.** Antilles from Guadeloupe to Trinidad, adjacent Venezuela and Colombia. Forests.

**32. *Moquilea longicuspidata* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472926-2>

*Licania longicuspidata* Prance, *Kew Bull.* 50: 707 (1995). Type: Ecuador, Carchi, Tulcan Cantón, Parroquia Tobar Donoso, *G. Tipaz et al.* 1446 (holotype MO; isotype QCNE; phototype K).

**DISTRIBUTION AND HABITAT.** Ecuador. Premontane tropical rainforest; 650 – 1800 m.

**33. *Moquilea longipedicellata* (Ducke) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472927-2>

*Licania longipedicellata* Ducke, *Bull. Mus. Natl. Hist. Nat., Sér. 2, 4:* 725 (1932). Type: Brazil, Amazonas, Fonte Boa, rio Solimões, *A. Ducke* s.n. (holotype RB 23603; isotypes K, P, S, US).

**DISTRIBUTION AND HABITAT.** Colombia, Ecuador, Peru, and the upper part of Brazilian Amazonia. Riverine forest.

**34. *Moquilea longipetala* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472928-2>

*Licania longipetala* Prance, *Fl. Neotrop. Monogr.* 9: 62 (1972a). Type: Peru, Loreto, Río Mazan, Gamitanacocha, *J. M. Schunke* 288 (holotype NY; isotypes A, F, S, US).

**DISTRIBUTION AND HABITAT.** Amazonian regions of Peru, Bolivia and Brazil. Periodically flooded forest.

**35. *Moquilea macrocarpa* (Cuatrec.) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472929-2>

*Licania macrocarpa* Cuatrec., *Fieldiana, Bot.* 27 (2): 107 (Cuatrecasas 1951). Type: Colombia, Valle, Río Cajambre, Quebrada del Corosal, *J. Cuatrecasas* 17740 (holotype F; isotype COL).

**DISTRIBUTION AND HABITAT.** Panama, Colombia, Ecuador and Peru. Lowland forests to 600 m and in premontane rain forest in Panama.

**36. *Moquilea maranhensis* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472930-2>

*Licania maranhensis* Prance, *Fl. Neotrop. Monogr.* 9: 58 (1972a). Type: Brazil, Maranhão, Barra do Corda, A. Lisboa s.n. (holotype NY; isotypes MG 2462, RB).

**DISTRIBUTION AND HABITAT.** Brazil; known only from the type collection. River margin.

**37. *Moquilea maritima* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472931-2>

*Licania maritima* Prance, *Fl. Neotrop. Monogr.* 9: 44 (1972a). Type: Colombia, Chocó, south of Curiche, J. A. Duke 9659 (holotype NY).

**DISTRIBUTION AND HABITAT.** Colombia (Chocó). Endemic to coastal forests.

**38. *Moquilea megalophylla* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472932-2>

*Licania megalophylla* Prance, *Kew Bull.* 46: 105 (1991). Type: Ecuador, Pichincha, Centinela, km 12 Carretera Patricia Pilar-24 de Mayo, km 47 Santo Domingo -Quevado, en la cima de las montañas de Ila, C. H. Dodson, A. Gentry, W. Palacios & J. Zaruma 14484 (holotype MO; isotype K).

**DISTRIBUTION AND HABITAT.** Western Ecuador. Lower montane forest 600 – 900 m.

**39. *Moquilea minutiflora* Sagot (1883: 308).**

*Licania minutiflora* (Sagot) Fritsch (1889: 54), non *Licania minutiflora* Cuatrec. Type: French Guiana, Maroni, M. Mélinon s.n. (holotype P; isotypes A, BM, F, G, K, NY, R, US).

*Licania rondonii* Pilg. (Pilger 1923: 540). Type: Brazil, Mato Grosso, Cáceres ("São Luiz de Cáceres"), F. C. Hoehne 4602 (holotype B, lost; lectotype designated here, R; isotype SP).

*Moquilea riparia* Gleason (in Gleason & Smith 1934: 192); *Licania riparia* (Gleason) Standl. (Standley 1937: 258). Type: Brazil, Maranhão, Maracaçumé, Campo da Boa Esperança, R. L. Fróes 1961 (holotype NY; isotypes BM, F, K, MICH, MO, P, S).

**DISTRIBUTION AND HABITAT.** Guianas, Venezuela, Bolivia and Amazonian Brazil. Non-flooded forests and gallery forests.

**40. *Moquilea montana* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472933-2>

*Licania montana* Prance, *Brittonia* 28: 212 (1976). Type: Venezuela, Lara, vic. Laguna Negra, Loma de Los Naranjos, J. A. Steyermark, R. Smith & C. Espinoza 111541 (holotype NY; isotypes P, VEN).

**DISTRIBUTION AND HABITAT.** Venezuela; known only from the type collection. Cloud forest, at 1300 – 1500 m.

**41. *Moquilea palcazuensis* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472934-2>

*Licania palcazuensis* Prance, *PhytoKeys* 42: 2 (2014). Type: Peru, Pasco, Oxapampa, Palcazu Distr., Parque Nacional Yanachaga-Chemillén, Cerro Panjil-Ozuz, Permanent plot tree 24, 10°10'S, 75°10'W, 850 m, A. Monteagudo, A. Peña, R. Francis et al. 8250 (holotype K; isotypes AMAZ, HUT, MO, MOL, USM).

**DISTRIBUTION AND HABITAT.** Peru; known only from the type. Primary lowland rainforest.

**42. *Moquilea platypus* Hemsl. (Hemsley 1878: 9).**

*Licania platypus* (Hemsl.) Fritsch (1889: 53). Type: Panama, without precise locality, H. Cumíng 1272 (lectotype K, fide Prance 1972a: 55; isolectotype MO).

**DISTRIBUTION AND HABITAT.** From southern Mexico through Central America to northern Colombia. Forest, most common near rivers, but also in forest away from rivers.

**43. *Moquilea pyrifolia* (Griseb.) R. O. Williams (1932: 314)**

*Licania pyrifolia* Grisebach (1860: 230). Type: Trinidad-Tobago, Trinidad, without locality, W. Purdie s.n. (holotype K).

*Moquilea macrocarpa* Pittier (1938: 352). Type: Venezuela, Carabobo, Valencia in Parks and Gardens, H. F. Pittier 8202 (holotype VEN; isotypes F, GH, MICH, MO, US).

**DISTRIBUTION AND HABITAT.** Martinique to Trinidad, adjacent Venezuela and Colombia. Lowland forest and

riverine forest in open places. Widely cultivated for its edible fruit.

**44. *Moquilea salicifolia*** (Cuatrec.) Sothers & Prance **comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472935-2>

*Licania salicifolia* Cuatrec., *Fieldiana, Bot.* 27: 111 (Cuatrecasas 1951). Type: Colombia, Antioquia, Rionegro, *Bro. J. Daniel* 477 (holotype US; isotypes COL, F, GH, NY).

**DISTRIBUTION AND HABITAT.** Known only from the vicinity of the type locality in Colombia. A high altitude endemic.

**45. *Moquilea salzmännii*** Hook. f. (Hooker 1867: 21)  
*Licania salzmännii* (Hook. f.) Fritsch (1889: 49).  
Type: Brazil, Bahia, without precise locality,  
*P. Salzmänn* s.n. (holotype K; isotypes E, G, LE,  
MO, P).

**DISTRIBUTION AND HABITAT.** Brazil (Espírito Santo and Bahia). Restinga.

**46. *Moquilea silvatica*** (Glaz. ex Prance) Sothers & Prance **comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472936-2>

*Licania silvatica* Glaz. ex Prance, *Fl. Neotrop. Monogr.* 9: 90 (1972a). Type: Brazil, Espírito Santo, Serra de Itabapoana, *A. F. M. Glaziou* 10702 (holotype C; isotypes B, K, P).

*Licania silvatica* Glaz. (Glaziou 1906: 195), *nom. nud.*

**DISTRIBUTION AND HABITAT.** Brazil; known only from the type collection. Cerrado.

**47. *Moquilea subarachnophylla*** (Cuatrec.) Sothers & Prance **comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472938-2>

*Licania subarachnophylla* Cuatrec., *Fieldiana, Bot.* 27: 110 (Cuatrecasas 1951). Type: Colombia, Boyacá, Orocué, *O. Haught* 2629 (holotype F; isotypes A, COL, NY, US).

**DISTRIBUTION AND HABITAT.** Known only from central Colombia and Venezuela. Gallery forest along the rivers of the savannas.

**48. *Moquilea tachirensis*** (Prance) Sothers & Prance **comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472940-2>

*Licania tachirensis* Prance, *Fl. Neotrop. Monogr.* 9S: 30 (1989). Type: Venezuela, Táchira, Río San Buena, 10 km W of La Fundación, *R. L. Liesner, A. González & R. F. Smith* 9606 (holotype NY; isotypes MO, VEN).

**DISTRIBUTION AND HABITAT.** Venezuela; known only from the type collection. Primary forested areas on sandy soil, 700 – 1000 m.

**49. *Moquilea tambopatensis*** (Prance) Sothers & Prance **comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472981-2>

*Licania tambopatensis* Prance, *Fl. Neotrop. Monogr.* 9S: 36 (1989). Type: Peru, Madre de Dios, Tambopata Nature Reserve, laguna Coco Cocha, *V. A. Funk, B. Kahn & S. Wiser* 8415 (holotype NY; isotype US).

**DISTRIBUTION AND HABITAT.** Peru and Bolivia. Along river edges.

**50. *Moquilea tomentosa*** Benth. (Bentham 1840: 215)  
*Licania tomentosa* (Benth.) Fritsch var. *latifolia* Hook. f. (Hooker 1867: 21); *Licania tomentosa* (Benth.) Fritsch (1889: 52). Type: Brazil, Pernambuco, *G. Gardner* 992 (holotype K; isotypes BM, CGE, E, GH, NY, OXF, P, S, US).

*Pleragina odorata* Arruda ex H. Kost. (Koster 1816: 499), *nom. inval.*

*Licania tomentosa* (Benth.) Fritsch var. *angustifolia* Hook. f. (Hooker 1867: 21). Type: Brazil, Piauí, *G. Gardner* 2559 (holotype K; isotypes BM, GH, NY, OXF, P).

**DISTRIBUTION AND HABITAT.** Northeastern, southeastern and southern Brazil. Native to the coastal restinga forest, but widely cultivated outside the region, especially in Amazonia.

**51. *Moquilea unguiculata*** (Prance) Sothers & Prance **comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472982-2>

*Licania unguiculata* Prance, *Fl. Neotrop. Monogr.* 9: 60 (1972a). Type: Brazil, Amazonas, Rio Negro, above mouth of rio Curicuriari, *A. Ducke* s.n. (holotype K; isotypes NY, RB 23599).



**DISTRIBUTION AND HABITAT.** Colombia, Peru and Brazilian Amazonia. Non-flooded forest.

**52. *Moquilea vasquezii* (Prance) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472983-2>

*Licania vasquezii* Prance, *Kew Bull.* 47: 251 (1992).  
Type: Peru, Loreto, Caballococha, road to Cashillo-Cocha, R. Vásquez & J. Jaramillo 12726 (holotype K; isotype MO).

**DISTRIBUTION AND HABITAT.** Peru; known only from the type collection. Primary swamp forest.

**53. *Moquilea velata* (Cuatrec.) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472984-2>

*Licania velata* Cuatrec., *Fieldiana, Bot.* 27: 60 (Cuatrecasas 1950). Type: Colombia, Valle, Río Calima, Quebrada La Brea, J. Cuatrecasas 21179 (lectotype F, fide Prance 1972a: 88; isolectotypes COL, MAD, P).

**DISTRIBUTION AND HABITAT.** Colombia; collected only in the Pacific coastal regions of Valle. Forest.

**54. *Moquilea veneralensis* (Cuatrec.) Sothers & Prance comb. nov.**

<http://www.ipni.org/urn:lsid:ipni.org:names:60472985-2>

*Licania veneralensis* Cuatrec., *Fieldiana, Bot.* 27: 109 (Cuatrecasas 1951). Type: Colombia, Valle, Río Yurumanguí, Veneral, J. Cuatrecasas 15786 (holotype F; isotype COL).

**DISTRIBUTION AND HABITAT.** Northwestern Colombia. Terra firme forest.

**VIII. *Licania* Aublet, *Hist. Pl. Guiane* 1: 119, t. 45 (Aublet 1775).**

*Hedycrea* Schreb. (Schreber 1789: 160), *nom. superfl. illegit.* Type: *Licania incana* Aubl.

*Licania* sect. *Cymosa* Prance (1967: 226). Type: *Licania hypoleuca* Benth.

*Licania* sect. *Pulverulenta* Prance (1967: 226). Type: *Licania coriacea* Benth.

*Trees.* Leaf lanate, pulverulent-furfuraceous, pulverulent-farinaceous, or glabrous, with or without stomatal cavities. Petiole with a pair of glands present or not. Bracteoles usually much shorter than or rarely equalling calyx, not enclosing flower buds. Inflorescences racemose panicles, panicles or spikes. Petals absent. Stamens 2–7 (8–11), rarely more than 8 (8–11 only in *L. mollis*, *L. stewardii* and *L. majuscula*), unilateral or less frequently inserted in a complete circle; filaments shorter than or equalling the calyx lobes, mostly free to base (a few species with filaments slightly connate at base) and glabrous or less often sparsely pubescent. Ovary pilose, tomentose, hirsutulous, inserted at the base of receptacle. Fruit globose to elliptic, to 10 × 6 cm, epicarp tomentose, pubescent, pulverulent, or smooth; endocarp glabrous or variously pilose within. Fig. 3A.

**DISTRIBUTION.** A genus of c. 100 species, two of which imperfectly known, distributed throughout Central and South America and in the Leeward Islands, from Mexico and Costa Rica to southeastern Brazil.

**NOTES.** The genus *Licania* s.s. (= core *Licania*) now comprises the former sections *Licania*, *Cymosa* and *Pulverulenta* of subgen. *Licania*, and the apetalous species of sect. *Hymenopus* of the previous classification, and three new species described since the last monograph of the family (Prance & Sothers 2003a, b). A priori here we have not circumscribed sections *Cymosa* and *Pulverulenta*, despite species appearing in subclades within the *Licania* clade, and these may in fact represent sections of *Licania* s.s., but at present we are not proposing any sections. *Licania* s.s. holds morphological affinities with *Leptobalanus* (both genera are apetalous), but differ in the number and the exertion of stamens. In Fig. 1 *Licania* appears in a clade with *Hirtella*, and distant to *Leptobalanus* and *Moquilea*.

**Key to species of *Licania*** (key does not include *L. roraimensis* and *L. tepuiensis* as they are known from incomplete material)

1. Leaf undersurface glabrous
  2. Leaves thin and membranous, the base cuneate, the venation equally prominent on both surfaces; receptacle urceolate; east-central Brazil. . . . . **38. *L. glazioviana***
  2. Leaves thick and coriaceous, the base usually rounded to cordate, rarely rounded-subcuneate (to cuneate in *L. marleneae*), the venation obscure on upper surface; receptacle conical to globose-cupuliform
    3. Leaves rounded to obtuse at apex, rarely exceeding 9 cm in length
      4. Flowers c. 3 mm long; petioles terete; E Brazil. . . . . **55. *L. littoralis***

4. Flowers c. 2 mm long; petioles usually canaliculate
  5. Inflorescence and flowers with brown pubescence; stamens 3; venation of leaf lower surface often papillose; stipules intrapetiolar; Venezuela, Guyana . . . . . **33. L. fanshawei**
  5. Inflorescence and flowers grey-puberulous or glabrescent; stamens 5; venation of leaf lower surface smooth-papillose; stipules adnate to extreme base of petiole
    6. Leaf 2.5 – 6.5 cm long, the apex and base rounded; Guianas . . . . . **48. L. irwinii**
    6. Leaf 5.5 – 9.5 cm long, the apex acute, the base cuneate; Brazil (C Amazonia) . . . **57. L. marleneae**
3. Leaves distinctly acuminate at apex, usually exceeding 8 cm in length
  7. Midrib slightly impressed above; petioles canaliculate; French Guiana . . . . . **26. L. cyathodes**
  7. Midrib prominulous above; petioles terete
    8. Flowers 2.5 – 3.5 mm long, ferruginous-brown-pubescent; stipules 4 – 7 mm long, persistent; Venezuela, Guianas, Brazil (Amazonia) . . . . . **76. L. polita**
    8. Flowers 1.5 mm long, grey-brown-pubescent; stipules small, caducous; Colombia, Venezuela, Brazil (Pará) . . . . . **85. L. silvae**
1. Leaf undersurface pubescent, either pulverulent or tomentose or lanate
  9. Flowers in small cymules, on long slender secondary branches (peduncles) less than 0.5 mm thick and attached to primary inflorescence branches; pedicels usually 0.25 – 3 mm long, rarely absent; fruit often very small, usually not exceeding 2 cm in length
  10. Leaf lower surface with stomatal cavities or thick, coarse, deeply cut venation, lanate-arachnoid
    11. Bracteoles large and enclosing groups of flower buds; flowers sessile; peduncles of cymules short and rather thick; Venezuela, Guianas . . . . . **30. L. densiflora**
    11. Bracteoles small and not enclosing groups of flower buds; flowers pedicellate; peduncles of cymules long and slender
      12. Inflorescence and exterior of flowers ferruginous-tomentose; young stems ferruginous-tomentellous (fruit 3 – 5 mm long, stipitate, densely tomentose, in *L. cuprea*)
        13. Flowers c. 2 mm long; stipules c. 5 mm long; stamens 3; Guyana. . . . . **24. L. cuprea**
        13. Flowers c. 6 mm long; stipules 7 – 10 mm long; stamens 6 – 7; Brazil (Espírito Santo) **6. L. arianeae**
      12. Inflorescence and exterior of flowers grey-puberulous or grey- or brown-tomentose; young stems glabrous or puberulous (fruit 1 – 2 cm long, not stipitate)
        14. Midrib impressed for entire length; petioles 7 – 14 mm long; leaves oblong-lanceolate; Brazil (Amazonia) . . . . . **45. L. impressa**
        14. Midrib plane throughout or impressed at base only; petioles 2 – 10 mm long; leaves ovate to oblong
          15. Leaf apex rounded; leaves orbicular-ovate, petioles 8 – 10 mm long; stamens 7; E Brazil . . . . . **83. L. santosii**
          15. Leaf apex acute to acuminate; leaves elliptic; petioles 2 – 7 mm long; stamens 3 – 7
            16. Leaf lower surface with lanate pubescence obscuring venation; stamens 6 – 7; C Brazil . . . . . **29. L. dealbata**
            16. Leaf lower surface pubescent only in the mouth of stomatal cavities, the reticulations glabrous; stamens 3 – 5
              17. Leaves ovate, broadest near base, 3 – 8.5 cm long; stipules axillary; Widespread. . . . . **44. L. hypoleuca**
              17. Leaves oblong-elliptic, broadest about middle, 5 – 13 cm long; stipules adnate to petiole base; Venezuela, Guianas, Brazil (Amazonia), Ecuador, Peru . . . . . **70. L. pallida**
    10. Leaf lower surface with a very fine, plane or prominulous venation, usually pulverulent-farinaceous
      18. Exterior of flowers and branches of inflorescence entirely glabrous or glabrescent; fruit exterior often drying purple
        19. Leaves oblong-lanceolate to oblong, the lower surface white-lanate; Brazil (Amazonia) **39. L. gracilipes**
        19. Leaves ovate to oblong, the lower surface sparsely grey-pulverulent-farinaceous; Venezuela, Guianas, Brazil (Amazonia), Colombia . . . . . **73. L. parvifructa**
      18. Exterior of flowers and usually branches of inflorescence puberulous to tomentose; fruit exterior grey to brown
        20. Leaf apex rounded, the margins revolute; inflorescence glabrous; Brazil (Pará, Bahia) **27. L. cymosa**
        20. Leaf apex acuminate, the margins not revolute; inflorescence usually puberulous or tomentose
          21. Fruit elongate-pyriform, to 2.5 cm long, the exterior with short rufous-velutinous pubescence; either inflorescence and exterior of flowers brown-tomentellous or petioles 7 – 12 mm long

22. Petioles 3 – 6 mm long, terete; inflorescence and flowers brown-tomentellous; leaves triangular or nearly so; W Indies . . . . . **92. L. ternatensis**
22. Petioles 7–12 mm long, canaliculate; inflorescence and flowers grey-puberulous; leaves oblong; Trinidad, Guianas, Amazonia . . . . . **59. L. membranacea**
21. Fruit ovoid to pyriform, rarely exceeding 1.2 cm long; exterior of flowers grey-puberulous or glabrescent; petioles 3 – 6 mm long
23. Leaves 6.5 – 16 cm long; midrib and primary veins prominent on upper surface; rachis and branches of inflorescence glabrescent; Guianas, Brazil (Amapá) . . . . . **74. L. piresii**
23. Leaves 2.5 – 10 cm long; midrib plane or prominulous on upper surface; rachis and branches of inflorescence puberulous
24. Inflorescence spreading, the rachis 1 – 15 mm thick; lower leaf surface pulverulent; Venezuela . . . . . **36. L. furfuracea**
24. Inflorescence compact, the rachis 0.5 mm thick; lower surface tomentellous; widespread . . . . . **44. L. hypoleuca**
9. Flowers sessile or subsessile on primary branches of inflorescence or on short (less than 0.5 mm long) thick peduncles only; pedicels usually sessile; fruit rarely less than 2 cm long
25. Leaf lower surface pulverulent-farinaceous
26. Leaf with rounded to acute apex, the margins usually revolute
27. Flowers 1.5 – 2 mm long; receptacle campanulate-cupuliform
28. Young branches and inflorescence densely tomentose; inflorescence to 4 cm long, recurved; Venezuela, Guyana . . . . . **11. L. boyanii**
28. Young branches and inflorescence branches glabrous; inflorescence usually exceeding 4 cm long, erect; Guyana . . . . . **13. L. buxifolia**
27. Flowers c. 3 mm long; receptacle urceolate
29. Leaves predominantly orbicular, occasionally oblong-elliptic, the apex rounded to retuse; Amazonia (Venezuela, Brazil) . . . . . **68. L. orbicularis**
29. Leaves elliptic, the apex acute
30. Receptacle narrowly urceolate-cylindrical; calyx lobes lanceolate; Brazil (Amazonas, Rondônia) . . . . . **66. L. niloi**
30. Receptacle broadly urceolate; calyx lobes deltoid; Venezuela, Guianas, Brazil (Amazonia) . . . . . **20. L. coriacea**
26. Leaf with well-developed acumen, the margins not revolute
31. Flowers 3 – 4 mm long; receptacle campanulate or urceolate
32. Receptacle campanulate; leaves 8.5 – 10 cm broad; Ecuador . . . . . **25. L. cuyabensis**
32. Receptacle urceolate, leaves to 8 cm broad
33. Leaf apex caudate; leaves 4 – 5.5 cm long, chartaceous; exterior of receptacle red-brown-pubescent contrasting with white pubescence on interior of calyx lobes; Brazil (Rondônia) . . . . . **91. L. teixeirae**
33. Leaf apex acuminate or acute; leaves 4 – 15 cm long, usually coriaceous; exterior of receptacle and calyx lobes grey-pubescent
34. Venation of leaf lower surface minutely reticulate, forming a network with less than 0.25 mm between reticulations; reticulation apparent because of absence of pubescence on veins; leaves thin-chartaceous; stipules usually caducous; western Amazonia (Peru, Colombia, Brazil, Venezuela) . . . . . **96. L. urceolaris**
34. Venation and reticulation coarse, with 1 – 2 mm between reticulations; pubescence obscuring much of veins; leaves thick-coriaceous; stipules persistent
35. Leaf apex with finely pointed, well-developed acumen; rachis of inflorescence glabrous; Costa Rica, Panama, Guianas, Brazil (Pará) . . . . . **1. L. affinis**
35. Leaf apex acute or with short blunt acumen; rachis of inflorescence pubescent; Venezuela, Guianas, Brazil (northern Amazonia) . . . . . **20. L. coriacea**
31. Flowers 1.5 – 2 mm long; receptacle campanulate
36. Primary veins slightly impressed on upper surface; fruit exterior sordid-rufous-pubescent; branches of inflorescence densely tomentose to puberulous
37. Leaves thick-coriaceous; stipules caducous; flowers in clusters on short thick peduncles; stamens 3; Colombia (Pacific Coast) . . . . . **37. L. glauca**

37. Leaves thin, chartaceous-membranous; stipules persistent; flowers on primary and secondary branches of inflorescence; stamens 6 – 7; Guianas, Brazil (Amapá, Pará) . . . . . **28. L. davillifolia**
36. Primary veins plane or prominent on upper surface; fruit exterior glabrous, drying yellow; branches of inflorescence glabrous to puberulous
38. Leaves 11 – 13 (– 18) × 4 – 8 cm; Guianas, Brazil (Amazonia) . . . . . **32. L. elliptica**
38. Leaves 4 – 10 (– 12) × 2 – 5.5 cm; Amazonia (Bolivia, Brazil, Guianas, Peru, Venezuela) . . . . . **15. L. canescens**
25. Leaf lower surface densely lanate-arachnoid or with stomatal cavities, never pulverulent
39. Flowers 6 – 7.5 mm long, stamens often connate for ½ their length or free
40. Stamens connate for ½ their length; leaves prominently reticulate but without stomatal cavities; petioles eglandular; Guyana, Suriname . . . . . **21. L. couepiifolia**
40. Stamens free to base; leaves with conspicuous stomatal cavities; petioles with 2 glands near base of lamina; Brazil (Amapá) . . . . . **64. L. naviculistipula**
39. Flowers not exceeding 5.5 mm in length; stamens free almost to base
41. Leaf base distinctly cordate to subcordate; leaves usually ovate-orbicular
42. Leaves triangular-ovate, 10 – 16 cm long, membranous; Peru (Loreto) . . . **95. L. trigonioides**
42. Leaves orbicular to ovate, 3 – 9 cm long, usually coriaceous
43. Young stems hispid; lower surface of leaves with hirsutulous-hispid venation, the apex with well-developed acumen; Venezuela (Amazonas) . . . . . **19. L. cordata**
43. Young stems puberulous to tomentose; lower surface of leaves glabrous or lanate on venation, the apex acute or bluntly acuminate
44. Flowers 4.5 – 5.5 mm long; receptacle urceolate; stipules 5 – 6 mm long; Venezuela (Amazonas) . . . . . **35. L. foldatsii**
44. Flowers 1.5 – 3.5 mm long; receptacle campanulate; stipules 1 – 3 mm long
45. Leaves submembranous, the lower surface with deeply cut venation, the pubescence occurring in cavities and hard to remove; fertile stamens 5 – 11
46. Stamens 8 – 11; petioles c. 5 mm long; stipules 3 – 6 mm long; Amazonian Colombia, Venezuela, Brazil . . . . . **62. L. mollis**
46. Stamens 5 – 6; petioles 1.5 – 3 mm long; stipules 2 – 2.5 mm long; Amazonian Venezuela, Colombia . . . . . **41. L. hebantha**
45. Leaves thick-coriaceous, the lower surface with shallow venation, not forming cavities, the lanate pubescence easily rubbed off; fertile stamens 3; Venezuela
47. Pubescence obscuring venation; stipules adnate to extreme base of petiole . . . . . **88. L. steyermarkii**
47. Pubescence not obscuring venation; stipules axillary . . **90. L. subrotundata**
41. Leaf base rounded to cuneate; leaves only rarely ovate-orbicular
48. Midrib and primary veins distinctly impressed on leaf upper surface
49. Leaf lower surface with well-developed stomatal cavities filled with lanate pubescence; petioles 8 – 17 mm long
50. Stomatal cavities conspicuous because of glabrous venation; leaves 4 – 8.5 cm long; Venezuela, Brazil (Amazonas) . . . . . **22. L. crassivenia**
50. Stomatal cavities less conspicuous because of puberulous venation; leaves (8 –) 10 – 25 cm long
51. Leaf apex acute; flowers 1.5 – 2 mm long; Ecuador . . . . . **4. L. apiknae**
51. Leaf apex acuminate; flowers 1.5 – 5 mm long; Brazil and Guianas
52. Flowers c. 1.5 – 2.5 mm long; inflorescence much branched, predominantly axillary; fertile stamens 3 with 4 staminodes; petioles conspicuously 2 – 4-glandular; Suriname . . . . . **49. L. jimenezii**
52. Flowers 3 – 5 mm long; inflorescence little branched, terminal; fertile stamens 6 – 11, staminodes absent; petiole glands inconspicuous
53. Receptacle conical, 4 – 5 mm long; fruit tomentellous, the stipe 2 – 6 mm long; leaf lower surface brown-lanate; Guianas, Brazil

- (Amazonas) . . . . . **56. L. majuscula**
- 53.** Receptacle campanulate, 2.5 – 3 mm long; fruit pulverulent, the stipe 8 – 15 mm long; leaf lower surface white-lanate; Venezuela, Guianas, Brazil (Amazonas) . . . . . **2. L. alba**
- 49.** Leaf lower surface without stomatal cavities but often prominently reticulate; petioles 2 – 6 (– 8) mm long
- 54.** Exterior of receptacle sparsely puberulous, the pubescence not completely covering the surface; leaves oblong-lanceolate; widespread . . . . . **50. L. kunthiana**
- 54.** Exterior of receptacle densely tomentose to tomentellous, the pubescence completely covering the surface; leaves oblong to elliptic
- 55.** Leaves 2.5 – 5.5 cm long, not prominently reticulate beneath; petioles 1.5 – 3 mm long; Venezuela (Bolívar) . . . . . **42. L. hitchcockii**
- 55.** Leaves 5 – 22 cm long, prominently reticulate beneath; petioles 4 – 8 mm long
- 56.** Flowers c. 3.5 – 5 mm long; receptacle broadly cupuliform; leaves orbicular with rounded apex, the lower surface hirsute along venation; Guyana . . . . . **82. L. sandwichii**
- 56.** Flowers 2 – 3 mm long; receptacle campanulate; leaves oblong to elliptic, acute to acuminate at apex, the lower surface usually tomentellous, rarely hirsute on venation
- 57.** Leaf lower surface with parallel secondary veins, giving a prominently reticulate appearance; pubescence brown; primary veins 7 – 10; Venezuela, Guianas, Brazil (Amazonia) . . . . . **53. L. laxiflora**
- 57.** Leaf lower surface with diffuse secondary veins, less prominent; pubescence rufous; primary veins 5 – 6; Venezuela, Guianas . . . . . **81. L. rufescens**
- 48.** Primary veins and usually midrib plane or prominent on upper surface
- 58.** Exterior of flowers and inflorescence branches grey-puberulous, the pubescence not completely covering surfaces
- 59.** Receptacle campanulate; leaves without stomatal cavities; wide-spread . . . . . **50. L. kunthiana**
- 59.** Receptacle urceolate; leaves with shallow stomatal cavities; Brazil (Rondônia) . . . . . **9. L. bellingtonii**
- 58.** Exterior of flowers densely tomentellous or tomentose, the pubescence completely covering surfaces
- 60.** Leaf apex rounded, obtuse or bluntly acute, or rarely short-apiculate (never acuminate)
- 61.** Lanate pubescence of leaf lower surface hard to remove, covering deep stomatal cavities
- 62.** Leaf veins 9 – 11; dense pubescence covering stomatal cavities receptacle urceolate; stamens 4; Guyana . . . . . **17. L. compacta**
- 62.** Leaf veins 13 – 15; stomatal cavities visible; receptacle campanulate; stamens 7 – 8; Ecuador . . . . . **18. L. condoriensis**
- 61.** Lanate pubescence of leaf lower surface easily removed, revealing little protruding venation, stomatal cavities absent; receptacle usually campanulate, urceolate in *L. ovalifolia* and *L. savannarum* only
- 63.** Receptacle urceolate; stipules 3 – 5 mm long, adnate to petiole well above base
- 64.** Stamens 3; leaves thickly coriaceous; petioles 4 – 7 mm long; Guianas, Brazil (Amapá) . . . . . **69. L. ovalifolia**
- 64.** Stamens 9 – 11; leaves chartaceous; petioles 1.5 – 2.5 mm long; Brazil (Amazonas) . . . . . **87. L. stewardii**
- 63.** Receptacle usually campanulate, rarely urceolate; stipules 1 – 3 mm long, axillary or adnate to extreme base of petiole
- 65.** Leaves ovate-orbicular, the apex often shortly apiculate
- 66.** Lanate pubescence obscuring venation; stipules adnate to extreme base of petiole; Venezuela (Bolívar, Amazonas) . . . . . **88. L. steyermarkii**
- 66.** Lanate pubescence not obscuring venation; stipules axillary; Venezuela



- (Distrito Federal, Aragua) ..... **90. L. subrotundata**
65. Leaves oblong-lanceolate to elliptic, the apex rounded, acute or acuminate
67. Stipules adnate to petiole base; petioles 8 – 12 mm long; inflorescence branches very sparsely puberulous; stamens 5; Brazil (Bahia) ..... **7. L. bahiensis**
67. Stipules axillary, caducous; petioles 2 – 7 mm long; inflorescence branches densely puberulous or tomentellous; stamens 3
68. Leaves oblong-elliptic, sparsely lanate, the lower surface minutely reticulate; primary veins 9 – 11; petioles 4 – 7 mm long; receptacle campanulate; Colombia ..... **14. L. caldasiana**
68. Leaves oblong to oblong-lanceolate, the lower surface densely farinaceous-lanate with obscured venation; primary veins 5 – 8; petioles 2 – 3 mm long; receptacle campanulate-urceolate; Brazil, Venezuela (Amazonas) ..... **84. L. savannarum**
60. Leaf apex distinctly acuminate or sharply acute
69. Leaves 3 – 4 cm long, with 2 conspicuous glands at junction of petiole with upper surface of lamina; Guyana ..... **61. L. microphylla**
69. Leaves predominantly large, exceeding 5 cm long, lacking conspicuous glands
70. Stamens 3
71. Leaf lower surface with stomatal cavities
72. Leaf venation glabrous or glabrescent, hence conspicuous, with glands present at base of lower surface; leaves coriaceous; stipules less than 1.5 mm broad at base; Peru, Brazil, Colombian Amazonia ..... **94. L. triandra**
72. Leaf venation pubescent, lanate pubescence covering entire leaf and obscuring stomatal cavities of lower surface, lacking glands at leaf base; leaves chartaceous; stipules 2.5 mm broad at base; Brazil (Pará) ..... **93. L. tocantina**
71. Leaf lower surface with prominent venation but no stomatal cavities, the venation pubescent and hence less conspicuous
73. Stipules caducous, petioles glabrous or tomentose; receptacle campanulate
74. Petioles tomentose when young; leaves elliptic to oblong, with well-developed acumen; primary veins 7 – 9 pairs; Venezuela, Guianas, Brazil ..... **31. L. discolor**
74. Petioles glabrous; leaves oblong-lanceolate, finely apiculate; primary veins 10 – 12 pairs; Brazil (Amazonia) ..... **3. L. apiculata**
73. Stipules persistent, petioles glabrous or puberulous when young; receptacle campanulate or urceolate
75. Inflorescence 8 – 15 cm long, spreading, with numerous primary branches; lower leaf surface brown-lanate; receptacle campanulate; Colombia, Venezuela, Guianas, Brazil (Amazonia, Bahia) ..... **60. L. micrantha**
75. Inflorescence 5 – 6 cm long, with a few primary branches; lower leaf surface whitish-grey-pubescent; receptacle urceolate
76. Leaf apex with a finely pointed acumen; leaves thin-membranous; French Guiana, Brazil (Amapá) ..... **77. L. pruinosa**
76. Leaf apex acute to bluntly acuminate; leaves coriaceous
77. Leaves thinly coriaceous, 4.5 – 10.5 × 2 – 5.5 cm; flowers 4 – 5 mm long; interior of receptacle pubescent on upper portion; E-central Brazil ..... **67. L. nitida**
77. Leaves thickly coriaceous, 3 – 5.5 × 2 – 3 cm; flowers 2 mm long; interior of receptacle glabrous on upper

- portion; Brazil (NW Amazonia) . . . . **5. L. aracaensis**
- 70.** Stamens 4 – 8 (– 10)
- 78.** Leaf lower surface with deep, extremely conspicuous stomatal cavities, the pubescence confined to cavities made obvious by almost glabrous venation
- 79.** Inflorescence and flowers ferruginous-pubescent; stipules 1 – 2 mm long × 1 – 1.5 mm broad at base, persistent, ferruginous; leaf apex acute to bluntly acuminate; E-central Brazil . . . . . **78. L. riedelii**
- 79.** Inflorescence and flowers grey-puberulous; stipules 2 – 4 mm long, 0.2 – 0.5 mm broad at base, persistent or caducous, pubescent but not ferruginous; leaf with well-developed acumen
- 80.** Bracteoles persistent, lanceolate; upper surface of midrib impressed; stipules caducous; Brazil (Amazonia). . . . . **12. L. bracteata**
- 80.** Bracteoles caducous, triangular; upper surface of midrib plane; stipules small but persistent
- 81.** Inflorescence branches thick; flowers subsessile; fruit exterior ferruginous-velutinous; Venezuela, Guianas, central and western Amazonia . . . . . **72. L. parviflora**
- 81.** Inflorescence branches slender; flowers distinctly pedicellate; fruit exterior reddish-brown, short-pulverulent; Venezuela, Brazil (Amazonas) . . . . . **70. L. pallida**
- 78.** Leaf lower surface with poorly developed stomatal cavities or none, venation pubescent
- 82.** Petioles 1.5 – 2 cm long; inflorescence rachis and branches glabrous or glabrescent; Guianas, Brazil (Pará) . . . . . **79. L. robusta**
- 82.** Petioles to 1 cm long (to 1.5 cm in *L. bahiensis* and *L. lamentanda*); inflorescence rachis and branches usually densely tomentose or tomentellous
- 83.** Inflorescence predominantly of axillary and terminal spikes, terminal inflorescences rarely little branched or with minute spikes along rachis
- 84.** Leaf lower surface deeply reticulate, with poorly developed stomatal cavities
- 85.** Leaves lanceolate, apex acuminate; stamens 6 – 8; Venezuela (Amazonas), Brazil (Roraima) . . . . . **52. L. lanceolata**
- 85.** Leaves ovate-elliptic, apex abruptly acuminate; stamens 4; Colombia, Venezuela (Aragua) . . . . . **75. L. pittieri**
- 84.** Leaves oblong to ovate-elliptic, the lower surface not deeply reticulate, lacking stomatal cavities
- 86.** Flowers 2.5 mm long; receptacle broadly cupuliform; inflorescence puberulous; reticulate venation of leaf lower surface conspicuous; E-central Brazil . . . . . **86. L. spicata**
- 86.** Flowers 1.5 – 2 mm long; receptacle campanulate; inflorescence tomentose; venation of leaf lower surface inconspicuous except in *L. nelsonii*
- 87.** Flowers in short, dense, minute spikes attached to long rachis; Suriname . . . . . **89. L. stricta**
- 87.** Flowers solitary along rachis or in dense glomerules, but not in minute spikes
- 88.** Leaf lower surface conspicuously reticulate; stipules adnate to base of petiole; receptacle

- rufous-pubescent; flowers densely and evenly clustered along inflorescence rachis; large tree; Brazil (Amazonas) . . . **65. L. nelsonii**
- 88.** Leaf lower surface lanate, not conspicuously reticulate; stipules axillary; receptacle grey-brown pubescent; flowers in dense glomerules or small groups; small shrub to medium sized tree (15 m)
- 89.** Leaves thin and membranous, the acumen finely pointed; flowers in dense glomerules; inflorescences largely axillary; Venezuela, Guianas, Brazil (Bahia, Pará) . . . **54. L. leptostachya**
- 89.** Leaves thick and coriaceous, the acumen usually blunt; flowers in small groups or solitary but not glomerulate; inflorescences largely terminal; Venezuela, Guianas, Brazil (Amazonia) . . . **46. L. incana**
- 83.** Inflorescence of terminal and sub-terminal racemose panicles
- 90.** Leaves lanceolate; low shrub or subshrub; Venezuela (Amazonas), Brazil (Roraima). . . . **52. L. lanceolata**
- 90.** Leaves ovate to oblong-lanceolate; trees or tall shrubs
- 91.** Stipules 3 – 10 mm long and at least 1 mm broad at base, distinctly adnate to petiole or intrapetiolar, persistent and obvious
- 92.** Midrib distinctly impressed above; bracteoles 0.2 – 1.5 mm long
- 93.** Inflorescence ferruginous-pubescent; petioles canaliculate; stipules adnate to petiole well away from axil; Bolivia, Brazil (Pará) . . . **71. L. paraensis**
- 93.** Inflorescence grey-puberulous; petioles terete; stipules intrapetiolar or adnate to inside of extreme base of petiole
- 94.** Leaves with a finely pointed acumen; primary veins 11 – 12 pairs, the lower surface glandular at base; Brazil, Colombia, Venezuela (northwestern Amazonia) . . . **97. L. vaupesiana**
- 94.** Leaves with blunt acumen; primary veins 6 – 8 pairs, the lower surface eglandular at base; E-central Brazil . . . **7. L. bahiensis**
- 92.** Midrib plane or prominulous above; bracteoles 1.5 – 3 mm long
- 95.** Leaves velutinous beneath; stipules fimbriate; Ecuador. . . . **98. L. velutina**
- 95.** Leaves not velutinous beneath; stipules with entire margin
- 96.** Leaves membranous; flowers c. 2 mm long, grey-tomentellous; inflorescence grey-puberulous; stamens 5; Brazil (Amapá) . . . **58. L. maxima**
- 96.** Leaves coriaceous; flowers 3 – 3.5 mm long, brown-tomentose; inflorescence brown-tomentose; stamens 8 – 11; Amazonian Colombia, Peru, Venezuela,

- Brazil . . . . . **62. L. mollis**
- 91.** Stipules usually less than (rarely exceeding) 2.5 mm long and very narrow to base, on outside of axils or adnate to extreme base of petiole, caducous or persistent, often inconspicuous
- 97.** Stipules adnate to extreme base of petiole, persistent or subpersistent
- 98.** Petioles 7 – 15 mm long; lamina 7 – 16 × 3 – 8 cm; stipules subpersistent
- 99.** Petioles glabrous; leaves not deeply reticulate; Brazil (Amazonas) . . . . . **16. L. cidii**
- 99.** Petioles tomentellous even when old, leaf lower surface deeply reticulate; Brazil (Pará and central) . . . . . **10. L. blackii**
- 98.** Petioles 2 – 6 mm long; lamina 3 – 12 × 2.2 – 5.5 cm; stipules persistent
- 100.** Leaf lower surface with stomatal cavities. . . . . **72. L. parviflora**
- 100.** Leaf lower surface without stomatal cavities
- 101.** Flowers 1.5 – 2 mm; inflorescence and flowers sparse- grey puberulous. . . . . **50. L. kunthiana**
- 101.** Flowers 2.5 mm; inflorescence and flowers dense-brown tomentose. . . . . **63. L. monteagudensis**
- 97.** Stipules axillary, caducous or persistent
- 102.** Petioles 10 – 15 mm long, receptacle velutinous on exterior; Brazil (Bahia)
- 103.** Leaves thickly coriaceous with recurved margins; apiculate at apex; flowers 4.5 – 5.5 mm long . . . . . **51. L. lamentanda**
- 103.** Leaves chartaceous, finely acuminate at apex; flowers 2 – 2.5 mm long . . . . . **8. L. belemii**
- 102.** Petioles 2 – 10 mm long, receptacle rarely velutinous (only in *L. rodriguesii*)
- 104.** Leaf lower surface with smooth inconspicuous reticulation, the pubescence easily removed; primary veins widely spaced, 1.2 – 2.5 cm apart; exterior of receptacle velutinous; Brazil (Amazonas) . . . . . **80. L. rodriguesii**
- 104.** Leaf lower surface with deeply cut reticulation, and hence pubescence hard to remove; primary veins not more than 1 cm apart; exterior of receptacle tomentellous
- 105.** Receptacle globose; upper surface of youngest leaves appressed-strigose, soon becoming glabrous; inflorescence of axillary spikes and terminal panicles; E-central Brazil . . . . . **86. L. spicata**

105. Receptacle campanulate; upper surface of youngest leaves glabrous; inflorescence of terminal and sub-terminal racemose panicles
106. Leaves oblong-lanceolate; midrib slightly impressed above . . . . .47. **L. indurata**
106. Leaves ovate-elliptic to oblong; midrib plane above
107. Inflorescence much branched, spreading, lax; lower leaf surface rufous pubescent; Venezuela, Guianas, N Brazil.....81. **L. rufescens**
107. Inflorescence densely eroded, compact, little-branched; lower leaf surface grey-brown pubescent
108. Leaves finely acuminate, the acumen 8 – 12 mm long; stipules caducous; Ecuador . . . . .  
...40. **L. harlingii**
108. Leaves bluntly acuminate, obtuse or with abrupt acumen 0 – 6 mm long; stipules usually persistent (caducous in *L. ferreirae*)
109. Stipules caducous; leaf apex abruptly acuminate, the acumen 4 – 6 mm long; young leaves with large glands at junction with petiole; Brazil (Amazonas).....34. **L. ferreirae**
109. Stipules persistent, 1 – 3 mm long; leaf apex obtuse, acute or bluntly acuminate; young



leaves without large glands at junction with petiole

110. Petioles soon becoming glabrous; leaf apex bluntly acuminate; young fruit pyriform; Brazil (Central)...43.

**L. hoehnei**

110. Petioles tomentose, becoming less so with age; leaf apex obtuse to acute; young fruit cylindrical, becoming pyriform; Panama, Trinidad, Venezuela ....23.

**L. cruegeriana**

1. **Licania affinis** Fritsch (1889: 50). Type: Guyana, R. & R. Schomburgk 822 (holotype W; isotypes CGE, G, K, P). *Licania schomburgkiana* Klotzsch in M. R. Schomb. (Schomburgk 1848: 1199), *nom. nud.*

**DISTRIBUTION AND HABITAT.** Costa Rica, Panama, Guianas and N Brazil (Pará). Riverine and periodically flooded forest.

2. **Licania alba** (Bernoulli) Cuatrec. (Cuatrecasas 1964: 588).

*Theobroma alba* Bernoulli (1869: 14). Type: Guyana, 'Essequibo and Cuyounie', C. F. Appun 1 (holotype K).

*Licania venosa* Rusby (1920: 26). Type: Venezuela, Delta Amacuro, H. H. Rusby & R. W. Squires 423 (holotype NY; isotypes A, BM, F, GH, MICH, MO, S, US, VEN, Z).

*Licania longifolia* Benoist (1922: 252). Type: French Guiana, L. C. Richard s.n. (lectotype P, fide Prance & Sothers 2003a: 146).

**DISTRIBUTION AND HABITAT.** Guianas and adjacent Venezuela and Brazil (Amapá, Amazonas, Pará). Primary forest.

3. **Licania apiculata** Prance (1972a: 151). Type: Brazil, Amazonas, Rio Cuieiras, W. A. Rodrigues & L. Coelho 4881 (holotype NY; isotype INPA).

**DISTRIBUTION AND HABITAT.** N Brazil (Amazonas); known only from the Rio Cuieiras. Beaches and open habitats beside rivers.

4. **Licania apiknae** Prance (2014: 4). Type: Peru, Amazonas, Bagua Prov., Imaza Distr., Comunidad Aguaruna de Putuim, Monte Alto de Putuim, 5°00'54"S, 78°22'44"W, 500 m, C. Diaz, S. J. Kayip, & P. Atamain 7016 (holotype K; isotype MO).

**DISTRIBUTION AND HABITAT.** Known only from Peru. Habitat unknown.

5. **Licania aracaensis** Prance (1976: 223). Type: Brazil, Amazonas, Serra Aracá, J. M. Pires 15027 (holotype IAN; isotypes INPA, NY, RB).

**DISTRIBUTION AND HABITAT.** Brazil (Amazonas). Endemic to the summit of the sandstone mountain, at c. 1000 m.

6. **Licania arianeae** Prance (1989: 44). Type: Brazil, Espírito Santo, Linhares, Reserva Florestal CVRD, D. A. Foli 228 (holotype RB; isotypes CVRD, NY).

**DISTRIBUTION AND HABITAT.** Brazil (Espírito Santo). Restinga and tabuleiro forests.

**7. *Licania bahiensis*** *Prance* (1972a: 165). Type: Brazil, Bahia, Ilhéus, *H. P. Vellozo* 736 (holotype R; isotype NY).

**DISTRIBUTION AND HABITAT.** Brazil; known only from the type collection. Coastal forest.

**8. *Licania belemii*** *Prance* (1972a: 172). Type: Brazil, Bahia, Belmonte, *R. P. Belém & Pinheiro* 3211 (holotype UB; isotypes NY, RB).

**DISTRIBUTION AND HABITAT.** E Brazil (Bahia and Espírito Santo). Common in forests.

**9. *Licania bellingtonii*** *Prance* (1972a: 145). Type: Brazil, Rondônia, Santa Bárbara, 15 km E of Km 117 of Porto Velho-Cuiabá Highway, *G. T. Prance & J. F. Ramos* 7000 (holotype NY; isotypes INPA, K, P, US).

**DISTRIBUTION AND HABITAT.** NW Brazil (Amazonas and Rondônia). Non-flooded forest.

**10. *Licania blackii*** *Prance* (1972a: 167). Type: Brazil, Tocantins [Goiás], Araguaína, *G. T. Prance & N. T. Silva* 58989 (holotype NY; isotypes K, RB, UB).

**DISTRIBUTION AND HABITAT.** Bolivia, Peru, and Brazil in Amazonia, and S to the borders of the planalto central. Gallery forest, and secondary forest in open places.

**11. *Licania boyanii*** *Tutin* (1940: 255). Type: Guyana, Bartica-Potaro road, *T. G. Tutin* 293 (holotype BM; isotypes K, NY, RB, U, US).

**DISTRIBUTION AND HABITAT.** Venezuela and Guyana. Wallaba forest and forest on slopes.

**12. *Licania bracteata*** *Prance* (1972a: 155). Type: Brazil, Amazonas, Manaus, Estrada do Aleixo, *A. Ducke* 293 (holotype K; isotypes AA, F, IAN, NY, S, US).

**DISTRIBUTION AND HABITAT.** Peru and Brazil (vicinity of Manaus and the lower rio Negro). Non-flooded forest.

**13. *Licania buxifolia*** *Sandwith* (1931: 369). Type: Guyana, Moraballi Creek, near Bartica, *N. Y. Sandwith* 327 (holotype K; isotypes NY, P, RB, U).

**DISTRIBUTION AND HABITAT.** Guyana. Wallaba forest.

**14. *Licania caldasiana*** *Cuatrec.* (Cuatrecasas 1951: 106). Type: Colombia, without locality, *J. C. Mutis* 3868 (holotype US; isotypes F, MA).

**DISTRIBUTION AND HABITAT.** Colombia; known only from the type collection, which lacks detailed field notes.

**15. *Licania canescens*** *Benoist* (1919: 514). Type: French Guiana, Maroni, *M. Mélinon* s.n. (lectotype P, fide *Prance* 1972a: 134; isolectotypes GH, K).

**DISTRIBUTION AND HABITAT.** Guianas, Venezuela, Bolivia, Peru and widespread in Amazonian Brazil. Riverine and periodically flooded forest.

**16. *Licania cidii*** *Prance* (1992: 247). Type: Brazil, Amazonas, Mun. de Jutai, São Francisco, *C. A. Cid Ferreira et al.* 8352 (holotype INPA; isotypes K, NY).

**DISTRIBUTION AND HABITAT.** Peru and western Amazonian Brazil in the rio Solimões region. Forest on terra firme.

**17. *Licania compacta*** *Fritsch* (1889: 52). Type: Guyana, Roraima, *R. & R. Schomburgk* 519 (812) (holotype W; isotypes BM, BR, CGE, F, G, K, L, NY, OXF, P, W).

*Licania flavicans* *Klotzsch* in *M. R. Schomb.* (Schomburgk 1848: 1198), *nom. nud.*

**DISTRIBUTION AND HABITAT.** Guyana (vicinity of Mt Roraima); known only from the type. Habitat unknown.

**18. *Licania condoriensis*** *Prance* (2013: 72). Type: Ecuador, Zamora-Chinchi, El Pangui, Cordillera del Cóndor, plateau of Contrafuerte, Tres Patines, W of main Cóndor ridge above Jardín Botánico of Ecuacorriente Copper Company, 03°37'48"S, 78°26'50"W, 1685 m, *D. Neill & W. Quizhpe* 15076 (holotype K; isotypes MO, QCNE).

**DISTRIBUTION AND HABITAT.** Known only from Ecuador, at mid-altitudes.

**19. *Licania cordata*** *Prance* (1972a: 136). Type: Venezuela, Amazonas, NW base of Cerro Yapacana, *B. Maguire & J. J. Wurdack* 34505 (holotype NY; isotypes K, P).

**DISTRIBUTION AND HABITAT.** Venezuela (Cerro Yapacana, where it is reported to be abundant) and in Amazonian Brazil (Amazonas). Savannas.

**20. *Licania coriacea* Benth.** (Bentham 1840: 221). Type: Guyana, banks of Essequibo R., *R. & R. Schomburgk* 50 (holotype K; isotypes BM, BR, CGE, G, L, OXF, P, US).

*Licania pallidula* Standl. (Smith 1940: 286). Type: Venezuela, Bolívar, *A. S. Pinkus* 89 (holotype F; isotypes GH, K, NY, US).

**DISTRIBUTION AND HABITAT.** Guianas, Venezuela and C & N Amazonia in Brazil. Non-flooded forest.

**21. *Licania couepiifolia* Prance (1972a: 134).** Type: Guyana, Shodikar Creek, Essequibo R., *A. C. Smith* 2839 (holotype NY; isotypes A, F, K, MAD, P, S, U, US).

**DISTRIBUTION AND HABITAT.** Guianas. Lowland forest.

**22. *Licania crassivenia* Spruce ex Hook. f.** (Hooker 1867: 14). Type: Brazil, Amazonas, rio Uaupés, *R. Spruce* 2678 (lectotype K, fide Prance 1972a: 140; isolectotypes BM, BR, CGE, OXF, P, W).

**DISTRIBUTION AND HABITAT.** Venezuela and Brazil (Amazonas). Caatinga.

**23. *Licania cruegeriana* Urb.** (Urban 1908: 352). Type: Trinidad-Tobago, Trinidad, Las Cuevas, *H. Crueger* 205 (2065 some sets) (holotype GOET; isotypes K, NY, TRIN).

**DISTRIBUTION AND HABITAT.** Panama, N coastal Venezuela and Trinidad-Tobago. Forests and coastal locations.

**24. *Licania cuprea* Sandwith (1937: 108).** Type: Guyana, Demerara R., *G. S. Jenman* 6300 (lectotype K, fide Prance 1972a: 117).

**DISTRIBUTION AND HABITAT.** Guyana. Wallaba forest and savanna margins. Flowering October to February.

**25. *Licania cuyabenensis* Prance (1999: 104).** Type: Ecuador, Sucumbios, Lago Agrio Cantón, Reserva Cuyabeno, Laguna Grande, *W. Palacios, G. Tipaz, Rubio, Gudiño & Aulestia* 9376 (holotype K; isotypes MO, QCNE).

**DISTRIBUTION AND HABITAT.** Ecuador; known only from the type collection. Lowland primary forest on terra firme.

**26. *Licania cyathodes* Benoist (1919: 513).** Type: French Guiana, *P. Sagot* s.n. (lectotype P, fide Prance 1972a: 113).

**DISTRIBUTION AND HABITAT.** French Guiana, Suriname and Venezuela. Riverine forests.

**27. *Licania cymosa* Fritsch (1889: 47).** Type: Brazil, Bahia, *J. S. Blanchet* 3200 (holotype W; isotypes F, G, GOET, OXF, P).

**DISTRIBUTION AND HABITAT.** Northern and northeastern Brazil (Bahia, Pará). Littoral forest and in secondary forest.

**28. *Licania davillifolia* Benoist (1919: 513).** Type: French Guiana, Maroni, *M. Mélinon* s.n. (lectotype P, fide Prance 1972a: 133; isolectotypes A, BM, F, GH, K, R, US).

**DISTRIBUTION AND HABITAT.** Guianas and in Brazil in E Amazonia (Amazonas, Amapá, Pará). Riverine forest and non-flooded forest.

**29. *Licania dealbata* Hook. f.** (Hooker 1867: 14). Type: Brazil, Bahia, Rio Preto, *G. Gardner* 2836 (holotype K; isotypes BM, CGE).

**DISTRIBUTION AND HABITAT.** Planalto of Central Brazil and in the northeast. Cerrados.

**30. *Licania densiflora* Kleinhoonte** (in Pulle 1925: 383). Type: Suriname, Jan Passie, *B. W. (Boschwezen)* 5346 (lectotype U, fide Prance 1972a: 117).

*Licania kanukuensis* Standl. (in Smith 1939: 182). Type: Guyana, NW slopes of Kanuku Mts, Moku-Moku Creek, *A. C. Smith* 3420 (holotype F; isotypes A, IAN, K, LE, MO, NY, P, U, US).

**DISTRIBUTION AND HABITAT.** Guianas and adjacent Venezuela and Brazil. Primary forest on high ground and slopes.

**31. *Licania discolor* Pilg.** (Pilger 1914: 137). Type: Brazil, Roraima, Surumu, Serra de Mairary, *E. Ule* 8393 (holotype B, destroyed; lectotype K, fide Prance 1972a: 151; isolectotypes L, LA, MG).

**DISTRIBUTION AND HABITAT.** Guianas and adjacent Venezuela and Brazil. Forest on high ground, especially on slopes.

**32. *Licania elliptica* Standl.** (Standley 1937: 255). Type: Brazil, Amazonas, near mouth of rio Embira, trib. of rio Tarauacá, *B. A. Krukoff* 5014 (holotype F; isotypes A, BM, K, LE, M, MICH, MO, NY, S, U, US).

*Licania paniculata* Fanshawe & Maguire (Maguire 1948a: 323). Type: Suriname: Toekoemoetoe Creek, *B. Maguire* 24068 (holotype NY; isotypes A, BR, F, K, US).

**DISTRIBUTION AND HABITAT.** Guianas and Amazonia (Peru and Brazil). Primary forest.

**33. *Licania fanshawei* Prance (1972a: 112).** Type: Venezuela, Delta Amacuro, Río Cuyubini, Cerro La Paloma, *J. A. Steyermark* 87557 (holotype NY).

**DISTRIBUTION AND HABITAT.** Guianas and Venezuela, in the Orinoco delta. Primary forest and in the delta area.

**34. *Licania ferreirae* Prance (1999: 104).** Type: Brazil, Amazonas, Município de Alvarães, road Alvarães-Vila Nogueira, *C. A. Cid Ferreira* 8442 (holotype INPA; isotypes CAS, K, MO, NY).

**DISTRIBUTION AND HABITAT.** NW Brazil; known only from the type collection. Terra firme forest.

**35. *Licania foldatsii* Prance (1972a: 136).** Type: Venezuela, Amazonas, Río Atabapo, Santa Cruz, *E. Foldats* 3857 (holotype VEN 49613; isotype NY).

**DISTRIBUTION AND HABITAT.** Venezuela (Upper Orinoco and Río Negro). Savannas and river margins.

**36. *Licania furfuracea* Prance (1976: 221).** Type: Venezuela, Bolívar, El Dorado-Santa Elena Rd, km 251 – 253, *J. A. Steyermark* 111390 (holotype NY; isotype VEN).

**DISTRIBUTION AND HABITAT.** Venezuela; known only from the type collection. Tall forest, beside a small stream.

**37. *Licania glauca* Cuatrec.** (Cuatrecasas 1951: 109). Type: Colombia, Valle, highway Buenaventura to Cali, *E. P. Killip & J. Cuatrecasas* 39000 (holotype F; isotypes COL, K, MO, NY, S, US).

**DISTRIBUTION AND HABITAT.** Colombia and Ecuador. Pacific coastal forest.

**38. *Licania glazioviana* Warm.** (Warming 1874: 68). Type: Brazil, Rio de Janeiro, Rio de Janeiro, Tijuca, *A. F. M. Glaziou* 2561 (holotype C; isotypes BR, K, P).

**DISTRIBUTION AND HABITAT.** Southeastern Brazil. Forests and possibly coastal restingas.

**39. *Licania gracilipes* Taub.** (Taubert 1892: 8). *Licania gracilis* Taub., *loc. cit.*, *nom. nud.* Type: Brazil, without locality, *A. F. M. Glaziou* 13800 (holotype B, destroyed; lectotype K, fide Prance & Sothers 2003a: 129; isolectotypes C, P).

*Licania dukei* Maguire (1948c: 29). Type: Brazil, Amazonas, *A. Ducke* 248 (holotype NY; isotypes K, R, RB).

**DISTRIBUTION AND HABITAT.** Amazonian Brazil, Venezuela and Colombia. Non-flooded forest.

**40. *Licania harlingii* Prance (1979a: 9).** Type: Ecuador, Napo, c. 6 km S of Puerto Napo, *H. Lugo* S. 1054 (holotype GB; isotype NY).

**DISTRIBUTION AND HABITAT.** Western Amazonia: Bolivia, Colombia, Ecuador, Peru and Brazil (Acre). Terra firme forest.

**41. *Licania hebantha* Mart. ex Hook. f.** (Hooker 1867: 17). Type: Colombia, Amazonas, Monte Araracoara, *C. F. P. Martius* s.n. (holotype M).

**DISTRIBUTION AND HABITAT.** Amazonian Colombia and Brazil (Amazonas). Savannas.

**NOTE.** A leaf fragment at K was erroneously cited as an isotype of this species (Prance 1972a; Prance & Sothers 2003a), but is most probably a fragment from a collection by Wied-Neuwied. We are unable to identify to which species the fragment belongs.

**42. *Licania hitchcockii* Maguire** (in Maguire & Wurdack 1957: 477). Type: Venezuela, Bolívar, Uaipan Tepui, *K. D. Phelps & A. S. Hitchcock* 407 (holotype NY; isotype VEN).

**DISTRIBUTION AND HABITAT.** Venezuela; known only from two inadequate collections. Forested slopes.

**43. *Licania hoehnei* Pilg.** (Pilger 1923: 541). Type: Brazil, São Paulo, São Paulo, Butantã, *F. C. Hoehne*

1494 (syntype B, destroyed; lectotype SP, fide Prance 1972a: 171; isotypes A, SPF, US).

**DISTRIBUTION AND HABITAT.** Bolivia and east-central Brazil (Mato Grosso, Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro, São Paulo). Forests.

**44. *Licania hypoleuca* Benth.** (Bentham 1844: 91). Type: Panama, *R. B. Hinds* s.n. (holotype K; isotype LE).

**44a. *Licania hypoleuca* Benth. var. *hypoleuca***

*Licania microcarpa* Hook. f. (Hooker 1867: 15). Type: Venezuela, San Carlos, *R. Spruce* 3696 (lectotype K, fide Prance 1972a: 126; isoelectotypes BM, BR, C, CGE, F, GH, GOET, LD, LE, NY, OXF, P, RB, TCD, W).

*Licania grisea* Kleinhoonte (in Pulle 1925: 382). Type: Suriname, Sectie O, *B. W. (Boschwezen)* 3392 (lectotype U, fide Prance, 1972a: 126; isotypes A, MO).

*Licania parvifolia* Pittier (1938: 351), *nom. illegit. non L. parvifolia* Huber (1909). Type: Venezuela, Bolívar, Ciudad Bolívar, *E. G. Holt & W. Gehringer* 69 (holotype VEN; isotypes F, NY, US).

*Licania parviflora* Benth. var. *conduplicata* Maguire (1952: 253). Type: Venezuela, Bolívar, *J. A. Steyermark* 60277 (holotype NY; isotypes F, VEN).

**DISTRIBUTION AND HABITAT.** A wide ranging variety from Southern Mexico to Bolivia, the Guianas, Venezuela, Colombia, Peru and scattered localities in NE and Amazonian Brazil. Sandy soils in forest and savannas.

**44b. *Licania hypoleuca* var. *foveolata* Prance (1972a: 127).** Type: Brazil, Amazonas, rio Curicuriari, *R. E. Schultes & López* 9719 (holotype US; isotype IAN).

**DISTRIBUTION AND HABITAT.** Brazil (Amazonas). Forest.

**45. *Licania impressa* Prance (1972a: 118).** Type: Brazil, Amazonas, Manaus, Colônia dos Franceses, *A. Ducke* s.n. (holotype K; isotype RB 25032).

**DISTRIBUTION AND HABITAT.** Eastern and central part of Brazilian Amazonia. Non-flooded forest.

**46. *Licania incana* Aubl.** (Aublet 1775: 119).

*Hedycrea incana* (Aubl.) J. F. Gmel. (Gmelin 1796: 428); *Chrysobalanus incanus* (Aubl.) M. Gómez (1887: 39). Type: French Guiana, *J. B. C. F. Aublet* s.n. (holotype BM; isotype P-Rousseau; phototype BR).

*Licania crassifolia* Benth. (Bentham 1840: 221); *Licania leptostachya* Benth. var. *crassifolia* (Benth.) Benoist (1919: 512). Type: Guyana, *R. & R. Schomburgk* 388

(381 some sets) (holotype K; isotypes BM, CGE, L, NY, OXF, P, TCD, US, W).

**DISTRIBUTION AND HABITAT.** Venezuela, Guianas, N and NE Brazil. Savannas, savanna margins and savanna forests.

**47. *Licania indurata* Pilg.** (Pilger 1923: 542). Type: Brazil, São Paulo, Santo André, Paranapiacaba, Alto da Serra, *E. Schwebel* 81 (holotype B, destroyed; lectotype R, fide Prance 1972a: 170; isotypes NY, SP, SPF; phototypes F, GH, US).

**DISTRIBUTION AND HABITAT.** SE Brazil (Rio Janeiro and São Paulo).

**48. *Licania irwinii* Prance (1972a: 113).** Type: Suriname, Wilhelmina Mts, 3 km SSE of Juliana Top, *H. S. Irwin, G. T. Prance, T. Soderstrom & N. Holmgren* 55002 (holotype NY; isotypes K, P).

**DISTRIBUTION AND HABITAT.** Guianas, Venezuela and Brazil (Amazonas). Forested slopes.

**49. *Licania jimenezii* Prance (1972b: 7).** Type: Suriname, Nickerie Distr., Falawatra, *H. Jiménez-Sáa* 1549 (holotype NY; isotypes LBB, P).

**DISTRIBUTION AND HABITAT.** Known only from Guyana and Suriname. Rainforests.

**50. *Licania kunthiana* Hook. f.** (Hooker 1867: 16). Type: Guyana, Pirara, *R. & R. Schomburgk* 728 (lectotype K, fide Prance 1972a: 145; isoelectotypes BM, BR, CGE, GH, L, NY, OXF, P, US, W).

*Licania hypargyrea* Malme (1930: 12). Type: Brazil, Mato Grosso, Chapada dos Guimarães (Santa Anna da Chapada), *G. O. A. Malme* 2378 (holotype S; isotypes LD, R).

*Licania parviflora* Benth. var. *submembranacea* Maguire (1952: 254). Type: Venezuela, Monagas, Quebrada Pajarral, Río Caripe, NE of Alto Aguacate, *J. A. Steyermark* 62173 (holotype NY; isotypes F, VEN).

**DISTRIBUTION AND HABITAT.** A wide ranging species from Costa Rica to Bolivia, the Guianas, Venezuela, Peru and throughout Brazil. Non-flooded forest, riverine forest, cerrados, or secondary forest.

**51. *Licania lamentanda* Prance (1989: 51).** Type: Brazil, Bahia, Mun. de Ilhéus, 4 km N of Olivença, *S. A. Mori, B. M. Boom & A. M. de Carvalho* 13673 (holotype CEPEC; isotypes K, NY).



**DISTRIBUTION AND HABITAT.** Brazil (Bahia). Restinga on sandy soil, 25 m altitude, growing with many individuals of piçaba palm (*Attalea funifera* Mart. ex Spreng.).

**52. *Licania lanceolata* Prance (1972a: 158).** Type: Venezuela, Amazonas, Río Guainía, Sabana El Venado, *B. Maguire & J. J. Wurdack* 35568 (holotype NY).

**DISTRIBUTION AND HABITAT.** Venezuela (Upper Orinoco region) and N Brazil. Savannas.

**53. *Licania laxiflora* Fritsch (1889: 46).** Type: Guyana, *R. & R. Schomburgk* 976 (holotype W; isotypes K, P).

*Licania gracilis* Kleinhoonte (Pulle 1925: 382). Type: Suriname, Gonini R., *B. W. (Boschwezen)* 3791 (holotype U; isotypes K, NY).

*Licania macrophylla* Klotzsch (in Schomburgk 1848: 1198), *nom. nud.*

**DISTRIBUTION AND HABITAT.** Guianas and Amazonian Brazil and Venezuela. Non-flooded forest and clump wallaba forest.

**54. *Licania leptostachya* Benth. (Bentham 1840: 220).** Type: Guyana, bank of Rupununi R., *R. & R. Schomburgk* 111 (holotype K; isotypes CGE, F, G, L, LE, TCD, NY, P, US, W).

*Licania incana* var. *axilliflora* Sagot (1883: 305); *Licania leptostachya* var. *axilliflora* (Sagot) Fritsch (1889: 46); *Licania axilliflora* (Sagot) Hochr. (Hochreutiner 1910: 273). Type: Guyana, Roraima, *R. & R. Schomburgk* 868 (holotype NY; isotypes BM, K, IAN, P, W).

**DISTRIBUTION AND HABITAT.** Guianas, Venezuela and northern and northeastern Brazil. Common along river margins and also found in Atlantic coastal Brazil.

**55. *Licania littoralis* Warm. (Warming 1874: 67).** Type: Brazil, Rio de Janeiro, Rio de Janeiro, Restinga da Tijuca, *A. F. M. Glaziou* 6168 (holotype C; isotypes F, K, P, R).

**55a. *Licania littoralis* Warm. var. *littoralis***

**DISTRIBUTION AND HABITAT.** E Brazil, from Paraíba to Rio de Janeiro. Confined to coastal restingas and coastal forests.

**55b. *Licania littoralis* var. *cuneata* Kuhlmann. (Kuhlmann 1940: 77).** Type: Brazil, Espírito Santo, Linhares, Rio Doce, Lagoa do Durão, *J. G. Kuhlmann* 208 (holotype RB; isotype NY).

**DISTRIBUTION AND HABITAT.** Brazil; known only from the type collection. In restinga vegetation.

**56. *Licania majuscula* Sagot (1883: 306).** Type: French Guiana, Maroní R., *M. Mélinon* s.n. (holotype P; isotypes BM, GH, K, NY, P, US).

*Licania hostmannii* Fritsch (1889: 42). Type: Suriname, *W. R. Hostmann & A. Kappler* 1250 (holotype W; isotypes BM, C, CGE, F, K, LE, NY, P, S, U).

**DISTRIBUTION AND HABITAT.** Guianas and Amazonian Brazil. Upland forest and high riverine forest.

**57. *Licania marleneae* Prance (1976: 218).** Type: Brazil, Amazonas, Manaus-Porto Velho Hwy., between Castanho and Tupana rivers, *M. F. Silva* 873 (holotype INPA; isotype NY).

**DISTRIBUTION AND HABITAT.** Brazil; known only from the type. Rainforest on terra firme.

**58. *Licania maxima* Prance (1972a: 165).** Type: Brazil, Amapá, Oiapoque, road between Oiapoque and Clevelândia, *B. Maguire, J. M. Pires & C. Maguire* 47081 (holotype NY; isotypes IAN, MG, P).

**DISTRIBUTION AND HABITAT.** Brazil; known only from the type collection. Riverine forest.

**59. *Licania membranacea* Sagot ex Laness. (Lanessan 1886: 130).**

*Licania galibica* Benoist (1919: 515). Type: French Guiana, Karouary, *P. Sagot* 1081 (holotype P; isotypes BM, BR, GOET, K, NY, S, W).

**DISTRIBUTION AND HABITAT.** Trinidad, the Guianas, Venezuela and Brazil. Forested slopes and non-flooded forest.

**60. *Licania micrantha* Miq. (Miquel 1851: 20).** Type: Suriname, *W. R. Hostmann* 1257 (holotype U; isotypes C, F, GH, K, LE, NY, P, W).

**60a. *Licania micrantha* Miq. subsp. *micrantha***

*Licania helvola* Spruce ex Hook. f. (Hooker 1867: 18), *nom. nud.*

*Licania anisophylla* Standl. (Standley 1937: 253).  
Type: Brazil, Amazonas, B. A. Krukoff 8451 (holotype NY; isotypes A, BM, BR, F, K, MO, NY, P, S, US).

**DISTRIBUTION AND HABITAT.** Widespread from Costa Rica to the Guianas, Venezuela, Colombia, Peru, Amazonian Brazil and Bolivia. Its known range has been recently extended west of the Andes in Colombia (Chocó and Valle) and in Brazil (Bahia). Non-flooded forests and Atlantic coastal forests.

**60b. *Licania micrantha* subsp. *atabapoensis* Prance (1995: 717).** Type: Venezuela, Amazonas, Atabapo Dept., Cabeceras del Río Yudi, F. Delgado 1799 (holotype PORT; isotype K).

**DISTRIBUTION AND HABITAT.** Venezuela; known from the type collection. Forest on terra firme.

**61. *Licania microphylla* Fanshawe & Maguire (Maguire 1948a: 322).** Type: Guyana, Potaro R., D. B. Fanshawe 1078 (F. D. 3814) (holotype NY; isotype K).

**DISTRIBUTION AND HABITAT.** Guyana; known only from the type collection. Forest.

**62. *Licania mollis* Benth. (Bentham 1840: 219).** Type: Brazil, Amazonas, R. & R. Schomburgk 910 (holotype K; isotypes BM, CGE, F, G, GH, L, NY, OXF, P, TCD, US, W).

*Licania lucida* J. F. Macbr. (Macbride 1934: 369). Type: Peru, Loreto, Mishuyaru near Iquitos, G. Klug 462 (holotype F; isotypes NY, US).

**DISTRIBUTION AND HABITAT.** Amazonian Colombia, Peru, Venezuela and Brazil (Amazonas and Roraima). River banks and river islands and in riverine forest on sandy soil.

**63. *Licania monteagudensis* Prance (2014: 6).** Type: Peru, Pasco, Distr. Palcazu, Parque Nacional Yanachaga-Chemillén, Estación Biológica Paujil, 10°43'S, 74°54'W, 800 m, A. Monteagudo, G. Ortiz & R. Francis 5164 (holotype K; isotypes AMAZ, MO, MOL, USM).

**DISTRIBUTION AND HABITAT.** Peru. Primary rainforest.

**64. *Licania naviculistipula* Prance (1972a: 398).** Type: Brazil, Espírito Santo, Linhares, Vale do Rio Doce, R. P. Belém 3814 (holotype NY; isotypes FHO, SP, UB).

**DISTRIBUTION AND HABITAT.** E & SE Brazil (Bahia, Espírito Santo). Margin of secondary forest.

**65. *Licania nelsonii* Prance (1989: 53).** Type: Brazil, Amazonas, 3 km S of Serra Aracá, W. A. Rodrigues et al. 10501 (holotype INPA; isotypes NY, RB).

**DISTRIBUTION AND HABITAT.** NW Brazil (Amazonas). Igapó forest in sandy soil.

**66. *Licania niloi* Prance (1972a: 129).** Type: Brazil, Rondônia, Porto Velho, N. T. Silva 392 (holotype NY; isotypes IAN, K).

**DISTRIBUTION AND HABITAT.** Bolivia and N Brazil (Amazonas, Rondônia). Primary forest.

**67. *Licania nitida* Hook. f. (Hooker 1867: 17).**

*Licania coriacea* Benth. var. *nitida* (Hook. f.) Fritsch (1889: 49). Type: Brazil, Bahia, Jacobina, J. S. Blanchet 3290 (holotype BM; isotypes BR, F, G, K, LE, NY, P, W).

**DISTRIBUTION AND HABITAT.** SE and C Brazil. Cerrados.

**68. *Licania orbicularis* Spruce ex Hook. f. (Hooker 1867: 13).** Type: Venezuela, Amazonas, Río Guainía, above mouth of Río Casiquiare, R. Spruce 3760 (lectotype K, fide Prance 1972a: 129; isolectotypes BM, BR, CGE, NY, P, TCD, W).

**DISTRIBUTION AND HABITAT.** Amazonian Venezuela and adjacent Brazil (Amazonas). Riverine forest and savanna margins.

**69. *Licania ovalifolia* Kleinhoonte (Pulle 1933: 180).** Type: Suriname, Brownsberg, B. W. (Boschwezen) 6457 (holotype U; isotypes IAN, K, NY).

*Licania stahelii* Kleinhoonte (Pulle 1933: 181). Type: Suriname, Brownsberg, B. W. (Boschwezen) 6818 (holotype U; isotypes IAN, K, NY).

**DISTRIBUTION AND HABITAT.** Guianas and Brazil (Amapá). Primary forest.

**70. *Licania pallida* Spruce ex Sagot (1883: 306).***Licania parviflora* var. *pallida* Hook. f. (Hooker 1867: 18).Type: Brazil, Amazonas, Managuirí, *R. Spruce* 1576 (lectotype P, fide Prance 1972a: 119; isolectotypes BM, BR, C, CGE, E, F, K, LE, M, NY, OXF, TCD).*Licania pallida* Spruce ex Hook. f. (Hooker 1867: 18), *nom. nud.*, in *synon.***DISTRIBUTION AND HABITAT.** Guianas and Venezuela to Brazilian Amazonia, Peru and Ecuador. Non-flooded forest.**71. *Licania paraensis* Prance (1972a: 163).** Type: Brazil, Pará, Santarém, Piquiatuba, *A. Ducke* s.n. (holotype K; isotypes NY, RB 8818).**DISTRIBUTION AND HABITAT.** Amazonian Brazil, Peru and Bolivia. Non-flooded forest.**72. *Licania parviflora* Benth. (Bentham 1840: 221).***Licania parviflora* var. *subfalcata* Spruce ex Hook. f. (Hooker 1867: 18). Type: Brazil, rio Uaupés, near Panuré, *R. Spruce* 2885 (holotype K; isotypes F, G, NY, RB).*Licania parviflora* f. *brevifolia* Fritsch (1889: 51). Type: Brazil, Amazonas, rio Negro, *R. & R. Schomburgk* 977 (holotype K; isotypes BM, CGE, F, G, L, OXF, P, W).*Licania parviflora* f. *longifolia* Fritsch (1889: 51). Type: Brazil, Amazonas, Tefé, *E. Poeppig* 2770 (holotype not traced).**DISTRIBUTION AND HABITAT.** Guianas, Venezuela, and Amazonia in Colombia, Peru, Brazil. Periodically flooded and riverine forest.**NOTE.** The type specimen of *Licania parviflora* f. *longifolia*, *Poeppig* 2770, was cited by Fritsch (1889: 51) as pro parte, with the type of *Leptobalanus egensis* (synonym of *Leptobalanus octandrus* subsp. *pallidus*) having the same number. We have only seen the part of the specimen which refers to *Leptobalanus egensis*.**73. *Licania parvifruca* Fanshawe & Maguire (Maguire 1948b: 374).** Type: Guyana, Berbice-Rupununi Cattle Trail, *A. A. Abraham* 258 (lectotype NY, fide Prance 1972a: 121; isolectotypes K, U).**DISTRIBUTION AND HABITAT.** Guianas, Venezuela, Colombia and Amazonian Brazil. Primary forests.**74. *Licania piresii* Prance (1972a: 124).** Type: Brazil, Amapá, rio Araguari, junction with rio Mururú, *J. M. Pires*, *W. A. Rodrigues* & *G. C. Irvine* 50435 (holotype NY).**DISTRIBUTION AND HABITAT.** Guianas and Brazil (Amapá). Non-flooded forest.**75. *Licania pittieri* Prance (1992: 249).** Type: Venezuela, Aragua, P. N. Henri Pittier, *A. Cardozo et al.* 1397 (holotype MY; isotype K).**DISTRIBUTION AND HABITAT.** Venezuela (coastal Cordillera) and Colombia. Cloud forest at 1,100 – 2,200 m.**76. *Licania polita* Spruce ex Hook. f. (Hooker 1867: 17).** Type: Brazil, Amazonas, rio Uaupés, near Panuré, *R. Spruce* 2676 (lectotype K, fide Prance 1972a: 115; isolectotypes BM, BR, C, CGE, E, F, GH, GOET, LD, LE, NY, OXF, P, RB, W).*Licania polita* f. *angustifolia* Fritsch (1889: 42). Type: Brazil, Amazonas, rio Uaupés, Panuré, *R. Spruce* 2762 (lectotype K, fide Prance & Sothers 2003a: 124; isolectotypes BM, BR, C, F, GOET, LD, LE, OXF, P).*Licania poeppigii* Fritsch (1889: 49). Type: Brazil, Amazonas, Tefé, *E. Poeppig* 2785 (holotype W; isotypes BR, G, GOET).*Licania laurifolia* Huber (1909: 365). Type: Brazil, Pará, Oriximiná, rio Cuminá-mirim, lower rio Trombetas, *A. Ducke* s.n. (holotype MG 7958; isotype BM).*Licania laxa* Fanshawe & Maguire (Maguire 1948a: 321). Type: Guyana, Essequibo R., Kuriki Rapids, *D. B. Fanshawe* 1665 (*F.D.* 4401) (holotype NY; isotype K).**DISTRIBUTION AND HABITAT.** Guianas, Venezuela and Amazonian Brazil. Non-flooded and periodically flooded forest.**77. *Licania pruinosa* Benoist (1919: 516).** Type: French Guiana, Cayenne, *L. C. Richard* s.n. (holotype P).**DISTRIBUTION AND HABITAT.** French Guiana and adjacent Brazil. River and island margins.**78. *Licania riedelii* Prance (1972a: 155).** Type: Brazil, Minas Gerais, Catas Altas, Serra do Caraça, *L. Riedel* 518 (holotype NY; isotype US).**DISTRIBUTION AND HABITAT.** SE Brazil (Minas Gerais and Rio de Janeiro). Forested regions.**79. *Licania robusta* Sagot (1883: 306).** Type: French Guiana, Maroní R., *M. Mélinon* s.n. (1862) (holotype P; isotypes A, BM, F, GH, K, NY, R, US).

*Licania pachystachya* Kleinhoonte (Pulle 1925: 384).  
Type: Suriname: Sectie O, B. W. (*Boschwezen*) 2729  
(holotype U; isotype P).

**DISTRIBUTION AND HABITAT.** Guianas and Brazil (Pará).  
Primary forest.

**80. *Licania rodriguesii*** Prance (1972a: 168). Type:  
Brazil, Pará, Breves, rio Jaburuzinho, A. Ducke s.n.  
(holotype K; isotype RB 18812).

**DISTRIBUTION AND HABITAT.** French Guiana and Brazil-  
ian Amazonia (Amazonas, Pará). Non-flooded forest.

**81. *Licania rufescens*** Klotzsch ex Fritsch (1889: 52).  
Type: Guyana, Roraima, R. & R. Schomburgk 601 (935B)  
(holotype W; isotypes BR, CGE, K, NY, P).  
*Licania rufescens* Klotzsch in M. R. Schomb.  
(Schomburgk 1848: 1103), *nom. nud.*

**DISTRIBUTION AND HABITAT.** Guianas and adjacent  
Venezuela and Brazil (Pará). Primary forest on slopes  
and high ground.

**82. *Licania sandwithii*** Prance (1972a: 142). Type:  
Guyana, Upper Mazaruni Distr., Tuibarodai trail,  
R. Boyan 92 (F.D. 7916) (holotype NY; isotype K).

**DISTRIBUTION AND HABITAT.** Guyana and Central Ama-  
zonian Brazil (Amazonas). Terra firme forests.

**83. *Licania santosii*** Prance (1979b: 28). Type: Brazil,  
Bahia, Itacaré, J. Almeida & T. S. dos Santos 150 (holotype  
CEPEC; isotypes AAU, FHO, MO, NY, U, US).

**DISTRIBUTION AND HABITAT.** Known only from Brazil  
(Bahia). Coastal region.

**84. *Licania savannarum*** Prance (1972a: 149). Type:  
Venezuela, Amazonas, Río Pacimoni, 50 km above  
mouth, B. Maguire, J. J. Wurdack & G. S. Bunting 37584  
(holotype NY; isotype K).

**DISTRIBUTION AND HABITAT.** Venezuela (Upper Río  
Orinoco region) and Brazil (Amazonas; Rio  
Negro region). Savannas or open places by river  
margins.

**85. *Licania silvae*** Prance (1972a: 115). Type: Brazil,  
Tocantins, Cariri do Tocantins, Belém-Brasília road,

30 km south of Gurupi, G. T. Prance & N. T. Silva  
58968 (holotype NY; isotypes K, UB).

**DISTRIBUTION AND HABITAT.** Amazonian Brazil, Co-  
lombia, Peru, Guianas and Venezuela. Non-flooded  
forest.

**86. *Licania spicata*** Hook. f. (Hooker 1867: 16).  
*Moquilea organensis* Miers (1879: 374); *Licania*  
*organensis* (Miers) Fritsch (1889: 59). Type: Brazil,  
Rio de Janeiro, Organ Mts, J. Miers 4095 (holotype  
K; isotypes BM, P).

**DISTRIBUTION AND HABITAT.** C and SE Brazil. Forested  
regions on hills.

**87. *Licania stewardii*** Prance (1976: 223). Type: Brazil,  
Amazonas, Manaus-Caracarái Rd, km 130, W. C.  
Steward et al. P20251 (holotype INPA; isotypes FHO,  
K, MO, NY, P, US).

**DISTRIBUTION AND HABITAT.** Colombia and northern  
Brazil in Amazonas and Roraima. Low campina  
forest around a sandstone rock outcrop in an  
area where the original forest has now been  
destroyed. Common around the vicinity of the  
type location.

**88. *Licania steyermarkii*** Maguire (1952: 254). Type:  
Venezuela, Bolívar, Río Karuai, base of Sororopan  
Tepui, 1220 m, J. A. Steyermark 60768 (holotype NY;  
isotypes F, MO, VEN).

**DISTRIBUTION AND HABITAT.** Venezuela and Colombia.  
Forests.

**89. *Licania stricta*** Kleinhoonte (Pulle 1925: 380). Type:  
Suriname, beside the Maratakka River, B. W.  
(*Boschwezen*) 3463 (holotype U).

**DISTRIBUTION AND HABITAT.** Suriname; known only  
from the type collection. River margin.

**90. *Licania subrotundata*** Maguire (1952: 255). Type:  
Venezuela, Distrito Federal, Cordillera del Avila,  
between Pico del Galipán and Boca del Tigre,  
J. A. Steyermark 56917 (holotype NY; isotypes F,  
VEN).

**DISTRIBUTION AND HABITAT.** Venezuela (Coastal Cordil-  
lera). Confined to the highland cloud forest.



**91. *Licania teixeirae*** Prance (1989: 47). Type: Brazil, Rondônia, Itapuã do Oeste, Mineração Santa Bárbara, L. O. A. Teixeira 728 (holotype INPA; isotypes FHO, K, NY).

**DISTRIBUTION AND HABITAT.** Brazil; known only from the type collection. Forest.

**92. *Licania ternatensis*** Hook. f. ex Duss (1896/1897: 259). Type: Leeward Is., Guadeloupe, Houëlmon, Vieux-Habitants, La Bouillante, Trois Rivières, A. Duss 2868 (lectotype NY, fide Prance & Sothers 2003a: 130; isolectotype US).

*Licania ternatensis* Hook. f. (Hooker 1893: 251), *nom. nud.*

**DISTRIBUTION AND HABITAT.** Lesser Antilles from Guadeloupe to Grenada. Forests and forested slopes.

**93. *Licania tocantina*** Prance (1983: 28). Type: Brazil, Pará, Breu Branco, rio Tocantins, Tucuruí, M. G. Silva & R. Bahia 3508 (holotype MG; isotypes INPA, NY, RB).

**DISTRIBUTION AND HABITAT.** N Brazil; known only from near the type locality. Terra firme forest.

**94. *Licania triandra*** Mart. ex Hook. f. (Hooker 1867: 18). *Licania micrantha* Miq. var. *triandra* (Mart. ex Hook. f.) Fritsch (1889: 50). Type: Brazil, Amazonas, Panuré, rio Uaupés, R. Spruce 2490 (2409 in some sets) (lectotype K, fide Prance 1972a: 140; isolectotypes BR, C, CGE, GH, GOET, LD, LE, NY, P, W).

*Licania pulchravenia* Killip & Cuatrec. (Cuatrecasas 1951: 106). Type: Colombia, Vaupés, J. Cuatrecasas 7054 (holotype COL; isotype F (fragments)).

**DISTRIBUTION AND HABITAT.** Amazonia: Venezuela, Colombia, Peru and Brazil (Acre, Amazonas). Non-flooded forest.

**95. *Licania trigonioides*** J. F. Macbr. (Macbride 1934: 368). Type: Peru, Loreto, near Mishuyacu, Iquitos, G. Klug 449 (holotype F; isotypes NY, US).

**DISTRIBUTION AND HABITAT.** Peru; known only from the type. Forest.

**96. *Licania urceolaris*** Hook. f. (Hooker 1867: 15). Type: Brazil, Amazonas, rio Uaupés, R. Spruce 2422 (lectotype K, fide Prance 1972a: 131; isolectotypes BM, BR, C, CGE, E, GH, GOET, LD, LE, NY, OXF, P, RB, W).

**DISTRIBUTION AND HABITAT.** Western Amazonia in Venezuela, Colombia, Peru, Brazil (Acre, Amazonas). Non-flooded forest.

**97. *Licania vaupesiana*** Killip & Cuatrec. (Cuatrecasas 1951: 105). Type: Colombia, Vaupés, Río Cuduyarí, tributary of Río Vaupés, J. Cuatrecasas 6837 (holotype COL; isotype fragments F, US).

*Licania parviflora* var. *grandifolia* Hook. f. (Hooker 1867: 19). Type: Colombia, Amazonas, C. F. P. Martius s.n. (holotype M).

**DISTRIBUTION AND HABITAT.** Venezuela, Amazonian Colombia and Brazil (Amazonas). Riverine forest.

**98. *Licania velutina*** Prance (1992: 638). Type: Ecuador, Pastaza, Pastaza Cantón, 20 km S of Curaray, V. Zak & S. Espinoza 5052 (holotype K; isotypes MO, QCNE).

**DISTRIBUTION AND HABITAT.** Ecuador; known only by two collections from a single locality. Tropical moist forest.

### Imperfectly known species

**1. *Licania roraimensis*** Standl. (Smith 1940: 286). Type: Guyana, A. S. Pinkus 61 (holotype F; isotypes GH, K, NY, S, US).

**DISTRIBUTION AND HABITAT.** Known only from the type collection, which is a very poor specimen with young fruit. No habitat information given. This is closely related to *Licania micrantha* and may be conspecific with it.

**2. *Licania tepuiensis*** Prance (1972a: 174). Type: Venezuela, Bolívar, Ilu-Tepui, Gran Sabana, B. Maguire 33389 (holotype NY).

**DISTRIBUTION AND HABITAT.** Known only from the type collection; flowers unknown. Low open woodland at edge of mesa, 4500 ft. [c. 1350 m] elevation.

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## Appendix 1

List of taxa used in the molecular analyses with an indication of markers obtained for each taxon. All DNA extracted from silica-gel dried leaf material, except those marked with an \*, which were extracted from herbarium specimens at the Royal Botanic Gardens, Kew (K). Taxa in bold represent additions to our analyses that were not included in Sothers 2010 or Sothers *et al.* 2014. For *Licania* s.l., species names from the previous classification are used.

Species	Collector/ number	DNA N° MWC	<i>rbcL</i>	<i>matK</i>	<i>ndhF</i>	ITS	<i>Xdh</i>
<i>Acioa edulis1</i>	Sothers 1512; Brazil, Amazonas, BR-174, Reserva de Fruticultura do INPA. Cultivated	30797	√	√	√	√	√
<i>Acioa edulis2</i>	Sothers 1541; Brazil, Amazonas, rio Urucu, Área de Exploração da Petrobrás	34568	√	√	√	√	√
<i>Acioa guianensis</i>	Mansano 04/279; Brazil, R.J., Rio de Janeiro, Jardim Botânico. Cultivated	20138	√	√	√	√	√
<i>Acioa longipendula1</i>	Sothers 263; Brazil, Amazonas, Manaus, Reserva Florestal Ducke	28047	√	√	√	√	√
<i>Acioa longipendula2</i>	Sothers 1490; Brazil, Amazonas, Manaus, grounds of INPA	35106	√	√	√	√	√
<b><i>Afrolicania elaeosperma</i></b>	Gabon	<b>5K</b>	√partial	√	√	√	<b>X</b>
<i>Angelesia splendens</i>	Chase 2120; Indonesia, Bogor IV.H.97a	2120	√	√	√	√	√
<i>Atuna racemosa</i>	Chase 2118; Indonesia, Bogor IV.H.18	2118	√	√	√	√	√
<b><i>Bafodeya bema</i></b>	<b>Cheek 16149; Guinea-Conakry, Kindia prefecture, Koulékouré</b>	<b>42729</b>	√	√	√	√	√
<i>Chrysobalanus icaco atacorensis</i>	van der Burgt 910; Cameroon, Korup National Park, NW plot near P transect	28907	√	√	√	√	√
<i>Chrysobalanus icaco icaco1</i>	Sothers 1524; Brazil, Bahia, Mun. de Olivença	30798	√	√	√	√	√
<b>*<i>Chrysobalanus icaco icaco2</i></b>	<b>Kami 270; Congo (Brazzaville), Northeast of Pointe Noire along the coast</b>	<b>40411</b>	√	√	√	√	√
<i>Couepia belemii1</i>	Sothers 1518; Brazil, Bahia, Mun. de Itacaré	30800	√	√	√	√	√
<i>Couepia belemii2</i>	Sothers 1531; Brazil, Espírito Santo, Linhares, Res. Natural da CVRD	34571	√	√	√	√	√
<b>*<i>Couepia bernardii</i></b>	<b>Grández 1506; Peru, Maynas Prov., Puerto Almendras</b>	<b>45918</b>	√partial	√	√	√	<b>X</b>
<i>Couepia bondarii</i>	Sothers 1517; Brazil, Bahia, EMARC Gregório Bondar	30801	√	√	√	√	√
<i>Couepia bracteosa1</i>	Ribeiro 1550; Brazil, Amazonas, Manaus, Reserva Florestal Ducke	28042	√	√	√	√	√
<i>Couepia bracteosa2</i>	Mori 25554; French Guiana, Nouragues Field Station	16613	√	√	√	√	√
<i>Couepia caryophylloides</i>	Sothers 1455; Brazil, Amazonas, ZF-2, Reservas do PDBFF	30851	√	√	√	√	√
<i>Couepia coarctata</i>	Sothers 1519; Brazil, Bahia,	30850	√	√	√	√	√

<i>Couepia excelsa</i>	Mun. de Itacaré Sothers 1453; Brazil, Amazonas, ZF-2, Reservas do PDBFF	30852	√	√	√	√	√
<i>Couepia glabra1</i>	Sothers 1516; Brazil, Amazonas, ZF-2, Reservas do PDBFF	30803	√	√	√	√	√
<i>Couepia glabra2</i>	Sothers 1460; Brazil, Amazonas, ZF-2, Reservas do PDBFF	30894	√	√	√	√	√
<i>Couepia grandiflora</i>	Sothers 1507; Brazil, Brasília, Distrito Federal, Jardim Botânico	28052	√	√	√	√	√
<i>Couepia guianensis glandulosa</i>	Vicentini 578; Brazil, Amazonas, Manaus, Reserva Florestal Ducke	28046	√	√	√	√	√
<i>Couepia guianensis guianensis</i>	Sothers 1451; Brazil, Amazonas, Manaus, Reserva Florestal Ducke	28045	√	√	√	√	√
<i>Couepia habrantha</i>	Sothers 1464; Brazil, Amazonas, ZF-2, Reservas do PDBFF	30804	√	√	√	√	√
<i>Couepia impressa</i>	Sothers 1529; Brazil, Pernambuco, Restinga de Ariquindá	34570	√	√	√	√	√
<i>Couepia joaquinae</i>	French Guiana, Nouragues	NH200492	√	√	√	√	√
<i>Couepia magnoliifolia1</i>	Sothers 1538; Brazil, Amazonas, Manaus, Reserva Florestal Ducke	35097	√	√	√	√	√
<i>Couepia magnoliifolia2</i>	Sothers 1462; Brazil, Amazonas, Manaus, Reserva Florestal Ducke	30888	√	√	√	√	√
<b>*<i>Couepia monteclarensis</i></b>	<b>Maas 9807; Brazil, Espírito Santo, Linhares, Reserva Natural da CVRD</b>	<b>38008</b>	√	√	√	√	<b>X</b>
<i>Couepia morii</i>	Sothers 1470; Brazil, Amazonas, ZF-2, Reservas do PDBFF	30853	√	√	√	√	√
<b><i>Couepia multiflora</i></b>	<b>Dexter 5603; French Guiana</b>	<b>45917</b>	√ <b>partial</b>	√	√	√	√
<i>Couepia obovata1</i>	Costa 350; Brazil, Amazonas, Manaus, Reserva Florestal Ducke	28049	√	√	√	√	√
<i>Couepia obovata2</i>	Sothers 1452; Brazil, Amazonas, Manaus, Reserva Florestal Ducke	35091	√	√	√	√	√
<i>Couepia ovalifolia1</i>	Sothers 1509; Brazil, Rio de Janeiro, RJ, Barra da Tijuca, Lote 2	28054	√	√	√	√	√
<i>Couepia ovalifolia2</i>	Sothers 1534; Brazil, Espírito Santo, Linhares, Reserva Natural da CVRD	35096	√	√	√	√	√
<i>Couepia paraensis</i>	Sothers 1510; Brazil, Amazonas, Manaus, Praia Dourada	30799	√	√	√	√	√
<b>*<i>Couepia paraensis cerradoana</i></b>	<b>Duarte 47; Brazil, Mato Grosso, Mun. Novo Santo Antônio</b>	<b>35408</b>	√	√ <b>partial</b>	√	√	√
<i>Couepia parvifolia</i>	Oliveira 1713; Brazil, R.J., Rio de Janeiro, Estrada da Vista Chinesa, Km 1	28053	√	√	√	√	√
<b>*<i>Couepia polyandra</i></b>	<b>Amith 1530; Mexico</b>	<b>45285</b>	√	√	√	√	√
<i>Couepia rankiniae</i>	Sothers 1454; Brazil, Amazonas, ZF-2, Reservas do PDBFF	30854	√	√	√	√	√
<i>Couepia robusta</i>	Sothers 167; Brazil, Amazonas, Manaus, Reserva Florestal Ducke	28050	√	√	√	√	√
<i>Couepia rufa1</i>	Sothers 1668; Brazil,	34569	√	√	√	√	√

<i>Couepia rufa</i> 2	Pernambuco, Recife, Campus UFRPE Sothers 1526; Brazil, Pernambuco, Recife, Mata Dois Irmãos	35413	√partial	√	√	√	√
<i>Couepia sandwichii</i>	Sothers 1465; Brazil, Amazonas, ZF-2, Reservas do PDBFF	30855	√	√	√	√	√
<i>Couepia schottii</i> 1	Sothers 1501; Brazil, Rio de Janeiro, Restinga da Marambaia	21383	√	√	√	√	√
<i>Couepia schottii</i> 2	Sothers 1532; Brazil, Espírito Santo, Linhares, Reserva Natural da CVRD	35095	√	√	√	√	√
<i>Couepia spicata</i> 1	Sothers 1471; Brazil, Amazonas, ZF-2, Reservas do PDBFF	30856	√	√	√	√	√
<i>Couepia spicata</i> 2	Sothers 1556; Brazil, Amazonas, rio Urucu, Área de Exploração da Petrobrás	35100	√	√	√	√	√
<i>Couepia subcordata</i>	Sothers 1511; Brazil, Amazonas, Manaus, Campus da UFAM	30802	√	√	√	√	√
* <i>Couepia uiti</i>	Parada 26; Bolivia, Santa Cruz, Prov. German Busch, Laguna La Gaiba	35407	√partial	√	√	√	X
<i>Couepia ulei</i> 1	Sothers 992; Brazil, Amazonas, Manaus, Reserva Florestal Ducke	28051	√	√	√	√	√
<i>Couepia ulei</i> 2	Souza 393; Brazil, Amazonas, Manaus, Reserva Florestal Ducke	30891	√	√	√	√	√
* <i>Dactyladenia campestris</i>	<b>M'Boungou 459; Congo (Brazzaville), Mayombe hills, near Niari River</b>	<b>40410</b>	√	√	√	√	√
* <i>Dactyladenia aff. floretti</i>	<b>Mpandzou 1326a; Congo Brazzaville</b>	<b>42736</b>	√partial	√	√	√	√
<i>Dactyladenia pallescens</i>	Van der Burgt 904; Cameroon, Korup National Park	28908	√	√	√	√	√
* <i>Dactyladenia scabrifolia</i>	<b>Jongkind 7569; Guinea</b>	<b>45927</b>	√	√	√	√	X
* <i>Dactyladenia cf. scabrifolia</i>	<b>Haba 188; Guinea-Conakry, A l'est de Whisky 1, a l'ouest de Canga, Simandou Range</b>	<b>40275</b>	√	√	√	√	√
<i>Dactyladenia cf. smeathmanii</i>	<b>van der Burgt 1430; Sierra Leone, Southern Sula Mountains, southeast of Bumbuna, along Tonkolili river</b>	<b>45926</b>	√	√	√	√	√
<i>Dactyladenia staudtii</i>	van der Burgt 672; Cameroon, Korup National Park, P transect plots	28909	√	√	√	√	√
<i>Exellodendron barbatum</i>	De Granville 6121; French Guiana	A110225	√	√	√	√	√
* <i>Gaulettia amaraliae</i>	Stevenson et al. 1011; Brazil, Amazonas, rio Negro	42732	√	√	√	√	√
<i>Gaulettia canomensis</i> 1	Hopkins 1438; Brazil, Amazonas, Manaus, Reserva Florestal Ducke	28043	√	√	√	√	√
<i>Gaulettia canomensis</i> 2	Sothers 1456; Brazil, Amazonas, ZF-2, Reservas do PDBFF	30890	√	√	√	√	√
<i>Gaulettia canomensis</i> 3	Sothers 1473; Brazil, Amazonas, Manaus, Reserva Florestal Ducke	34574	√	√	√	X	√

<i>Gaulettia elata1</i>	Assunção 502; Brazil, Amazonas, Manaus, Reserva Florestal Ducke	28044	√	√	√	√	√
<i>Gaulettia elata2</i>	Sothers 1450; Brazil, Amazonas, Manaus, Reserva Florestal Ducke	35090	√	√	√	√	√
<i>Gaulettia parillo</i>	Without collector and number; French Guiana, Montagne Tortue	M17116625	√	√	√	√	X
<i>Grangeria porosa1</i>	Briggs 274; Madagascar	40403	√partial	√	√	√	X
* <i>Grangeria porosa2</i>	Nusbaumer 2726; Madagascar	45283	√partial	√	√	√	√
<b><i>Hirtella corymbosa</i></b>	<b>Sothers 1533; Brazil, Espírito Santo, Linhares, Res. Natural da CVRD</b>	<b>40405</b>	√	√	√	√	√
<i>Hirtella mutisii</i>	Homeier et al. 3476; Ecuador, Napo, Parque Nacional Sumaco- Galeras	35104	√	√	√	√	√
<i>Hirtella myrmecophila</i>	Sothers 1503; Brazil, Amazonas, Manaus, Reserva Florestal Ducke	28912	√	√	√	√	√
<i>Hirtella physophora</i>	Sothers 1539; Brazil, Amazonas, Manaus, Reserva Florestal Ducke	35098	√	√	√	√	√
* <i>Hirtella recurva</i>	Homeier et al. 2190; Ecuador, Zamora- Chinchi, Reserva Biológica San Francisco	35410	√partial	√	√	√	√
<i>Hirtella rodriguesii</i>	Sothers 1475; Brazil, Amazonas, Manaus, Reserva Florestal Ducke	35093	√	√	√	√	√
<i>Hirtella sprucei</i>	Sothers 1530; Brazil, Espírito Santo, Linhares, Res. Natural da CVRD	35094	√	√	√	√	√
<i>Hirtella thouarsiana</i>	Schatz et al. 3816; Madagascar, Station Forestiere Farankaraina	16120	√partial	√	√	√	√
* <i>Hirtella zanzibarica</i>	Crawford 603; Mozambique	45925	√	√	√	√	√
* <i>Hunga gerontogea</i>	Pillon 221; New Caledonia	40269	√	√	√	√	√
* <i>Kostermanthus robustus</i>	Tree number 1099; Semenggoh Arboretum, Sarawak, Malaysia	38005	√partial	√	√	√partial	X
<i>Licania adolphoduckei</i>	Tree number 435-02; Brazil, Amazonas, Manaus, Reserva Florestal Ducke	40407	√	√	√	√	√
<i>Licania affinis</i>	Brazil	GD500	√	√partial	√	X	X
<i>Licania alba</i>	French Guiana, Paracou	P00610185	√	√	√	X	√
<i>Licania amapaensis</i>	French Guiana	4K	√partial	√	√	√	X
<i>Licania apetala</i>	Tree number 2266-02; Brazil, Amazonas, Manaus, Reserva Florestal Ducke	40278	√partial	√partial	√	√	X
* <i>Licania arborea</i>	Ibarra Manríquez 6065; Mexico	45278	√partial	√	√	√	√
<i>Licania bracteata</i>	Sothers 688; Brazil, Amazonas, Manaus, Reserva Florestal Ducke	45284	√	√	√	√	X
<i>Licania brittoniana</i>	Peru	JH2/286	√	√	√	X	X
<i>Licania canescens</i>	Tree number 440-02; Brazil, Amazonas, Manaus, Reserva Florestal Ducke	40409	√partial	√	√	√	√
<i>Licania caudata</i>	Tree number 4609-02; Brazil, Amazonas, Manaus, Reserva Florestal Ducke	45920	√partial	√	√	√	√
<i>Licania celiae</i>	Homeier et al. 3567; Ecuador, Napo, Parque Nacional Sumaco- Galeras	35102	√	√	√	√	√
<i>Licania cordata</i>	Brazil	MHT486	√	√	√	X	√
<i>Licania coriacea</i>	Tree number 428-02; Bra- zil, Amazonas, Manaus, Reserva Florestal Ducke	42726	√	√	√	√	√
<i>Licania discolor</i>	Brazil	VIC2411	√	√	√	X	√

<i>*Licania divaricata</i>	<i>Gillespie 725; Guyana</i>	45924	√partial	√partial	√	X	X
<i>Licania egleri</i>	<i>Sothers 1545; Brazil,</i> Amazonas, rio Urucu, Área de Exploração da Petrobrás	37996	√	√	√	√	X
<i>Licania emarginata</i>	<b>Peru</b>	<b>JH1/168</b>	√	√	√	X	√
<i>Licania glabrifolia</i>	<b>French Guiana, Bafog</b>	<b>B445068</b>	√	√	√	X	X
<i>Licania gracilipes</i>	<b>Tree number 1124-02; Bra-</b> <b>zil, Amazonas, Manaus,</b> <b>Reserva Florestal Ducke</b>	<b>42724</b>	√	√	√	√	√
<i>Licania granvillei</i>	<b>French Guiana</b>	<b>Q451</b>	√	√	√	X	√
<i>Licania guianensis</i>	<b>French Guiana, Nouragues</b>	<b>PE1075</b>	√	√	√	X	√
<i>Licania harlingii</i>	<i>Homeier et al. 3755;</i> Ecuador, Napo, Cordillera Galeras	35105	√	√	√	√	√
<i>Licania heteromorpha1</i>	<i>Sothers 1474; Brazil,</i> Amazonas, Manaus, Reserva Florestal Ducke	35092	√	√	√	√	√
<i>Licania heteromorpha2</i>	<i>Sothers 1554; Brazil,</i> Amazonas, rio Urucu, Área de Exploração da Petrobrás	35099	√	√	√	√	√
<i>Licania cf. hypoleuca</i>	<b>Ribeiro 1449; Brazil,</b> <b>Amazonas, Manaus,</b> <b>Reserva Florestal Ducke</b>	<b>45282</b>	√	√	√	√	√
<i>Licania impressa</i>	<b>Tree number 3893-02; Bra-</b> <b>zil, Amazonas, Manaus,</b> <b>Reserva Florestal Ducke</b>	<b>40408</b>	√partial	√	√	√	√
<i>Licania incana</i>	<b>Guyana</b>	<b>SL9</b>	√	√	√	X	√
<i>Licania irwinii</i>	<b>French Guiana</b>	<b>KD5287</b>	√	√	√	X	√
<i>Licania intrapetiolaris</i>	<b>Peru</b>	<b>PA12</b>	√	√partial	√	X	X
<i>Licania laevigata</i>	<b>Tree number 282-02; Bra-</b> <b>zil, Amazonas, Manaus,</b> <b>Reserva Florestal Ducke</b>	<b>45919</b>	√partial	√	√	√	√
<i>Licania lanceolata</i>	<b>Brazil</b>	<b>FM206</b>	√	√	√	X	X
<i>Licania latifolia</i>	<b>French Guiana, Nouragues</b>	<b>PE5397</b>	JQ898727	X	X	X	X
<i>Licania latistipula</i>	<b>French Guiana</b>	<b>JC040</b>	√partial	√partial	√	X	X
<i>Licania laxiflora</i>	<b>Tree number 357-02; Bra-</b> <b>zil, Amazonas, Manaus,</b> <b>Reserva Florestal Ducke</b>	<b>42739</b>	√partial	√	√	√	√
<i>Licania leptostachya</i>	<b>French Guiana?</b>	<b>MNHN5693</b>	√	√	√	X	X
<i>Licania licaniiiflora</i>	<b>French Guiana</b>	<b>3K</b>	√partial	√	√	X	X
<i>Licania longistyla</i>	<b>Tree number 491-02; Bra-</b> <b>zil, Amazonas, Manaus,</b> <b>Reserva Florestal Ducke</b>	<b>40276</b>	√partial	√partial	√	√	X
<i>Licania macrocarpa1</i>	<i>Homeier 1603; Ecuador</i>	38001	√	√	√	√	X
<i>Licania macrocarpa2</i>	<i>Homeier 3481; Ecuador,</i> Napo, Cocodrilos	38000	√	√	√	√	√
<i>Licania macrophylla</i>	<b>Tree number 239-02; Bra-</b> <b>zil, Amazonas, Manaus,</b> <b>Reserva Florestal Ducke</b>	<b>45921</b>	√partial	√	√	√	√
<i>Licania majuscula</i>	<b>French Guiana, Acarouany</b>	<b>A110139</b>	√	√	√	√	X
<i>Licania membranacea</i>	<b>French Guiana</b>	<b>M17116059</b>	√	√	√	X	√
<i>Licania michauxii</i>	<b>USA</b>	<b>MNHN20553</b>	√	√	√	X	√
<i>Licania micrantha</i>	<b>Homeier 3627; Ecuador</b>	<b>40406</b>	√partial	√	√	√	√
<i>Licania minutiflora</i>	<i>Sothers 1555; Brazil,</i> Amazonas, rio Urucu, Área de Exploração da Petrobrás	37999	√	√	√	√	√
<i>Licania niloi</i>	<b>Tree number 219-02; Bra-</b> <b>zil, Amazonas, Manaus,</b> <b>Reserva Florestal Ducke</b>	42725	√	√	√	√	√
<i>Licania oblongifolia</i>	<i>Sothers 1544; Brazil,</i> Amazonas, rio Urucu, Área de Exploração da Petrobrás	37995	√	√	√	√	√
<i>Licania octandra</i>	<b>Tree number 215-02; Bra-</b> <b>zil, Amazonas, Manaus,</b> <b>Reserva Florestal Ducke</b>	<b>40277</b>	√partial	√	√	√	X
<i>Licania orbicularis</i>	<b>Guyana</b>	<b>SL7</b>	√	√	√	X	√
<i>Licania ovalifolia</i>	<b>French Guiana</b>	<b>P00610120</b>	√	√	√	X	√
<i>Licania parviflora</i>	<i>Sothers 1548; Brazil,</i> Amazonas, rio Urucu,	37997	√	√	√	√	√



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<i>*Licania platycalyx</i>	Aguilar 3643; Costa Rica, Limón, Cantón de Pococi	42734	√partial	√partial	√	√		X
<i>Licania pyrifolia</i>	Venezuela, Hacho Pintero	AF28563	√	√	√	X		√
<i>Licania reticulata</i>	Tree number 499-02; Brazil, Amazonas, Manaus, Reserva Florestal Ducke	42738	√partial	√	√	√		√
<i>Licania riverae</i>	iBOL	GenBank	JQ591082	JQ587249	X	X		X
<i>Licania rodriguesii</i>	Tree number 245-02; Brazil, Amazonas, Manaus, Reserva Florestal Ducke	42727		√	√	√		√
<i>Licania sandwithii</i>	Tree number 214-02; Brazil, Amazonas, Manaus, Reserva Florestal Ducke	42728	√partial	√	√	√		√
<i>Licania sclerophylla</i>	Sothers 1549; Brazil, Amazonas, rio Urucu, Área de Exploração da Petrobrás	37998	√	√	√	√		√partial
<i>Licania sprucei</i>	Baraloto 3496; French Guiana, Paracou	P01860159	√	√	√	√		√
<i>Licania tomentosa</i>	Sothers s.n.; Brazil, Rio de Janeiro, Barra da Tijuca; cultivated	45923		√partial	√	√		X
<i>Licania urceolaris</i>	Peru	JH6/576a	√	√	√	X		√
<i>Magnistipula butayei</i> subsp. <i>korupensis</i>	van der Burgt 659; Cameroon, Korup National Park, near P transect, near P plot	38002	√	√	√	√		√partial
<i>Magnistipula multinervia</i>	van der Burgt 917; Cameroon, Korup National Park, NW plot, near P transect	28906	√	√	√	√		√
<i>Magnistipula tamenaka</i>	Schatz et al. 3680; Madagascar, Masoala Peninsula	16117	√	√	√	√		√
<i>Maranthes chrysophylla</i>	van der Burgt 773; Cameroon, Korup National Park, NW plot near P transect, subplot 35MN	28905	√	√	√	√		√
<i>Maranthes corymbosa</i>	Prance 30902; Malaysia, Selangor, grounds of Forest Research Institute	35089	√	√	√	√		√
<i>*Maranthes gabumensis</i>	M'Boungou 428; Congo, Mayombe hills, near Niari River	40412	√partial	√	√	√		√
<i>Maranthes glabra</i>	van der Burgt 1489; Sierra Leone, Southern Sula Mountains, Tonkolili R. near village Kegbema	40274	√	√	√	√		√
<i>*Maranthes panamensis</i>	Thomsen 1000; Costa Rica, Aguabuena, Osa Peninsula	42735	√partial	√partial	√	√		X
<i>*Neocarya macrophylla</i>	James 23; Sierra Leone, Tagrim Point, Lungi, NE of Ferry terminal	40273	√	√	√	√		√
<i>Parastemon urophyllus</i>	Sarawak 100485	28911	√	√	√	√		√
<i>Parinari curatellifolia</i>	Haba 81; Guinea-Conakry, Piste entre le village Kosseino et le Mt Captain Hook (Mt Simandou Nord)	35412	√partial	√	√	√		√
<i>Parinari excelsa</i>	French Guiana	B429025	√partial	√	√	√		X
<i>Parinari occidentalis</i>	Homeier et al. 3709; Ecuador, Napo, Parque Nacional Sumaco-Galeras	35103	√	√	√	√		√
<i>Parinari montana</i>	Sothers 1661; Brazil, Amazonas, rio Urucu, Área de Exploração da Petrobrás	35101	√	√	√	√		√
<i>Parinari parva</i>	Prance 30899; Malaysia,	35411	√	√	√	√		√

	Johore, Endau-Rompin N.P.							
<i>Parinari sumatrana</i>	Chase 2119; Indonesia, Bogor IV.H.21a	2119	✓	✓	✓	✓	✓	✓
<i>Balanops vieillardii</i>	MacKee 38214; New Caledonia	1816	✓	✓	✓	✓	✓	✓
<i>Euphronia guianensis</i>	Mori 23699; Venezuela, Bolívar, Gran Sabana, Salto Kama	1057	✓	✓	✓	✓	✓	✓
<i>Tapura guianensis</i>	Tree number 557-04; Bra- zil, Amazonas, Manaus, Reserva Florestal Ducke	1039	✓	✓	✓	✓	✓	✓
<i>Trigonia eriosperma</i>	Prance P30842; Brazil	3948	✓	✓	✓	✓	✓	✓

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