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SYSTEMATICS OF LIABUM ADANSON (ASTERACEAE, LIABEAE)

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ABSTRACT. *Liabum* (Asteraceae), one of the most important genera of the tribe Liabeae in terms of number of species and extent of overall distribution, was the subject of a revisionary study. The genus consists of perennial herbs, subshrubs, or shrubs, rarely scandent shrubs or small trees, without latex, with opposite, tripliveined leaves, radiate, heterogamous capitula, and yellow corollas. The morphology and anatomy of *Liabum* were studied; in addition, a principal component analysis of 100 samples representing the morphological variation and geographic distribution of *Liabum* in the Caribbean was conducted, resulting in recognition of a single highly variable species, *L. umbellatum*. Descriptions, illustrations, and maps for each species, and the first key distinguishing the species of *Liabum* are presented. This revision recognizes 22 species distributed from southeastern Mexico to northwestern Argentina, and in Cuba, Jamaica, and Hispaniola, including two new species from Ecuador and Peru, *Liabum dillonii* D. G. Gutiérrez & Katinas and *L. robinsonii* D. G. Gutiérrez & Katinas, respectively. The main center of species diversity for the genus is in Peru. In addition, new synonyms are proposed, and 151 names of taxa are excluded from *Liabum*. *Liabum onoserifolium* S. Díaz & Rodríguez-Cabeza from Colombia is transferred to the genus *Munnozia* as *Munnozia onoserifolia* (S. Díaz & Rodríguez-Cabeza) D. G. Gutiérrez & Katinas.

INTRODUCTION

The Neotropical genus *Liabum* Adans., with 22 species, is the second largest genus in the tribe Liabeae of family Asteraceae (Dillon et al. 2009; Gutiérrez 2010; Robinson & Funk 2011; Funk et al. 2012). Its species are perennial herbs, subshrubs, or shrubs (rarely scandent shrubs or small trees) without latex, the leaves are opposite and tripliveined, and the capitula are radiate and heterogamous (i.e., with pistillate ray florets and bisexual disc florets), with both kinds of florets having yellow corollas. The genus is distributed from southeastern Mexico to northwestern Argentina, mainly concentrated in the Andean ranges of Ecuador and Peru, as well as in the West Indies (Cuba, Jamaica, and Hispaniola). *Liabum* is the only member of the Liabeae with species in the Caribbean and in Brazil. *Liabum* is distinguished from closely related genera such as *Dillandia* V. A. Funk & H. Rob., *Inkaliabum* D. G. Gut., *Oligactis* (Kunth) Cass., and *Sampera* V. A. Funk & H. Rob. by a combination of the following characters: tripliveined leaves, umbelliform or corymbiform

cymes, long style branches, absence of glandular hairs on the cypselae, and quadrangular crystals in the cypsela wall (Gutiérrez 2010).

Liabum was established by Adanson (1763) on the basis of one Jamaican species. Bentham (1873) then greatly expanded the generic concept of *Liabum*. This broad concept of the genus was generally accepted and used by subsequent authors. Through the study of new characters in more recent treatments (Robinson & Brettell 1974; Robinson 1983), *Liabum* was returned to a narrower concept. A revision of *Liabum* has been lacking but is needed. For example, a controversial issue in the genus has been how many species are present in the Caribbean, given the degree of variation in the general morphology of the taxa there. The purpose of this study, therefore, was to review the morphology and taxonomy of these and other species of *Liabum*.

TAXONOMIC HISTORY

Patrick Browne (1756) described and illustrated the first species of *Liabum*, from Jamaica, as a dubious taxon under the genus *Solidago* L. Browne did not give it a binomial, and therefore it was not validly published. Two years later, Browne sold his collection to Linnaeus (Stafleu & Cowan 1976), who published the species as *Amellus umbellatus* L. (Linnaeus 1759a) together with the South African *A. lychnites* L. (now the type species of *Amellus* L., a genus in the tribe Astereae).

The generic name *Liabum* was created by Adanson (1763) based on *Amellus umbellatus* of Linnaeus. The generic name is probably an anagram of the Latin *lăbium*, meaning lip (Cassini 1823). Adanson characterized *Liabum* by the opposite leaves, the inflorescence either a solitary terminal capitulum or multiple capitula in a corymbose arrangement, the involucre with imbricate phyllaries, the chaffy receptacle, the 2–3-dentate ray corollas, the 5-lobed disc corollas, and the barbellate pappus. *Amellus umbellatus* has all of these characters except the terminal, solitary capitulum, probably an indication that Adanson inadvertently included one feature of the second Linnaean species of *Amellus* in his description of *Liabum*.

In the following years, several genera were created that were later considered synonyms of *Liabum*. In 1803 Willdenow, unaware of Adanson's description of *Liabum*, proposed the new genus *Starkea* Willd. for *Amellus umbellatus*. Humboldt and Bonpland (1812) described the genus *Andromachia* Humb. & Bonpl. with the single species *A. igniaria* Humb. & Bonpl. (=*Liabum igniarium* (Humb. & Bonpl.) Less.) from the South American Andes. In 1824, La Llave and Martínez de Lexarza described the monotypic genus *Allendea* La Llave & Lex. with the species *A. lanceolata* La Llave & Lex. (=*Liabum asclepiadeum* Sch. Bip.) from Mexico.

Kunth (1818), in studying Humboldt and Bonpland's collections, described nine new South American species of *Andromachia* and grouped them into three sections (Table 1): (1) Sect. *Andromachia* Humb. & Bonpl. (four new species and *A. igniaria*), characterized by a branched herbaceous habit, opposite, abaxially white-tomentose leaves, corymbose inflorescences with numerous multi-flowered capitula, and yellow ray corollas; (2) Sect. *Chrysactinium* Kunth (two species), characterized by herbaceous habit (caulescent or acaulescent), abaxially lanose leaves, solitary, long-pedunculate capitula, and gold or yellowish ray corollas; and (3) Sect. *Oligactis* Kunth (three species), characterized by a subshrubby habit, opposite, abaxially white-tomentose leaves, capitula in corymbs or panicles, axillary or terminal few-flowered capitula, and 3–7 white ray corollas. The sections *Oli-*

TABLE 1. Infrageneric classification of *Andromachia* and *Liabum* through time and current generic position of some species originally associated with *Liabum*.

Kunth 1818	Lessing 1831	Candolle 1836, 1838	Bentham 1873	Hoffmann 1894	Current systematics (genera); this work
Andromachia	*Liabum*	*Liabum*	*Liabum*	*Liabum*	*Liabum*
Section *Andromachia*	Section *Andromachia*	Section *Pleionactis*	Section *Andromachia*	Section *Andromachia*	*Liabum* (Andromachia group)
A. igniaria	*L. igniarium*	*L. igniarium*	-	-	
A. melastomoides	*L. melastomoides*	*L. melastomoides*	-	-	
A. solidaginea	*L. solidagineum*	*L. solidagineum*	-	-	
A. grandiflora		*L. grandiflorum*	-	-	
A. verbascifolia	*L. verbascifolium*	*L. verbascifolium*	-	-	*Ferreyranthus*
	L. floribundum	-	-	-	*Liabum* (Andromachia group)
	L. jussieui	-	-	-	*Munnozia* (subgenus *Munnozia*)
	L. hieracioides	-	-	-	*Chrysactinium*
Section *Chrysactinium*	Section *Chrysactinium*	Section *Chrysactinium*	Section *Chrysactinium*	Section *Chrysactinium*	
A. acaule	*L. acaule*	*L. acaule*	-	-	
A. hieracioides	-	*L. hieracioides*	-	-	
	L. grandiflorum	-	-	-	*Liabum* (Andromachia group)
		Section *Starkea*	Section *Starkea*	Section *Starkea*	*Liabum* (Liabum group)
	L. umbellatum (as *L. brownei*)	*L. umbellatum* (as *L. brownei*)	-	-	
		L. jussieui	-	-	*Munnozia* (subgenus *Munnozia*)
Section *Oligactis*	Section *Oligactis*	Section *Oligactis*	Section *Oligactis*	Section *Oligactis*	*Oligactis*
A. nubigena	*L. nubigenum*	*L. nubigenum*	-	-	
A. sessiliflora	*L. sessiliflorum*	*L. sessiliflorum*	-	-	
A. volubilis	*L. volubile*	*L. volubile*	-	-	
	Section *Platylepis*	Section *Platylepidea*	-	-	*Sinclairia*
		L. floribundum	-	-	*Liabum* (Andromachia group)
	L. deppeanum	*L. deppeanum*	-	-	*Sinclairia*
	Section *Stenophyllum*	Section *Stenophyllum*	-	-	*Diplostephium* (Astereae)
	L. ericoides	*L. ericoides*	-	-	
			Section *Paranephelium*	Section *Paranephelius*	*Paranephelius*
			Section *Erato*	Section *Andromachia*	*Erato*
			Section *Munnozia*		*Munnozia* (subgenus *Munnozia*)
			Section *Kastnera*		*Munnozia* (subgenus *Kastnera*)
			Section *Sinclairia*		*Sinclairia*

gactis and *Chrysactinium* were later raised to generic level by Cassini (1825) and Weddell (1857), respectively.

Cassini (1817, 1823) was the first to propose the genera *Andromachia* and *Starkea* to be congeneric with *Liabum* and to establish a clear difference between *Liabum* and *Amellus*. Cassini (1823) also created the illegitimate names *Liabum bonplandii* Cass. and *L. brownei* Cass. for *L. igniarium* (Humb. & Bonpl.) Less. and *L. umbellatum* (L.) Sch. Bip., respectively. The name *L. brownei* was erroneously cited in several works (e.g., Cabrera 1947; Robinson & Brettell 1974; Robinson 1983) as *Liabum*'s type species, but the correct type species name is *L. umbellatum* (see discussion under *Liabum umbellatum*). Some years later, Cassini (1829, 1830) grouped *Liabum* together with *Cacosmia* Kunth, *Munnozia* Ruiz & Pav., and *Oligactis* as members of the subtribe Liabinae in the Vernonieae.

Lessing (1831) transferred all of the species of *Andromachia* to *Liabum*. He maintained Kunth's (1818) infrageneric classification of *Andromachia* in *Liabum* and described two new sections, *Platylepis* Less. and *Stenophyllum* Less. (Table 1).

Initially, Candolle (1836) maintained *Andromachia* and *Liabum* as independent genera with two sections in each one: sects. *Pleionactis* DC. and *Oligactis* in *Andromachia*, and sects. *Starkea* (Willd.) DC. and *Chrysactinium* (Kunth) DC. in *Liabum.* Two years later, however, Candolle (1838) recognized *Andromachia* as a synonym of *Liabum* and added the sections *Platylepidea* and *Stenophyllum* (Table 1).

In the following years, some authors added new species to *Liabum* (e.g., Schultz Bipontinus 1847, 1863; Grisebach 1862). Schultz Bipontinus (1863) wrote the first key to species of *Liabum* to determine the Caribbean species and properly transferred *Amellus umbellatus* to *Liabum*.

Toward the end of nineteenth century, Bentham (1873) made a profound change in the taxonomy of *Liabum* (Table 1). He established a broad concept of *Liabum* by including within it several other genera with a capillary pappus from subtribe Liabinae of tribe Senecioneae. Bentham established nine sections for *Liabum*, some of which had been independent genera (e.g., *Erato* DC., *Munnozia*, *Paranephelius* Poepp., *Sinclairia* Hook. & Arn.). Hoffmann (1894) reduced Bentham's classification to five sections (Table 1).

In general, later authors (e.g., Hieronymus 1894; Kuntze 1898; Blake 1927; Urban 1929; Cuatrecasas 1953; Ferreyra 1965) agreed with the broad concept of *Liabum*, with few authors supporting a narrow concept (e.g., Rydberg 1927; Cabrera 1954). Between the years 1881 and 1973, several authors described or transferred to *Liabum* more than 70 species or varieties. This broad concept of *Liabum* included more than 100 species (e.g., Adams 1972; Nash 1976; Cabrera 1978). Rydberg (1927) was the first to propose the new tribe Liabeae in his work on some North American and Caribbean tribes of Asteraceae. He included the genera *Liabellum* Rydb., *Liabum*, *Megaliabum* Rydb., *Sinclairia*, and *Sinclairiopsis* Rydb. in Liabeae. Robinson and Brettell (1973) superfluously elevated Cassini's section Liabinae of Vernonieae to the tribal level and designated *Liabum* as the type genus of Liabeae, but one year later they (Robinson & Brettell 1974) recognized the correct author's citation of the tribe to be Liabeae (Cass.) Rydb. Robinson and Brettell (1974) supported a narrow concept of *Liabum* on the basis of their analysis of both microcharacters (e.g., pollen, style branches, crystals and trichomes of the cypselae) and macrocharacters (habit, leaf venation, inflorescence, and pappus), but they did not establish an infrageneric classification. This was a new and important starting point, however, in the taxonomy of *Liabum*.

Robinson (1983) made the first detailed systematic survey of the Liabeae, which

included generic redelimitations and extended descriptions. He postulated that the genus *Oligactis* sensu lato (14 species) was close to *Liabum*, but that it differed in habit, leaf venation, and type of cypsela trichomes (occasionally some traits of *Oligactis* s.l. appear in *Liabum*, but not all together in the same species). Robinson (1983) recognized three subtribes within Liabeae: Liabinae (*Liabum* and eight other genera), Munnoziinae (four genera), and Paranepheliinae (two genera). Bremer (1994), using a morphological cladistic analysis, recognized Munnoziinae and Paranepheliinae as monophyletic but found Liabinae to be paraphyletic. Therefore, he postulated that there were no reasons for dividing Liabeae into subtribes. Additional cladograms based on morphological characters (Funk et al. 1996) showed Munnoziinae, Paranepheliinae, and some generic groups of Liabinae (clades of *Ferreyranthus* H. Rob. & Brettell-*Liabum*-*Oligactis* s.l. and *Microliabum*-*Liabellum*-*Sinclairia*) to be monophyletic, but the whole subtribe Liabinae to be again paraphyletic. The monophyly of Munnoziinae was questioned in a further molecular study (Kim et al. 2003). The results of recent molecular investigations of Liabeae (Dillon et al. 2009; Funk et al. 2012) have recovered consistent placements for all taxa (except for *Cacosmia*). Four main clades are resolved in these phylogenies: Liabinae, Munnoziinae, Paranepheliinae, and Sinclairiinae. Currently, subtribe Liabinae contains the genera *Dillandia*, *Ferreyranthus*, *Inkaliabum*, *Liabum*, *Oligactis* sensu stricto (five species), and *Sampera* (Gutiérrez 2008, 2010; Funk et al. 2012). These studies, based on a classical taxonomic point of view of *Liabum*, support *Liabum* as monophyletic and sister to *Sampera*. *Inkaliabum* was not included in these analyses.

MATERIALS AND METHODS

This revision included an examination of over 4,000 herbarium specimens, some of them in the form of digital images and photographs, from major herbarium collections of the world. In a few cases the data from specimens were supplemented with information from the literature. In addition, field observations of species were made in Argentina (*Liabum acuminatum* Rusby) and in Panama and Venezuela (*Liabum asclepiadeum*). For microscopic examination of morphological characters, vegetative and reproductive parts from herbarium material were rehydrated, treated with a clearing process (Dizeo de Strittmatter 1973), stained with 2% safranin, and mounted on microscope slides. Free-hand transverse sections of plant organs were made from dried material that had been rehydrated. Drawings were made with a camera-lucida attachment using both a Wild M5 stereomicroscope and Olympus CH2 compound microscope. Light micrographs were taken with a Nikon Coolpix S10. For scanning electron microscopy (SEM) studies, fresh or rehydrated herbarium material was critical point dried, or dry material was placed directly on the stubs and coated with gold. The samples were scanned and photographed in a JEOL JSM-T 100 SEM.

General terminology for morphological and anatomical structures follows Font Quer (1973) and Harris & Wolf Harris (1994). Terminology for leaf architecture follows Hickey (1973), for trichomes follows Ramayya (1962a, 1962b), and for terms specific to Asteraceae follows Small (1919) and Bremer (1994).

All species of *Liabum* were macro- and micromorphologically analyzed (stems, leaves, stomata, and trichomes) (see Appendix). At least 20 specimens per species were morphologically studied whenever possible. Two capitula at the same stage of maturity and two to five florets per specimen were analyzed. For anatomical studies at least two

specimens per species were analyzed. Some species of *Liabum* (see Appendix) were sampled for pollen studies (15 grains per specimen) and supplemented with information from the literature.

In order to analyze morphometric variation among the Caribbean *Liabum* populations, we took measurements from 100 specimens (types specimens and additional collections) (Table 2) making three measurements per organ trait for 22 vegetative and reproductive characters from specimens of *Liabum* from Cuba, Hispaniola, and Jamaica: (1) leaf blade length, (2) leaf blade width, (3) petiole length, (4) pubescence of leaf adaxial surface, (5) length of the inflorescence peduncle, (6) phyllary length, (7) phyllary width, (8) ray floret corolla length, (9) ray floret corolla limb length, (10) ray floret corolla limb width, (11) ray floret corolla tube width, (12) disc floret corolla length, (13) disc floret corolla limb length, (14) disc floret corolla limb width, (15) disc floret corolla tube width, (16) disc floret corolla lobe length, (17) disc floret corolla lobe width, (18) anther length, (19) anther connective appendage width, (20) cypsela length, (21) cypsela width, and (22) pappus length (Table 3).

Leaf measurements (1–4): Leaf blade length was measured from the base of the blade and to its apex. Leaf blade width was measured at its broadest point. Petiole length was measured from the base of the petiole to the base of leaf blade. Given the gradual winged character of the petiole, the base of the leaf blade was defined in the point where the margin conspicuously changes its direction (Fig. 4D). Pubescence of the leaf adaxial surface was recorded as either present or absent (glabrous).

Inflorescence measurements (5–7): Length of the inflorescence peduncle was measured in terminal capitula. Inner phyllary length was measured between the base of the phyllary and its apex, and its width was measured at the midpoint of the total length of the phyllary.

Ray floret measurements (8–11): Ray floret corolla length was measured from the limb apex up to the insertion of the corolla tube on the ovary or cypsela. Tube length was measured from the notch of the corolla to the insertion of the corolla with the ovary or cypsela. Tube width was measured at the midpoint of the total tube length. Limb length was measured from the notch of the corolla to the limb apex. Limb width was measured at the midpoint of the limb length.

Disc floret measurements (12–19). Disc floret corolla length was measured from the apex of lobes to the insertion of the corolla tube on the ovary or cypsela. Tube length was measured from the insertion of the stamens with the corolla up to the insertion of the corolla with the cypsela. Tube width was measured at the midpoint of the tube length. Limb length was measured from the insertion of the stamens on the corolla to the limb apex. Limb width was measured at the midpoint of the limb length. Lobe length was measured from the bases of lobes to their apices, and lobe width was measured at the base of each lobe. Anther length was measured from the appendages apices to the anther bases. Width of the appendage was measured at its broadest point.

Cypselae and pappus measurements (20–22). Length and width of the fruit were measured. Width of the cypsela was measured at the midpoint of the cypsela length. Pappus length was measured from the base up to the apices of the longer inner series.

We performed a Principal Component Analysis (PCA) on the correlation matrix to characterize the morphological variance among the specimens analyzed. Statistical analyses were performed using PAST (Hammer et al. 2001).

TABLE 2. Specimens measured for the statistical analysis of Caribbean *Liabum* populations. Collector and collector number, herbarium, number of plants analyzed per sheet/s (N = 100 individual plants), island of collection, species identification using keys in floristic treatments (Liogier 1964; Liogier 1996), and acronyms used in Fig. 12 are indicated. In some cases there were several complete plants mounted on the same sheet, in other cases one complete plant was on an individual sheet but there were duplicates from several herbaria, and in a few cases one complete plant was on a unicate sheet kept at a single herbarium.

SPECIMENS	HERBARIA	NUMBER OF PLANTS	ISLANDS	SPECIES	ACRONYM
Wright 289	F, GH, MO	4	Cuba	*L. crispum*	Cr
*Ventosa et al. s.n. (*HAC 42554)	LP	1	Cuba	*L. cubense*	Cu
Ventosa et al. s.n. (HAC 42552)	LP	2	Cuba	*L. wrightii*	Wr
Wright 288	F, GH, MO	9	Cuba	*L. wrightii*	Wr
Ekman 14745	F	1	Cuba	*L. wrightii*	Wr
Wright 2871	GH	1	Cuba	*L. wrightii*	Wr
Judo 1482	GH	1	Hispaniola	*L. subacaule*	Su
Ekman 12578	GH, US	2	Hispaniola	*L. ovatifolium*	Ov
Türckheim 3113	F, GH, MO, US	10	Hispaniola	*L. subacaule*	Su
Ekman 1548	US	1	Hispaniola	*L. selleanum*	Se
Ekman 5346	GH	1	Hispaniola	*L. polycephallum*	Po
Valeur 56	F, GH, MO	6	Hispaniola	*L. subacaule*	Su
Fuentes 1635	GH	3	Hispaniola	*L. subacaule*	Su
Fuentes 959	GH	1	Hispaniola	*L. subacaule*	Su
Liogier 19903	F	3	Hispaniola	*L. ovatifolium* or *L. polycephalum*	Ov-Po
Liogier 11063	GH	1	Hispaniola	*L. subacaule*	Su
Liogier 14130	GH	2	Hispaniola	*L. subacaule*	Su
Liogier 11533	GH	2	Hispaniola	*L. subacaule*	Su
Liogier 11754	F	3	Hispaniola	*L. subacaule*	Su
Ekman 1870	GH	2	Hispaniola	*L. subacaule*	Su
Ekman 13012	GH	2	Hispaniola	*L. subacaule*	Su
Gastony et al. 394	GH	1	Hispaniola	*L. subacaule*	Su
Lavastre 964	GH	3	Hispaniola	*L. subacaule*	Su
Zanoni et al. 42442	MO	1	Hispaniola	*L. ovatifolium*	Ov
Mejía & Zanoni 4975	MO	1	Hispaniola	*L. ovatifolium*	Ov
Leonard & Leonard 14518	GH	1	Hispaniola	*L. poiteaui*	Poi
Leonard & Leonard 13726	MO	1	Hispaniola	*L. poiteaui*	Poi
Ekman 10392	F, GH	6	Hispaniola	*L. subacaule*	Su
Howard & Howard 8166	GH	1	Hispaniola	*L. subacaule*	Su
Howard 12087	GH	1	Hispaniola	*L. selleanum* or *L. barahonense*	Se-Ba
Howard & Howard 8158	GH	1	Hispaniola	*L. selleanum*	Se
Howard & Howard 8179	GH	3	Hispaniola	*L. subacaule*	Su
Crosby et al. 535	F, GH	2	Jamaica	*L. umbellatum*	Um
Crosby et al. 859	F, GH, MO	4	Jamaica	*L. umbellatum*	Um
Alexander s.n.	GH	1	Jamaica	*L. umbellatum*	Um
West & Arnold 119	GH	1	Jamaica	*L. umbellatum*	Um
Nicholson 25	F, GH, MO	3	Jamaica	*L. umbellatum*	Um
Stearn 566	GH	1	Jamaica	*L. umbellatum*	Um
Yuncker 18202	F	1	Jamaica	*L. umbellatum*	Um
Hunnewell 14406	GH	3	Jamaica	*L. umbellatum*	Um
Philipson 1118	MO	1	Jamaica	*L. umbellatum*	Um
Harris 10844	F	1	Jamaica	*L. umbellatum*	Um
Maxon & Killip 194	F	1	Jamaica	*L. umbellatum*	Um
Anderson & Sternberg 3113	GH, MO	1	Jamaica	*L. umbellatum*	Um
Adams 10803	MO	1	Jamaica	*L. umbellatum*	Um
Bertero s.n.	MO	1	Jamaica	*L. umbellatum*	Um

TABLE 3. Morphological characters, their statistics (mean, ± standard deviation, and range), and their factor loadings on the first two principal components in PCA of Caribbean specimens of *Liabum*. The variance of each principal component is also given.

CHARACTERS	MEAN (STANDARD DEVIATION) (RANGE)	PC1	PC2
(1) Leaf blade length (cm)	6.26 (±3.38) (1.6–14.0)	0.7141	-0.06019
(2) Leaf blade width (cm)	3.15 (±1.79) (0.8–8.7)	0.3409	-0.03504
(3) Petiole length (cm)	4.45 (±3.01) (0.5–15.0)	0.5585	-0.09729
(4) Leaf adaxial surface pubescence	Present/absent	-0.05613	-0.02087
(5) Peduncle length of the inflorescence (cm)	2.16 (±2.19) (0.1–10.5)	0.2013	-0.03925
(6) Phyllary length (cm)	0.97 (±0.18) (0.6–1.8)	0.006489	0.008503
(7) Phyllary width (mm)	5.03 (±1.63) (1.0–8.0)	-0.03315	-0.2076
(8) Ray florets corolla length (mm)	10.57 (±2.13) (5.4–17.5)	0.08893	0.7639
(9) Ray florets corolla limb length (mm)	5.16 (±1.61) (1.1–11.0)	0.04489	0.5564
(10) Ray florets corolla limb width (mm)	0.32 (±0.06) (0.17–0.45)	0.0001062	0.005697
(11) Ray florets corolla tube width (mm)	0.11 (±0.02) (0.08–0.16)	0.0008275	0.000411
(12) Disc florets corolla length (mm)	7.92 (±1.01) (6.3–11.4)	0.05023	0.1829
(13) Disc florets corolla limb length (mm)	1.48 (±0.64) (0.7–3.8)	0.02381	0.07929
(14) Disc florets corolla limb width (mm)	0.63 (±0.11) (0.42–0.91)	0.004881	0.01278
(15) Disc florets corolla tube width (mm)	0.18 (±0.03) (0.11–0.26)	0.001062	0.003188
(16) Disc florets corolla lobes length (mm)	1.52 (±0.29) (1.03–2.53)	0.01962	0.04369
(17) Disc florets corolla lobes width (mm)	0.26 (±0.04) (0.18–0.37)	0.00233	0.003846
(18) Anther length (mm)	2.14 (±0.64) (1.60–3.31)	0.01566	0.04275
(19) Connective appendage width (mm)	0.15 (±0.02) (0.11–0.19)	0.000071	0.001363
(20) Cypsela length (mm)	1.48 (±0.36) (0.8–2.38)	0.0149	0.00063
(21) Cypsela width (mm)	0.32 (±0.08) (0.17–0.54)	0.001133	0.0001229
(22) Pappus length (mm)	6.58 (±0.79) (4.10–8.27)	0.05656	0.06116
Variance (%)		52.267	14.031

MORPHOLOGY AND ANATOMY

Habit. Four different habit types occur within the genus: (1) Acaulescent or sub-acaulescent perennial herbs, with rosulate leaves (*L. umbellatum*), (2) Caulescent perennial herbs, with leaves clustered at the end of the stem (*L. grandiflorum* (Kunth) Less. and *L. umbellatum*), (3) Perennial herbs with leaves spread also along principal and secondary branches (e.g., *L. acuminatum*, *L. amplexicaule* Poepp., and *L. steinbachii* H. Rob.), and (4) Subshrubs or shrubs (rarely small trees), with leaves spread into principal and secondary branches (e.g., *L. acuminatum*, *L. saloyense* Domke, and *L. solidagineum* (Kunth) Less.). Shrubs and subshrubs are usually erect, but in some species (e.g., *L. kingii* H. Rob., *L. saloyense*, *L. wurdackii* Ferreyra) the stems are tall and slender and lean on other plants, and are thus somewhat scandent.

Many species show variation in their habit. For example, plants of *Liabum acuminatum* may be either perennial herbs or subshrubs, plants of *L. solidagineum* may be subshrubs, shrubs, or sometimes small trees, and plants of *L. umbellatum* may be either caulescent or sub-acaulescent perennial herbs.

Latex. The occurrence of latex has been considered one of the diagnostic characters of Liabeae. However, all genera of subtribe Liabinae, as it is currently circumscribed (Funk et al. 2012, Gutiérrez & Luna 2013), seem to lack latex. The only mention of milky juice in *Liabum* was found on the label of one specimen of *L. kingii* (*Stuessy & Nesom 5808*, LP),

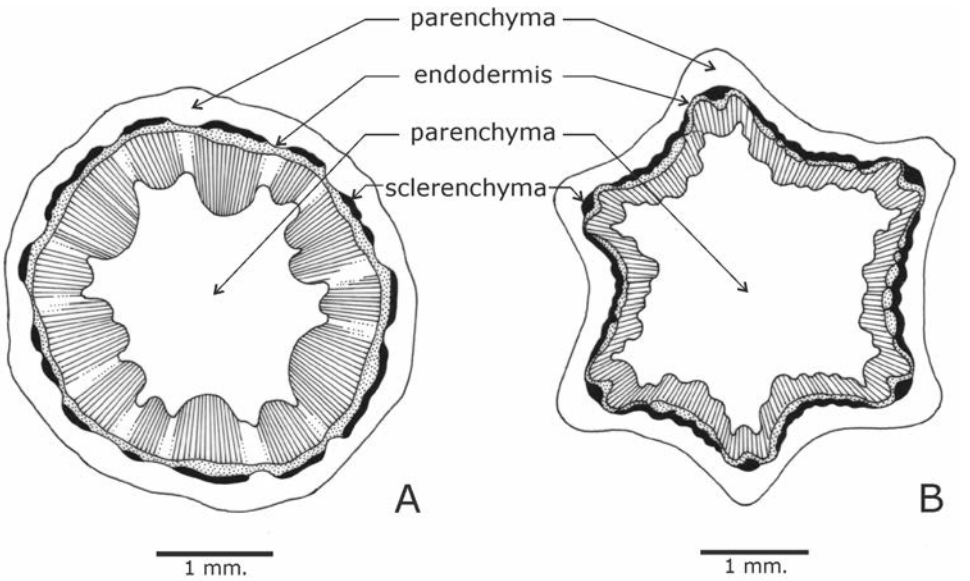

FIG. 1. Stem transections. A. Herb (*L. umbellatum*, *Wright 288*, F). B. Subshrub (*L. floribundum*, *Mille 1995*, MO).

although the label of another specimen of the same species (*King & Almeda 7936*, US) reads: "without milky sap." In this work we confirm the absence of latex in *Liabum*.

Stem. The stem may be long, reaching 6 m in height, or short to very reduced in acaulescent herbs, and in cross-section circular to conspicuously hexagonal from the presence of ribs of sclerenchyma (Fig. 1A, B). Most species have stems that are densely tomentose, with a white or ochraceous, persistent tomentum constituted of the same type of trichomes found on the leaves.

Anatomical studies of the stem anatomy are scarce, except for the work of Carlquist (1962a, b) on *Liabum igniarium* (sub *L. bonplandii*) and other genera of Liabeae. All species of *Liabum* sampled in this study show that the stem cross-section in herbs (Fig. 1A) basically consists of a uniseriate epidermis, several layers of parenchyma tissue occasionally containing druses, and an endodermis layer surrounding the vascular bundles. In most dicotyledons, including Asteraceae, the endodermis is not obvious and consists of a more or less clearly defined layer of cells that are distinguishable from neighboring cells in containing starch (Metcalfe & Chalk 1957, Lersten 1997). Each vascular bundle is surrounded on the outer side by a sclerenchyma sheath. The pith may be parenchymatous or absent. A typical secondary structure characterizes the stems of shrubs and subshrubs (Fig. 1B), with the vascular bundles becoming connected by formation of secondary tissues from a continuous vascular cambium.

Pseudostipules. The pseudostipules are irregular foliaceous elements arising at the base of the petiole. Pseudostipules show different degrees of development (Fig. 2A–E), and in some cases, they are lacking from the leaves on the terminal branches (*L. asclepiadeum*, *L. solidagineum*). Pseudostipules are completely lacking in the Antillean species

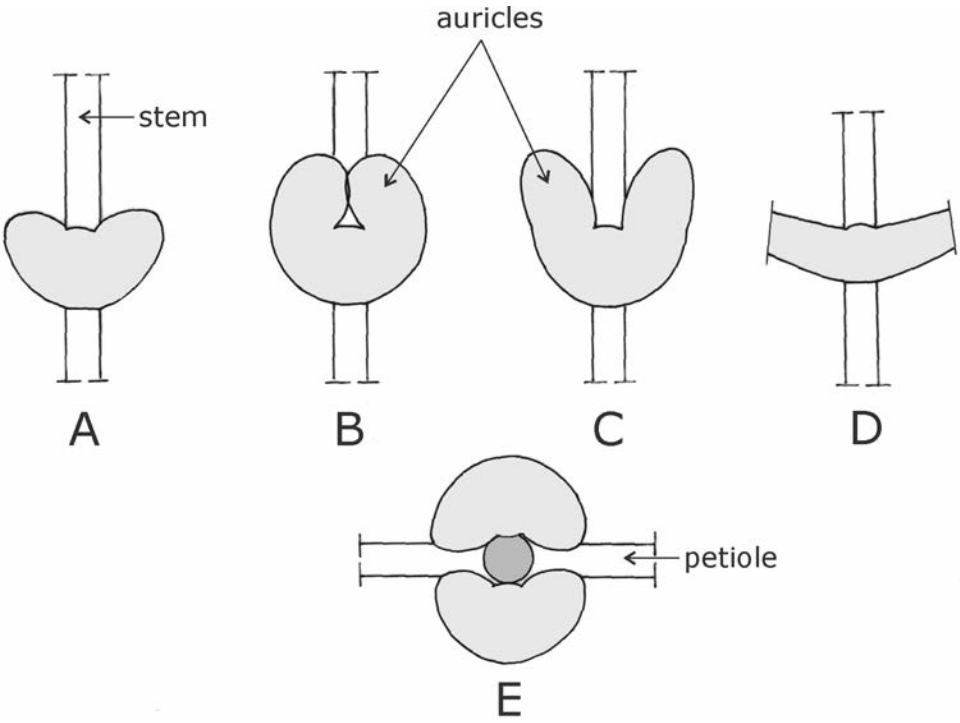

FIG. 2. Pseudostipules. A–D. Lateral view. A. Pseudostipule not auriculate. B. Pseudostipule with convergent auricles. C. Pseudostipule with divergent auricles. D. Pseudostipule not disciform. E. Upper view of a pair of non-auriculate pseudostipules.

L. umbellatum and in some continental species (e.g., *L. acuminatum*, *L. melastomoides* (Kunth) Less.). The pseudostipules are usually disciform (therefore sometimes referred to as "nodal discs" in the literature) but may also be auriculate (Fig. 2B, C), with the auricles of opposing leaves convergent and overlapping, or divergent (e.g., *L. igniarium*, *L. saloyense*, *L. kingii*). In most species with winged petioles, the pseudostipules are continuous with the wings (Figs. 2D, 3A), except in *L. robinsonii* D. G. Gut. & Katinas, where the petiole wings end distal to the petiole base. Pseudostipules are subglabrous or arachnoid-pubescent adaxially and white-tomentose abaxially.

Leaves. The leaves are opposite and usually decussate, sometimes rosulate, or clustered at the apex of the stem in some caulescent herbs. They are short-petiolate (e.g., *L. acuminatum* with petioles 1–3.5 cm long, *L. grandiflorum* with petioles 0.8–2.5 cm long) or long-petiolate (e.g., *L. robinsonii* D. G. Gut. & Katinas with petioles 3.5–8.5 cm long), or inconspicuously petiolate (*L. umbellatum*) (Fig. 4A–D). Petioles may be wingless (Fig. 4A) or completely or partially winged with narrow or wide wings (Fig. 4B, C), continuous or not with the pseudostipules; when continuous, the petiole wings are very well demarcated from the leaf blade base and have the same width throughout (Fig. 4B). The inconspicuous type of petiole is a gradual extension of the leaf blade toward the leaf base, wider near the blade and narrowing to the stem (Fig. 4D).

Leaf blades may be simple and elliptic (e.g., *L. umbellatum*), narrowly elliptic (e.g., *L.*

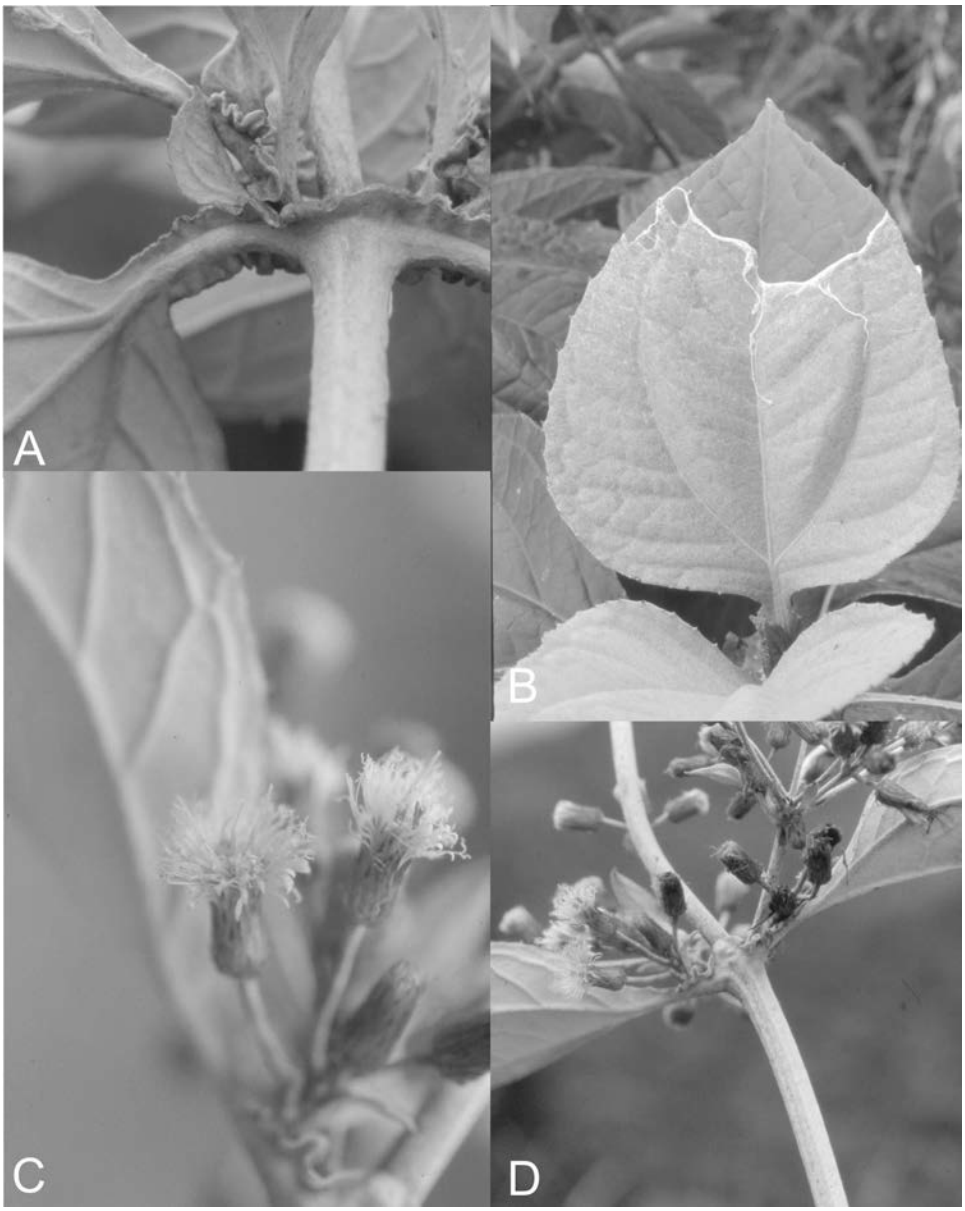

FIG. 3. General morphology of *Liabum*: *L. asclepiadeum* Sch. Bip. A, B. Vegetative morphology. A. Pseudostipules, showing the pseudostipule continuous with the winged petiole. B. Leaf, showing the evanescent adaxial indument. C, D. Reproductive morphology. C. Detail of capitula. D. Lax inflorescence. (Photos by J. M. Bonifacino.)

acuminatum), ovate (e.g., *L. umbellatum*), or sub-triangular (e.g., *L. grandiflorum*, *L. robinsonii*) in shape (Fig. 4A–D). The margins may be mucronate-serrate or serrulate, rarely denticulate, and planate in cross-section (revolute only in *L. melastomoides*). The texture is coriaceous or chartaceous. The blade base shows considerable variation, predominantly cuneate but may also be decurrent, rounded, cordate, or truncate (Fig. 4A–D). The

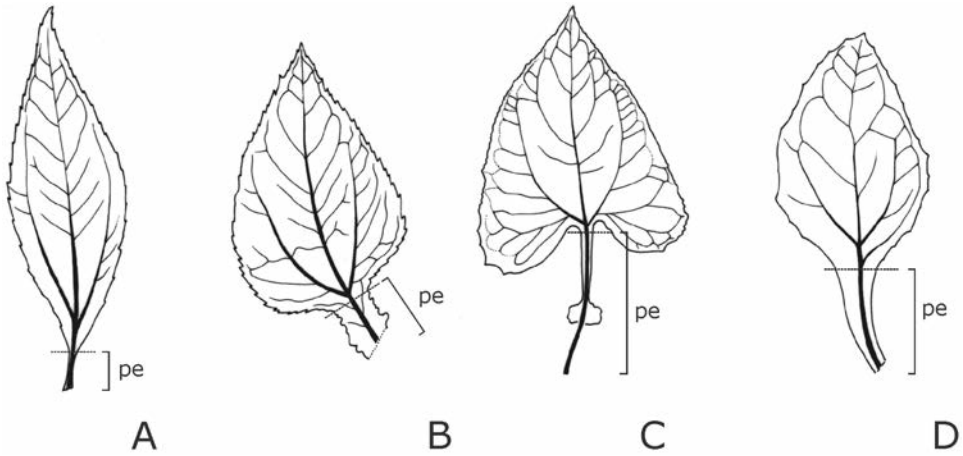

FIG. 4. Variation in leaf morphology. A. Elliptic blade and non-winged petiole. B. Sub-triangular blade with rounded base and winged petiole. Note the sharp distinction between the petiole and the leaf blade base. C. Sub-triangular blade with cordate base and partially winged petiole with auricles. D. Ovate blade and inconspicuously petiolate. Note the gradual extension of the leaf blade toward the leaf base. pe = petiole.

blade apex is acuminate or acute, sometimes attenuate. The surface of the leaves is usually smooth and flat, but the surface is sometimes bullate in specimens of *L. umbellatum* and *L. grandiflorum*. Stomata are commonly abaxial and slightly elevated (Fig. 7C), rarely adaxial in depressions on the marginal teeth.

Typically, the leaves of *Liabum* are tripliveined (sensu Harris & Harris 1994; Fig. 4A, B), i.e., with one central main vein and two lateral main veins arising from the midvein above the blade base (acrodromous; Hickey 1973), and thus different from a triveined leaf, in which the three main veins arise from a common point at the base of the blade. The lateral main veins are basally either parallel to the margin or not, and are variable in length, with the two veins reaching the apex of the blade in some species or not reaching the apex in others. Sometimes other basal secondary veins are present in sub-triangular leaves (actinodromous; Hickey 1973) (Fig. 4C). The tripliveined condition is not conspicuous in the Antillean species *Liabum umbellatum* (Fig. 4D), which approaches a pinnate condition.

The blade in cross-section is bifacial and amphistomatic. The cuticle on the uniseriate epidermis is thicker in chartaceous leaves. The stomata are anomocytic (Fig. 7C), commonly abaxial and slightly elevated; when adaxial, they are usually found in depressions on the marginal teeth. Guard cell length ranges from 15 to 25 μm. A sub-epidermal hypodermis is found in some specimens at the level of the midvein, on the adaxial side. The mesophyll, with 1–3 palisade layers, may contain druses. The midvein has a reduced abaxial sclerenchymatous sheath that sometimes extends to the adaxial side. There is adaxial and abaxial sub-epidermal collenchyma at the midvein level.

There is usually a marked difference in the amount of pubescence on the adaxial versus the abaxial surface of the blade in species of *Liabum*. Adaxially, some species have glabrous leaves (e.g., *L. melastomoides*, *L. kingii*), hirsute (e.g., *L. floribundum*, *L. grandiflorum*), or strigose (e.g., *L. umbellatum*), sometimes mixed with an arachnoid and evanescent indumentum (e.g., *L. asclepiadeum*, *L. umbellatum*) (Fig. 3B). Abaxially, leaves are usually white- or sometimes ochraceous-tomentose (e.g., *L. solidagineum, L. eriocaulon* Poepp.). Sometimes the tomentum is mixed with brownish hairs (this color in dried speci-

mens), which may be distributed along the main veins (*L. floribundum*, *L. saloyense*) or across the surface of the blade (specimens of *L. floribundum* and *L. saloyense*).

Vegetative Hairs. Vegetative hairs or trichomes can be classified into four types:

(a) Aseptate-flagellate hairs (Fig. 5A): Usually white in color and found on branches, the lower surfaces of leaves, and on capitulum peduncles, producing a tomentose pubescence. Sometimes such hairs are located on the upper surfaces of leaves, and on phyllaries of the involucre, producing an arachnoid pubescence. These hairs have a simple foot and a uniseriate body. The stalk is 1 (–2)-celled, cylindrical or slightly tapering proximally, the cells are usually longer than broad, and the cross and lateral walls are thin. The head is 1-celled, very long, coiled, flagellate, tubular, usually sharply delimited from the stalk, remaining intact, the lateral walls are thin, swollen basally, the apex is acute; it has a vanishing content.

(b) Bulbiferous flagellate hairs with simple foot (Fig. 5B): Typically white in color, sometimes brownish or reddish. Usually found on branches, the lower surface of leaves, especially on main veins, and capitula peduncles, producing a tomentose pubescence. In some specimens they may appear on the upper surface of leaves and are early deciduous. Ramayya (1962a) called this type "bulbiferous flagellate hair type I." The foot is simple and the body is uniseriate. The stalk is 1–6-celled, cylindrical, the cells usually longer than broad, the terminal cells (1 or more) swollen and spherical or oblong in shape, collapsing early or not collapsing, and the cross and lateral walls are thin; it has a translucid and vanishing content. The head is 1-celled, very long, coiled, tubular, flagellar, slightly narrower than the basal cells of stalk, collapsing early or not collapsing, tapering distally, and the basal and lateral walls are thick.

(c) Bulbiferous flagellate hairs with compound foot (Fig. 5C): These are similar to hairs described under (b) but the foot is compound (many-celled) and the body is uniseriate to basally biseriate or multiseriate, the stalk is 1- to usually many-celled and conical, and the terminal cells collapse early. They are usually found on the upper surface of leaves producing a strigose or hirsute pubescence, on branches, petioles, and main veins of the lower surfaces of leaves. In specimens of *L. floribundum* and *L. saloyense* these hairs appear mixed with the tomentose pubescence of the abaxial side of the leaves, producing a dotted aspect. Ramayya (1962a) called this hair type "bulbiferous flagellate hair type II."

(d) Simple biseriate glandular hairs with a head (Fig. 5D): Found on the lower surface of leaves covered by non-glandular hairs. Ramayya (1962a) called this type "simple biseriate glandular hairs subtype α." The foot is 1–2-celled and the body is biseriate, the cells of one row are opposite or sub-opposite to the cells of the other row; it has a translucent and vanishing content. The stalk is 1–3-celled in each row, the cells are isodiametric or slightly longer than broad, and the inner and outer walls are thin. The head is 1–2-celled in each row, variable in shape, demarcated from the stalk or continuous with it, and the two terminal cells are not distinct or are slightly distinct like a vesicle; the inner and outer walls are thin.

Inflorescences. The capitula of *Liabum* are borne in cymose inflorescences, which may be scapose or, more commonly, non-scapose. Scapose cymes are umbelliform, with one main floral axis, which may be either branched or unbranched (Fig. 6A, B); rarely there may be two or three additional axes borne in the axils of leaves. This inflorescence type is found exclusively in herbaceous species with clustered leaves, i.e., *L. umbellatum* and occasionally *L. grandiflorum*. The cymes are laxly arranged (Fig. 6A) when peduncles of

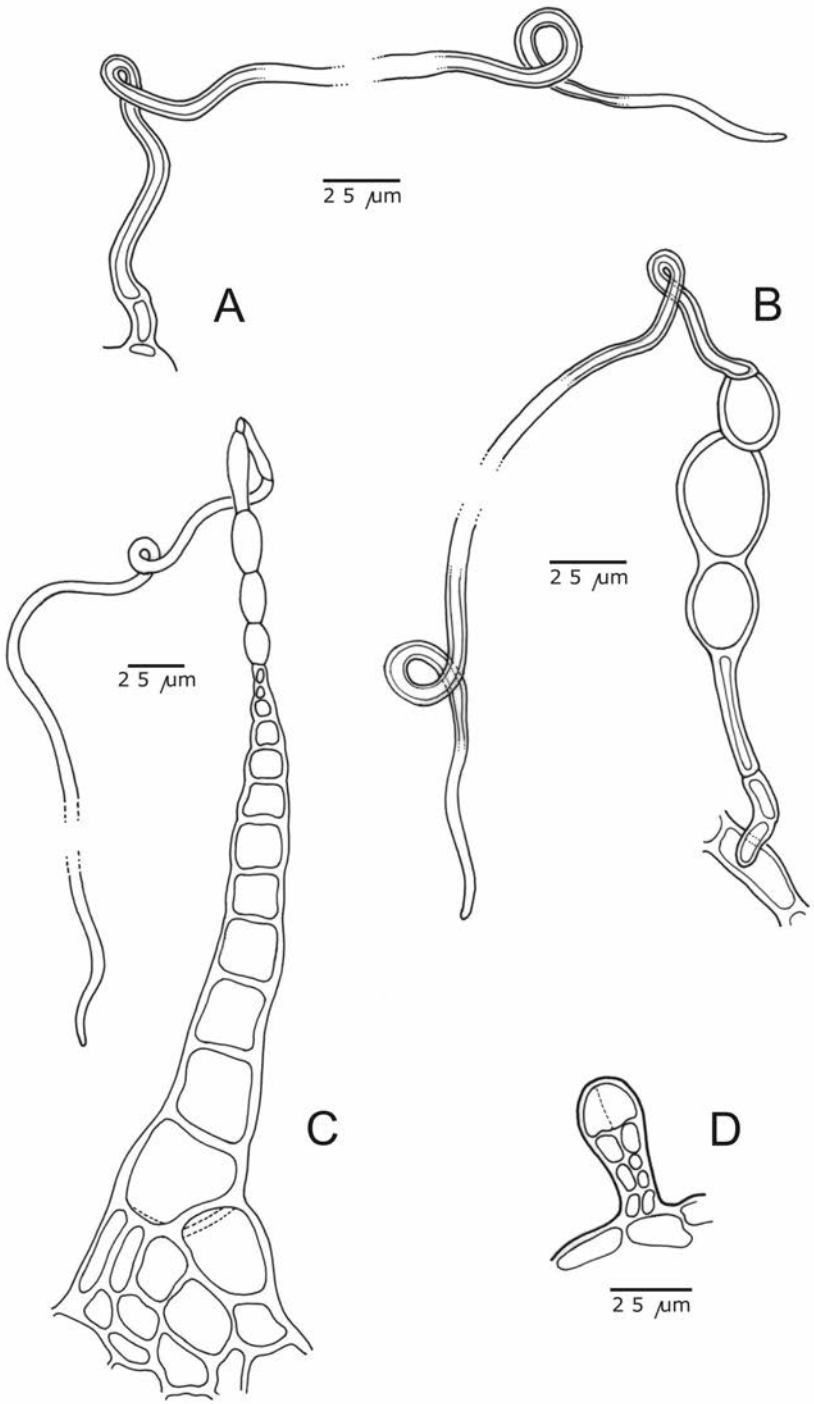

FIG. 5. Vegetative hairs. A. Aseptate-flagellate hair (*L. wurdackii*, *Sánchez & Dillon 8010*, F). B. Bulbiferous flagellate hair, with simple foot (*L. umbellatum*, *Liogier 11533*, GH). C. Bulbiferous flagellate hair, with compound foot (*L. floribundum*, *Játiva & Epling 24*, NY). D. Simple biseriate glandular hair, with head (*L. umbellatum*, *Crosby et al. 859*, F).

capitula are long, and may be few- to many-headed, or they may be densely arranged with subsessile capitula when peduncles are very short, as in some individuals of *L. umbellatum* (Fig. 6B).

All non-scapose inflorescences have numerous floral axes in addition to the one terminal, branched axis (Fig. 6C–G). All inflorescence branches are opposite and form complex third-order inflorescences. The capitula are arranged in umbelliform, sometimes corymbiform or rarely glomerulose, cymes, these grouped in turn into corymbiform or racemiform secondary cymes. They may be laxly or densely arranged. In lax inflorescences (Fig. 6C) the main branches are long, usually with numerous or few, long-pedunculate capitula. In dense inflorescences (Figs. 3C, D, 6D–F) the main branches are long, usually with numerous short-pedunculate capitula. When the capitula are sessile or subsessile (Fig. 6G) they form glomerulose cymes; this inflorescence type occurs only in *L. melastomoides*.

Capitula. The capitula are heterogamous, radiate with conspicuous marginal ray corollas (e.g., *L. floribundum*, *L. igniarium*, *L. wurdackii*) or sub-radiate with the limb of the marginal ray corollas linear and inconspicuous (e.g., *L. umbellatum*, *L. asclepiadeum*)

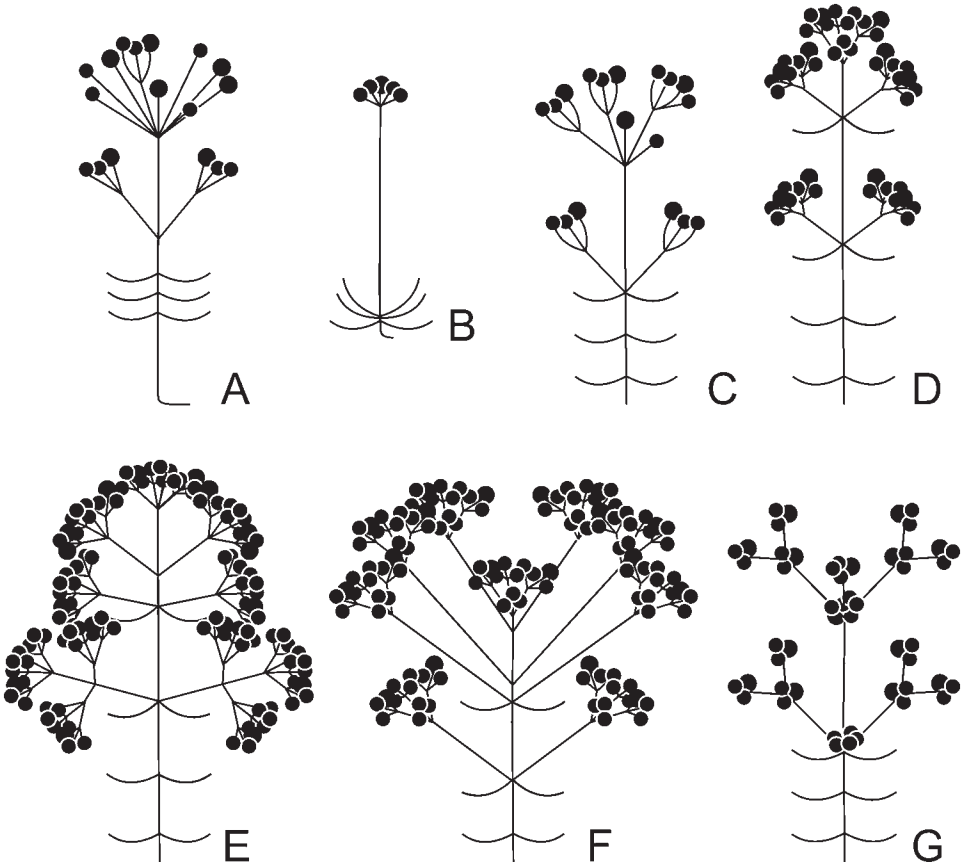

FIG. 6. Inflorescences. A, B. Scapose umbelliform cymes. A. Many-headed cymes. B. Few-headed cymes. C–G. Non-scapose cymes. C. Long-pedunculate cymes. D. Short-pedunculate cymes. E. Many-headed capitulescence with lateral branches shorter than the main axis. F. Many-headed capitulescence with lateral branches longer than the main axis. G. Glomerulose cymes.

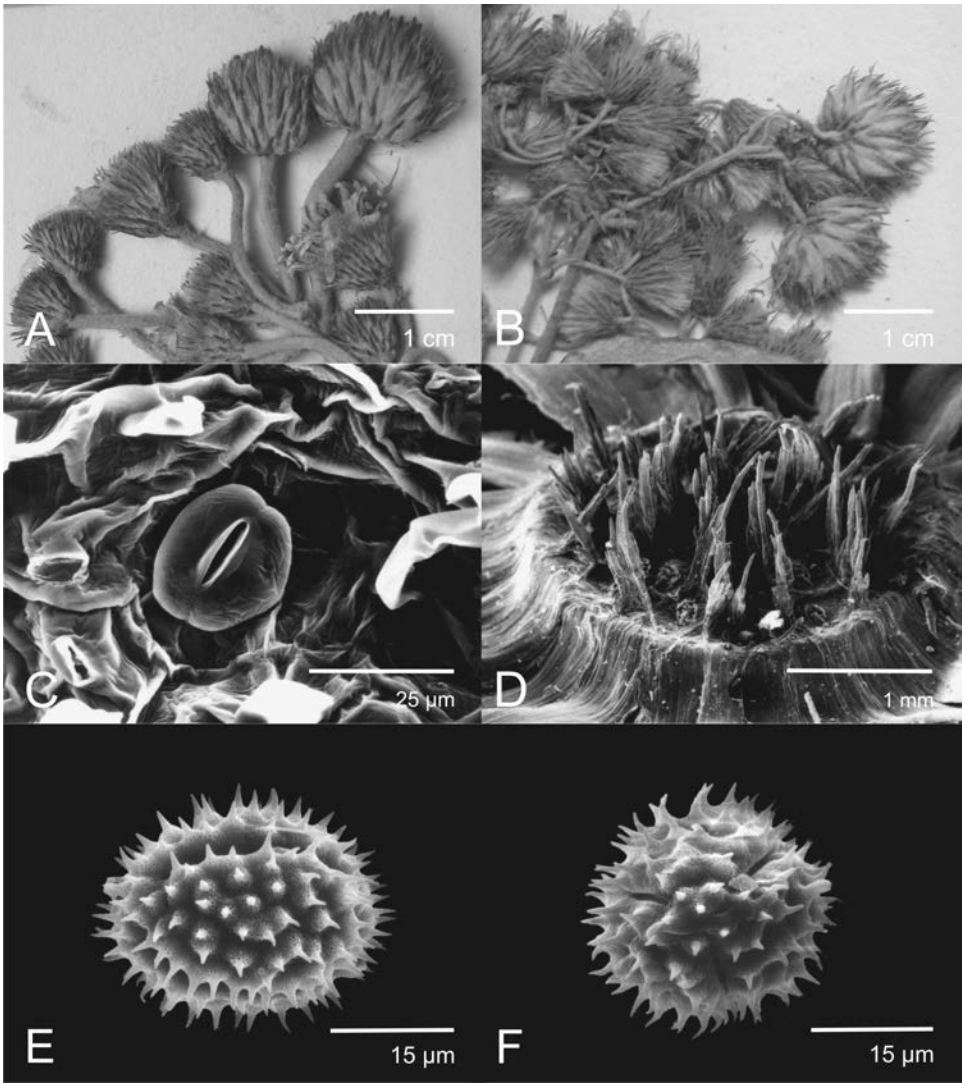

FIG. 7. A, B. Galls in capitula of *Liabum*. A. Galls in *L. igniarium*. B. Galls in *L. solidagineum*. C. Scanning electron micrograph of slightly elevated abaxial stoma (*L. umbellatum*, *Liogier 11533*, GH). D. Scanning electron micrograph of setiferous receptacle (*L. melastomoides*, *Rusby & Pennell 466*, NY). E, F. Scanning electron micrographs of pollen grains of *L. umbellatum* (*Liogier 11533*, GH). E. Equatorial view. F. Polar view.

(Fig. 3C). The capitula are sessile or subsessile to long-pedunculate. It is common to find an increase in capitulum size together with increased pubescence of phyllaries and alteration in size and shape of florets and fruits in specimens of *L. barclayae* H. Rob., *L. igniarium*, and *L. solidagineum*, due to the attack of insects that produce galls (Fig. 7A, B). The involucre is broadly campanulate (e.g., some specimens of *L. umbellatum*, *L. wurdackii*), campanulate (e.g., *L. acuminatum*, *L. solidagineum*), or hemispherical (e.g., *L. kingii*, *L. saloyense*), with 50–150 imbricate phyllaries arranged in (4–) 5–7 (–8) series. The phyllaries are coriaceous, with a conspicuous central vein, scabrate on the apex and margin, plane or slightly twisted, and completely green or purple at the apex. From the outer series to the

inner one there is a gradual transition from short-ovate phyllaries that are acute at the apex and pubescent or glabrous, to linear or narrowly ovate ones that are acute or attenuate at the apex and sparsely pubescent or glabrous.

The receptacle is flat or slightly convex, and setiferous with irregularly laciniate setae that surround each depression (Fig. 7D).

Florets. In *Liabum* the marginal florets have ray corollas and the central or disc florets have tubular corollas. The ray florets (Fig. 8A, B) are pistillate, fertile, and lack staminodia. The number of ray florets varies from (10–) 20–140 per capitulum. The ray corolla is yellow or orange, and may be glabrous or pubescent. The ray corolla limb may be linear, narrowly elliptic, obovate, or ovate in shape; it is 1–4-veined and 2–3-dentate or entire at the apex. It is common to find druses in the parenchyma tissue and 1–2 stomata at the limb apex, usually associated with trichomes. The style of the ray florets is bifid, with long, filiform, curly or curved branches that are narrowly obtuse at the apex (Fig. 8C). Externally, the branches are glabrous or with a few papillae toward the apex; internally, the branches are completely covered by stigmatic papillae. The style lacks a nectary at its base.

The tubular disc florets (Fig. 8D–F) are hermaphroditic and fertile, and they vary from 15–90 per capitulum. The corolla is yellow and may be glabrous or pubescent. The narrow basal part is called the tube, and the gradually to abruptly broadened, more distal portion of the corolla is called the limb. The limb is further differentiated into a funnel-shaped throat and five free lobes. A few stomata are common on the abaxial surface, near the tips of the lobes. The tube of corolla may be equal to, shorter than, or longer than the limb; the lobes are very deep in *L. saloyense* and *L. kingii*. The anthers are pale yellowish, linear, short-calcarate (i.e., pollen-containing thecae are prolonged below the point of filament insertion) and short-caudate (the bases of the thecae have tails of sterile cells: Fig. 8I–J). The apical appendage (the connective tissue prolonged toward the anther apex) is smooth, planate, ovate or triangular, and apically rounded (Fig. 9A). The anther tails are papillose to digitate when the papillae are very long (Fig. 8J). An anther collar or filament collar, a region of the filament with more thick-walled and differently shaped cells immediately below the anther, is conspicuous and cylindrical (Fig. 8K). The endothecial cells are long, with different types of thickenings: a) radial thickenings in the radial walls (e.g., *L. igniarium*) (Fig. 9B), b) "U" thickenings in the radial walls and in one of the tangential walls of the cell (e.g., *L. asclepiadeum*, *L. vargasii* H. Rob.) (Fig. 9C), and c) polarized thickenings in the transverse walls of the endothecial cells (e.g., *L. barclayae*, *L. igniarium*, *L. melastomoides*) (Fig. 9D). Commonly, there are transitions from one type to the other in the same anther and it is not possible to assign one particular type to each species. The style is broadest at the base and the two style branches are usually shorter and less coiled than the style branches of the ray florets (Fig. 8G). Externally, the branches are hispidulous, with sweeping hairs (which act as pollen presenters) formed by one-celled papillae that are triangular in shape, apically acute, and pointing toward the apex (Fig. 8H). The sweeping hairs extend down the style proximal to the bifurcation point a distance less than the length of the style branches (Fig. 8G). The inner surface of the branches has a continuous stigmatic surface. The style has a nectary at its base.

Corolla Hairs and Papillae. Marginal and central corollas may be glabrous or pubescent with flagellate hairs, twin hairs, glandular hairs, and papillae. These types may be divided into the following subtypes:

(a) Bulbiferous flagellate hairs with a simple foot (Fig. 10A; they are similar to the

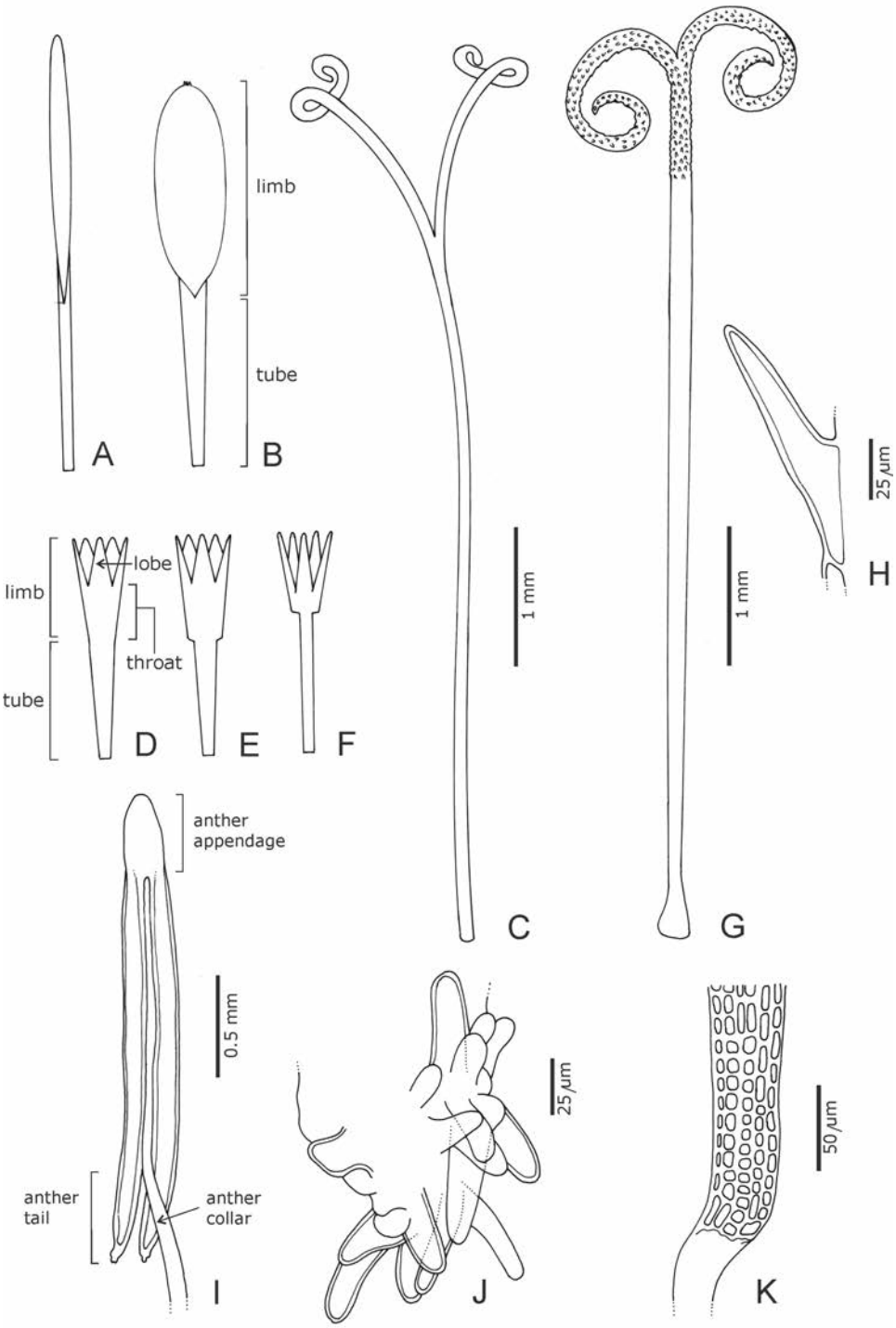

FIG. 8. Florets of *Liabum*. A–C. Ray florets. A. Corolla of *L. acuminatum* with linear limb. B. Corolla of *L. grandiflorum* with elliptic limb. C. Style. D–H. Disk florets. D. Corolla of *L. acuminatum* with tube gradually broadened into the limb. E. Corolla of *L. dillonii* with tube abruptly broadened into the limb, shallowly lobed. F. Corolla of *L. saloyense* with tube abruptly broadened into the limb, deeply lobed. G. Style. H. Detail of sweeping hair. I. Stamen. J. Papillose base of anther. K. Anther collar. (Based on: C, G, H, J, *L. saloyense*, *Jaramillo & Zak 7903*, MO; I, K, *L. melastomoides*, *Pennell 5854*, US.)

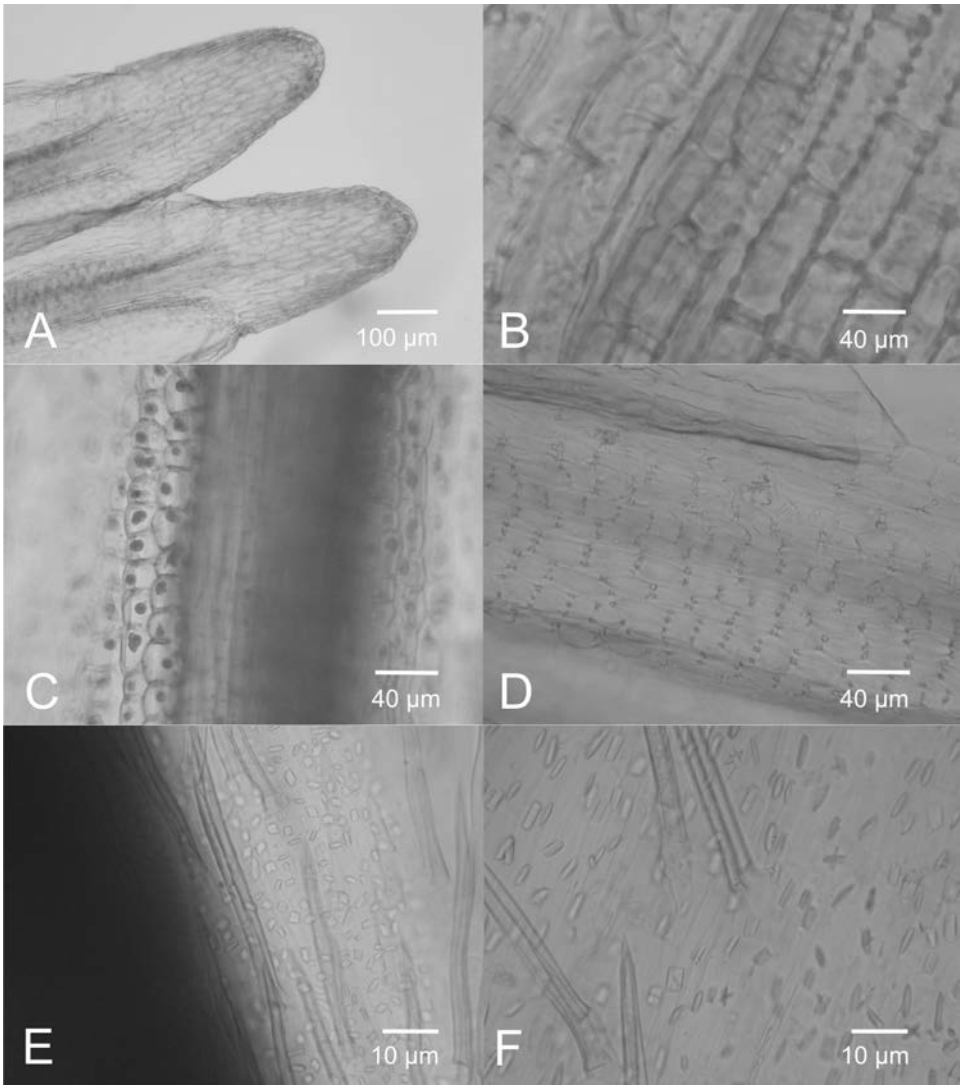

FIG. 9. Floral and fruit features. A. Apical anther appendage. B–D. Endothecial thickenings. B. Radial. C. "U" thickenings. D. Polarized. E, F. Cypsela crystals. E. Quadrate. F. Rectangular. (Based on: A–D, *L. igniarium*, *Zak & Jaramillo 2058*, NY; E, F, *L. melastomoides*, *Pennell 5854*, US.)

vegetative ones) are usually found on the external side of the disc corolla lobes, near the apex.

(b) Aseptate-flagellate hairs (Fig. 10B; similar to the vegetative ones) are usually found on the external side of the disc corolla lobes, near the apex.

(c) Typical twin hairs or "Zwillingshaare" (Hess 1938) (Fig. 10C) are basically formed by two triangular or rectangular, short, basal cells (one sometimes reduced), and two elongated, cylindrical hair cells, with thick walls, completely united with each other on their longitudinal walls or diverging, equal in length or one shorter. They are usually found near the lobe apices of the disc corollas.

(d) Atypical twin hairs (Fig. 10D) (Freire & Katinas 1995) are ontogenetically derived from the typical twin hairs, but differ in aspect by the septation of the hair cells to form 4–8-celled hairs. The cell walls are very thick and usually one hair cell is longer. They are usually found on the lobes of the central corollas and on the limb apex of the marginal corollas.

(e) Simple biseriate glandular hairs, with a head (Fig. 10E) differ from the vegetative trichomes of the same type because they are longer, with 8–14 cells in two rows, the head is always demarcated from the stalk, and the cell walls of the stalk are thicker. They are usually found on the external side of the central corolla lobes, near the apex.

(f) Simple biseriate glandular hairs, without a head (Fig. 10F) have 4–8 (–12) cells in two rows and can be opposite, sub-opposite, or alternate. The cell walls are thin, occassionally thicker at the apex of the hair. The hair apex is obtuse or acute, 1–2-celled. They are usually found in the middle of the central and marginal corollas. When these hairs are found on the lobes of the central corollas, they have an acute apex and all the cells have thick walls.

(g) Long papillae or 1-celled hairs (Fig. 10G) are transitional forms between hairs and papillae, since they are formed by the enlargement of one epidermal cell, and the cell is acute at the apex, with thick walls; they are grouped in tufts. They are usually found at the apex of central and marginal corollas.

(h) Short, acute papillae or spicules (Font Quer 1973) (Fig. 10H) are another transitional form between a papilla and a hair. They are caused by the enlargement of one epidermal cell (but much shorter than in the long papillae) and are usually acute at the apex, with thick walls and grouped in tufts. They could be interpreted as shorter forms of the long papillae but, although coexisting with them, the short papillae appear to be independent entities with limited growth. Transitional forms between long and short papillae were not seen. These papillae are usually found at the apex of both the ray and disc corollas.

(i) Short, rounded papillae (Fig. 10I) fit the definition of the term "papillae" according to Font Quer (1973) since they are the enlargement of one epidermal cell, short and with the apex rounded; the walls may be thin or thick. They are abundant on the outer and inner side of lobes of the disc corollas, and they are also common on the limb apex of the ray corollas.

Cypselae. The cypselae of ray and disc florets are morphologically similar. These are cylindrical, ellipsoid, or obconic, generally with a conspicuous carpopodium at the base (Figs. 18E, 27E). The apex of the cypsela is widened in the pappus insertion area. Cypselae are slightly to strongly 8–10-costate and sericeous.

Some cypsela features, such as the type of hairs and crystals, are very important from a taxonomic point of view, as they help to distinguish *Liabum* from other genera of the tribe. Twin hairs typically cover the cypselae of the species of *Liabum*. The analysis of many specimens of *Liabum* shows the absence of glandular hairs on the cypsela of *Liabum* and that this thus constitutes a good character to distinguish *Liabum* from related genera. It is true that glandular hairs may be sparsely found, one or two hairs per cypsela, in a few specimens of some species such as *L. umbellatum* and *L. wurdackii*, but this does not alter the utility of the character. Despite these exceptions, it can be considered that cypselae of all the species of *Ferreyranthus*, *Oligactis*, and *Sampera* have abundant glandular hairs on the cypsela. *Liabum ferreyri* and *L. sandemanii* also have abundant glandular hairs on the cypsela similar to those of *Oligactis* and *Sampera*, and have been excluded in this work from *Liabum* (see Excluded Names). The cypsela hairs of *Ferreyranthus* are

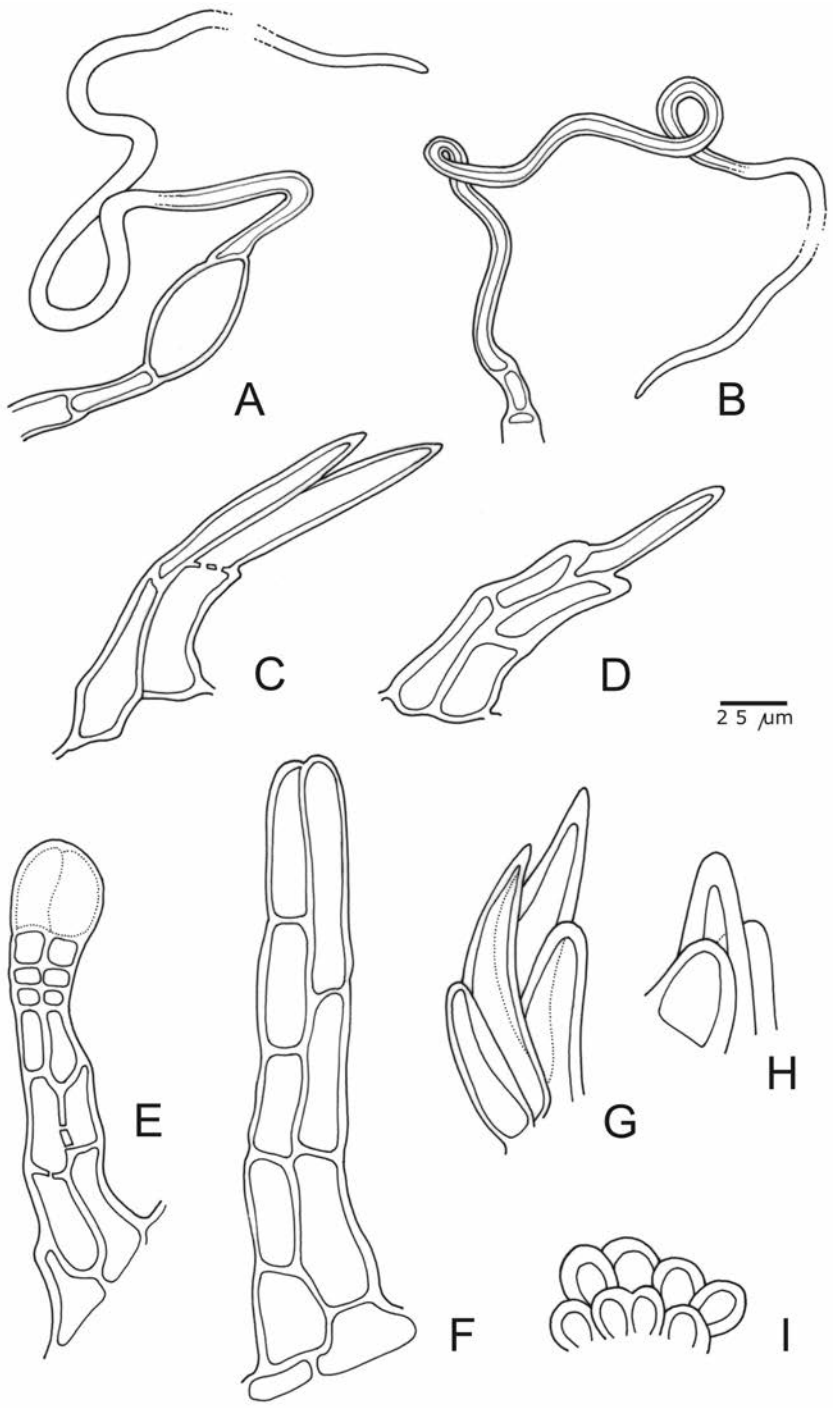

FIG. 10. Corolla hairs. A. Bulbiferous flagellate hair (*L. asclepiadeum*, *Hammel et al. 6875*, F). B. Aseptate-flagellate hair (*L. asclepiadeum*, *Hammel et al. 6875*, F). C. Typical twin hair (*L. saloyense*, *Jaramillo & Zak 7903*, MO). D. Atypical twin hair (*L. igniarium*, *Funk 11458*, US). E. Simple biseriate glandular hair, with head (*L. steinbachii*, *Steinbach 8152*, MO). F. Simple biseriate glandular hair, without head (*L. saloyense*, *Jaramillo & Zak 7903*, MO). G. Long papillae (*L. umbellatum*, *Crosby et al. 535*, F). H. Short, acute papillae (*L. vargasii*, *Vargas 10182*, US). I. Short, rounded papillae, with thick walls (*L. solidagineum*, *Cook & Gilbert 895*, US).

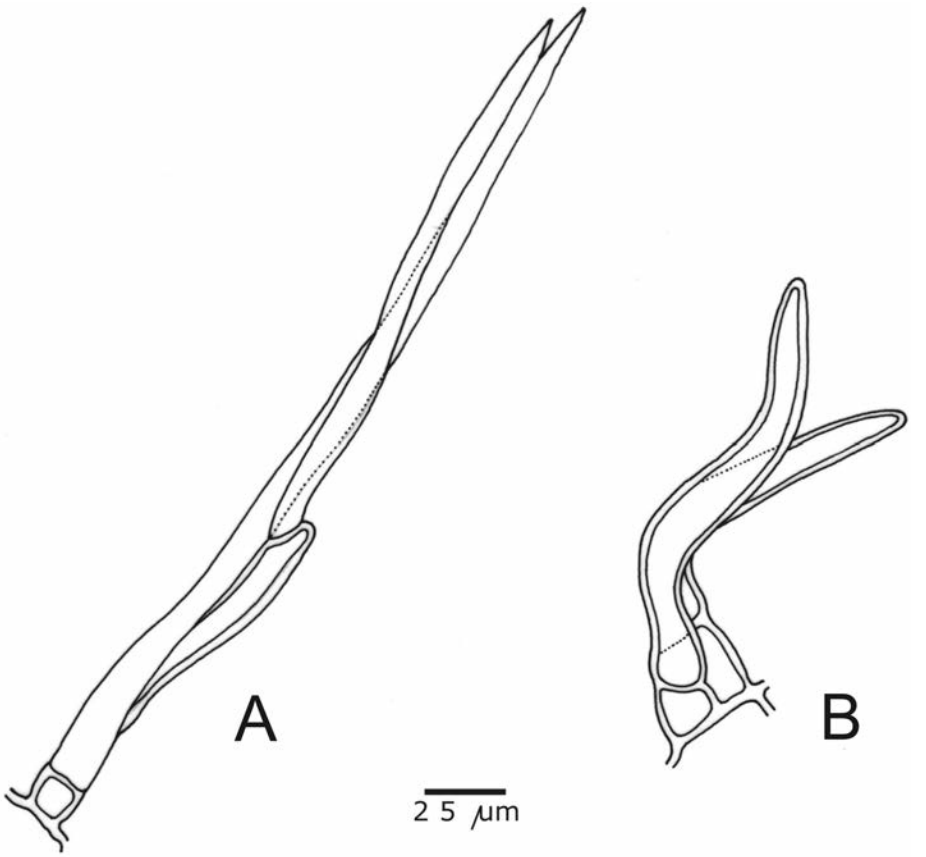

FIG. 11. Cypsela twin hairs. A. Without diverging tips. B. With diverging tips. (Based on *L. melastomoides*, *Pennell 5854*, US.)

morphologically different: the glandular head of the hairs is conspicuously broader (Dillon and Sagástegui Alva 1994; our own observations) and similar to those of *Cacosmia* (Nordenstam 1977b; our own observations).

The cypsela hairs in *Liabum* are:

(a) Typical twin hairs or "Zwillinghaare" (Hess 1938) (Fig. 11A, B) similar to those described for the corollas. They usually have the hair cells completely united with each other on their longitudinal walls or sometimes the cells are apically diverging, equal in length or one cell shorter, sometimes septate; this variation may be found in the fruits of a single individual. This type of hair is common in all species of *Liabum*. Cypselae with this type of hair are sometimes described as "setuliferous," "setiferous," or "setulose" in the literature.

(b) Simple biseriate glandular hairs with a head are similar to the hairs covering the vegetative organs and corollas (cf. Figs. 5D, 10E).They are very occasionally found in a few specimens of some species such as *L. umbellatum* and *L. wurdackii*.

The cypselae of *Liabum* characteristically have one crystal inside each cell of the pericarp. The crystals appear to be made of calcium oxalate (Nordenstam 1977a). Crystals occur in several distinct forms, namely quadrate (Nordenstam 1977b), short and quadrate

(Fig. 9E) to somewhat longer and rectangular (Fig. 9F) with either acute or obtuse extremes, and occasionally they are narrow and somewhat acicular. The presence of similar cypselar crystals is shared, for example, with *Dillandia* (Funk & Robinson 2001), *Inkaliabum* (our observations), *Oligactis* (our observations), and *Sampera* (our observations). Robinson (1983) proposed that these crystals were present in the common ancestral type of all existing Liabeae and then were lost in most members of the tribe. In this way, the crystals in *Liabum* and the other genera are interpreted as either a reversion or a weak relic of the ancestral condition (Robinson 1983).

Pappus. *Liabum* usually has a basic type of biseriate capillary pappus but sometimes it can be somewhat paleate, consisting of an outer series of few, short (1–4 mm long), denticulate bristles. Occasionally this outer series is lacking. The inner series consists of numerous, denticulate, longer (4–12 mm long) bristles, widened or not at the apex. The pappus is yellow, yellowish-white, or yellowish-orange, and generally the color varies within a species.

Pollen. The pollen of *Liabum* (see Appendix) is tricolporate and spheroidal to prolate, varying in size P = E = 25–35 μm. The colpi are long and the endoapertures lalongate. The exine is echinate and the tectum perforate. The spines are unevenly distributed in groups, with confluent bases (Fig. 7E, F).

Stix (1960) performed the initial studies of pollen in *Liabum* sensu lato, and recognized three palynological types in the tribe Liabeae: the andromachioides-type, the ovatum-type, and the umbellata-type. According to Stix (1960), the umbellata-type, which included *Liabum solidagineum*, *L. umbellatum*, and one species of *Munnozia*, has small columellae under each spine and some basal columellae among spines.

On the other hand, Robinson and Marticorena (1986) found that the pollen grains of the species of *Liabum* have small size, spines unevenly distributed in small groups on the pollen surface, shorter stouter tips of the spines, and ecaveate exine (i.e., without a cavea or space between exine layers above the foot layer).

Our observations on pollen size and distribution of spines on the pollen surface agree with these previous analyses. We have not studied the internal structure of the pollen grains.

GENERIC RELATIONSHIPS

Cassini (1819, 1830) proposed a close relationship among *Liabum*, *Munnozia, Oligactis*, and *Cacosmia*. Candolle (1836) associated *Liabum* with *Andromachia* (under which *Oligactis* was a section), *Alibum* Less. (now a synonym of *Munnozia*), *Cacosmia*, and two genera that now belong to the tribe Astereae.

Other genera that have been associated with *Liabum* are *Sinclairia* (Hooker & Arnott 1841), *Paranephelius* (Poeppig 1843), *Microliabum* (as *Liabellum* Cabrera non Rydb.; Cabrera 1954), *Chionopappus* Benth. (Blake 1935; Cabrera 1954), and *Philoglossa* Benth. (Sandwith 1956; Stuessy 1973; Robinson & Cuatrecasas 1973).

On the basis of morphology, Robinson and Brettell (1974) associated *Liabum* with *Sinclairia* and *Oligactis* s.l. (including *Sampera*) in generic keys. Three years later, Nordenstam (1977a) included the genus *Zycona* Kuntze as a synonym of *Liabum*. *Zycona* is

now considered to be a synonym of *Schistocarpha* Less. in the tribe Heliantheae (Rydberg 1927; Robinson 1979).

Robinson (1983) proposed the first evolutionary scheme among the genera of Liabeae. According to him, *Liabum* and *Oligactis* s.l. are two distinct but closely related genera of subtribe Liabinae linked by the occurrence of quadrangular crystals in the cypsela wall and the usually long style branches of the disc florets. Both genera also share the lack of latex (a feature shared also with *Ferreyranthus*) and the pale yellow anthers with papillose tails. *Liabum* and *Oligactis* s.l. also share pollen grains of 25–35 μm in diameter (the smallest in the tribe), ecaveate exine with thick and numerous columellae under each spine, and pollen spines with a compact tip (Robinson 1983; Robinson & Marticorena 1986; Dillon et al. 2009). According to Robinson (1983), *Liabum* is distinguished from *Oligactis* s.l. by its generally non-scandent habit, tripliveined leaves, umbelliform inflorescences, and cypselae covered exclusively by twin hairs.

Morphology-based cladistic analyses (Funk 1985; Bremer 1994; Funk et al. 1996) supported the *Liabum*-*Oligactis* s.l. relationship, and in most of these studies, the generic pair was sister to *Ferreyranthus*. In a molecular phylogenetic study of some genera of Liabeae (Gutiérrez et al. 2007), using sequences of the nuclear internal transcribed spacer (ITS) 1 and 2 and the 5.8S gene, *Liabum* was sister to *Dillandia*. More recent molecular studies with both ITS and plastid DNA sequences (*matK*, *ndhF*, and *trnL-trnF*) (Dillon et al. 2009; Funk et al. 2012) placed five genera in subtribe Liabinae: *Dillandia*, *Ferreyranthus*, *Liabum*, *Oligactis*, and *Sampera*. In these phylogenies, *Liabum* was monophyletic (13 sampled species) and sister to *Sampera*, both genera were then sister to the pair *Oligactis*-*Dillandia*, and the genus *Ferreyranthus* was sister to the whole group. In these publications, the five genera were characterized by the lack of latex, with *Liabum* being the only genus with tripliveined leaves; the other genera are pinnately veined. *Ferreyranthus* (eight species) is an Andean genus of subshrubs to small trees that ranges from Ecuador to southern Peru, at 1300–3000 m in elevation (Dillon & Sagástegui Alva 1994; Dillon et al. 2009; Gutiérrez 2010; Funk et al. 2012). It differs from *Liabum* by the sheathing petiole bases, the cypsela bearing glandular hairs with short foot and big terminal cells, and prismatic and elongate cypsela crystals. *Dillandia* (three species) consists of small herbs with pseudo-dichasial cymes and ranges from Colombia to northern Peru (Funk & Robinson 2001; Gutiérrez 2010). While it differs from *Liabum* in leaf venation, it shares the occurrence of bullate leaves, inflorescences of 1–7 capitula, and cypselae with only twin hairs and quadrate crystals. *Oligactis* (five species) is confined to cloud forests from western Venezuela to Colombia; one species reaches the forests of Panama and Costa Rica (Gutiérrez 2008; Gutiérrez 2010). It is a genus distinctive by its scandent habit with slender stems, capitula grouped in axillary or terminal inflorescences, few florets per capitulum, papillose apical appendages of the anthers, and glandular cypselae with quadrate crystals. *Sampera* (eight species) consists of scrambling shrubs with terminal inflorescences, 15–55 florets per capitulum, smooth apical appendages of the anthers, and cypselae with twin hairs, glandular hairs, and quadrate crystals. It ranges from Colombia to northern Peru with the major concentration of species in Ecuador (Dillon et al. 2009; Funk & Robinson 2009; Gutiérrez 2010; Funk et al. 2012).

The new monotypic genus *Inkaliabum* from Peru (Gutiérrez 2010) has the long style branches, the pinnate leaf venation, and the absence of latex that place the genus in subtribe Liabinae, according to the most recent circumscription of this subtribe (Funk et al. 2012). *Inkaliabum* is morphologically similar to *Liabum*, *Oligactis*, and *Sampera* but can be easily differentiated from them by the combination of slender scandent habit, pinnately

veined leaves, inflorescences with few capitula, ca. 200 linear phyllaries, long style branches, and eglandular cypselae (Gutiérrez 2010).

LIABUM IN THE CARIBBEAN

Liabum diversity in the Caribbean has been difficult to assess, since most characters are variable, and morphological gaps among described species are not very evident. Schultz Bipontinus (1863) made the first attempt to understand the diversity of *Liabum* in the Caribbean and differentiated species on the basis of leaf blade shape and the pubescence of the adaxial leaf surface. Urban (1931) also noted this morphological diversity, as shown, for example, in his description of *L. subacaule*, with leaves ranging from glabrous to adaxially densely pubescent. The main characters employed by other authors (e.g., Liogier 1964; Liogier 1996) to recognize species were: leaf blade length and shape, cutting of the leaf margin, leaf adaxial surface pubescence, petiole length, involucre size, shape and pubescence of the phyllaries, type of inflorescence, ray floret limb length and width, and pappus length.

Depending upon the taxonomic criteria emphasized, the number of species recognized from this region has therefore ranged widely (Table 4). For example, Grisebach (1864), Urban (1921), and Adams (1972) recognized a highly variable *Liabum umbellatum*, inhabiting Cuba, Jamaica, and Hispaniola, while Robinson (1983) reported 11 species of *Liabum* from these islands. Also, many floristic treatments did not include all three islands, and the keys to species allowed recognition of taxa on some of the islands but not on the others. All of these treatments were based on small numbers of specimens, the largest being 24 (Urban 1931). In addition, we recently demonstrated in a detailed morphological study that *L. oblanceolatum* from Hispaniola actually belongs to the genus *Chaptalia* Vent. (Mutisieae) (Gutiérrez & Katinas 2006).

The most recent molecular phylogenies including Liabeae (Dillon et al. 2009; Funk et al. 2012) have supported recognition of all Caribbean taxa of *Liabum* as a monophyletic group but did not provide detail about relationships among the Caribbean populations sampled. Therefore, we conducted a principal component analysis (PCA) to examine morphometric variation in vegetative and reproductive traits (see Materials and Methods) that have been used in the past to distinguish different Caribbean species. Statistical analyses have proven to be useful in recognition of morphologically infraspecific close taxa or species (e.g., Martínez-Azorín et al. 2007; Robyn et al. 2008; Sun et al. 2008; Grossi et al. 2011).

The PCA revealed that the first principal component accounts for 52.27% of total variation and the two first principal components account for 66.3%. Table 3 summarizes the information of these two first principal components and the loadings of each variable measured. The plots of the principal components show that the variation of the Caribbean species of *Liabum* is included within the intraspecific variation of *L. umbellatum* (Fig. 12).

The analysis showed that morphological trait variation that has been used to distinguish the Caribbean species of *Liabum* is continuous and does not allow the recognition of separate taxa. Thus, we consider here a single, highly variable species, *L. umbellatum*. These results partially or totally agree with Urban (1921), Moore (1936), Adams (1972), and Turner (1996) (see Table 4). In this way, *L. umbellatum* becomes the only species of the genus *Liabum* distributed in Cuba, Hispaniola, and Jamaica.

TABLE 4. Caribbean species of *Liabum* on each island, as treated chronologically by different authors. The number of species and the number of specimens cited in each treatment is indicated. (–) species not present, (*) species not treated, and (=) synonym.

SYSTEMATICS/ ISLAND	URBAN (1921)	RYDBERG (1927)	URBAN (1929, 1931)	MOORE (1936)	MOSCOSO (1943)	LIOGIER (1964)	ADAMS (1972)	ROBINSON (1983)	LIOGIER (1996)	TURNER (1996)	GUTIÉRREZ & KATINAS (2006; THIS WORK)
Cuba	*L. umbellatum*	*L. umbellatum*	*	*L. umbellatum*	*	*L. umbellatum*	*L. umbellatum*	–	*	*	*L. umbellatum*
		L. crispum	*	*	*	*L. crispum*	*	*L. crispum*	*	*	= *L. umbellatum*
		L. cubense	*	*	*	*L. cubense*	*	*L. cubense*	*	*	= *L. umbellatum*
		L. wrightii	*	*	*	*L. wrightii*	*	*L. wrightii*	*	*	= *L. umbellatum*
			L. longipes	*	*	= *L. wrightii*	*	= *L. wrightii*	*	*	= *L. umbellatum*
Jamaica	*L. umbellatum*	*L. umbellatum*	*	*L. umbellatum*	*	*L. umbellatum*	*L. umbellatum*	*L. umbellatum*	*	*	*L. umbellatum*
Hispaniola	*L. umbellatum*	*L. umbellatum*	– (confused with *L. selleanum* and *L. subacaule*)	*L. umbellatum*	*L. umbellatum* (but some specimens confused with *L. selleanum* and *L. subacaule*)	*L. umbellatum*	*L. umbellatum*	–	– (confused with *L. selleanum* and *L. subacaule*)	–	*L. umbellatum*
		L. crispum	– (confused with *L. barahonense*)	*	– (confused with *L. barahonense*)	*L. crispum*	*	–	*	–	= *L. umbellatum*
		L. cubense	– (confused with *L. poiteaui*)	*	– (confused with *L. poiteaui*)	*L. cubense*	*	–	– (confused with *L. poiteaui*)	–	= *L. umbellatum*
		L. subacaule	*L. subacaule*	*	*L. subacaule*	*	*	*L. subacaule*	*L. subacaule*	= *L. poiteaui*	= *L. umbellatum*
		L. domingense	= *L. subacaule*	*	= *L. subacaule*	*	*	= *L. subacaule*	= *L. subacaule*	= *L. poiteaui*	= *L. umbellatum*
			L. barahonense	*	*L. barahonense*	*	*	*L. barahonense*	*L. barahonense*	= *L. poiteaui*	= *L. umbellatum*
			L. oblanceolatum	*	*L. oblanceolatum*	*	*	*L. oblanceolatum*	*L. oblanceolatum*	= *L. poiteaui*	= *Chaptalia angustata*
			L. ovatifolium	*	*L. ovatifolium*	*	*	*L. ovatifolium*	*L. ovatifolium*	= *L. poiteaui*	= *L. umbellatum*
			L. poiteaui	*	*L. poiteaui*	*	*	*L. poiteaui*	*L. poiteaui*	*L. poiteaui*	= *L. umbellatum*
			L. polycephalum	*	*L. polycephalum*	*	*	*L. polycephalum*	*L. polycephalum*	= *L. poiteaui*	= *L. umbellatum*
			L. selleanum	*	*L. selleanum*	*	*	*L. selleanum*	*L. selleanum*	= *L. poiteaui*	= *L. umbellatum*
Number of species	1	6	7	1	8	4	1	11	7	1	1
Number of cited specimens	14	2	24	12	0	0	4	0	14	5	105

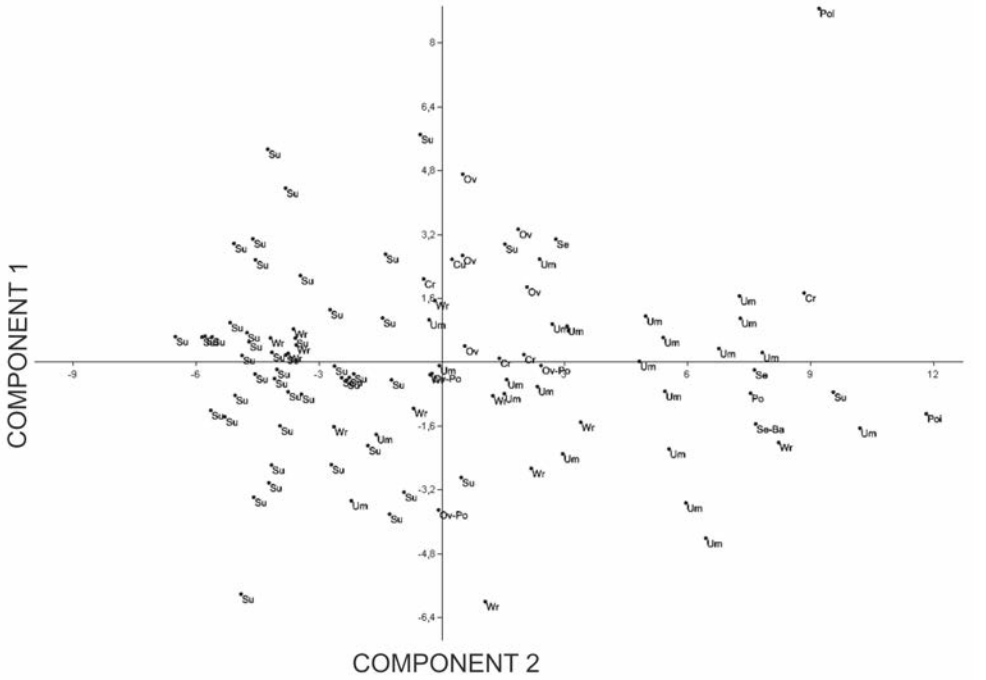

FIG. 12. Principal component analysis (PCA) from correlation matrix of quantitative characters. Plot of principal component 1 versus principal component 2. See TABLE 2 for acronyms.

LIABUM SPECIES GROUPS

Two *Liabum* species groups are recognized in this work on the basis of morphological characters: type of capitulum, ray floret limb shape, number of teeth at the apex of ray floret corollas, and number of limb veins of the ray floret corolla. In general, these groups agree with those already recognized in much earlier taxonomic studies (i.e., Kunth 1818, Lessing 1831, Candolle 1836, 1838). With two exceptions, this also agrees with monophyletic groups established in the most recent phylogenetic studies based on molecular markers (Dillon et al. 2009; Funk et al. 2012).

The Andromachia Group includes 17 species: *Liabum barclayae, L. dillonii* D. G. Gut. & Katinas, *L. floribundum*, *L. grandiflorum*, *L. igniarium*, *L. kingii*, *L. macbridei* H. Rob., *L. melastomoides*, *L. nigropilosum* Hieron., *L. robinsonii*, *L. saloyense*, *L. saundersii* H. Rob., *L. solidagineum*, *L. steinbachii*, *L. stipulatum* Rusby, *L. vargasii*, and *L. wurdackii.* This group is centered in the Andes, from Venezuela to Bolivia. Members of the Andromachia Group are herbs, subshrubs, or shrubs (rarely small trees), with radiate capitula, and ray florets with elliptic or obovate corolla limbs that are tridentate at the apex and have four veins. According to Dillon et al. (2009) and Funk et al. (2012), *L. kingii* and *L. vargasii* are closely related to *L. asclepiadeum* and *L. acuminatum*, respectively, based on molecular data.

The Liabum Group includes five species: *L. acuminatum*, *L. amplexicaule* Poepp., *L. asclepiadeum*, *L. eriocaulon*, and *L. umbellatum*. This group is widespread from southeastern Mexico to northwestern Argentina, with representatives in Brazil and in the Caribbean.

They are erect herbs with basally or apically rosulate leaves, shrubs, or subshrubs, with sub-radiate capitula, and ray florets with linear corolla limbs that are usually entire at the apex and have 1–3-veins. According to Dillon et al. (2009) and Funk et al. (2012), this group may be monophyletic but includes *L. kingii* and *L. vargasii*, despite their ray corollas, which are more like those of the Andromachia Group.

DISTRIBUTION AND HABITATS

Liabum, with 22 species recognized here, is the second largest genus of Liabeae after *Munnozia*, which has 47 species (Dillon et al. 2009; Funk et al. 2012; this work, p. 101). *Liabum* is the most widely distributed genus of the tribe and the only one with representatives in the West Indies and in Brazil (Fig. 13). The species of *Liabum* are distributed from southeastern Mexico through Central America to the Andes of South America, where they range from Venezuela to northwestern Argentina (Fig. 13A).

From a biogeographic point of view, *Liabum* is confined to the Neotropical region (Cabrera & Willink 1980). In South America, *Liabum* occupies areas associated with the Andean ranges with the Amazonian, Pacific, and Yungas provinces having the majority of the species, and the Venezuelan and Chacoan provinces having fewer (Fig. 13B). Farther north the genus is found in the Mesoamerican, Pacific, and Caribbean provinces (Fig. 13C).

Most species are centered in the Andean ranges of Bolivia (5 spp.), Colombia (8), Ecuador (11), and Peru (14), rarely reaching 4600 m (*L. solidagineum*). These species inhabit humid premontane forests, montane tropical forests, subtropical forests (rain or cloud), or dry transitional forests, the margins of rivers and streams, and disturbed environments. Usually they grow on clay, humus, and rocky soils, the latter sometimes derived from limestones. The West Indies are home to one species found in lowland and upland moist forests associated with limestone areas.

According to the biogeographic studies of Liabeae (Funk et al. 1996, 2012; Dillon et al. 2009), the tribe probably originated in the northern (from Venezuela and northwestern Colombia to northwestern Peru) and central (from northern to south-central Peru) areas of the Andes. According to Funk et al. (2012), *Liabum* migrated from its original area in the Central Andes to the north and the south, with introductions to Central America eventually reaching southern North America and the Greater Antilles (Cuba, Jamaica, and Hispaniola). Also, according to these authors, the presence of *Liabum* in southern North America and Central America probably resulted from gradual terrestrial range expansion, whereas the Caribbean species may be the result of long distance dispersal from the northern Andes.

Because of its Andean-centered distribution, it is very probable that the Andean orogeny may have played the most important role in the biogeographic history of the South American species of *Liabum*. The Huancabamba deflection (also known as the Huancabamba Depression or the North Peruvian Low) in northern Peru (Fig. 13A) and the recently established dispersal barrier between the Northern and Central Andes (the "Western Andean Portal") may be the biggest barriers (Funk et al. 1996, 2012; Antonelli et al. 2009). However, large intermontane valleys cannot be dismissed as additional possible barriers to dispersal (Young et al. 2007).

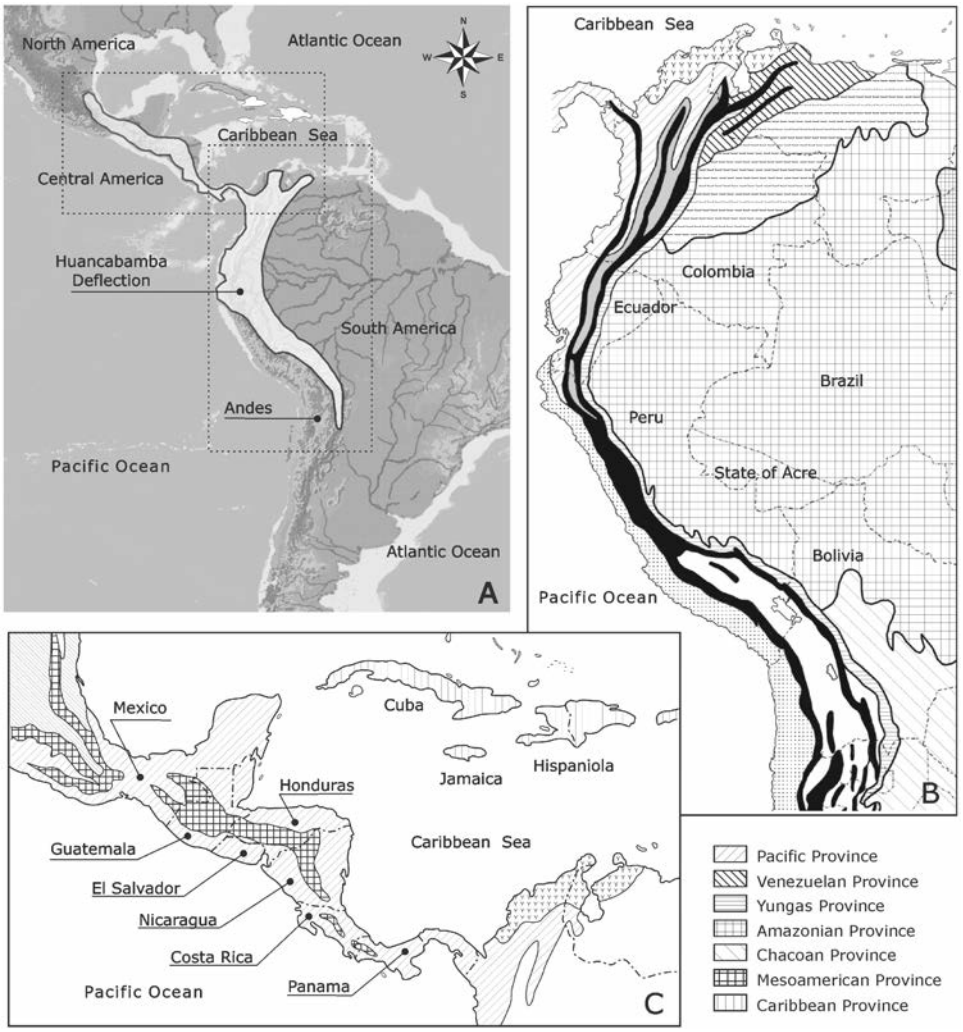

FIG. 13. Geographic distribution of the genus *Liabum* and biogeographic provinces. A. Geographic distribution of *Liabum* (in white). B. Biogeographic provinces of South America. C. Biogeographic provinces of Central America. Only biogeographic provinces mentioned in the text have been indicated. (Redrawn from Cabrera & Willink 1980.)

TAXONOMY

Liabum Adanson, Fam. Pl. (Adanson) 2: 131. 1763.—TYPE: *Liabum umbellatum* (Linnaeus) Schultz Bipontinus [=*Amellus umbellatus* Linnaeus, Syst. Nat., ed. 10: 1225. 1759].

Starkea Willdenow, Sp. Pl., ed. 4, 3(3): 2216. 1803. *Liabum* section *Starkea* (Willdenow) Candolle, Prodr. [A. P. de Candolle] 5: 97. 1836. *Liabum* subgenus *Starkea* (Willdenow) Schultz Bipontinus, J. Bot. 1: 237. 1863.—TYPE: *Starkea umbellata* (Linnaeus) Willdenow [=*Liabum umbellatum* (Linnaeus) Schultz Bipontinus].

Andromachia Humboldt & Bonpland, Pl. Aequinoct. [Humboldt & Bonpland] 2: 104. 1812 ["1809"]. *Liabum* section *Andromachia* (Humboldt & Bonpland) Lessing, Linnaea 6: 699. 1831. *Andromachia* section *Pleionactis* Candolle, Prodr. [A. P. de Candolle] 5: 95. 1836.—TYPE: *Andromachia igniaria* Humboldt & Bonpland [=*Liabum igniarium* (Humboldt & Bonpland) Lessing].

Allendea La Llave & Lexarza, Nov. Veg. Descr. [La Llave & Lexarza] 1: 10. 1824.—TYPE: *Allendea lanceolata* La Llave & Lexarza [=*Liabum asclepiadeum* Schultz Bipontinus].

Subshrubs, shrubs, or perennial caulescent (rarely acaulescent) herbs, rarely small trees or scandent shrubs, sparsely branched or unbranched, without latex; stems costate or not costate, terete or scarcely to strongly hexagonal in cross-section, densely white-tomentose, sometimes ochraceous-tomentose, rarely glabrous; nodes usually, but not always, with interpetiolar, chartaceous pseudostipules, these commonly fusing into a complete or partial leafy disc, with or without conspicuous auricles, auricles oriented toward the stem apex, glabrescent adaxially, densely white-tomentose abaxially. Leaves simple, opposite, usually scattered along the main stem and branches, in some herbaceous species either basally rosulate or clustered at the shoot apex; leaf blades chartaceous, sometimes coriaceous, ovate to elliptic, sometimes subtriangular or rarely obovate, apex acute, attenuate, or acuminate, base cuneate, rounded, truncate, or decurrent, sometimes cordate, margins mucronate-serrate or serrulate, planate, rarely revolute; venation acrodromous with a central midvein and two conspicuous lateral main veins, occasionally with additional conspicuous basal secondary veins (actinodromous), rarely with the lateral main veins inconspicuous and the leaf appearing to have pinnate venation (*L. umbellatum*); upper surface usually smooth, rarely bullate, glabrous or glabrescent, sometimes hirsute or strigose, sometimes mixed with arachnoid pubescence, abaxially densely white-tomentose, sometimes ochraceous-tomentose; petiolate, sometimes inconspicuously petiolate when blade decurrent, petiole wingless or winged, wings narrow or wide. Inflorescences terminal, umbelliform, corymbiform, or glomerulose cymes, few- or many-headed; capitula radiate or sub-radiate, heterogamous, sessile or pedunculate, peduncles tomentose. Involucre campanulate or sometimes hemispherical; phyllaries 50–150, (4–) 5–7 (–8)-seriate, imbricate, coriaceous, greenish or sometimes reddish toward the apex; outer series shorter, ovate, apex acute, arachnoid-pubescent or glabrous; inner series linear, apex attenuate and erect, rarely twisted, glabrous. Receptacle epaleate, fimbriate to chaffy, chaff laciniate surrounding depressions. Ray florets pistillate, fertile, without staminodia, (10–) 20–150; corolla yellow or orange, limb linear, elliptic or obovate to ovate, usually 4-veined with apex 3-dentate or 1–3-veined with apex entire or rarely 2-dentate, glabrous or pubescent; style shaft glabrous, without a nectary at the base; style branches long, filiform, rounded at the apex, curved to coiled, glabrous, rarely papillose at the apex. Disc florets bisexual, fertile, 15–90; corolla yellow, tubular, funnelform, deeply 5-lobed, tube usually gradually expanded into the throat (connate portion of the limb), rarely abruptly expanded (e.g., *L. saloyense*), glabrous or pubescent; stamens with thecae pale yellow, calcarate, short-caudate, tails digitate or papillose, apical appendage ovate to sub-triangular, smooth; filament smooth, anther collar with conspicuous thickenings; endothecial cells with polarized, radial and "U" thickenings; style shaft hispidulous distally, with a nectary at the base; style branches long, filiform, rounded at the apex, curved to coiled, externally hispidulous, the sweeping hairs extending down the style proximal to the bifurcation point a distance less than the length of the style branches. Cypselae cylindrical, ellipsoidal or obconical, brownish, with conspic-

uous basal carpopodia, slightly or strongly 8–10-costate, pubescent with twin hairs; walls with quadrate to short-rectangular, rarely somewhat acicular, crystals. Pappus biseriate, yellow, yellowish-white, or yellowish-orange; outer series of a few short scabrous capillary bristles, or absent; inner series of long, numerous, scabrous capillary bristles. Pollen tricolporate, spheroidal to prolate, P = E = 25–35 μm; colpi long, endoapertures lalongate; exine echinate, tectum perforate; spines unevenly distributed in groups, with confluent bases (Fig. 7E, F).

Liabum includes 22 species, these distributed from southeastern Mexico, Central America, and the West Indies to western South America from Venezuela south to northwestern Argentina, mainly in the Andes and but also in western Brazil.

Key to the Species of Liabum

1. Inflorescences scapose.
   2. Stems with pseudostipules; leaves ovate or less commonly subtriangular, scattered along the main stems and branches, rarely clustered at the stem apex; limb of ray corollas 3-dentate, 4-veined; Ecuador and Peru. 8. *L. grandiflorum*
   2. Stems without pseudostipules; leaves ovate, clustered at the apex of the stem or in a basal rosette; limb of ray corollas entire, 1–3-veined; Cuba, Jamaica, and Hispaniola. 20. *L. umbellatum*
1. Inflorescences not scapose, capitula arranged in umbelliform, corymbose, or glomerulose cymes.
   3. Petioles not winged or only winged in the upper part by short decurrence of the blades.
      4. Stems usually without pseudostipules at the nodes.
         5. Leaves with the two main lateral veins extending to the lamina apex; capitula sub-radiate; ray corollas linear. 1. *L. acuminatum*
         5. Leaves with the two main lateral veins extending at least to the midpoint of the lamina but not to the lamina apex; capitula radiate; ray corollas elliptic to obovate.
            6. Inflorescences of umbelliform or corymbiform cymes; capitula usually pedunculate, peduncles up to 5 mm long; leaf apex attenuate; leaf blade ovate or narrowly ovate. 17. *L. solidagineum*
            6. Inflorescences of glomerulose, or sometimes densely umbelliform or corymbiform cymes; capitula sessile or pedunculate, peduncles, if present, up to 2.5 mm long; leaf apex acute or attenuate; leaf blade ovate. 12. *L. melastomoides*
      4. Stems with pseudostipules at the nodes.
         7. Involucre hemispherical.
            8. Leaves abaxially primarily white-tomentose but with tomentum mixed with brownish hairs. 15. *L. saloyense*
            8. Leaves white-tomentose abaxially, without brownish hairs.
               9. Pseudostipules with auricles; disc corollas with lobes longer than the throat; ray and disc corollas lacking twin hairs (visible at 5× magnification or higher). 10. *L. kingii*
               9. Pseudostipules without auricles; disc corollas with lobes equal to or shorter than the throat; ray and disc corollas occasionally with twin hairs (visible at 5× magnification or higher). 5. *L. dillonii*
         7. Involucre campanulate.
            10. Leaves with the two main lateral veins extending to the lamina apex.
               11. Leaf blade elliptic, rarely ovate, 1.5–5 cm wide; leaf base always cuneate; involucre 7.5–9 mm long, 6.5–9 mm wide; ray floret corolla limb 3.5–4.5 mm long. 2. *L. amplexicaule*
               11. Leaf blade ovate, 5–8 cm wide; leaf base cuneate, rounded, or slightly cordate; involucre ca. 6.5 mm long, 5.5 mm wide; ray floret corolla limb 2–2.5 mm long. 6. *L. eriocaulon*
            10. Leaves with the two main lateral veins extending at least to the midpoint of the lamina but not to the lamina apex.
               12. Leaf blade subtriangular.
                  13. Leaves glabrous adaxially, white-tomentose without brownish hairs abaxially. 19. *L stipulatum*

13. Leaves hirsute adaxially, white-tomentose, the tomentum mixed with brownish hairs (rarely absent) on the veins abaxially. 7. *L. floribundum*
12. Leaf blade elliptic to ovate.
14. Perennial caulescent herbs; ray floret corollas 15.5–20 mm long. 18. *L. steinbachii*
14. Subshrubs, shrubs, or small trees; ray floret corollas up to 13 mm long.
15. Pseudostipules 1.5–3.5 cm long. 9. *L. igniarium*
15. Pseudostipules 0.5–1 cm long.
16. Capitulum peduncles 1–1.5 mm long.
17. Leaf blades chartaceous, base cuneate; inflorescence umbelliform, lax, with 20–50 capitula; involucre 6–7.5 mm long, 5.5–7 mm wide. *4. L. barclayae*
17. Leaf blades coriaceous, base rounded or truncate, occasionally cuneate; inflorescence umbelliform or corymbiform, dense, with more than 50 capitula; involucre 4.5–6 mm long, 3–5 mm wide. 17. *L. solidagineum*
16. Capitulum peduncles 5–20 mm long.
18. Ray florets 40–50 with corollas yellow or orange. 22. *L. wurdackii*
18. Ray florets 25–35 with corollas yellow.
19. Leaf blade broadly ovate, up to 12.5 cm wide; leaf apex acute; inflorescence umbelliform with 25–50 capitula; involucre 6.5–7 mm long; ray floret corolla limb 6.5–7.5 mm long. 11. *L. macbridei*
19. Leaf blade ovate, up to 7 cm wide; leaf apex attenuate; inflorescence umbelliform or corymbiform, with more than 50 capitula; involucre 5–6.5 mm long; ray floret corolla limb 5–5.5 mm long. 21. *L. vargasii*

3. Petioles winged at least from blade to petiole midpoint, often winged for the entire length; when reaching only to the midpoint of the petiole the wings ending in conspicuous lobes; petioles of upper leaves sometimes wingless.
20. Capitula sub-radiate; limb of ray corolla linear, 1–3-veined. 3. *L. asclepiadeum*
20. Capitula radiate; limb of ray corolla elliptic to obovate, 4-veined.
21. Leaf blades subtriangular; involucre 5–8 mm wide.
22. Petiole wings present from the blade to the midpoint of the petiole, not continuing to the pseudostipules, ending in conspicuous lobes. 14. *L. robinsonii*
22. Petioles winged to the base, the wings continuous with the pseudostipules. 13. *L. nigropilosum*
21. Leaf blades ovate; involucre 8–13 mm wide.
23. Leaf base rounded or cuneate; leaf surface glabrescent adaxially, white tomentose abaxially; ray floret corolla limb 5.5–6.5 mm long; disc floret corolla limb 4–5.5 mm long; corollas orange or orange-yellowish. 16. *L. saundersii*
23. Leaf base usually truncate or sub-cordate; leaf surface glabrous or hirsute adaxially, white tomentose usually with coarsely stiff hairs on the main veins abaxially; ray floret corolla limb 4.5–5.5 mm long; disc floret corolla limb 3.5–4 mm long; corollas yellow. 8. *L. grandiflorum*

1. Liabum acuminatum Rusby, Descr. S. Amer. Pl. 161–162. 1920.—Type: Bolivia. Department unknown: Machichoirisa, 3500 ft, 3 Aug 1902, *R. S. Williams 1605* (holotype: NY, digital image!; isotypes: GH! K, digital image! UC, digital image! US!).

Liabum falcatum Rusby, Descr. S. Amer. Pl. 161. 1920.—Type: Colombia. Magdalena: Agua Dulce, Santa Marta, 2200 ft, 20 Jan 1898/1899 (or Jan 1898/1901), *H. H. Smith 2012* (holotype: NY, digital image!; isotypes: BR, COL, E, F, digital images! GH! K, LL, MO, P, PH, digital images! US! WIS, digital image!).

Perennial caulescent erect herbs to subshrubs, 0.3–1 m tall; stems costate or not costate, terete or hexagonal in cross-section, densely and persistently white-tomentose;

pseudostipules absent. Leaves scattered along the main stem and branches; leaf blades 6–17 cm long, 1.5–5 cm wide, chartaceous, narrowly elliptic or elliptic, rarely ovate or obovate, apex acute or attenuate, base cuneate, margin mucronate-serrate, venation acrodromous, with the pair of lateral veins reaching the apex of the blade, surface smooth, green, glabrous adaxially, densely white-tomentose abaxially; petioles 1–3.5 cm long, not winged. Inflorescence not scapose, umbelliform, dense, rarely lax, with more than 50 capitula; capitula sub-radiate, pedunculate, peduncles up to 12 mm long, densely white-tomentose. Involucre 7–9 mm long, 4.5–7 mm wide, campanulate; phyllaries 85–90 in 5–7 series, 1.5–8.5 mm long, 0.5–0.7 mm wide, greenish, outermost phyllaries ovate, apex acute, pubescence arachnoid, innermost phyllaries linear, apex attenuate, glabrescent; receptacle with chaff 1.5–3 mm long. Ray florets 85–120; corolla 8–9.5 mm long, yellow, glabrous or slightly pubescent, tube 4.5–5.5 mm long, 0.15–0.2 mm wide, limb 3.5–4.0 mm long, 0.25–0.3 mm wide, linear, 1–3-veined, apex entire or slightly 2-dentate; style 6–11 mm long, branches 1.5–2.2 mm long. Disc florets ca. 15; corolla 7–8.5 mm long, tubular, tube 3.5–4.5 mm long, ca. 0.2 mm wide, gradually expanded into the limb, yellow, glabrescent, limb 3.5–4 mm long, 0.5–0.7 mm wide, lobes 1.4–1.8 mm long, ca. 0.5 mm wide, shorter than the throat, pubescent at the apex; anthers 1.8–2.5 mm long, apical appendage 0.45–0.5 mm long, tails 0.2 mm long; style 9–15 mm long, branches 1.7–2 mm long, papillae covering style branches and extending down the shaft of the style a distance less than the length of the branches. Cypselae 1.1–1.5 mm long, ca. 0.3 mm wide, cylindrical to ellipsoid. Pappus bristles pale yellow, white-yellowish, or yellowish-orange, scabrous; outer series up to 2 mm long, sometimes absent; inner series 6.5–9 mm long. Chromosome number unknown. Fig. 14A–E.

Phenology. Collected in flower from April to November.

Distribution (Fig. 14F). Northern Colombia, Ecuador, Peru, western Brazil, Bolivia, and northwestern Argentina (Gutiérrez 2003); premontane or montane tropical moist forests, ravines and sandbanks of river margins and river-beds, and disturbed areas; 260–1100 m. This species is here reported for Colombia for the first time.

Representative Specimens. **Argentina.** Salta: Dept. Orán, Aguas Blancas, finca El Arrazayal, Río Pescado, *Palací 738* (SI). **Bolivia.** Beni: valle del Río Quinquibey, camino a San Borja, *Beck 12711* (SI, US); Rurrenabaque, Río Tuichi, *Fournet 494* (US); Prov. Ballivián, Carmen Florida, Río Beni, 7 km from Rurrenabaque, 14°30′S, 67°30′W, *Williams 990* (NY).—La Paz: Carrasco, near Antahuacana, *Cárdenas 6076* (US); Prov. Alto Beni, Río Quiquibey, *Fournet 533* (US); Abel Iturralde, Parque Nacional Madidi, río Tuichi, arroyo Rudidi, 14°20′57″S, 67°48′01″W, *Fuentes et al. 5332* (CTES); Franz tamayo, Quendenque, cerca de la embocadura del río Quendenque, 14°58′47″S, 67°47′23″W, *Miranda et al. 13* (LP); Bopi river valley, *Rusby 332* (NY); Prov. Sud Yungas, Alto Beni, Concesión de San José de Popoy, *Vargas & Seidel 2021* (US).—Santa Cruz: Parque Nacional Amboró, cerro Amboró, Río Isama, *Lewis & Clark 37730* (MO, US); Parque Nacional Amboró, Río Saguayo, 17°40′S, 63°43′W, *Nee 38833* (F, MO, NY, SI); Prov. Ichilo, Parque Nacional Amboró, 9 km SW of Huaytu, Río Agua Blanca, W of Río Cheyo, 17°38′S, 63°40′W, *Nee 38888* (F, MO, NY, US); Prov. Florida, Río Sillar, canyon of Río Bermejo, 9 km to Santa Cruz, 8°10′S, 63°35′W, *Nee 38923* (F, MO, NY); Prov. Andrés Ibañez, La Miel, 17 km WSW de Santa Cruz, 17°48′S, 63°21′W, *Saldías 727* (NY); Parque Nacional Amboró, ca. 15 km SE Río Pitasama from the Río Surutú, 17°44′S, 63°40′W, *Solomon & Urcullo 14118* (MO, US); Prov. Lara, cuenca del Surutú, *Steinbach 2963* (GH, LIL, SI). **Brazil.** Acre: Mun. Tarahuacá, Rio Muru, 12 km above confluence with Rio Tarahuacá, *Prance et al. 7310* (MO, NY, US); São Francisco, *Ule 9906* (US). **Ecuador.** Napo: Cantón Archidona, carretera Hollín-Loreto, km 50, S del volcán Sumaco, 0°38′S, 77°27′W, *Cerón & Hurtado 6624* (MO, US). **Peru.** Amazonas: entre Imacita y Pongo de Rentena, *Ferreyra 19483* (US).—Cuzco: Prov. Cuzco, Distr. La Convención, Camisea, 11°52′S, 72°56′W, *Acevedo & Ramírez 9939* (US); Distr. Camanti, Maniri, 8 km W de Quincemil, Río Maniri hacia el Río Araza, 13°17′S, 70°48′W, *Timaná & Astete 636* (MO); Prov. Quispicanchi, Cadena, *Vargas 6224* (F); Prov. Paucartambo, Kosñipata-Socorro, *Vargas 10237* (US); without locality, *Vargas 16443* (US).—Huánuco: Prov. Leoncio Prado, Distr. Rupa Rupa, Jacintillo, Río Monzón, *Schunke 10334* (F, MO, NY).—Loreto: Previsto, *Woytkowski 7562* (MO).—Madre de Dios: Prov. Manu, Parque

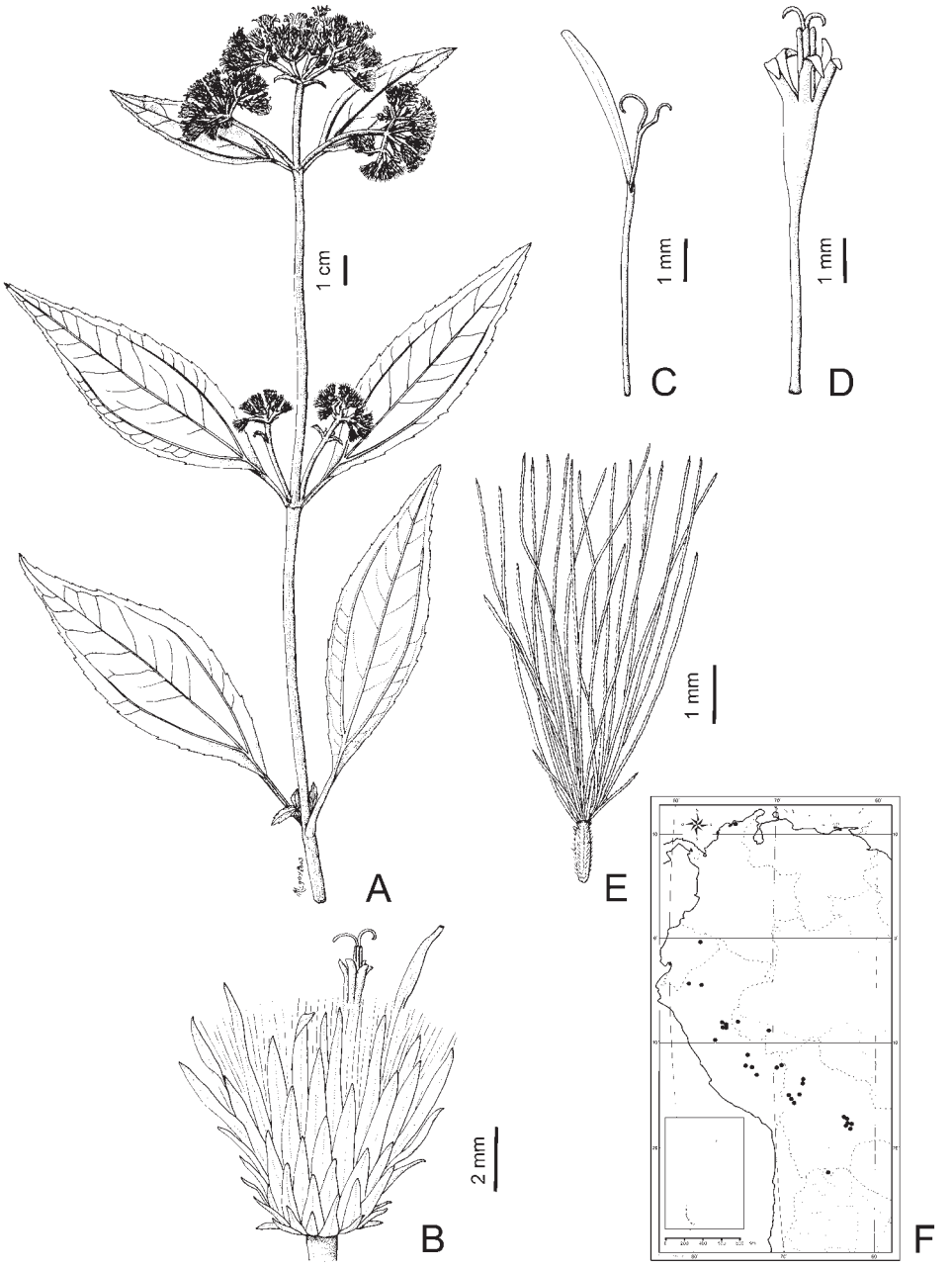

FIG. 14. *Liabum acuminatum* Rusby. A. Habit (branch). B. Capitulum (only some florets shown). C. Ray floret. D. Disc floret. E. Cypsela and pappus. F. Distribution. (Based on: A–B, *Beck 12711*, SI; C–E, *Nee 38833*, SI.)

Nacional del Manu, Río Manu, Cocha Cashu Station, *Foster & Terborgh 6650* (F); Manu Park, Cocha Cashu uplands, 11°45′S, 71°00′W, *Núñez 5920* (MO).—Puno: ad ripas fluviosum prope San Roman, *Lechler 2396* (NY).—Ucayali: road to Divisoria, km 59 from Tingo María to Pucallpa, *Allard 21342* (F, US); Yurac, between Divisoria and Pucallpa, *Allard 22167* (F); Prov. Coronel Portillo, Boquerón, *Ferreyra 16050* (MO); Boquerón, Río Yurac Yacu, *Seibert 2081* (F, MO, US).

Liabum acuminatum resembles *L. amplexicaule* and *L. eriocaulon* in its reproductive characters but differs by lacking pseudostipules. Occasionally, *L. eriocaulon* lacks pseudostipules, but the leaf blade of that species is ovate instead of elliptic as in *L. acuminatum*. Some specimens (e.g., *Prance et al. 7310*) differ in having leaves ovate and obovate on the same plant.

In its protologue, *L. falcatum* was differentiated from *L. acuminatum* by its long internodes, more or less falcate leaf blades, and capitula ca. 8 mm long. Later, Robinson (1976) differentiated *L. falcatum* from *L. acuminatum* and *L. amplexicaule* by the presence of hairs on the disc corolla in the former. However, these features are part of the infraspecific variation of *L. acuminatum*, and *L. falcatum* is proposed in this work as a synonym of *L. acuminatum*.

Colombia represents the northern limit of distribution of *L. acuminatum* and corresponds to the type locality of *L. falcatum*; we did not find other specimens of this species from Colombia other than the type.

H. H. Smith's Colombian plant collections present many typification problems. A single collection number may represent plants from two or more populations or may indicate collections taken from the same population but collected months apart (Ayers & Boufford 1988). As far as we can determine, all duplicates of *Smith 2012* seem to represent the same collection made on the same date, and all are thus considered types of the name *L. falcatum*.

2. Liabum amplexicaule Poeppig, Nov. Gen. Sp. Pl. (Poeppig & Endlicher) 3: 43. 1843.—Type: Peru. San Martín: Crescit in insulis arenosis fluminis Tocache Peruviae orientalis, Aug 1830, *Poeppig s.n. [D.2055]* (lectotype, here designated: W-28616, digital image!; isolectotype: W-28615 [Tocache, Huallaga, *Poeppig s.n.*], digital image!).

Liabum ulei Hieronymus in Ule, Verh. Bot. Vereins Prov. Brandenburg 48: 206–207. 8 Mar 1907 ["1906"].—Types: Peru. San Martín: Tarapoto, 320 m, Oct 1902, *Ule 6384* (holotype: B [destroyed], FM 18134!; lectotype, here designated: F, digital image!); Peru. Loreto: Pongo de Cainarachi, Sep 1902, *Ule 6384* (epitype, here designated: K, digital image!).

Perennial caulescent erect herbs to subshrubs, 0.4–2 m tall; stems costate or not costate, terete or hexagonal in cross-section, densely and persistently white-tomentose; pseudostipules 0.5–1.5 mm long, without auricles, green, glabrous adaxially, densely white-tomentose abaxially. Leaves scattered along the main stem and branches; leaf blades 6–19 cm long, 1.5–5 cm wide, chartaceous, narrowly elliptic or elliptic, rarely ovate, apex acute or attenuate, base cuneate, margin mucronate-serrate, venation acrodromous, with the pair of lateral veins usually reaching the apex of the blade, surface smooth, green glabrous adaxially, densely white-tomentose abaxially; petioles 1–3 cm long, not winged. Inflorescence not scapose, umbelliform, dense, rarely lax, with more than 50, occasionally as few as 12, capitula; capitula sub-radiate, pedunculate, peduncles up to 10 mm long, densely white-tomentose. Involucre 7.5–9 mm long, 6.5–9 mm wide, campanulate;

phyllaries 80–90 in 5–7 series, 1.5–8 mm long, 0.5–0.85 mm wide, greenish, outermost phyllaries ovate, apex acute, pubescence arachnoid, innermost phyllaries linear, apex attenuate, glabrescent; receptacle with chaff 1.5–3 mm long. Ray florets 85–110; corolla 8–10.5 mm long, yellow, glabrous or slightly pubescent, tube 4.5–6 mm long, 0.15–0.2 mm wide, limb 3.5–4.5 mm long, 0.25–0.4 mm wide, linear, 1–3-veined, apex entire or inconspicuously 2-dentate; style 7–7.2 mm long, branches 1–1.3 mm long. Disc florets 12–15; corolla 7–8 mm long, tubular; tube 3.5–4 mm long, ca. 0.2 mm wide, gradually expanded into the limb, yellow, glabrescent, limb 3.5–4 mm long, 0.5–0.7 mm wide, lobes 1.4–1.8 mm long, ca. 0.25 mm wide, shorter than the throat, pubescent at the apex; anthers 2–2.3 mm long, apical appendage 0.5–0.6 mm long, tails 0.2–0.3 mm long; style 8–10 mm long, branches 1.7–2 mm long, papillae covering style branches and extending down the shaft of the style a distance equal to the length of the branches. Cypselae 1.1–1.5 mm long, 0.3–0.4 mm wide, cylindrical to ellipsoid. Pappus bristles pale yellow, white-yellowish, yellowish-orange, scabrous; outer series 1–1.5 mm long, sometimes absent; inner series up to 7.5 mm long. Chromosome number: $n = 16–19$II (Strother & Panero 1994). Fig. 15A–E.

Phenology. Collected in flower from June to November.

Distribution (Fig. 15F). Southwestern Colombia, Ecuador, Peru, southwestern Brazil, and Bolivia; wet tropical forests, margins of rivers and sandbanks, and margins of roads in rocky and sandy soils; 200–1100 (–1500) m (one collection in Peru at 3720 m, *J. Infantes 3544a*, LIL). This species is here reported from Brazil for the first time.

Local Names. Botoncillo (*Schunke 12512*), ëzwëë ui mullka (*Montalvo 60*), is-la-huasca (*Schultes & Smith 2099*, Ingano), shia (*Ríos & Vivanco 396*, Quichua).

Representative Specimens. **Bolivia.** Beni: Prov. General Ballivián, Rurrenabaque, Río Beni, *Beck 18643* (US).—La Paz: Prov. B. Saavedra, Area Natural de Manejo Integrado de Apolobamba, Pauje Yuyo, 1.8 km NE de la comunidad, 15°02′19″S, 68°26′54″W, *Cayola et al. 1193* (CTES). **Brazil.** Acre: Mun. Assis Brasil, basin of the Río Acre (basin of Río Purus), 10°56′S, 69°29′W, *Daly et al. 9631* (US). **Colombia.** Putumayo: Mocoa, *Schultes & Smith 2099* (GH). **Ecuador.** Napo: Estación Biológica Jatun Sacha, Río Napo, 8 km E de Misahualli, 01°45′S, 77°36′W, *Cerón 1686* (MO); Río Napo, Río Huambuno, 3 km from Campana Cocha, 00°55′S, 77°25′W, *Neill et al. 7706* (MO); Isla San Rafael, Ahuano, 77°35′W, 01°06′S, *Ríos & Vivanco 396* (NY).—Zamora-Chinchipe: Cantón Nangaritza, Miazi, Río Nangaritza, 78°42′W, 04°16′S, *Palacios et al. 8596* (MO, US). **Peru.** Amazonas: Río Cenepa, quebrada Kachaig, vicinity of Huampami, ca. 5 km E of Chávez Valdivia, 78°30′W, 04°30′S, *Ancuash 1499* (US); Prov. Bagua, Río Marañón above Cascadas de Mayasi near Campamento Subteniente Montenegro, km 276–280 of Marañón road, *Wurdack 1819* (GH, LP, NY).—Huánuco: cerca de Tingo María, *Ferreyra 2265* (LIL, MO, US); entre Venenillo y Aucayacu, Río Huallaga, *Ferreyra 4358* (MO, US); Prov. Huánuco, Distr. Churubamba, hacienda Éxito, Río Ysabel, *Mexía 8134* (F, GH, MO, NY, US).—Junín: La Merced, *Macbride 5358* (F, GH, LP, US); Río Ene at Río Quipachiari, *Madison 10423-70* (US).—La Libertad: Prov. Huamachuco, Sartimbamba, 3720 m, *Infantes 3544a* (LIL).—Loreto: Pumayacu between Balsapuerto and Moyobamba, *Klug 3183* (F, GH, MO, NY, US).—Madre de Dios: Río Manu, Cocha Cashu station, *Foster 7030* (F); Parque Nacional del Manu, Río Manu, Cocha Cashu station, 71°25′W, 11°50′S, *Foster 9788* (F); Prov. Manu, Distr. Manu, Río Manu, playa 16 above the Boca, *Foster & Augspurger 3150* (MO, US).—Pasco: Prov. Oxapampa, Río Palcazu between Shiringamazú and Loma Linda, 75°11′W, 10°16′S, *Smith & Salick 8386* (F, US).—San Martín: Pongo de Cainarachi, Río Cainarachi, tributary of Río Huallaga, *Klug 2638* (F, GH, LP, MO, NY, US); Juan Jui, Alto Río Huallaga, *Klug 3844* (F, GH, MO, NY, US); km 46 of Tarapoto-Yurimaguas, Río Cainarache, 06°24′S, 76°18′W, *Knapp & Mallet 8188* (F, MO, US); Tocache, *Poeppig 164* (W); Prov. San Martín, Distr. Tarapoto, Tarapoto a Yurimaguas, km 10, *Rimachi 4793* (MO); Tarapoto-Jurimaguas, km 7, *Sagástegui 6868* (LP); Prov. Mariscal Cáceres, Distr. Tocache Nuevo, Santa Rosa de Mishollo, 4 km de Puerto Pizana, *Schunke 4881* (F, NY, US); Distr. Uchiza, Cachiyacu de Lepuna, *Schunke 7300* (MO, NY); Prov. Lamas, Distr. Alonso de Alvarado, San Juan de Pacaizapa, km 72, carretera Tarapoto-Moyobamba, *Schunke 9755* (MO, US); Distr. Tocache Nuevo, quebrada Cachiyacu de Huaquisha, *Schunke 12512* (F, LP, MO, NY, US); prope Tarapoto, *Spruce 4143* (GH, NY); Alto Río Huallaga, Tarapoto, *Williams 6733* (F).—Ucayali: Boquerón, 92 km from Tingo María to Pucallpa, *Allard 21743* (US); Prov. Coronel Portillo, Río San Alejandro, *Montalvo 60* (US); Panguana, 74°56′W, 09°37′S, Río Yuyapichis, affluent to Río Pachitea, *Seidenschwarz 167/1* (F); lower Aguaytia,

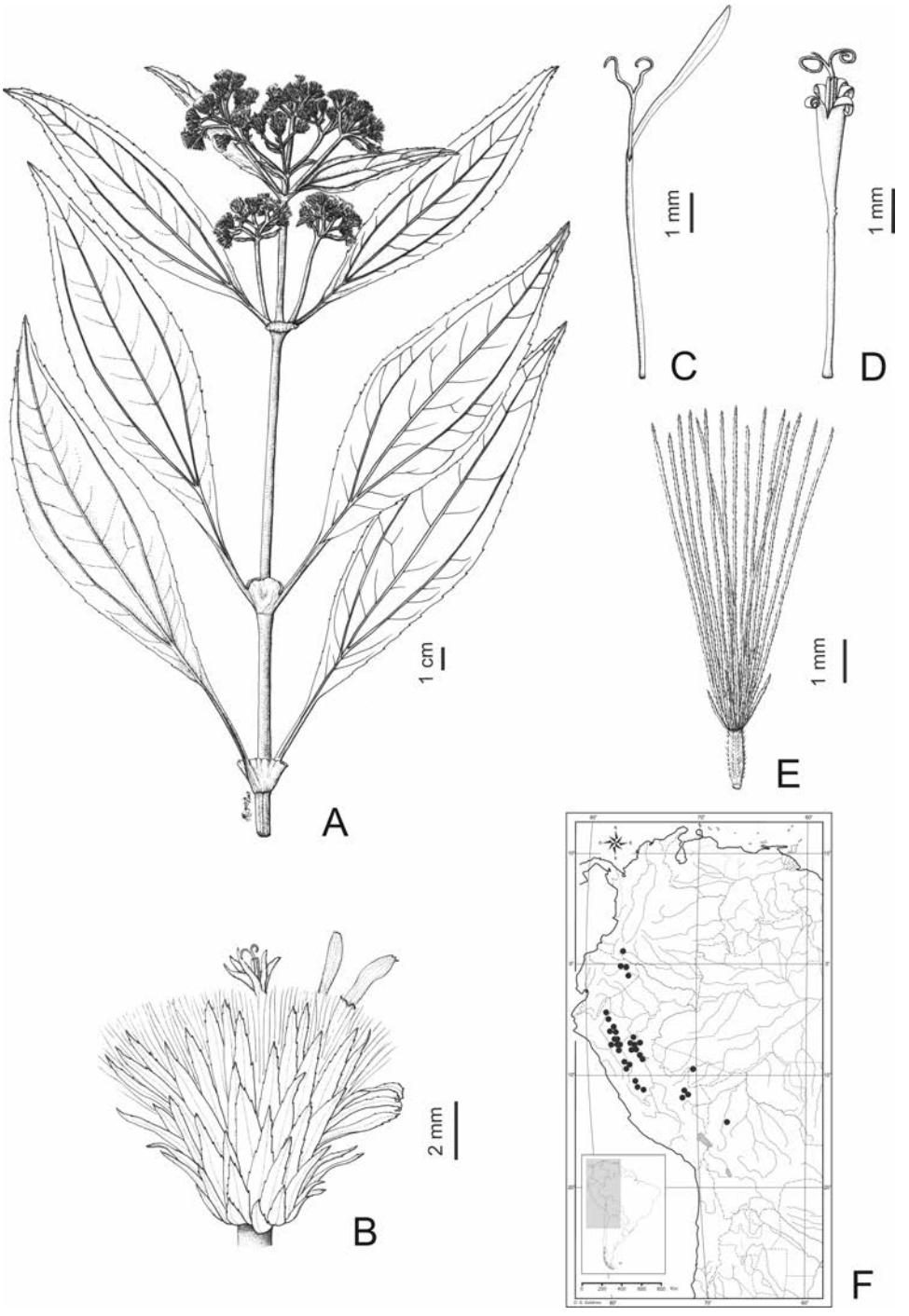

FIG. 15. *Liabum amplexicaule* Poepp. A Habit (branch). B. Capitulum (only some florets shown). C. Ray floret. D. Disc floret. E. Cypsela and pappus. F. Distribution. (Based on: A–B, *Schunke 4881*, NY; C–E, *Schunke 9755*, MO.)

Tessmann 3154 (NY); Prov. Padre Abad, on an island in Río Chino near Boquerón, *Woytkowski et al. 34392* (F, LIL, MO, US).

Liabum amplexicaule can be distinguished from *L. acuminatum* by the presence of pseudostipules at the nodes and from *L. eriocaulon* by the elliptic leaves, smaller involucres, and shorter limbs of the ray floret corollas.

Two specimens deposited in W correspond with the types of *Liabum amplexicaule*. Both specimens have the same locality, collection date, and collector name but differ in the collector number given by Poeppig: *Poeppig 164* and *Poeppig 3055*. Therefore, we have selected as lectotype the specimen *Poeppig 3055* kept at W, which fits very well with the original diagnosis of the species.

The holotype of *L. ulei* kept at B was destroyed during WWII. Therefore, we selected as lectotype the isotype deposited in F since no other original material was found. This specimen at F, however, consisting of a fragment, does not allow a clear recognition of this species. For purposes of the precise application of the name of *L. ulei*, an epitype is also designated here. This specimen, kept at K, fits accurately with the diagnosis of *L. ulei* and was collected by Ule who labeled this specimen with the same collector number.

A magical use was attributed to this species to blow up or scare away the rain ("para soplar la lluvia") (*Montalvo 60*). An infusion of the plants is also reported to be employed against menstrual pain (*Ríos & Vivanco 396*).

3. Liabum asclepiadeum Schultz Bipontinus, Linnaea 20: 521. 1847.—TYPE: VENEZUELA. Distrito Federal: Caracas, ad rivulum Anauco locis scopulosis, umbrosis, Jan/Feb, *Moritz 300* (lectotype, here designated: P-285908, digital image!; isolectotypes: F, P-285909, digital images!).

Allendea lanceolata La Llave & Lexarza, Nov. Veg. Descr. [La Llave & Lexarza] 1: 10. 1824, non *Liabum lanceolatum* (Ruiz & Pavon) Schultz Bipontinus, 1853.—TYPE: MEXICO. Veracruz: "… non longe à S. Jose [San José] del Corral" [now General Juan José Baz], *de La Llave s.n.* (holotype: G, digital image!).

Liabum caliense Hieronymus, Bot. Jahrb. Syst. 28: 623–624. 1901.—TYPE: COLOMBIA. Valle del Cauca: crescit in silvis apertis Andi[n]um occidentalium in Prov. Cali prope San Antonio de Cali, 1500–2000 m, *Lehmann 7974* (holotype: B [destroyed], photo FM 18093!; lectotype here designated: K, digital image!, fragment US, digital image!).

Liabum bourgeaui Hieronymus in Ule, Verh. Bot. Vereins Prov. Brandenburg 48: 208. 1907.—TYPE: MEXICO. Veracruz: Valleé de Cordova [Córdoba], Mar 1865–1866, *Bourgeau 2205* (syntype: B [destroyed], photo FM 18092!; lectotype here designated: G, digital image!; isolectotypes: BM, digital image! F! GH! L, digital image! MSC fragment, digital image! NY, digital image! P, S, digital image! US, digital image!).

Liabum subumbellatum Rusby, Descr. S. Amer. Pl. 159. 1920.—TYPE: COLOMBIA. Cauca: on the Río Palace [Palací], highlands of Popayán, 1500–1600 m, Nov 1886, *Lehmann 1146* (holotype: NY, digital image!; isotype: F, digital image!).

Perennial caulescent erect herbs to subshrubs, 0.25–2.5 m tall; stems costate or not costate, terete or hexagonal in cross-section, densely and persistently white-tomentose; pseudostipules present, or occasionally absent from the distal nodes, 0.2–1 mm long, without auricles, green, glabrous adaxially, densely white-tomentose abaxially. Leaves scat-

tered along the main stem and branches; leaf blades 8–20 cm long, 4–15 cm wide, chartaceous, elliptic or broadly elliptic, sometimes ovate or broadly ovate, rarely narrowly ovate, apex acute or attenuate, base cuneate, margin mucronate-serrate, venation acrodromous, with the pair of lateral veins reaching the apex of the blade, surface smooth, green, glabrous adaxially, sometimes with persistent arachnoid pubescence, densely white-tomentose abaxially; petioles up to 5 cm long, winged, wings up to 0.5 cm wide. Inflorescence not scapose, umbelliform, dense, with more than 50 capitula; capitula sub-radiate, sessile or pedunculate, peduncles, if present, up to 10 mm long, densely white-tomentose. Involucre 7.5–9 mm long, 5.5–7 mm wide, campanulate; phyllaries 80–90 in 5–7 series, 1.5–7.5 mm long, 0.4–0.65 mm wide, greenish, sometimes reddish toward the apex, outermost phyllaries ovate, apex acute, pubescence arachnoid, innermost phyllaries linear, apex attenuate, glabrescent; receptacle with chaff 1–2.5 mm long. Ray florets 90–110; corolla 7.5–8.5 mm long, yellow, glabrous or slightly pubescent, tube 4–4.5 mm long, ca. 0.2 mm wide, limb 3.5–4 mm long, 0.3–0.4 mm wide, linear, 1–3-veined, apex entire or slightly dentate; style 5–7.5 mm long, branches 1.2–2.2 mm long. Disc florets 35–55; corolla 6.2–7.5 mm long, tubular, tube 2.7–3.5 mm long, ca. 0.2 mm wide, gradually expanded into the limb, yellow, glabrescent, limb 3.5–4 mm long, 0.7–1 mm wide, lobes shorter than the throat, ca. 1.5 mm long, 0.3 mm wide, pubescent at the apex; anthers ca. 3 mm long, apical appendage 0.5–0.8 mm long, tails 0.7–1 mm long; style 6–8 mm long, branches 1.2–2 mm long, papillae covering style branches and extending down the shaft of the style a distance equal to the length of the branches. Cypselae 1–1.5 mm long, ca. 0.4 mm wide, cylindrical or ellipsoid. Pappus bristles pale or whitish yellow, scabrous; outer series 1–2.5 mm long, sometimes absent; inner series 4.5–5 mm long. Chromosome number: $n = 9$, ca. 36II, 38II (Carr et al. 1999, sub *L. bourgeaui*; Olsen 1980, sub *L. bourgeaui*). Fig. 16A–E.

Phenology. Collected in flower throughout the year. Fruiting capitula may occur on the same plant with flowering ones.

Distribution (Fig. 16F). Southern Mexico and Central America to Colombia and Venezuela; premontane or montane areas and open wet or cloud forests, or sometimes dry scrublands, near rivers or dry riverbeds among rocks, and along road margins; 150–2700 m. The distribution of *L. asclepiadeum* is significantly expanded to the north and west in this treatment by inclusion of *L. bourgeaui* as a taxonomic synonym.

Local Names. b Tzuytez (*Alush Shilom Ton 8160*), papelillo (Guatemala: Nash 1976; *Steyermark 49761*), saq saq (*Wilson 41032*, Quecchí), "tz'ul itaj max" (*Brett 855*, Tzeltal).

Representative Specimens. **Colombia.** Antioquia: 13 km E de Bolívar, *Araque & Barkley 19An036* (F); Bocaná 7 km E de Medellín, *Araque & Barkley 19An065* (F); between Salgar and Main, Medellín-Quibdó, 05°56′N, 75°57′W, *Croat 69943* (MO); cerca de Palmitas, *Klevens et al. 35* (LIL); Mun. Jardín, entre Jardín y Río Sucio, 12 km de Jardín, 05°32′N, 79°49′W, *MacDougal & Roldán 3486* (MO); between Valdivia and Yarumal, *Metcalf & Cuatrecasas 30120* (LIL, MO); San Pedro, *Tomas Alberto 108* (F).—Chocó: La Mansa, *Araque & Barkley 19Ch029* (F, LIL); between Bolívar and Quibdó, 05°47′N, 76°19′W, *Croat 55883* (MO); Ansermanuevo-San José del Palmar, límite con el Valle del Cauca, Alto del Galápago, *Forero et al. 2843* (MO); Tutunendo-El Carmen, Alto Río Atrato, *Forero et al. 6077* (MO); 20 km W of Bolívar, *Gentry & Renteria 23698* (MO).—Cundinamarca: Quipile, vereda de La Sierra, *Uribe 2875* (NY).—Huila: arriba de Guadalupe en Resina, *Pérez Arbeláez & Cuatrecasas 8375* (F).—Valle del Cauca: Hoya del Río Cali, Pichindé, Alto de las Brisas, *Cuatrecasas 18225* (F); Cali to Buenaventura, *Evans & Villarreal 7289* (F); Ansermanuevo-San José del Palmar, 26 km E de San José del Palmar, *Forero et al. 2823* (MO); cuesta de Tocotá, Buenaventura-Cali, *Pittier 707* (F).—Without department and locality: *Linden 103* (MO). **Costa Rica.** Alajuela: La Calera de San Mateo, *Brenes 3640* (F); Los Angeles y La Paz de San Ramón, *Brenes 6090* (F); Cataratas de San Ramón, *Brenes 13533* (F, NY); San Pedro de San Ramón, *Brenes 21489* (F); Río La Paz, to Puerto Viejo, 10°12′N, 84°10′W, *Burger 11871* (F); near Cataratas de Angel, river from the crater on volcán Poas, *Funk et al. 3019* (US); Tilarán to Volcán Arenal SW side of Lake Arenal, *Funk et al. 10734* (US); finca La Constancia, Buena Vista, San Carlos, *Jiménez*

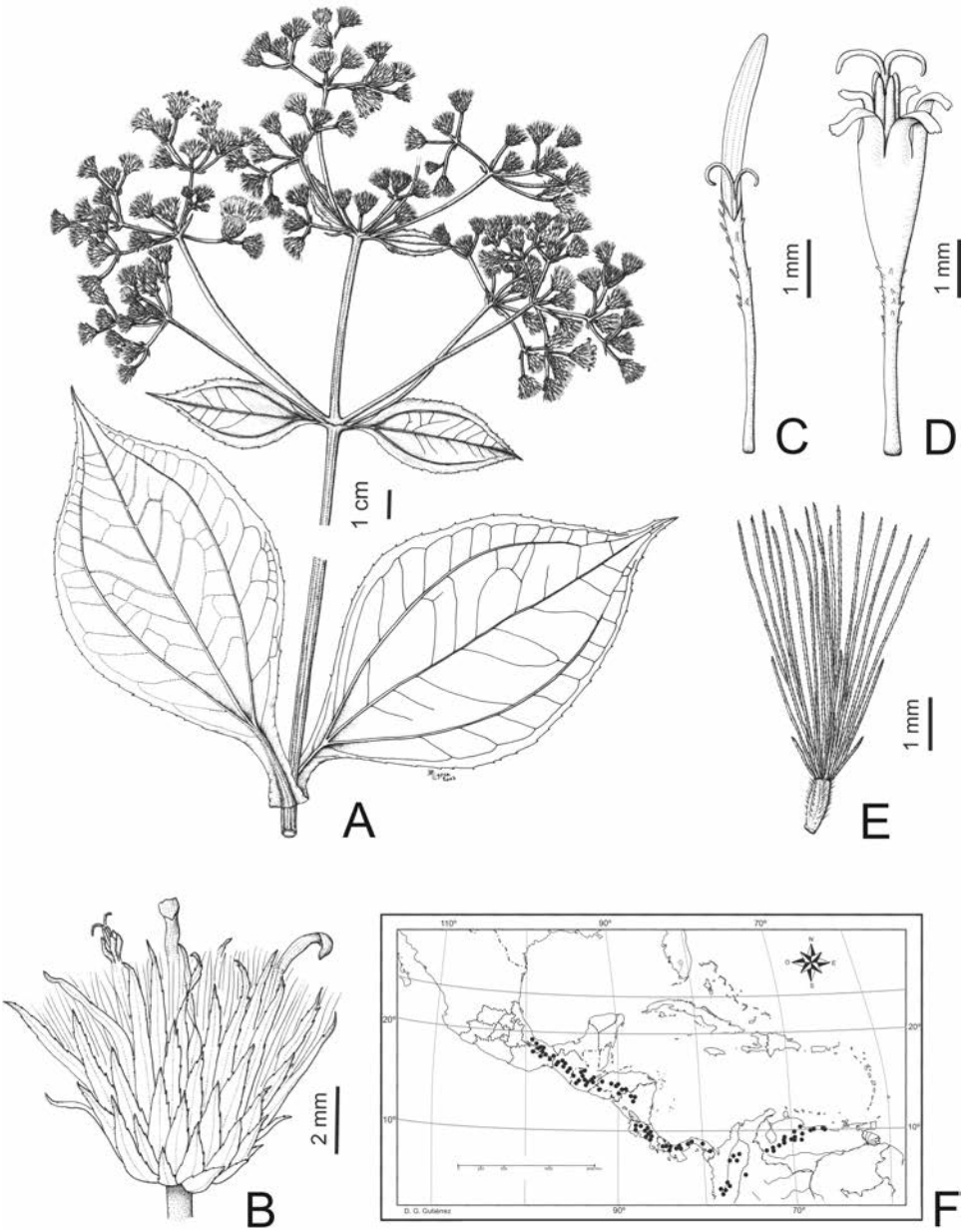

FIG. 16. *Liabum asclepiadeum* Sch. Bip. A. Habit (branch). B. Capitulum (only some florets shown). C. Ray floret. D. Disc floret. E. Cypsela and pappus. F. Distribution. (A–E based on *Skutch 3696*, MO.)

448, 568 (F, LIL, US); Tilarán and Nuevo Arenal to La Fortuna, *Kress et al. 4805* (US); SE of Lake Arenal to Volcán Arenal, *Kress et al. 4807* (US); Vera Blanca to San Miguel, 14 km from Vera Blanca, *Kress et al. 4808* (US); Vera Blanca to San Miguel, to Poás and Heredia, *Kress et al. 4811* (US); NNW of San Ramón, N of Balsa to San Lorenzo, 10°22′N, 84°30′W, *Liesner & Judziewicz 14891* (MO); along Río San Rafael, hacienda La Marina, NE of Villa Quesada, *Molina et al. 17415* (F); near La Laguna, S of Villa Quesada, *Molina et al. 17496* (F); Cantón San Carlos, Zapate, *Smith H478* (F); San Luis de Zarcero, *Smith H510* (F); N of San Ramón, *Wilbur & Stone*

10100 (F, GH, MO, US).—Cartago: Refugio Nacional de Vida Silvestre Tapantí, *Almeda et al. 6843* (US); Tapantí, *King & Castro 9997* (US); W bank Río Grande de Orosi, Tapantí, *Lent 887* (F, GH); Instituto Inter-Americano de Ciencias Agrícolas, Turrialba, *León 1489* (US); La Angostura-Turrialba, *Póveda et al. 4071* (F, MO); La Montural, a Carrillo, Parque Nacional Braulio Carrillo, *Sánchez et al. 436* (MO); Río Turrialba, *Smith 6611* (GH, US); Cartago, Dulce Nombre, *Standley 35923* (US).—Heredia: Alto La Palma between Paracito and Bajo La Hondura, *Croat 44477* (MO); Vara Blanca, Poás and Barba volcanoes, *Skutch 3696* (MO, NY); La Paz waterfall, near Cinchona, Volcán Poás, *L. Williams 19362* (F).—Limón: Reserva Biológica Hitoy Cerere, Río Hitoy, cordillera de Talamanca, 09°05′N, 83°25′W, *Herrera & Chacón 2506* (F, US); above Pacuare, Río Pacuare, *Williams 16216* (F).—Puntarenas: cerro Pando, Río Coton and the Río Negro, 08°55′N, 82°45′W, *Barringer & Gómez 22* (F); Río Naranjo, near Londres and Villa Nueva, 09°28′N, 84°28′W, *Burger et al. 12329* (F); between La Union (border of Panamá) and Coton, between Río Negro and Río Coto Brus, *Croat 26572* (MO); 5 mi N of Villa Nelly, *Gillis & Plowman 10072* (F, GH, MO); Rincón, península de Osa, *Godfrey 66525* (MO); between Cotoncito and Mellizas, *Gómez et al. 22709* (US); Cantón de Puntarenas, Monteverde, near Hotel Belmar above quebrada Máquina, 10°18′N, 84°48′W, *Haber 10592* (MO); Tigra to Sitio Cotón, cerro Chivo, Cotón river, *Hazlett 5249* (F); Santa Elena to Monteverde Forest Reserve, *Kress et al. 4803* (US); Monteverde Reserve to Peñas Blancas, *Norrbom AP 12* (US); cabeceras del Bkís [also Bekís, Bequís or Bquís river; old name for the upper part of the Río Ceibo], *Pittier 22* (GH, US).—San José: Río Claro valley, below La Palma NE of San Jerónimo, 10°03′N, 83°58′W, *Burger & Gentry 9086* (F); the General valley along the Interamerican Highway, 09°27′N, 83°43′W, *Burger & Barringer 11620* (F, NY); Reventazón Valley, *Cook & Doyle 334* (US); La Palma, *King et al. 9658* (MO, US); debajo de La Hondura, *King & Castro 10028* (US); Orosí to Reserva Tapantí, *Kress et al. 4812* (US); Alto San Juan, to Dominical, on El General valley, vicinity of San Isidro El General, *Molina et al. 18083* (F, MO, NY); San José, *Orozco 468* (F); San Carlos, *Orozco 352* (F); Cataraticas-San Ramón, *Póveda et al. 3004* (F); El General, *Skutch 4052* (GH, MO, NY, US); El General, *Skutch 4730* (F, US); La Hondura, *Standley 37666* (US); La Hondura, *Standley & Valerio 51861* (US).—Province unknown: without locality, *Kuntze s.n.* in 1874 (US). **El Salvador.** Ahuachapán: Mun. San Francisco Menéndez, hacienda San Benito, montaña de Tacho López, 13°49′N, 89°56′W, *Sandoval & Chinchilla 262* (MO). **Guatemala.** Alta Verapaz: San Juan Chamelco, *Hunnewell s.n.* in 1941 (NY), *17291* (GH); Sacapulas, ca. 6 km W of San Cristóbal Verapaz, *King & Renner 7114* (US); entre San Pedro Carchá y Sacoyoú, *Molina & Molina 12063* (MO, NY); NO de Tactic, 6 km a Estor, *Molina & Molina 12293* (F, NY); near Cobán, *Standley 69192* (F, NY); finca Socuyó, NE of Carchá, *Standley 70238* (F); near Pancajché, *Standley 70761* (F); E of Tactic, to Tamahú, *Standley 71335*, *71435* (F); Río Carchá, between Cobán and San Pedro Carchá, *Standley 89954* (F); near Tactic, Río Frío, *Standley 90459* (F); between San Cristóbal Verapaz and Chixoy, *Steyermark 43893* (F); Pansamalá, *Türckheim 898* [*J. D. Smith 98*] (F, GH, NY, US); Sachichá, *Türckheim 2123* (US); *Türckheim 8692* (F, GH, MO, NY, SI, US); between Tactic and Tamahú, 15°21′N, 90°17′W, *Williams et al. 40350* (F, US); about 10 km N of Cobán, *Williams et al. 42046* (F); vicinity of San Juan Chamelco, *Wilson 41032* (F).—Baja Verapaz: 4 km al S de Purulhá, camino Guatemala-Cobán, *Martínez & Téllez 13060* (MO).—Escuintla: between Río Jute and Río Pantaleón, between Escuintla and Santa Lucía Cotz, *Standley 63587* (F, GH, MO); finca Monterrey, Volcán de Fuego, *Standley 64546* (F, GH).—Guatemala: near Pireneos, above San Felipe, *Maxon & Hay 3558* (US); E of Tactic, to Tamahú, *Standley 71425* (F).—Huehuetenango: W of Aguacatán, to Huehuetenango, *Standley 81225* (F); puente El Aguilar, E of San Sebastián, *Standley 82821* (F); Cerro Victoria, Sierra de los Cuchumatanes, near Barillas, *Steyermark 49761* (F).—Izabal: Santo Tomás de Castilla, from Las Escobas, 88°38′W, 15°42′N, *Marshall et al. 268* (NY).—Quezaltenango: Santa María, *Kellerman 5296* (F); Volcano Santa María, El Palmar, *Kellerman s.n.* in 1907 (US); ca 28 km SW of Quezaltenango, *King & Renner 7021* (MO, NY, US); ca 33 km S of Quezaltenango, *King 7249* (MO, NY); ca 30 km S of Quezaltenango, *King 7253* (MO, NY, US); near Calahuaché, *Standley 67068* (F); near Muro, below Santa María de Jesús, *Standley 67171* (F); finca Azucena, above Colomba, *Standley 68006* (F); finca Pireneos, below Santa María de Jesús, *Standley 68190* (F, NY); above Mujuliá, between San Matín Chile Verde and Colomba, *Standley 85685* (F); between Finca Pirineos and Patzulín, *Standley 86687* (F); between Colomba and Las Mercedes, *Standley 87962* (F); near quebrada San Gerónimo, finca Pirineos, Volcán Santa María, between Santa María de Jesús y Calahuaché, *Steyermark 33323* (F); Volcán Zunil, opposite Santa María de Jesús, *Steyermark 35092* (F).—Quiché: without locality, *J. Aguilar 1332* (F).—Retalhuleu: Río Samalá, between San Sebastián and Santa Cruz Muluá, *Standley 88140* (F); Pueblo Nuevo, *Stricker 347* (US).—San Marcos: finca Vergel, near Rodeo, *Standley 68898* (F).—Santa Rosa: Río de la Plata, *Heyde & Lux 4525* (F, GH, NY, US).—Sololá: between Sololá and Panajachal, *Artamanoff s.n.* in 1939 (F); Panajachel, Lake Atitlán, *Hunnewell 14891* (GH, NY).—Suchitepequez: finca Moca, *Skutch 2117* (F, GH, NY, US).—Zacapa: between Río Hondo and waterfall, sierra de Las Minas, *Steyermark 29440* (F). **Honduras.** Copán: 5 km southwest of Santa Rosa de Copán, *Molina 11672* (F, NY, US).—Intibucá: Huise river, 9 km E of La Esperanza, *Molina & Molina 25576* (F, MO, NY).—La Paz: 5 km from Chinacla, *Molina & Molina 24223* (F, NY); Agua Blanca river, between Chinacla

and Planes de Mulle, *Molina & Molina 24318* (F).—Lempira: 5 km from Lepaera, *Molina 24138* (F, MO).—Ocotepeque: Yoroconte River, between El Moral and Sinuapa, *Molina 24178* (F). **Mexico.** Chiapas: Mun. Pueblo Nuevo Solistahuacán, above Pueblo Nuevo Silistahuacán, *Alush Shilon Ton 2883* (NY); Mun. Trinitaria Chiapas, km 18 Col. Cuauhtémoc, *Alush Shilon Ton 8160* (US); 3.4 mi from Tziscao camp, Lagos Montebello, near Guatemala, *Balogh 948* (US); Mun. La Trinitaria, at Lago of Monte Bello, 25 mi E of La Trinitaria, *Breedlove 9740* (F); Mun. Las Margaritas, valley of La Soledad from Las Margaritas to Campo Alegre, *Breedlove 33720* (MO); San Juan Cancuc, Sajkaleel, *Brett 855* (MO); near San Miguel, Los Lagos, 3 mi NW of Rancho San José, 34 mi SE of Comitán, *Carlson 1780* (F); Mun. Pueblo Nuevo Solistahuacán, near Rincón Chamula, *Clark 282* (NY); between Bochil and Pichucalco, 8 mi NW of Pueblo Nuevo Solistahuacan, *Croat 46338* (MO); from Lagos de Montebello to Dos Lagunas, km 4.5, *Croat 46575* (MO); Selva Negra, between Chiapa de Corso and Pichucalco, ca. 6 mi NW of Pueblo Nuevo Solistahuacan, 17°07′N, 92°52′W, *Croat & Hannon 65229* (MO); hacienda del Burrero, San Cristóbal a Chiapas, *Ghiesbreght 786* (GH); Mt. Tacaná, *Matuda s.n.* in 1938 (F); Vol. Tacaná, *Matuda 2331* (GH, MO, NY, US); Mt. Tacaná, *Matuda 2746* (GH, US); Mun. San Cristóbal de las Casas, Santa Cruz en San Filipe, *Méndez Ton & Martínez 9599* (NY); Mun. Altamirano, Puebla Nueva, *Pérez 141* (NY); hacienda del Burrero, Río Hondo, *Seler 2266* (GH, NY, US); 8 km from Ixtapa, Río Laja, 16°40′N, 93°00′W, *Stafford et al. 135* (MO); Mun. Unión Juárez, Col. Santo Domingo, *Ventura & López 1195* (US); Selva Negra, 14.5 km al NO [NW] de Pueblo Nuevo Solistahuacan, a Pichucalco, *Villaseñor & Thomas 821* (NY).—Oaxaca: Mun. Comaltepac, Distr. Ixtlán, S. Comaltepec, 17°33′N, 96°31′W, *Hernández & Martin 289* (US); Mun. Comaltepec, Distr. Ixtlán, Rancho Mameyal, 14°45′N, 96°30′W, *López Luna 443* (US); between Plunia and San Miguel Suchistepec, *Nelson 2503* (US).—Veracruz: Mun. Yecuatla, Naolinco to Misantla, 13 km S to Yecuatla and 6 km N to Paz de Enríquez, 19°51′N, 96°48′W, *Nee et al. 26400* (F, NY); Córdoba, *Plunkett 183* (F); Orizaba, *Gray s.n.* in 1885 (GH); near Jalapa, Barranca of Texolo, *Pringle 7837* (US), *Pringle 9187* (GH, US); Mun. Teocelo, Teocelo, *F. Ventura 850* (NY); Mun. Yecuatla, Plan de Almansa, *Ventura 3304* (F, NY). **Nicaragua.** Rivas: Isla Ometepe, Volcán Concepción, "Los Hatillos", 11°32–33′N, 85°36–37′W, *Robleto 1003* (MO); Volcán Concepción al SE de San Marcos, 11°32–33′N, 85°37–38′W, *Robleto 1900* (MO); Ometepe, NE del Volcán Concepción, sobre cauce grande que divide Los Angeles y Las Delicias, 11°33′N, 85°37′W, *Sandino 555* (MO), *567* (F, MO).—Without Department or Locality: *Wright s.n.* in 1853–1856 (GH). **Panama.** Chiriquí: Paso Ancho to Monte Lirio, valley of Río Chiriquí Viejo, *Allen 1587* (F, GH, MO, NY, US); Burica Peninsula, San Bartolo Límite, 20 km W of Puerto Armuelles, *Busey 555* (CTES, MO, NY); Palo Santo, 3 mi N of Volcán, *Croat 13544* (MO); N of Audubon Cabin, *Croat 13634* (MO); Burica Peninsula, quebrada Guanabanito beyond La Represa, 2 mi SW of Puerto Armuelles, *Croat 22042* (CTES, NY); to Cerro Colorado and Escopeta above Río San Félix, near San Félix, *Croat 33503* (MO); 11 km NW of Río Chiriquí Viejo, toward San Sereno, *D'Arcy 10745a* (CTES, MO, US); 13–20 km W of bridge at Río Chiriquí Viejo to San Sereno, *D'Arcy 10757* (MO, US); Concepción to Volcán, *D'Arcy 10774* (MO, US); Bajo Mono, *D'Arcy 11012* (MO, US); Río Chiriquí Viejo at Nueva California to cerro Pando, ca. 5 mi NW, *D'Arcy et al. 12954* (MO); Nueva California to Río Sereno, ca. 7 mi Río Chiriquí Viejo, *D'Arcy et al. 13021*, *13075* (MO); Boquete Distr., Chiquero, *Davidson 561* (F, GH, MO, US); cerro Colorado, *Folsom & Collins 1829* (F); between N Río Palo Alto and cerro Pate Macho, ca. 6 km NE of Boquete, 08°48′N, 82°23.5′W, *Grayum et al. 6393* (MO); Las Lagunas, W of Hato del Volcán, 82°40′W, 08°47′N, *Hamilton & Stockwell 3561* (MO); Alto Los Guerra, W Bombito, 82°37′W, 08°53′N, *Hamilton & Stockwell 3667* (MO); Río Colorado, 82°43′W, 08°50′N, *Hamilton & Krager 3780* (MO); La Fortuna hydroelectric project, Chiriquí River, *Hammel 2205* (F, MO); 3.5 mi NE of Boquete, Río Palo Alto, *Hammel 5727* (US); 7.5 mi Río Chiriquí Viejo to Río Sereno, *Hammel et al. 6875* (F, MO); between Los Planes de Hornito and Fortuna Lake, 08°40′N, 82°14′W, *Hampshire & Whitefoord 315* (F); Burica Peninsula, quebrada Melliza, 6 mi S of Puerto Armuelles, *Liesner 462 A* (NY, MO); vicinity of El Boquete, *Maxon 5232* (US); 1.5 mi W of cerro Punta, near Río Chiriquí Viejo, *McDaniel 10113* (MO); Las Lagunas, 2 mi SW El Volcán, *Tyson 853* (MO); NE of cerro Pando, NW of Nueva California, *Wilbur et al. 11010* (F, GH, MO, NY).—Coclé: El Valle, *I. Aguilar 2* (MO); 2 mi above El Valle to La Mesa, *Croat 13302* (NY, MO); S of El Valle, *D'Arcy et al. 13324* (MO); La Mesa, N of El Valle de Antón, *D'Arcy & Sytsma 14663* (MO); Cerro Pilon near El Valle, *Duke 12068* (3) (MO); La Mesa above El Valle, *Duke & Dwyer 15171* (NY); Distr. Penonomé, Río Guaybo, W of Cerro Pajita, 80°08′W, 08°38′N, *Webster 16825* (MO).—Darién: Serranía del Darién, cerro Tacarcuna, *Gentry & Mori 14098* (MO, US).—Panamá: La Laguna, *Galdames et al. 2910* (US); El Valle to La Mesa, *Tyson 6907* (MO).—Province unknown: Bismarck above Renonane, *R. Williams 261* (NY). **Venezuela.** Aragua: prope coloniam Tovar, *Fendler 655* (GH, MO); Río Tuy, NE of Maya, 7 km SE of Colonia Tovar, 10°21′N, 67°14′W, *Steyermark & Liesner 121846* (MO); Aragua, Parque Nacional, *L. Williams 12462* (F).—Barinas: Distr. Bolívar, La Soledad, 20 km SO [SW] Barinitas, 8°50N, 70°30′W, *Aymard & Ortega 2278* (MO).—Cojedes/Yaracuy: S Río Claro, *Saer 781* (F).—Distrito Federal: Las Adjuntas and Río Macarao, *Eggers 13265* (GH, US); Caracas, Chacao, *Otto 624* (GH, K, MO).—Falcón: Distr. Miranda, La Negrita to Curimagua, sierra de San Luis, near La Ciénaga, *Plowman et al.*

13430 (F).—Lara: Parque Nacional Yacambú, *Badillo 345* (MO); Sanare hacia Las Blanquitas, *Badillo 6679* (F); Parque Nacional Yacambú, SE de Sanare, *Benítez 1753* (F); Distr. Jiménez, Parque Nacional Yacambú, El Blanquito, 11–19 km SSE Sanare, *Bunting 4993* (NY); Distr. Morán, Humocaro Alto hacia Guaito, *van der Werff & Rivero 8736* (US).—Mérida: near San Eusebio, *Andrews 709* (NY); 35 km W of Mérida to La Carbonera, *Breteler 3603* (NY); 4.1–6.3 km E of Santo Domingo to Barinas, *King et al. 10535* (MO); 16.5–18.4 km E of Santo Domingo to Barinas, *King et al. 10546* (MO, US); 36.9–38.2 km W of Mérida to Jají and Azulita, Chorrera National Park, *King et al. 10579* (US); près Mérida, *Mocquerys s.n.* in 1893–1894 (LIL, LP, NY); Distr. Campo Elías, Río La González at La Chorilla, *Proctor et al. 49092* (US); between Hacienda Agua Blanca above La Azulita and Río Capaz, *Steyermark 56151* (F, NY).—Portuguesa: Distr. Sucre, km 37 Biscucuy hacia Tocuyo, 09°20′N, 69°58′W, *Rutkis 427* (MO); quebrada Cuchilla Alta, El Mosquito, Las Cruces, 09°15′N, 70°01′W, *Stergios et al. 6583* (MO).—Táchira: Cementos Táchira hacia Borotá, *Bono 4628* (MO).—Trujillo: between Trujillo and Bocono, *Alston 6455* (F, GH, NY).—Yaracuy: Depto. Bolívar, Mun. Aroa, hacia Aroa, entre Las Crucecitas y La Pila, *Fernández 3974* (NY); Sierra de Aroa, 9 km W of San Felipe, 0–3 km NE between Cocorote and Aroa, 15 km NW of Cocorote and 1 km SE of Los Cruceros, 10°21′N, 68°49′W, *Liesner & González 10044* (MO); Depto. Bruzual, km 11 Campo Elías-La Cumbre, *Trujillo 16069* (MO).—Zulia: Perija, *Hermano Gines 2117* (US).—State unknown: without locality, *Brother Elías 146* (F).

Originally, Hieronymus (in Ule 1907) recognized *L. bourgeaui* as resembling *L. asclepiadeum* (and its synonym *L. ulei*) but differing in having broader leaf blades, bigger capitula, longer involucres, and cuneate and decurrent leaf blade bases or with the petioles winged. Later authors (Standley 1938; Nash 1976: 460, fig. 6; Dillon 2001) employed the winged petioles to identify specimens of *L. bourgeaui* from Costa Rica, Guatemala, and Nicaragua. Specimens from Colombia (e.g., *Araque Molina & Barkley 19An036*) and Panama (e.g., *Busey 555*; Barkley 1975: 1254, fig. 96) may have either winged or wingless petioles. On the other hand, specimens of *L. asclepiadeum* from Venezuela have cuneate and decurrent leaf bases or narrowly winged petioles (Aristeguieta 1964; *Alston 6455*). Since the winged petiole, the only useful character to distinguish *L. bourgeaui* and *L. asclepiadeum*, can be present in both species, we propose here *L. bourgeaui* as a synonym of *L. asclepiadeum*.

Aristeguieta (1964) cited the specimen *Moritz 300* as being the type of *L. asclepiadeum*. However, there are two specimens kept at P with the same collector and collection number. We selected as lectotype the specimen P-285908, as specimen P-285909 (mounted with the specimen *Fedle 655*) lacks reproductive parts.

Rogers McVaugh labeled the specimen *La Llave s.n.* deposited in G, as the lectotype of *Allendea lanceolata*. Since the specimens of La Llave are kept at G (Stafleu & Cowan 1979) and because we could not find any publication regarding this decision, we consider (according to Article 9.8 of the ICN, McNeill et al. 2012) the specimen at G to be the holotype of *Allendea lanceolata*.

In the protologue of *Liabum bourgeaui*, Hieronymus did not indicate the collection number of the type specimens collected by Türckheim (J. D. Smith distribution number 98) or Heyde & Lux in Guatemala. We found the specimens *Türckheim 898* (*J. D. Smith 98*) and *Heyde & Lux 4525* (both kept at BM, F, G, GH, L, MSC, NY, S, and US) that coincide with the localities cited in the protologue and the other original data, including the herbarium number of J. D. Smith. Thus, these specimens are considered isosyntypes of *L. bourgeaui*. The syntypes kept at B were destroyed during World War II. Therefore, following Articles 9.9, 9.10, and Recommendation 9.A of the ICN (McNeill et al. 2012), we selected as lectotype the isosyntype *Bourgeau 2205* kept at G.

The stem and leaf pubescence of *L. asclepiadeum* is employed as tinder in Guatemala (Dept. Huehuetenango: Nash 1976). A decoction made from the leaves is used against edema (*Brett 855*). Acetylcholinesterase inhibitory activity was studied, and cytotoxic

activities were found in methanol extracts from this species (Mosquera et al. 2004; Niño et al. 2006).

4. Liabum barclayae H. Robinson, Phytologia 34: 286–287. 1976.—Type: Ecuador. Chimborazo: short distance S of Chunchí on road to Cuenca, ca. 2700 m, 27 July 1959, *Barclay & Juajibioy 8316* (holotype: US!; isotypes: MO, QCNE, WIS, digital images!).

Subshrubs or shrubs, 1–3 m tall; stems not costate, terete or slightly hexagonal in cross-section, densely and persistently white-tomentose; pseudostipules 0.5–1 cm long, without auricles, green, glabrescent adaxially, densely white-tomentose abaxially. Leaves scattered along the main stem and branches; leaf blades 8–12 cm long, 3.5–6.5 cm wide, chartaceous, ovate, apex acute or attenuate, base cuneate, margin mucronate-serrate, venation acrodromous, with the pair of lateral veins exceeding the midpoint of the blade but not reaching the apex, surface smooth, green, glabrous adaxially, densely white-tomentose abaxially; petioles 1–2 cm long, not winged. Inflorescence not scapose, umbelliform, lax, composed of 20–50 capitula; capitula radiate, pedunculate or sessile, peduncles, if present, up to 1.5 mm long, densely white-tomentose. Involucre 6–7.5 mm long, 5.5–7 mm wide, campanulate; phyllaries 50–55 in ca. 5 series, 1.5–5.5 mm long, 0.3–0.8 mm wide, greenish, outermost phyllaries ovate, apex acute, pubescence arachnoid, innermost phyllaries linear, apex attenuate, glabrescent; receptacle with chaff 1.5–2.5 mm long. Ray florets 20–30; corolla 7–12 mm long, yellow, glabrous or pubescent, tube 3–4 mm long, 0.2–0.3 mm wide, limb 4–8 mm long, 0.8–1.2 mm wide, obovate, 4-veined, apex 3-dentate; style ca. 8 mm long, branches ca. 4 mm long. Disc florets ca. 25; corolla 7–8 mm long, tubular, tube 3–4 mm long, 0.2–0.3 mm wide, gradually expanded into the limb, yellow, pubescent, limb 3–4 mm long, 0.7–0.9 mm wide, lobes 1.6–2 mm long, ca. 0.4 mm wide, approximately equal to the throat, pubescent at the apex; anthers 3.2–4 mm long, apical appendage ca. 0.5 mm long, tails 0.8–1 mm long; style 8–10 mm long, branches 3–4 mm long, papillae covering style branches and extending down the shaft of the style a distance equal to the length of the branches. Cypselae 1–1.2 mm long, 0.4–0.5 mm wide, cylindrical to ellipsoid. Pappus bristles pale yellow, scabrous; outer series 1–1.5 mm long, sometimes absent; inner series up to 6 mm long. Chromosome number unknown. Fig. 17A–E.

Phenology. Plants with flowering capitula were collected in June and July.

Distribution (Fig. 17F). Endemic to Central Ecuador; wet or somewhat dry montane forests, road margins, and cultivated areas; 1250–2700 m.

Representative Specimens. **Ecuador.** Chimborazo: Alausí, *Asplund 6790* (CTES); Cañar border, between Santa Rosa and Joyagshi, *Camp E4050* (NY).—Cotopaxi: around Pilaló, 79°02′W, 00°57′S, *Holm-Nielsen & Jeppesen 1199* (NY); Angamarca-El Corazón, below Pinllopata, 78°59′W, 01°08′S, *Holm-Nielsen & Andrade 18489* (US), 79°05′W, 01°09′S, *Holm-Nielsen & Andrade 18535* (US).—Tungurahua: 89.9 km W of Latacunga Pilaló, ca. 4.9 km E of Pilaló to Latacunga, *Panero & Clark 3005* (NY).

Liabum barclayae resembles *L. igniarium*, but differs by its smaller pseudostipules (0.5–1 cm long) and ovate, chartaceous leaves with an attenuate, rarely acuminate, apex. It is common for the plant to produce galls in capitula attacked by insects, which causes an increase in size of the involucre and in the amount of pubescence, as well as deformation of the florets and fruits.

This species was given a conservation status of Vulnerable by Montúfar (2000).

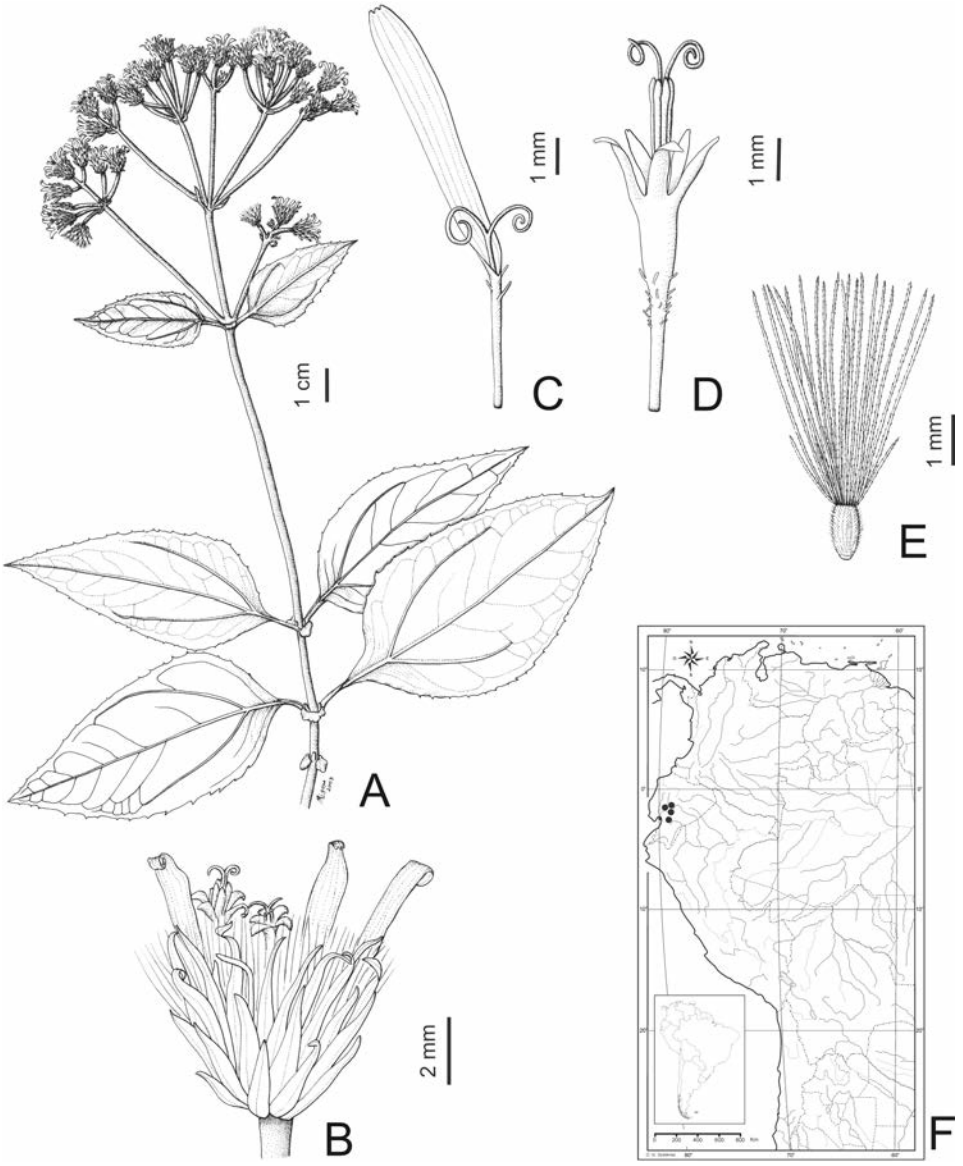

FIG. 17. *Liabum barclayae* H. Rob. A. Habit (branch). B. Capitulum (only some florets shown). C. Ray floret. D. Disc floret. E. Cypsela and pappus. F. Distribution. (A–E based on *Barclay & Juajibioy 8316*, US.)

5. Liabum dillonii D. G. Gutiérrez & Katinas, sp. nov.—TYPE. ECUADOR. Loja: carretera Loja-Zamora, km 16–24, 15 Aug 1983, *Jaramillo & Winnerskjold 5770* (holotype: F!).

Liabum dillonii is related to *L. kingii* and *L. saloyense* but differs by the absence of auricles on the pseudostipules, the absence of brownish hairs on the leaves, the lobes of the disc floret corollas equal to or longer than the throat, and the corollas pubescent with twin hairs.

Subshrubs or shrubs, sometimes climbing, 1–3 m tall; stems not costate, terete or slightly hexagonal in cross-section, with persistent or deciduous white-tomentose pubescence; pseudostipules up to 1.5 cm long, without auricles, green, glabrous adaxially, densely white-tomentose abaxially. Leaves scattered along the main stem and branches; leaf blades 4.5–16.5 cm long, 2.5–5.5 cm wide, chartaceous, ovate to narrowly ovate, apex attenuate, base cuneate, margin mucronate-serrate, venation acrodromous, with the pair of lateral veins reaching almost to the apex of the blade, surface smooth, green, glabrous or glabrescent adaxially, densely white-tomentose abaxially; petioles 0.5–4.5 cm long, not winged. Inflorescence not scapose, umbelliform or corymbiform, lax, with more than 50 capitula; capitula radiate, pedunculate, peduncles up to 8.5 mm long, densely white-tomentose. Involucre ca. 4.5 mm long, 5–5.5 mm wide, hemispherical; phyllaries 50–60 in 5–6 series, 1–4 mm long, 0.3–0.4 mm wide, greenish, outermost phyllaries ovate, apex acute, pubescence arachnoid, innermost phyllaries linear, apex attenuate, glabrescent; receptacle with chaff ca. 2 mm long. Ray florets 20–30; corolla 6.5–8 mm long, yellow, pubescent, tube 3–3.5 mm long, 0.35 mm wide, limb 3–4.5 mm long, 0.8–1 mm wide, elliptic to obovate, 4-veined, apex 3-dentate; style 6.5–7 mm long, branches 2.5–3 mm long. Disc florets 25–35; corolla 5.5–6.5 mm long, tubular, tube ca. 2.5 mm long, 0.2 mm wide, abruptly expanded into the limb, yellow, pubescent, limb 3–4 mm long, ca. 1 mm wide, lobes ca. 2 mm long, 0.35 mm wide, equal to or longer than the throat, pubescent at the apex; anthers 2–2.2 mm long, apical appendage 0.4–0.5 mm long, tails 0.5–0.8 mm long; style 5.5–6.2 mm long, branches 2–2.2 mm long, papillae covering style branches and extending down the shaft of the style a distance less than the length of the branches. Cypselae ca. 1 mm long, 0.35 mm wide, cylindrical to obconical. Pappus bristles yellowish orange, scabrous; outer series up to 1.7 mm long, sometimes absent; inner series up to 5.5 mm long. Chromosome number unknown. Fig. 18A–E.

Phenology. Plants with flowering capitula were collected in July and August.

Distribution (Fig. 18F). Ecuador and Peru; montane forests; 2000–2800 m.

REPRESENTATIVE SPECIMENS. **Ecuador.** BOLÍVAR: 15 km of road Chillanes-El Tambo, *van der Werff et al. 12425* (NY).—NAPO: Sendero Precooperativa Cordillera Oriental, 00°03′S, 77°49′W, *Jaramillo et al. 12480* (NY). **Peru.** SAN MARTÍN: Mariscal Cáceres, Río Abiseo National Park, Gran Pajaten, Río Montecristo, ca. 07°S, 77°W, *Young 4318* (F).

Liabum dillonii is described as climbing or a vine on some herbarium sheets, probably because taller plants may lie on other vegetation and thus appear scandent.

The name of this species honors Michael O. Dillon, a botanist from the United States of America (born 1947), who has made important contributions to the taxonomy of Asteraceae and to the flora of the Andes.

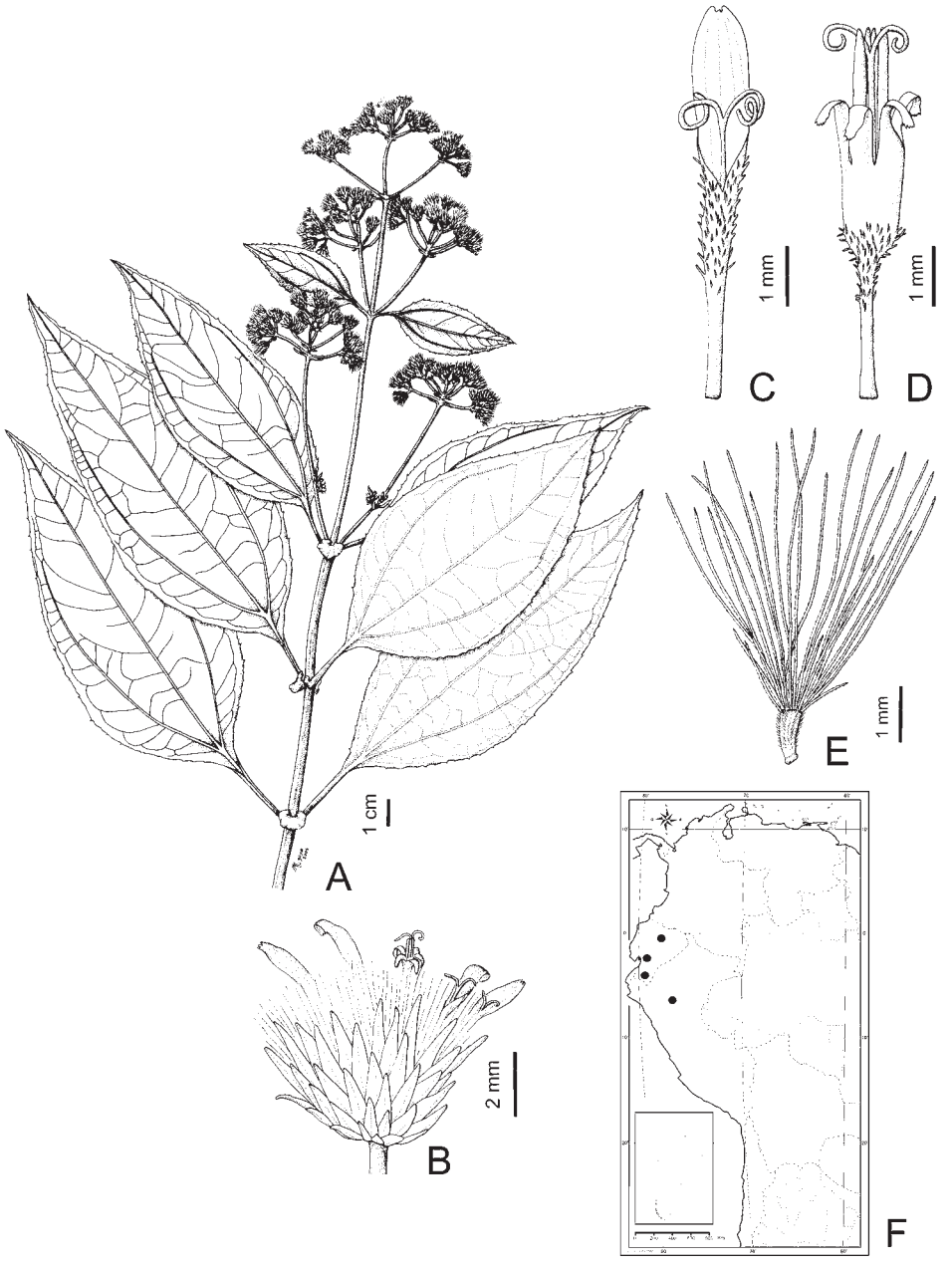

FIG. 18. *Liabum dillonii* D. G. Gutiérrez & Katinas. A. Habit (branch). B. Capitulum (only some florets shown). C. Ray floret. D. Disc floret. E. Cypsela and pappus. F. Distribution. (A–E based on *Jaramillo & Winner-skjold 5770*, F.)

6. Liabum eriocaulon Poeppig, Nov. Gen. Sp. Pl. (Poeppig & Endlicher) 3: 43 + pl. 249. 1843.—Type: Peru. Huánuco: crescit in Peruviae subandinae sylvis opacis circum Cuchero ["ad Pampayaco" on label], Aug 1829, *Poeppig s.n.* [D.1280] (holotype: W-0028614, digital image!).

Caulescent erect perennial herbs to subshrubs, 0.3–1.5 m tall; stems costate or not costate, terete or hexagonal in cross-section, densely and persistently white- or ochraceous-tomentose; pseudostipules 0.35–2.5 mm long, without auricles, green, glabrous adaxially, densely white-tomentose abaxially. Leaves scattered along the main stem and branches; leaf blades 10–14 cm long, 5–8 cm wide, chartaceous, ovate, apex acute or attenuate, base cuneate, rounded or slightly cordate, margin mucronate-serrate, venation acrodromous, with the pair of lateral veins reaching the apex of the blade, surface smooth, green, glabrous adaxially, densely white- or ochraceous-tomentose abaxially; petioles 2–5 cm long, not winged. Inflorescence not scapose, umbelliform, dense, rarely lax, with more than 50 capitula; capitula sub-radiate, sessile or pedunculate, peduncles up to 3 mm long, densely white-tomentose. Involucre ca. 6.5 mm long, 5.5 mm wide, campanulate; phyllaries ca. 85 in 5–7-series, 1–6 mm long, 0.4–0.6 mm wide, greenish, outermost phyllaries ovate, apex acute, pubescence arachnoid, innermost phyllaries linear, apex attenuate, glabrescent; receptacle with chaff 1.5–3 mm long. Ray florets ca. 85; corolla 6.5–7.5 mm long, yellow, glabrous or slightly pubescent, tube 4.5–5 mm long, ca. 0.15 mm wide, limb 2–2.5 mm long, 0.35–0.4 mm wide, elliptic, 4-veined, apex entire or slightly 3-dentate; style 7–8 mm long, branches 1.2–2 mm long. Disc florets ca.15; corolla 6.5–7.5 mm long, tubular, tube 3.5–4 mm long, ca. 0.2 mm wide, gradually expanded into the limb, yellow, glabrescent, limb 3–3.5 mm long, 0.5–0.6 mm wide, lobes 1.4–1.5 mm long, ca. 0.2 mm wide, shorter than the throat, pubescent at the apex; anthers 2.2–2.8 mm long, apical appendage 0.5–0.8 mm long, tails 0.18–0.2 mm long; style 8–9 mm long, branches 1.8–2 mm long, papillae covering style branches and extending down the shaft of the style a distance equal to the length of the branches. Cypselae ca. 1.5 mm long, 0.4 mm wide, cylindrical to ellipsoid. Pappus bristles white-yellowish or yellowish orange, scabrous; outer series 1–2.5 mm long, sometimes absent; inner series up to 7.5 mm long. Chromosome number unknown. Fig. 19A–E.

Phenology. Plants with flowering and fruiting capitula have been collected from June to December.

Distribution (Fig. 19F). Peru and Bolivia; near river valleys of subtropical montane forests or margins of rivers and roads, in rocky and sandy soils; 420–1700 m.

Representative Specimens. **Bolivia.** Beni: Prov. Ballivián, Carinavi-San Borja, serranías Pilón Bajas, 15°17′S, 67°04′W, *Smith & García 13766* (US).—Cochabamba: Prov. Chapare, San Rafael, *Steinbach 515* (GH, NY). **Peru.** Cuzco: Distr. Echatare, Cashiriari, 11°52′S, 72°39′W, *Beltrán et al. 3052* (US); Torontoy, Urubamba valley, *Cook & Gilbert 1094* (US); Calca, *Isern 26* (LP); Prov. La Convención, Distr. Echarate, Armihuari, 11°51′S, 72°46′W, *Núñez et al. 20088* (US); Prov. Convención, Kosqueñayvec, potrero, *Vargas 8237* (LIL).—Huánuco: Prov. Tingo María, La Divisoria, *Aldave & Fernández 5614* (LP); Prov. Leoncio Prado, Río Monzón near Río Huallaga at Tingo María, *Croat 21215* (MO, NY); ca. 20 km S of Tingo María to Huánuco, *Dillon 2694* (F, MO); near Divisoria, between Tingo María and Pucallpa, *Ferreyra 1106* (LIL, MO, US); between Huánuco and Tingo María, km 493, *Solomon 3356* (F, MO, NY); Prov. Huánuco, Éxito, Río Cayumba, *Vargas 71* (MO).—Junín: San Ramón, *Cabrera 10924* (LP); Prov. Tarma, San Ramón, *Cerrate 941* (MO); ca. 51 km NE of Tarma to San Ramón, *Dillon & Turner 1425* (F); Vítoc, *Soukup 4418* (US).—Pasco: Oxapampa, *Ellenberg 8919* (SI).—San Martín: Prov. Lamas, entre Yurimaguas y Tarapoto, *Ferreyra 17492* (MO); Distr. Campanilla, 7.4 km N of Pulcache, 07°43′S, 76°40′W, *Plowman & Schunke 11592* (GH, MO, NY, US); Prov. San Martín, Distr. Tarapoto, Tarapoto-Yurimaguas, km 12–16, *Rimachi 3887* (US); Distr. Tarapoto, Tarapoto a Yurimaguas, km

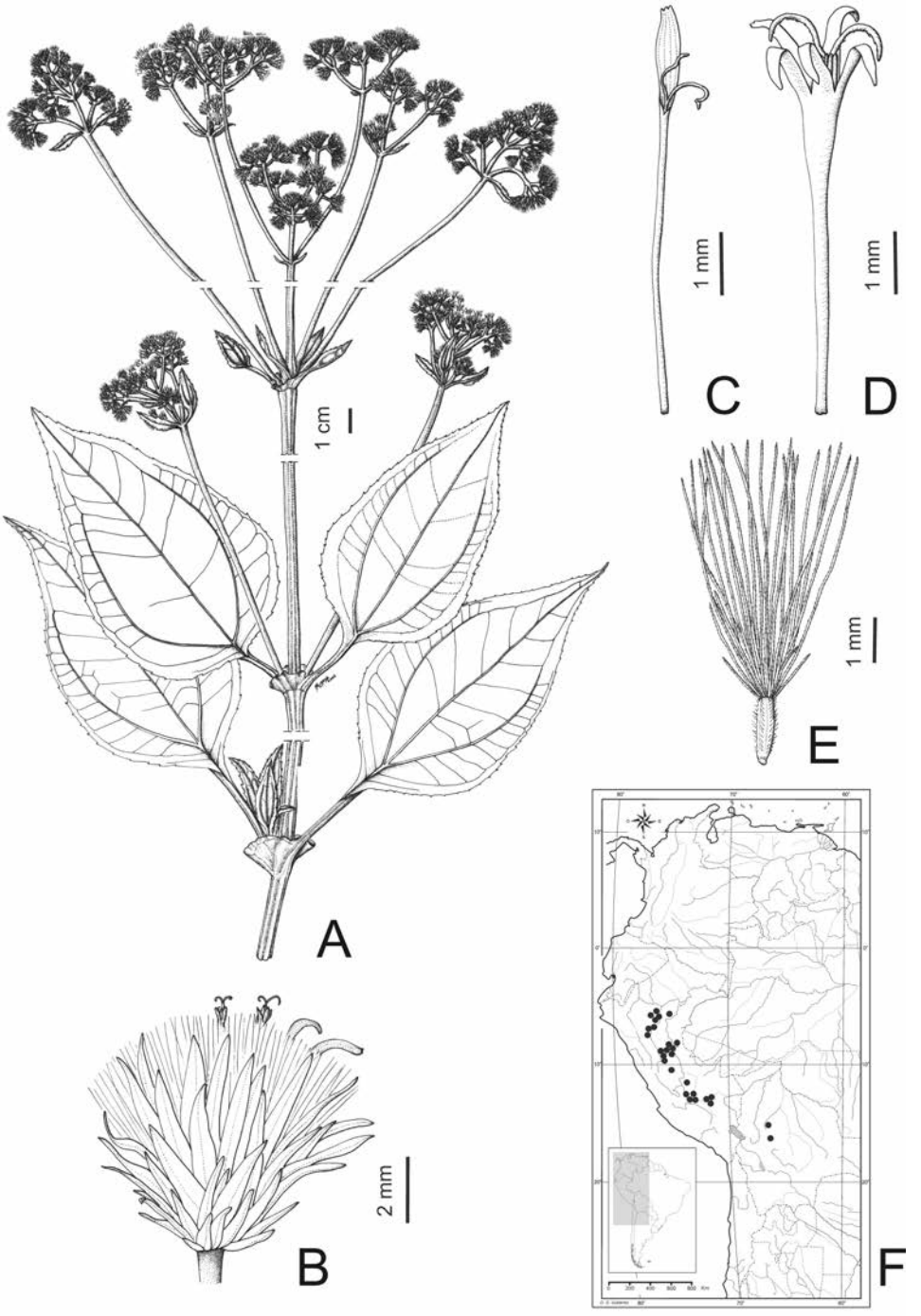

FIG. 19. *Liabum eriocaulon* Poepp. A. Habit (branch). B. Capitulum (only some florets shown). C. Ray floret. D. Disc floret. E. Cypsela and pappus. F. Distribution. (A–E based on *Dillon 2687*, F).

9–13, *Rimachi 4097* (F, MO, NY, US); Distr. Tarapoto, Tarapoto-Yurimaguas, km 13.5, *Rimachi 10089* (NY); Prov. Mariscal Cáceres, Tocache Nuevo, quebrada de Cachiyacu de Lopuna, a Progreso, *Schunke 7617* (MO, NY).—UCAYALI: Prov. Coronel Portillo, ca. 28 km NNE of Tingo María to Pucallpa, *Dillon 2687*, *2688* (F, MO); Divisoria, *Ferreyra 2214* (US); abajo de Divisoria entre Tingo María y Pucallpa, *Ferreyra 4322* (MO); Boquerón entre Tingo María y Pucallpa, *Ferreyra 8112* (MO, US); a Pucallpa, km 910, *Ridoutt s.n.* in 1943 (US).

As mentioned elsewhere, *L. eriocaulon* resembles *L. acuminatum* and *L. amplexicaule* in its reproductive characters, but differs from both species by the ovate rather than elliptic leaf blades.

In the original illustration of *L. eriocaulon* (Poeppig 1843, pl. 249), the pair of pseudostipules seems to be separated at each node. However, the holotype specimen deposited in W (*Poeppig 1280*) shows that the pseudostipules are actually fused at each node (Fig. 19A), a common trait in *Liabum*.

7. Liabum floribundum Willdenow ex Lessing, Linnaea 6: 702–703. 1831.—TYPE: ECUADOR. Pichincha: Cuencam Quitensium, alt. 1351 hex., *Humboldt s.n.* (ex herbarium Willdenow 16370) (holotype: B-W, digital image!).

Liabum eggersii Hieronymus, Bot. Jahrb. Syst. 28: 624–625. 1901. *L. solidagineum* var. *eggersii* (Hieronymus) Cuatrecasas, Anales Univ. Madrid, Ci. 4: 231. 1935.—TYPE: ECUADOR. Manabí: Crescit prope hacienda El Recreo, 28 Jul 1893, *Eggers 15042* (holotype: B [destroyed], photo FM 18100!; lectotype, here designated: LP!; isotypes: F, digital image, GH! K, M, S, US, digital images!).

Liabum nudicaule H. Robinson, Phytologia 35: 37. 1976.—TYPE: PERU. Junín: Prov. Tarma, Chanchamayo valley above La Merced at cumbre Yacumay [Yacunay] near summit, ca. 2000 m, 15 Aug 1957, *Hutchison 1191* (holotype: US!; isotypes: F, NY, UC, digital images!).

Subshrubs or shrubs, 1–5 m tall; stems slightly to strongly costate, hexagonal in cross-section, densely and persistently white-tomentose, sometimes glabrescent; pseudostipules ca. 1 cm long, without auricles, green, glabrous adaxially, densely white-tomentose abaxially. Leaves scattered along the main stem and branches; leaf blades 5.5–16.5 cm long, 3.5–11.5 cm wide, chartaceous, subtriangular, sometimes ovate, apex acute or short-acuminate, base truncate or cordate, sometimes decurrent, margin mucronate-serrate, venation acrodromous or actinodromous, with the pair of lateral veins exceeding the midpoint of the blade but not reaching the apex, surface smooth, green, hirsute adaxially, densely white-tomentose abaxially, usually with coarse stiff brownish hairs on the main veins; petioles 1.5–6.5 cm long, usually not winged. Inflorescence not scapose, umbelliform or corymbiform, dense, with more than 50 capitula; capitula radiate, pedunculate, peduncles up to 5 mm long, densely white-tomentose. Involucre 5–6 mm long, 5.5–6 mm wide, campanulate; phyllaries 50–75 in 5 series, 1.5–5 mm long, 0.25–0.5 mm wide, greenish, sometimes reddish toward the apex, outermost phyllaries ovate, apex acute, pubescence arachnoid, innermost phyllaries linear, apex attenuate, glabrescent; receptacle with chaff ca. 0.3 mm long. Ray florets 25–35; corolla 6–7.5 mm long, yellow, glabrescent or pubescent, tube 2.5–3 mm long, ca. 0.25 mm wide, limb 3.5–4.5 mm long, 0.9–1.1 mm wide, obovate, 4-veined, apex 3-dentate; style 5–6.5 mm long, branches 1.5–2 mm long. Disc florets 20–35; corolla 4.5–6.5 mm long, tubular, tube 1.5–2.5 mm long, ca. 0.25 mm wide, gradually expanded into the limb, yellow, glabrous or pubescent, limb 3–4 mm long, ca. 1 mm wide, lobes ca. 1.5 mm long, 0.35 mm wide, equal to or shorter than the throat, pubescent at the apex; anthers ca. 7 mm long, apical appendage 0.5–0.6 mm long, tails ca.

0.5 mm long; style 7–7.5 mm long, branches 1.5–2.2 mm long, papillae covering style branches and extending down the shaft of the style a distance less than the length of the branches. Cypselae 0.75–1 mm long, 0.3–0.4 mm wide, obconical. Pappus bristles pale yellow, whitish yellow, or yellowish-orange, scabrous; outer series 0.9–1.5 mm long, sometimes absent; inner series up to 4.5 mm long. Chromosome number: n = 18–20 + 1–2 fragments, ca. 20, 19 + 2, 6–7 fragments (Dillon & Turner 1982; Robinson at al. 1985, sub *L. eggersii*; Sundberg & Dillon 1986; Spooner et al. 1995). Fig. 20A–E.

Phenology. Collected in flower throughout the year.

Distribution (Fig. 20F). Ecuador to central Peru; humid montane forests (rain or cloud) or dry or transitional forests with semiarid scrub, margins of streams or rivers, and disturbed environments (roadsides, plantations, and secondary vegetation), on clay, humus, and rocky soils, sometimes on soils derived from limestone; 0–2700 m.

Local Names. Cabo (*Acosta 5210*), espalda blanca (*Acosta 5210*), sacha algodón (*Acosta 6125*, *6359*), shita menuda (*Llatas 1395*).

Representative Specimens. **Ecuador.** Azuay: Río Collay, 3–8 km N of Sevilla de Oro, *Camp E5195* (LIL, LP, NY); Cuenca, *Holway & Holway 969* (GH, NY); ca. 14 km SW of Girón, *King 6686* (MO, NY); Cuenca-San Joaquín-Angas, SO [SW] de Cuenca, entre Bayán y hacienda Pucán, *Jaramillo & Winnerskjold 5382* (F, NY); Azogues, ca. 5–6 km NE of Cuenca, *King & Garvey 6875* (F).—Bolívar: Charquiyacu, *Acosta 6125* (F); Limón, *Acosta 6359* (MO); cerro Copalillo, La Chorrera, *Játiva & Epling 24* (NY); Balsabambo, *Schimpff 270* (MO); Guaranda-Pablo de Atenas-Chillanes, sector Sicoto, 01°50′S, 79°05′W, *Zak & Jaramillo 2547* (F, MO, NY); Chillanes-Bucay, hacienda Tiquibuso, 01°50′S, 79°05′W, *Zak & Jaramillo* 2582 (F); entre Bola de Oro y Panecillo, 01°55′S, 79°05′W, *Zak & Jaramillo 2751* (F, MO, NY).—Cañar: Naranjapata, Río Chanchan, *Schimpff 588* (MO).—Carchi: Tulcán-Maldonado, 10 km from Maldonado, 78°06′W, 00°52′N, *Øllgaard & Balslev 8489* (F, MO, NY, US).—Chimborazo: entre Bucay y hacienda Rosa Mercedes, *Acosta 5210* (MO); hacienda El Carmen, Sibambe, *Acosta 5405* (F); cañon of the Río Chanchan near Huigra, *Camp E3196* (GH, MO, NY, US); Huigra, *Hitchcock 20359* (NY); Huigra, *Holway & Holway 820* (GH); ca. 13 km S of Guasuntos, *King 6609* (NY, US); Riobamba, ca. 39 km NE to Bucay, *King & Garvey 6961* (MO, NY); Chontapamba, between Puela and Baños, *Lugo 743* (F, MO, NY); General Elizalde (Bucay)-Pallatanga, 32 km from Pallatanga, 79°02′W, 02°09′S, *Øllgaard & Balslev 9004* (F, MO, NY, US); 10 km N to Huigra, above Tixan, *Panero & Clark 2902* (US); vicinity of Huigra, hacienda de Licay, *Rose & Rose 22199* (GH, NY, US), *Rose & Rose 22276* (NY), *Rose & Rose 23836* (GH, NY, US); 44.4 km SW of Cajabamba to Bucay, *Stuessy & Nesom 5845* (CTES, LP, SI).—El Oro: Portovelo near Zaruma, *Holway & Holway s.n.* in 1920 (US); between Paccha and Puente Grande, Pueblo Viejo, cordillera Suchiquilla, montaña Huahuel, cordillera de Dumán and Sambotambo, *Steyermark 54131* (NY).—Guayas: 20 km E of Durán, *Böcher et al. 178* (MO); cerro Azul above Casas Viejas, 22 km NW of Guayaquil to Salinas, *Dodson & Dodson 11527* (MO); Las Américas, *Fagerlind & Wibom 290* (GH, NY); near Bucay, *Haught 2889* (LP, MO, US); Teresita, 3 km W of Bucay, *Hitchcock 20500* (NY, US); Riobamba, ca. 33 km NE of El Triunfo, *King & Garvey 6949* (MO, US); Bosque Protector Cerro Blanco, a Salinas, km 15, 79°58′W, 02°10′S, *Rubio et al. 1871* (MO), *Rubio et al. 1986* (US).—Loja: without locality, *Espinosa 565* (F); carretera antigua Yangana-Vilcabamba, 1–6 km de Yangana, *Jaramillo et al. 8712* (F, NY); 2–10 km S of Oño to Saraguro, *King & Almeda 7820* (MO, US).—Los Ríos: Pichilingue, *Acosta 10790* (MO); Cantón Vinces, Jauneche Forest, between Mocachi and Palenque on estero Peñafiel, *Dodson et al. 7151* (MO, US); Jaureche, estero Peñafiel, *Gilmartin 338* (MO); hacienda Santa Lucía, Cantón Vinces, *Mexía 6577* (US).—Manabí: 21 km S of Jipijapa to Guayaquil, 23 km N of Cascol, *Gentry 12224* (MO); Canoa, *Mille 1995* (MO); Jipijapa to Pedro Carbo, 17 km SE of Jipijapa, *Plowman & Alcorn 14362* (F, NY, US); 43.8 km SW of El Carmen, *Stuessy et al. 4913* (MO); ca. 13 km E of Puerto del Cayo, 01°22′S, 80°40′W, *Webster 22639* (US).—Pichincha: Guaruma, km 38 de Saloya, *Acosta 11006* (F); Saloya, *Asplund 7354* (GH); Finlandia, 16 km E of Santo Domingo de los Colorados, *Gentry et al. 12151* (MO); 13 km E of Alluriquin, 35 km E of Santo Domingo, *Hansen et al. 7885* (US).—Tungurahua: entre Leito y La Cima, *Acosta 9043* (F); Valley of Río Pastaza, Hacienda Río Verde Grande, *Asplund 7842* (CTES); Negro, ca. 7 km E of Baños, *King 6541* (F, MO, NY); Riobamba, ca. 6 km SSW of Baños, *King & Garvey 6989* (MO, US); Cusatagua, vicinity of Ambato, *Pacchano 210* (US); Baños, Río Pastaza, *Schimpff 597* (MO); hacienda San Antonio, prope Baños, *Sydow 735* (US); San Antonio, Tungurahua volcano, *Tate 593* (US).—Without Province: Las Máquinas (W Andes), *Anthony & Tate 258* (US). **Peru.** Amazonas: Prov. Bagua, cordillera Colán SE of La Peca, *Barbour 3996* (US).—Cajamarca: Distr. San Juan, Huacraruco,

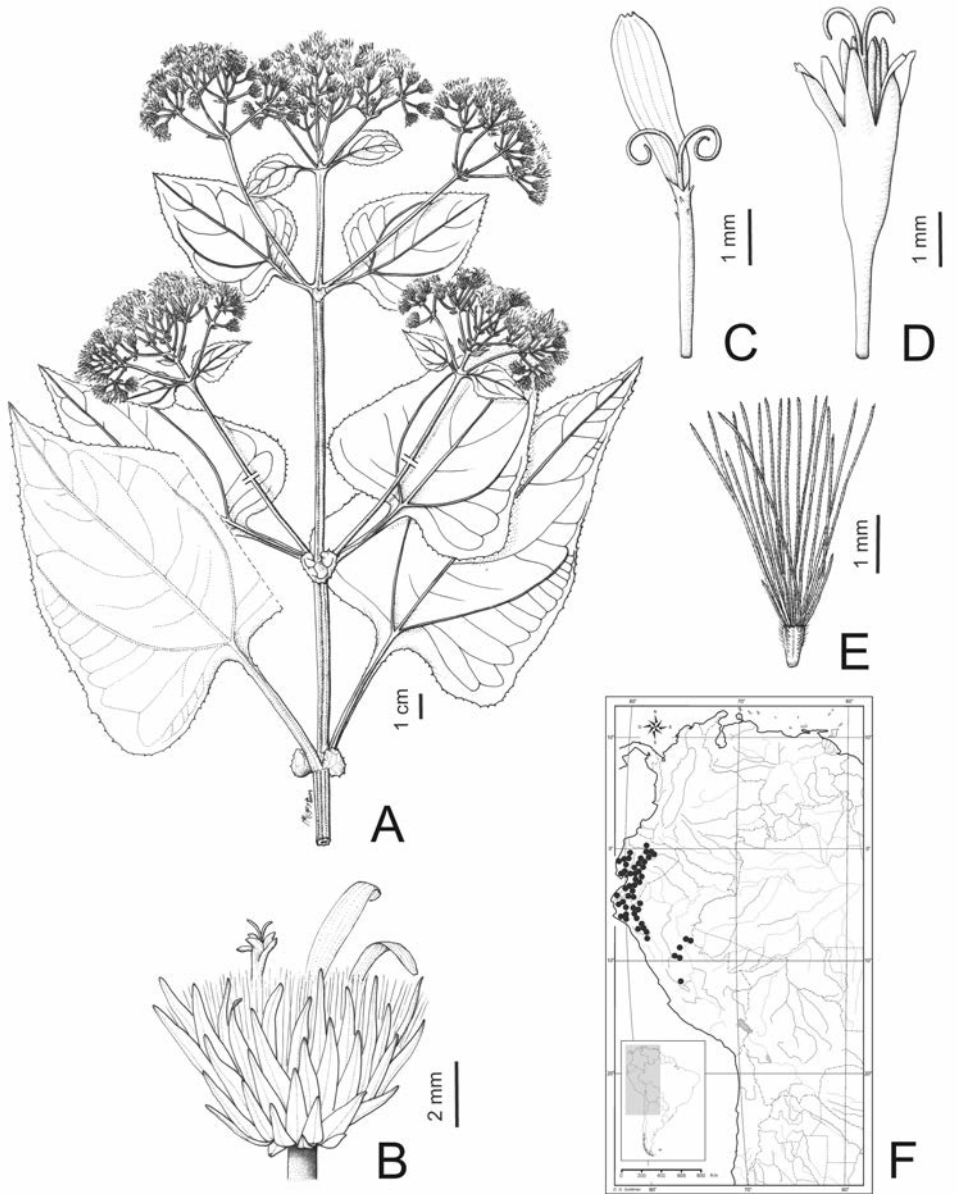

FIG. 20. *Liabum floribundum* Less. A. Habit (branch). B. Capitulum (only some florets shown). C. Ray floret. D. Disc floret. E. Cypsela and pappus. F. Distribution. (Based on: A–B, *King 6541*, MO; C–E, *Hutchinson & Bismarck 6337*, US.)

Cabanillas & Guevara 605 (F); Prov. Hualgayoc, San Miguel, *Díaz s.n.* in 1952 (US); ca. 33 km SW of Cajamarca to San Pedro de Lloc, *Dillon & Turner 1546* (F, MO); ca. 9 km above Cascas to Contumazá, 07°26′S, 78°47′W, *Dillon & Sagástegui 6067* (F); 7 km E of Cajamarca along to Celedin, *King & Bishop 9119* (US); km 131 near Pascamayo to Cajamarca, *Krukoff & Stevens 22050* (F, MO); Prov. Santa Cruz, a Chorro Blanco (Bosque de Monteseco), *Leiva & Lezama 915* (F); Prov. San Miguel, entre El Espino y El Trigal, Bolívar, *Llatas 3009* (F); Prov. Cajamarca, Namora-Matara, *Sagástegui 7747* (MO, NY); Prov. Cajamarca, Río Guayabamba (San Marcos), *Sagástegui 7765* (CTES); Prov. Contumazá, alrededores de Guzmango, *Sagástegui & Mostacero 9041* (US);

Huantum, Asunción, *Sagástegui et al. 10140* (F, MO, US); Contumazá-Chilete, Nanshá, *Sagástegui et al. 15034* (F); Prov. Cajabamba, valle de Condebamba, *I. Sánchez 2876* (F); entre El Gavilán y San Juan, a Pacasmayo, *I. Sánchez 5748* (F).—Cuzco: Vilcabamba, hacienda on Río Chinchao, *Macbride 5192* (F, US).—Huánuco: Prov. Huánuco, road to Mirador to Chinchao, *Mexía 4148* (GH, MO); Prov. Leoncio Prado, Distr. Hermilio Valdizan, cerca de la Divisoria, *Schunke 9432* (F, MO); Prov. Huánuco, cuesta de Carpish, *Vargas 5407* (F).—La Libertad: Prov. Otuzco, Simbal-La Cuesta, *López & Sagástegui 8015* (MO, NY).—Lambayeque: Prov. Ferreñafe, 15–20 km SW of Incahuasi, Río de La Leche, *Dillon & Skillman 4184* (F, MO, NY, US); Riopampa, bajada de Moyán, *Llatas 1375* (F); Prov. Lambayeque, Hualangal-Kerguer, Penachi, *Llatas 1395* (F); Pagay-puente, *Llatas 2560* (F).—Piura: Prov. Huancabamba, Palambla, Canchaque, *López et al. 8791* (F, MO, US); Palambla, *Soukup 4281* (F, LP).—Tumbes: Prov. Zarumilla, Distr. Matapalo, entre cerro San Carlos and Campo Verde, *Simpson & Schunke 484* (F).—Ucayali: Prov. Coronel Portillo, Aguaytía-Pucallpa, *M. Fernández 5681* (LP); entre Divisoria y Boquerón, *Ferreyra 16433* (MO).

The specimen of Humboldt deposited in B is the holotype of *L. floribundum* and is not the type of *Andromachia igniaria* (see comments in Hind & Jeffrey 2001: 2).

The holotype of *L. eggersii* kept at B was destroyed during World War II. Therefore, following Articles 9.9, 9.10, and Recommendation 9.A of the ICN (McNeill et al. 2012), we selected as lectotype the isotype deposited in LP. In the original description, *L. eggersii* was differentiated from *L. floribundum* by its appressed, white-tomentose abaxial leaf surface and bigger capitula. Later, Robinson (1978) differentiated *L. eggersii* from *L. floribundum* by lacking coarse hairs on the abaxial leaf surface. However, we did not find these or other morphological differences between *L. eggersii* and *L. floribundum*, and *L. eggersii* is proposed in this work as a synonym of *L. floribundum*.

In its protologue, *L. nudicaule* was differentiated from *L. eggersii* (sub *L. floribundum*) by its glabrous stems, more ovate leaf blades, and less truncate leaf blade bases. We did not find these or other morphological differences between *L. nudicaule* and *L. floribundum*, and *L. nudicaule* is proposed in this work as a synonym of *L. floribundum*.

Liabum floribundum is reported to be used against snakebite (*Acosta 6359*) and as forage for "cobayos" (Guinea pigs) (*Acosta 5210*). Guanolides, tricyclic sesquiterpenes, widespread triterpenes, and eudesmane and germacrane derivatives have been recorded in this species (Bohlmann et al. 1977; Bohlmann et al. 1980; Bohlmann et al. 1984; Jakupovic et al. 1988).

8. Liabum grandiflorum (Kunth) Lessing, Linnaea 6: 698. 1831. *Andromachia grandiflora* Kunth in Humboldt, Bonpland & Kunth, Nov. Gen. Sp. [H.B.K.], ed. folio, 4: 77–78. 1818 ["1820"]. *Diplostephium grandiflorum* (Kunth) Sprengel, Syst. Veg. (ed. 16) [Sprengel] 3: 544. 1826.—Type: Ecuador. Chimborazo: Crescit locis aridis prope urbem Alausi Quitensium, 1250 hex., July 1801, *Humboldt & Bonpland 3228* (lectotype, here designated: P-272952, digital image!; isolectotypes: B [3228, destroyed], fragment F!, photo FM 18105! P-272951, digital image!, fragment US!).

Liabum weberbaueri Muschler, Bot. Jahrb. Syst. 50(2/3), Beibl. 111: 78–79. 1913.—Types: Peru. Cajamarca: Infra hacienda La Tahoma prope Hualgayoc, 2600 m, 15 May 1904, *Weberbauer 4046* (holotype: B [destroyed], photo FM 18136!); Peru. Cajamarca: Prov. Chota, 2–3 km E of El Campamento, ca. 20 km WNW of Huambos, 06°24′23″S, 79°01′19″W, 22 Apr 1993, *Dillon et al. 6453* (neotype, here designated: F!).

Liabum amplexans S. F. Blake, J. Wash. Acad. Sci. 17: 292–293. 1927.—Type: Ecuador. Loja: Vicinity of Las Juntas, 29 Sept 1918, *Rose et al. 23232* (holotype: US!).

Perennial caulescent erect herbs, 0.4–1.4 m tall; stems not costate or only slightly costate, terete or slightly hexagonal in cross-section, densely and persistently white-tomentose, rarely glabrescent, sometimes with coarsely stiff brownish hairs near the petioles; pseudostipules 0.5–0.9 (–1.5) cm long, without auricles, green, glabrous adaxially, densely white-tomentose abaxially. Leaves scattered along the main stem and branches, sometimes clustered distally; leaf blades 4.7–11.3 cm long, 3.4–9 cm wide, chartaceous, ovate, sometimes subtriangular, apex acute or acuminate, base truncate or subcordate, sometimes cuneate, margin mucronate-serrate, venation acrodromous, with the pair of lateral veins exceeding the midpoint of the blade but not reaching the apex, surface smooth, sometimes bullate, green, glabrous or hirsute adaxially, densely white-tomentose abaxially, usually with coarsely stiff hairs on the main veins; petioles 0.8–2.5 (–3) cm long, winged, wings 0.3–0.9 cm wide, continuous with the pseudostipules. Inflorescence long-scapose or not scapose, umbelliform, branched or unbranched, lax, with 15–50 capitula; capitula radiate, pedunculate, peduncles up to 40 (–70) mm long, densely white-tomentose. Involucre 7–13 mm long, 8–13 mm wide, campanulate; phyllaries (65–) 80–140 in 5–6 series, 1.5–8.5 mm long, 0.4–0.8 mm wide, greenish, sometimes reddish toward the apex, outermost phyllaries ovate, apex acute, pubescence arachnoid, innermost phyllaries linear, apex attenuate, glabrescent; receptacle with chaff ca. 0.3 mm long. Ray florets 30–45; corolla 7–9.5 mm long, yellow, pubescent, tube 2.5–4 mm long, 0.2–0.3 mm wide, limb 4.5–5.5 mm long, 1–1.5 mm wide, obovate, 4-veined, apex 3-dentate; style 8–10 mm long, branches ca. 2.5 mm long. Disc florets 85–95; corolla 6–7.5 mm long, tubular, tube 2.5–3.5 mm long, ca. 0.3 mm wide, gradually expanded into the limb, yellow, glabrescent or pubescent, limb 3.5–4 mm long, ca. 0.7 mm wide, lobes 1–1.5 mm long, ca. 0.25 mm wide, shorter than the throat, pubescent at the apex; anthers 3–4 mm long, apical appendage 0.5–0.8 mm long, tails 0.5–0.7 mm long; style ca. 9 mm long, branches 2–2.5 mm long, papillae covering style branches and extending down the shaft of the style a distance equal to the length of the branches. Cypselae 1.2–1.9 mm long, 0.4–0.5 mm wide, obconical to ellipsoid. Pappus bristles pale yellow or yellowish orange, scabrous; outer series 1–1.5 mm long, sometimes absent; inner series 5.5–6 mm long. Chromosome number unknown. Fig. 21A–E.

Phenology. Plants with flowering capitula were collected from April to July.

Distribution (Fig. 21F). Southern Ecuador and northwestern Peru; hillsides of montane forests and road margins, clay and rocky soils; 900–3000 m, one specimen (*Leiva & Leiva 540a* from Otuzco province) from 270 m.

Representative Specimens. **Ecuador.** Loja: Quebrada de Chirino, *André 4702* (GH); between Loja and San Lucas, *Hitchcock 21452* (GH, NY).—Chimborazo: Alausí, *Asplund 6815* (CTES); between Huigra and Naranjapata, *Asplund 7749* (GH); Alausi, *Bonpland 3235* (P); Río Chanchan near Huigra, *Camp E3123* (F, GH, NY, MO). **Peru.** Amazonas: Prov. Chachapoyas, Utcubamba river valley, between Tingo and Samanaga, ca. 60 km from Chachapoyas, Chachapoyas-Celendín, 77°50′W, 06°28′S, *Smith & Cabanillas 7149* (MO, US).—Cajamarca: Distr. Choropampa, arriba de Choropampa, *Cabanillas & Guevara 433* (F); Distr. San Bernardino, El Alovishi, *Cabanillas & Guevara 515* (F); Distr. San Juan, sobre San Juan, *Cabanillas & Guevara 639* (F); Prov. Chota, alrededores de Llama, *López & Sagástegui 5313* (MO); Prov. Contumazá, alrededores de Guzmango, *Sagástegui 12746* (MO); Tambo La Lima, Cascas-Contumazá, *Sagástegui et al. 14646* (F); alrededores de San Pablo, *Sagástegui et al. 15378* (F); Prov. Cajamarca, Distr. San Juan, entre San Juan y La Asunción, *Sánchez 463* (F, LP); Prov. San Pablo, Distr. San Bernardino, Sangal, *Sánchez & Zarpán 627* (F); Distr. San Bernardino, San Pablo, quebrada El Chingo, *Sánchez & Zarpán 641* (F); Distr. San Juan, San Juan-Huacraruco, *Sánchez 715* (F); Prov. Hualgayoc, cerro La Llama de las Ventanillas, al SO [SW] de Bambamarca, *Sánchez et al. 5699* (F).—La Libertad: Prov. Otuzco, abajo de Piedra Gorda, Salpo-Samne, *Leiva & Leiva 540a* (F, US); Prov. Otuzco, Huaranchal, *López et al. 2678* (LP).—Piura: Prov. Ayabaca, Pingola, *López et al. 7808* (LP).

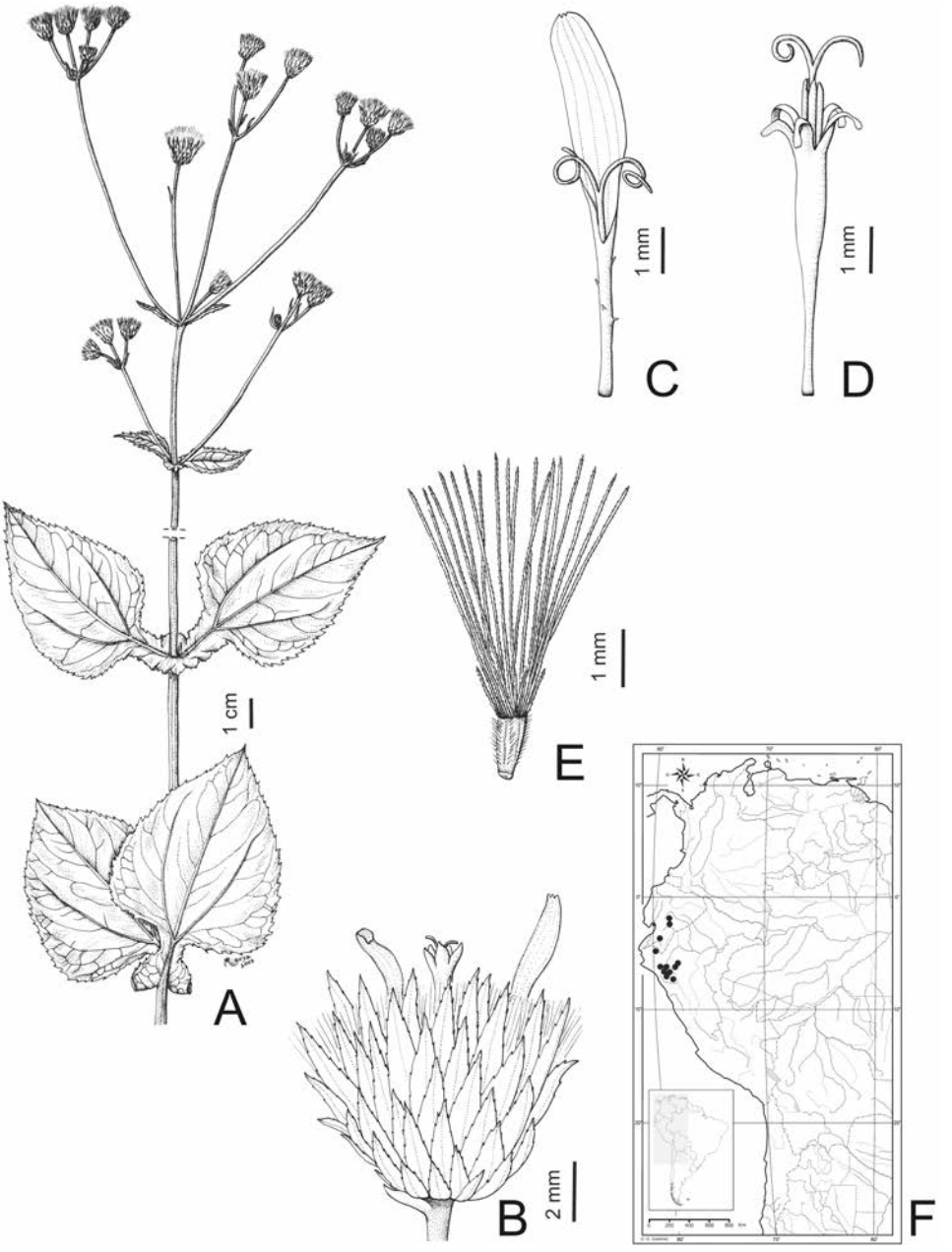

FIG. 21. *Liabum grandiflorum* (Kunth) Less. A. Habit (branch). B. Capitulum (only some florets shown). C. Ray floret. D. Disc floret. E. Cypsela and pappus. F. Distribution. (Based on: A–B, *Cabanillas & Guevara 433*, F; C–E, *Sagástegui 12746*, MO.)

There is morphological variation between small plants and large plants. In the smaller plants of *L. grandiflorum* the leaves are commonly clustered at the stem apex with a scapose umbelliform inflorescence (e.g., *Hitchcock 21452*, GH). On the other hand, in larger plants the leaves are distributed along the stem with a non-scapose but umbelliform and highly branched inflorescence (e.g., *J. Sánchez 715*, F).

9. Liabum igniarium (Humboldt & Bonpland) Lessing, Linnaea 6: 701. 1831. *Andromachia igniaria* Humboldt & Bonpland, Pl. Aequinoct. [Humboldt & Bonpland] 2: 104 + pl. 112. 1812. *Diplostephium igniarium* (Humboldt & Bonpland) Sprengel, Syst. Veg. (ed. 16) [Sprengel] 3: 544. 1826.—Type: Ecuador. Pichincha: près Chillo, situé à quatre lieues au sud-est de la ville de Quito, *Humboldt & Bonpland 2237* (lectotype, here designated: P, digital image!; isolectotypes: B [destroyed], photo FM 18109! K ["*Humboldt s.n.*"], digital image! fragment, US!).

Liabum lehmannii Hieronymus, Bot. Jahrb. Syst. 19(1): 61. 13 Apr 1894.—Type: Ecuador. Cuenca: Crescit in fruticetis densis prope Chagal et Molleturo in declivibus mediis Andi[n]um occidentalium, 2000–2600 m, Jul–Aug, *Lehmann 4896* (holotype: B [destroyed], photo FM 18111!; lectotype, here designated: K, digital image!, fragment US!).

Subshrubs or shrubs, 1–4 m tall; stems costate or not costate, terete or slightly hexagonal, densely and persistently white-tomentose; pseudostipules 1.5–3.5 cm long, with or without auricles, auricles up to 1.2 cm long, sometimes convergent and overlapping, green, glabrous adaxially, densely white-tomentose abaxially. Leaves scattered along the main stem and branches; leaf blades 5.5–18.5 cm long, 5.5–9 (–14) cm wide, chartaceous or coriaceous, ovate to broadly ovate or broadly elliptic, apex short-acuminate, base rounded or truncate, sometimes slightly cuneate, margin mucronate-serrate, venation acrodromous, with the pair of lateral veins exceeding the midpoint of the blade but not reaching the apex (in larger leaves a more basal, second pair of veins may be present), surface smooth, green, glabrous adaxially, densely white-tomentose abaxially; petioles 1.5–4.5 (–8) cm long, not winged. Inflorescence not scapose, umbelliform, lax, with more than 50 capitula; capitula radiate, pedunculate, peduncles up to 30 mm long, densely white-tomentose. Involucre 6–10 mm long, 6.5–10 mm wide, campanulate; phyllaries 60–75 in 5–7 series, 1.5–6 mm long, 0.5–1 mm wide, greenish, sometimes reddish toward the apex, outermost phyllaries ovate, apex acute, pubescence arachnoid, innermost phyllaries linear, apex attenuate, glabrescent; receptacle with chaff ca. 0.5 mm long. Ray florets 25–50; corolla 8–12.5 mm long, yellow, pubescent, tube 3.5–5.5 mm long, 0.2–0.25 mm wide, limb 4.5–7 mm long, 1–1.5 mm wide, obovate, 4-veined, apex 3-dentate; style 7.5–9.5 mm long, branches 2.5–3.2 mm long. Disc florets 35–60; corolla 7–9 mm long, tubular, tube 3.5–4.5 mm long, ca. 0.25 mm wide, gradually expanded into the limb, yellow, pubescent, limb 3.5–4.5 mm long, 0.5–1 mm wide, lobes 1.5–2 mm long, ca. 0.25 mm wide, shorter than the throat, pubescent at the apex; anthers 2.5–3 mm long, apical appendage 0.4–0.6 mm long, tails 0.2–0.5 mm long; style 7–10 mm long, branches 2–2.3 mm long, papillae covering style branches and extending down the shaft of the style a distance equal to the length of the branches. Cypselae 0.9–1.2 mm long, 0.3–0.4 mm wide, obconical to ellipsoid. Pappus bristles yellow or yellowish orange, scabrous; outer series 0.7–2 mm long, sometimes absent; inner series up to 6 mm long. Chromosome number unknown. Fig. 22A–E.

Phenology. Plants with flowering capitula were collected in February and from April to December.

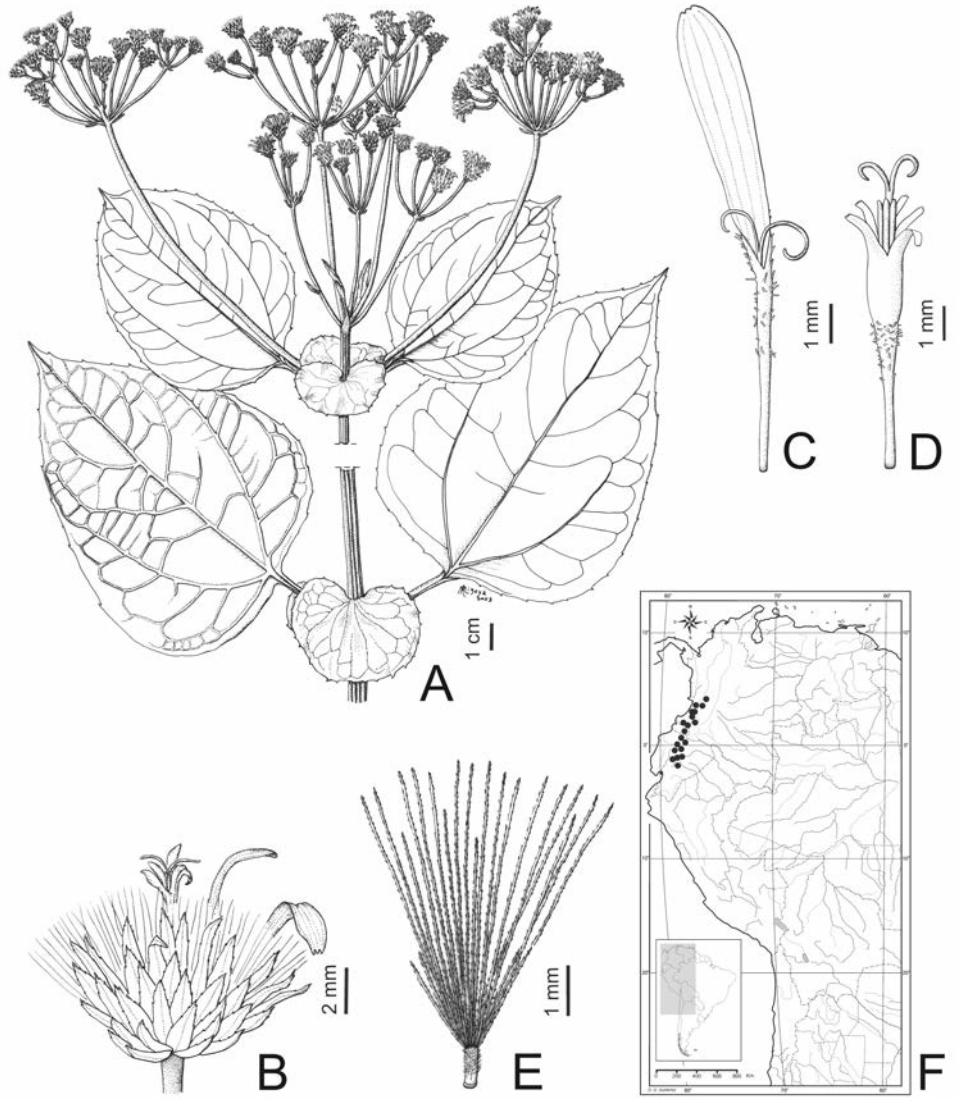

FIG. 22. *Liabum igniarium* (Humb. & Bonpl.) Less. A. Habit (branch). B. Capitulum (only some florets shown). C. Ray floret. D. Disc floret. E. Cypsela and pappus. F. Distribution. (Based on: A–B, *Flora Ecuatoriana 1093*, GH; C–E, *Peñafiel & Ortiz 249*, MO.)

Distribution (Fig. 22F). Southwestern Colombia to Ecuador (Carchi to Chimborazo Provinces); humid montane forests on humus and volcanic soils, secondary forests, stands of eucalyptus, and dry areas; 1690–3350 (–4300) m.

Local Names: Hierba de Santa María (Humboldt & Bonpland 1812: 104), machinbí (*Pennell & Killip 6381*), salvia (*Dryander 1644*), Santa María (*Lehmann 7970*).

Representative Specimens. **Colombia.** Cauca: between Silvia and Pitayó, *Core 59* (US); Carpinterías [Carpintero], entre cerros Munchique y Altamira, *Cuatrecasas & Pérez 6128* (F, US); entre Popayán y Puracé,

quebrada de Aguarregada, *Cuatrecasas 13767* (F); Puracé, Tablón, *Cuatrecasas 14545* (F); Río Vinagrita Tibia, Puracé, *Dryander 1644* (US); Silvia, *Espinal & Ramos 2978* (US); cerro Munchique, *Espinal & Ramos 3217* (US); W of Tambo, *Haught 5171* (F, LP, US); Paniquita, Popayán, *Lehmann 5261* (F, GH, K, LP, NY); [probably Popayán], *Lehmann 7970* (F, K, LP); Cuatro Esquinas to Río Piendamo, *Pennell & Killip 6381* (GH, US); Mount Puracé, *Pennell & Killip 6583* (US); Calaguala, Coconuco, *Pennell 7178* (GH, NY); San José, San Antonio, *Pennell & Killip 7429* (NY); Mount Trompo del Puerco, *Pennell 7510* (GH, NY, US); entre Popayán y Puracé, quebrada de Filipilla, *Pérez & Cuatrecasas 5821* (F, US); Coconuco, *Uribe 3794* (NY); El Tambo, Munchique, *von Sneidern 515* (F, GH, NY); El Tambo, Chisquío, *von Sneidern 5567* (US); Popayán, *Yepes 12* (F); Coconuco, *Yepes 345* (F).—Nariño: Túquerres, *André K263* (NY); E of Aponte, Río Majinsanoy, *Bristol 1183* (GH, US); region of Pedregal, between Pasto and Túquerres, S of Yacuanquer, *Schultes & Villareal 7872* (F, GH, US); Cebadal to Yacuanquer, km 15–25, *Schultes & Villareal 7937* (F, GH, US); Túquerres, *Triana 1140* (MO, US).—Quindio: Quindio, *Linden 1051* (F, GH); Mariquita, Quidio, *Triana 1141* (NY, US).—Valle del Cauca: Río Bugalagrande, Loma de Barragán, La Parilla a La Machuca, *Cuatrecasas 20754* (F); Río Bugalagrande, quebrada de La Palma, quebrada de los Osos, *Cuatrecasas 20933* (F).—Without Department: Quito-Popayán-Bogotá, *Hartwey 1088* (NY); *Lehmann 4699* (F, K), *7970* (F, K, LP); Parque Nacional Equinoccial, *von Retzell 62* (SI).
Ecuador. Bolívar: Vinchoa, *Acosta 5934* (F); Valley of Río Llangama near Guaranda, *Asplund 8217* (CTES); Guaranda-Pueblo Viejo, 12 km de Guaranda, *Larsen 85* (F).—Carchi: Cantón Tulcan, Olivos to Moran, *Mexia 7470* (F).—El Oro: Yacubiña, cordillera Chilchiles, Zaruma, *Espinosa 2089* (F).—Imbabura: near Otavalo, *Hart 1690* (GH, US); Imbabura, *Hirsch E65* (NY); laguna Cuicocha, 30 km W of Ibarra, 78°22′W, 00°18′N, *Holm-Nielsen et al. 6296* (NY); [probably Imbubura], *Lehmann 4699* (F, K); Cantón Ibarra, Tejera de Santa Lucía, *Mexia 7389* (F, US); Cotacachi-Apuela, 33–36 km from Cotacachi, 78°26′W, 00°20′N, *Øllgaard & Balslev 8736* (NY); Cantón Cotacachi, Reserva Ecológica Cotacachi-Cayapas, laguna Cuicocha, 78°22′W, 00°18′N, *Peñafiel & Trujillo 169* (MO, US), *Peñafiel & Ortiz 249* (MO, US), *Peñafiel et al. 404* (MO, NY, US); Cantón Cotacachi, Reserva Ecológica Cotacachi-Cayapas, laguna Cuicocha, islote Teodoro Wolff, 78°22′W, 00°18′N, *Peñafiel et al. 232* (MO, US), *Peñafiel et al. 322* (MO, NY, US); Cantón Cotacachi, Reserva Ecológica Cotacachi-Cayapas, laguna Cuicocha, 78°22′W, 00°18′N, *Peñafiel et al. 246* (MO, US); Cantón Cotacachi, Reserva Ecológica Cotacachi-Cayapas, laguna Cuicocha, islote Yerovi, 78°22′W, 00°18′N, *Peñafiel et al. 629* (MO); Cantón Cotacachi, Morocho, above Apuela, *Plowman et al. 3837* (GH); 2–2.5 km E of laguna Cuicocha, 00°18′N, 78°20′W, *Webster 23138* (US); Otonabo-Mojanda Cojas, hacienda Rubí, *Zak & Jaramillo 3501* (CTES, F, NY, US).—Pichincha: Patichubamba, Sangolqui, *Acosta 8293* (F); Guápulo, *Asplund 16693* (NY); Mount Pichincha, Quito, *Barclay et al. 7803* (US); cráter del volcán Pululahua, NW of Quito, *Barclay et al. 7882* (US); Reserva Geobotánica Pululahua, Parroquia Calacalí, 00°05′N, 78°30′W, *Cerón 1494* (F, MO, US); Cantón Quito, Reserva Geobotánica Pululahua, 00°05′N, 78°30′W, *Cerón & Benavídez 1909* (MO); Cantón Rumiñahui, Bosque Protector Pasochoa, 00°27′S, 78°28′W, *Cerón & Alarcón 4824* (MO); Panecillo, *Couthouy s.n.* in 1855 (GH, NY); cráter del Pululahua, *Flora Ecuatoriana 1092* (GH); pie del Pichincha, *Flora Ecuatoriana 1093* (GH); quebrada Miraflores, *Flora Ecuatoriana 1094* (GH); Pasachoa Forest Reserve, 00°30′S, 78°28′W, *Funk 11458*, *11459* (US); Pasochoa, S of Quito, 00°30′S, 78°30′W, *Gentry et al. 60286* (MO); W of Nono, *Harling et al. 10255* (F, MO, NY, US); [prope pagum Guapulo, ad Rumibamba, in Valle Chillo non longea Quito], *Hartweg 1088* (NY); monte Pichincha, *Heilborn 738* (F, US); Reserva de Pululahua, 20 km N of Quito, 00°00′, 78°30′W, *Hekker & Hekking 10055* (US); Quito, *E. Holway & M. Holway 932* (GH, NY); W of Quito above Miraflores, *Hudson 1169* (MO, NY); Quito, *Humboldt s.n.* (K); base of Pichincha and valley of Chillo, *Jameson s.n.* (NY); near Quito, *Jameson 14* (NY); towards the base of Pichincha, *Jameson 436*, *828* (F, GH, US); carretera Calacalí-Nieblí, Reserva Pululagua, *Jaramillo 9660* (F, NY); prope Quito, *Mille 595* (GH, MO, NY, US); slopes of Pichincha, W of Quito, *Ownbey 2607* (MO, US); Pululahua, *Padilla 1014* (MO); 12 km S of Quito a Latacunga, *Panero 781* (US); vicinity of Uyumbicho, *Penland & Summers 946* (F, GH); above Balsapampa, *Rimbach 787* (F, NY); km 37–50 along Río Saboya, *Steyermark 52545* (NY); 1 km W of Santa Rosa to Mindo, *Stuessy et al. 4875* (MO); Guapulo, prope Quito, *Sydow 36* (US); 20 km N of Quito, Ventana del Pululahua, *Vuilleumier 108* (GH); Quito-Nono entre Nono y Rundopampa, 00°03′S, 78°35′W, *Zak & Jaramillo 2058* (CTES, NY, US).—Tungurahua: between Baños and Mera above Río Pastaga, *Ornduff 9680* (NY).—Without Department: *Bonpland s.n.* (P).

Liabum igniarium is very similar to *L. barclayae* but differs in its wider leaves (up to 14 cm) and longer pseudostipules (1.5–3.5 cm). The formation of galls is common in this species (Fig. 7A), as is also the case in *L. barclayae* and *L. solidagineum*.

The pubescence of stems and leaves of *L. igniarium* plants is reported to be used as tinder (Humboldt & Bonpland 1812: 106; *Jameson 14*, *828*). It is also reportedly used as

an astringent (Humboldt & Bonpland 1812: 106) and for wounds (*Cerón 1494*). Humboldt and Bonpland (1812: 106) also suggested potential ornamental use of this species because of its appearance. The flowers are frequently fragrant.

10. Liabum kingii H. Robinson, Phytologia 34: 288–290. 1976.—Type: Ecuador. Tungurahua: Along the road to Puyo, ca. 2 km E of Río Negro, ca. 4300 ft, 21 Jan 1974, *King 6563* (holotype: US!; isotypes: F, MO, NY, digital images!).

Liabum trianae H. Robinson, Phytologia 34: 291–292. 1976.—Type: Colombia. Tolima: Central Cordillera, ca. 23 km west-southwest of Fresno, ca. 2350 m, 16–17 July 1965, *King, Guevara, and Forero 6006* (holotype: US!; isotypes: COL, digital image! F, digital image! NY!).

Subshrubs or shrubs, sometimes climbing, 0.5–2 m tall; stems not costate, terete or slightly hexagonal in cross-section, with dense persistent or deciduous white-tomentose pubescence; pseudostipules up to 1.5 cm long, with auricles, divergent or convergent and overlapping, up to 0.6 cm, green, glabrous adaxially, densely white-tomentose abaxially. Leaves scattered along the main stem and branches; leaf blades 4.5–12 cm long, 2.5–5.5 cm wide, chartaceous, ovate, apex acuminate or acute, base cuneate, margin mucronate-serrate, venation acrodromous, with the pair of lateral veins reaching the apex of the blade, surface smooth, glabrous or glabrescent adaxially, densely white-tomentose abaxially; petioles 0.5–4.5 cm long, not winged. Inflorescence not scapose, umbelliform or corymbiform, lax, with more than 50 capitula; capitula radiate, pedunculate, peduncles up to 8.5 mm long, densely white-tomentose. Involucre ca. 4.5 mm long, 5–5.5 mm wide, hemispherical; phyllaries 55–70 in 5–6 series, 1–4 mm long, 0.3–0.4 mm wide, greenish, sometimes purplish toward the apex, outermost phyllaries ovate, apex acute, pubescence arachnoid, innermost phyllaries linear, apex attenuate, glabrescent; receptacle with chaff ca. 2 mm long. Ray florets 20–45; corolla 7–11 mm long, yellow, pubescent, tube ca. 3 mm long, 0.2 mm wide, limb 4.5–7 mm long, ca. 1 mm wide, obovate, 4-veined, apex 3-dentate; style 5–5.5 mm long, style branches 1.5–2.5 mm long. Disc florets 21–51; corolla 5–7 mm long, tubular, tube ca. 3.5 mm long, 0.2 mm wide, abruptly expanded into the limb, yellow, pubescent, limb 2.5–3.2 mm long, ca. 1 mm wide, lobes ca. 2 mm long, 0.3 mm wide, longer than the throat, pubescent at the apex; anthers 3–3.2 mm long, apical appendage 0.7–0.8 mm long, tails 0.2–0.3 mm long; style 6.5–7.5 mm long, branches 1.8–2.2 mm long, papillae covering style branches and extending down the shaft of the style a distance less than the length of the branches. Cypselae ca. 1 mm long, 0.3 mm wide, obconical to ellipsoid. Pappus bristles yellowish orange, scabrous; outer series ca. 1 mm long, sometimes absent; inner series 4–5 mm long. Chromosome number: $n = 17–20$ (Robinson et al. 1985). Fig. 23A–E.

Phenology. Plants with flowering capitula have been collected in January, February, and from May to October.

Distribution (Fig. 23F). Western Colombia and Ecuador; volcanic, sandy, and rocky soils, rainy or cloud premontane tropical forests, margins of rivers, and in disturbed areas such as margins of roads; 1000–2800 m.

Representative Specimens. **Ecuador.** Imbabura: Lita, *Acosta 12283* (F).—Loja: Veracruz, *Lugo 26* (F, MO, NY).—Morona-Santiago: Cantón Palora, Río Palora, 78°55′W, 01°40′S, *Gudiño & Velasco 1524* (MO, US).—Napo: volcán Reventador, Baeza-Lago Agrio, *Jaramillo & Grijalva 12942* (F, NY); volcán El Reventador, *Jaramillo et al. 13106* (NY); entre Galindo y Río Malo, *Jaramillo & Grijalva 13223* (NY); to Tena, ca. 18 km N of Puyo, *King 6568* (F, MO, NY, US); Cantón El Chaco, Proyecto Hidroeléctrico Coca, Río Quijos, ca. 10 km al

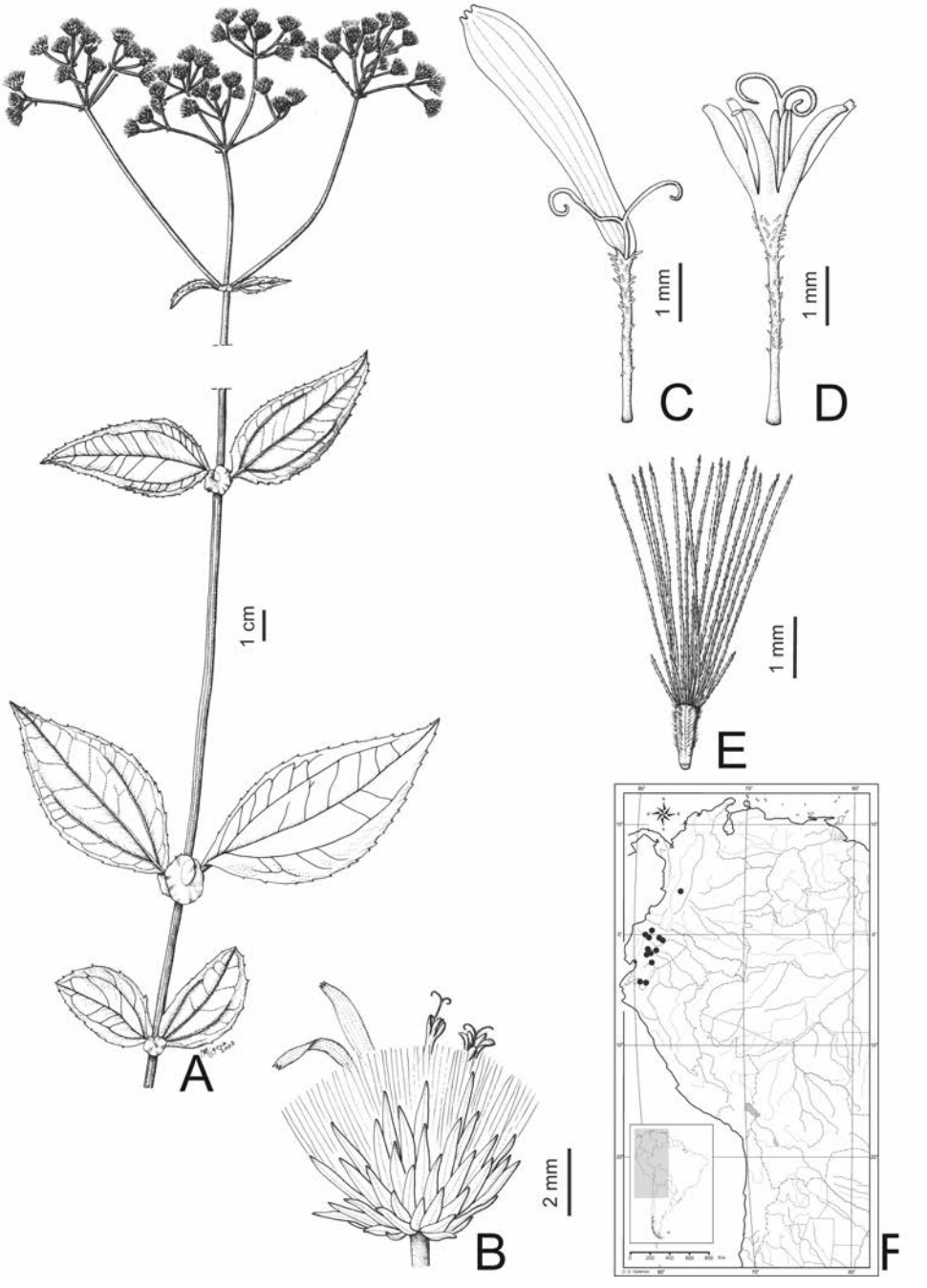

FIG. 23. *Liabum kingii* H. Rob. A. Habit (branch). B. Capitulum (only some florets shown). C. Ray floret. D. Disc floret. E. Cypsela and pappus. F. Distribution. (A–E based on *Stuessy & Nesom 5808*, LP.)

S de Reventador, 77°39′W, 00°11′S, *Palacios 5906* (MO, US).—Pastaza: Mera, Pindo path, *Harling et al. 10036* (F, MO, NY, US); ca. 5 km E of Mera, to Shell Mera, 78°05′W, 01°28′S, *Øllgaard et al. 35517* (F, MO, NY, US).—Tungurahua: El Topo, *Acosta 10284* (F); between Ambato and Baños, *D'Arcy 14000* (US); Baños, *Ellenberg 292* (US); Pastaza river, between Baños and Cashurco, *Hitchcock 21843* (NY, US); to Puyo, ca. 2 km E of Río Negro, *King 6555* (MO, NY); without locality, *Sodiro s.n.* in 1901 (US); in Andibus Ecuadorensibus [Tungurahua], *Spruce 5122* (F, NY); 5.3 km E of Río Verde to Puyo, *Stuessy & Jansen 4964* (MO); Baños toward Chaupi and volcán Tungurahua, *Stuessy & Nesom 5808* (CTES, LP).—Zamora-Chinchipe: 33 km E of Loja to Zamora, *King & Almeda 7936* (US); 38.2 km E of Reina del Cisne Church to Zamora, *Panero & Clark 2969* (NY).—Province uncertain: Pastaza River [runs through provinces of Morona-Santiago, Pastaza, Tungurahua], *Rimbach 279* (F, NY).

In its protologue, *L. trianae* was differentiated from *L. kingii* by its more closely serrate leaf margins, larger numbers of ray florets (ca. 38–45 versus ca. 25, respectively) and disc florets (ca. 50 versus ca. 25, respectively), and disc corollas with a longer throat (ca. 1–1.3 mm long versus ca. 0.5 mm long, respectively). With examination of a larger number of specimens, however, we found a continuous range of variation in all of these characters and therefore propose *L. trianae* to be a synonym of *L. kingii*. The Colombian type locality of *L. trianae* represents the northern limit of distribution of *L. kingii*.

In a recent phylogenetic study of Liabeae (Funk et al. 2012) the species *L. kingii* appears as sister to *L. asclepiadeum*. *Liabum kingii* is easily distinguishable from *L. asclepiadeum*, however, by its wingless petiole, auriculate disciform pseudostipules, hemispherical involucre, radiate capitulum, and the obovate and 4-veined limb of the ray florets. *Liabum kingii* resembles *L. dillonii* and *L. saloyense* in its general aspect, but differs from *L. dillonii* by its auriculate pseudostipules and from *L. saloyense* by its leaves lacking brownish hairs mixed with the abaxial white tomentum.

11. Liabum macbridei H. Robinson, Phytologia 34: 290–291. 1976.—Type: Peru. Huánuco: Río Huallaga Cañon below Río Santo Domingo, about 4000 ft, 3 June 1923, *Macbride 4224* (holotype: US!; isotypes: F, digital image! GH!).

Subshrubs or shrubs, sometimes climbing, 0.5–2.5 m tall; stems not costate, terete, densely and persistently white-tomentose; pseudostipules ca. 0.5 cm long, without auricles, glabrescent adaxially, densely white-tomentose abaxially. Leaves scattered along the main stem and branches; leaf blades 9.5–20.5 cm long, 6.5–12.5 cm wide, chartaceous, broadly ovate, apex acute, base cuneate, margin mucronate-serrate, venation acrodromous, with the pair of lateral veins exceeding the midpoint of the blade but not reaching the apex, surface smooth, glabrous adaxially, densely white-tomentose abaxially; petioles 2–4.5 cm long, generally not winged, occasionally narrowly winged distally by decurrence of blade. Inflorescence not scapose, umbelliform, lax, with 25–50 capitula; capitula radiate, pedunculate, peduncles up to 20 mm long, densely white-tomentose. Involucre 6.5–7 mm long, 5.5–7.5 mm wide, campanulate; phyllaries 55–80 in 5–6 series, 1–6 mm long, 0.4–0.6 mm wide, greenish, outermost phyllaries ovate, apex acute, pubescence arachnoid, innermost phyllaries linear, apex attenuate, glabrescent; receptacle with chaff ca. 2 mm long. Ray florets 25–35; corolla 10–12 mm long, yellow, pubescent, tube 3.5–4.5 mm long, ca. 0.35 mm wide, limb 6.5–7.5 mm long, 1–1.5 mm wide, obovate, 4-veined, apex 3-dentate; style ca. 8 mm long, branches 2.5–3 mm long. Disc florets 35–40; corolla 6–7 mm long, tubular, tube 2.5–3 mm long, 0.2–0.3 mm wide, gradually expanded into the limb, yellow, glabrescent or pubescent, limb 3.5–4 mm long, 0.8–0.9 mm wide, lobes 1.5–2 mm long, ca. 0.3 mm wide, equal to or shorter than the throat, pubescent at the apex; anthers 2.8–3 mm

long, apical appendage 0.6–1 mm long, tails 0.8–1 mm long; style 8–9.2 mm long, branches 2–3.2 mm long, papillae covering style branches and extending down the shaft of the style a distance equal to the length of the branches. Cypselae ca. 1 mm long, 0.4–0.5 mm wide, cylindrical to ellipsoid. Pappus bristles pale yellow or yellowish orange, scabrous; outer series ca. 1.5 mm long, sometimes absent; inner series up to 4.5 mm long. Chromosome number unknown. Fig. 24A–E.

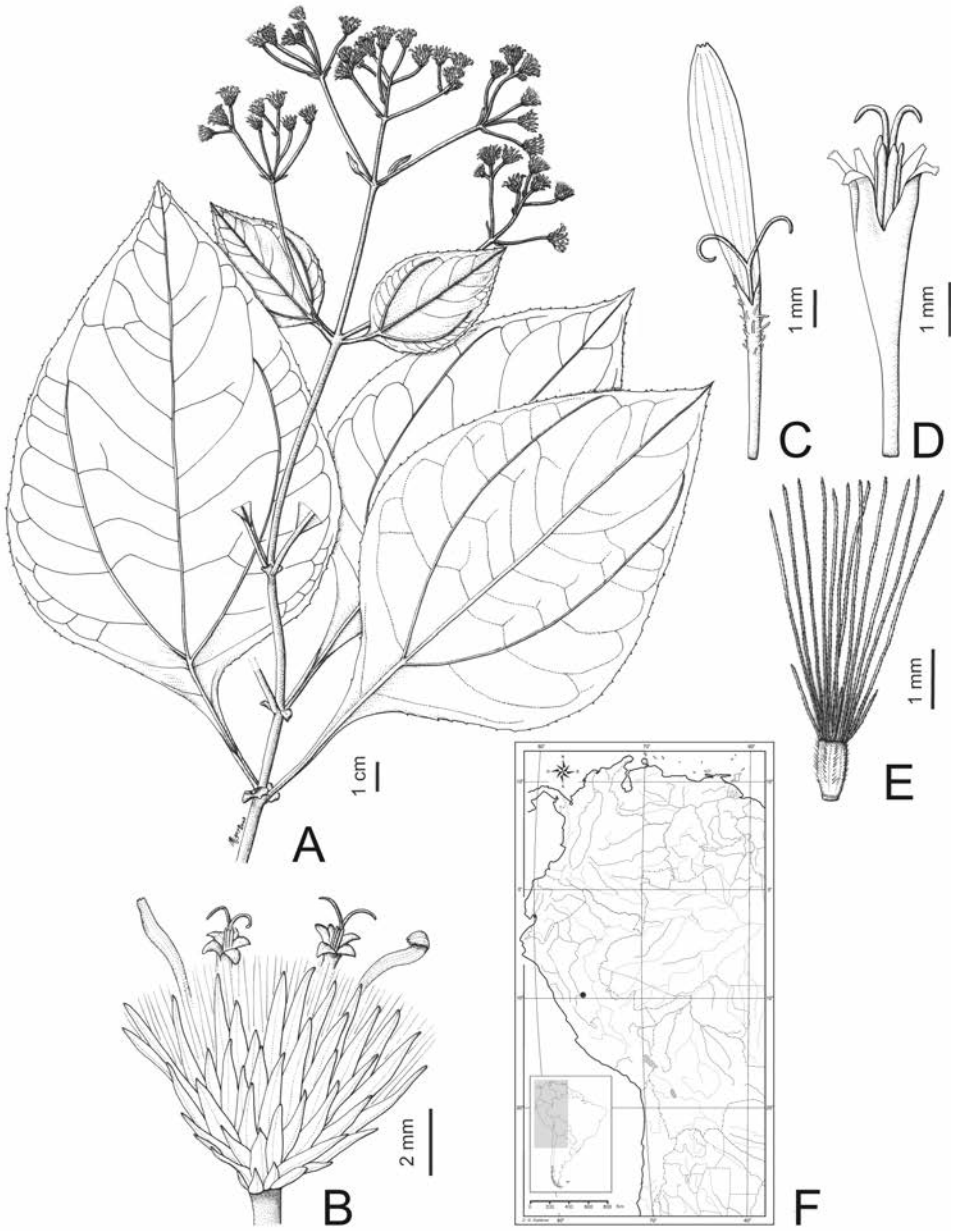

FIG. 24. *Liabum macbridei* H. Rob. A. Habit (branch). B. Capitulum (only some florets shown). C. Ray floret. D. Disc floret. E. Cypsela and pappus. F. Distribution. (A–E based on *Macbride 4224*, US.)

Phenology. Plants with flowering capitula were collected in June.

Distribution (Fig. 24F). Endemic to the Department of Huánuco, Peru, the only known specimen collected near the Huallaga River at ca. 1200 m.

Liabum macbridei resembles *L. vargasii* and *L. wurdackii* in general aspect but differs from *L. vargasii* by its broadly ovate leaf blade with an acute apex, inflorescence with up to 50 capitula, and involucre and ray floret corolla limbs as long as or longer than 6.5 mm and is distinguishable from *L. wurdackii* by its larger number of ray florets per capitulum (up to 35) and yellow ray corollas.

12. Liabum melastomoides (Kunth) Lessing, Linnaea 6: 699. 1831. *Andromachia melastomoides* Kunth in Humboldt, Bonpland & Kunth, Nov. Gen. Sp. [H.B.K.], ed. folio, 4: 79 + tab. 337. 1818 ["1820"]. *Diplostephium melastomoides* (Kunth) Sprengel, Syst. Veg. (ed. 16) [Sprengel] 3: 544. 1826.—TYPE: COLOMBIA. Tolima: Crescit in temperatis convallis Combeimae prope urbem Ibague Novo-Granatensium, alt. 700 hex., *Bonpland 1826* (holotype: P, digital image!; isotypes: B [destroyed], photo FM 18115! P, fragment US, digital images!).

Subshrubs or shrubs, 1–2 m tall; stems costate, slightly hexagonal, densely and persistently white-tomentose; pseudostipules absent. Leaves scattered along the main stem and branches; leaf blades 8.5–17.5 cm long, 3.5–7 cm wide, coriaceous, ovate, apex acute or attenuate, base rounded or truncate, occasionally cuneate, margin mucronate-serrate, venation acrodromous, with the pair of lateral veins exceeding the midpoint of the blade but not reaching the apex (in larger leaves a more basal, second pair of veins may be present), surface smooth to slightly bullate, glabrous or occasionally laxly white-tomentose adaxially, persistently or occasionally laxly white-tomentose, densely white- or ochraceous-tomentose abaxially; petioles 0.8–2.6 cm long, not winged. Inflorescence not scapose, glomerulose, sometimes densely umbelliform or corymbiform, with more than 50 capitula; capitula radiate, sessile or pedunculate, peduncles up to 2.5 (–7.5) mm long, densely white-tomentose. Involucre 5.5–7.5 mm long, 3.5–6 mm wide, campanulate; phyllaries 50–60 in 5–6 series, 1.5–6 mm long, 0.3–0.6 mm wide, greenish, sometimes purplish toward the apex, outermost phyllaries ovate, apex acute, pubescence arachnoid, innermost phyllaries linear, attenuate, glabrescent; receptacle with chaff ca. 0.5 mm long. Ray florets 20–25; corolla 6.5–8.5 mm long, yellow, pubescent, tube 3–4 mm long, ca. 0.25 mm wide, limb 3.5–4.5 mm long, 0.7–0.8 mm wide, obovate, 4-veined, apex 3-dentate; style 5–6 mm long, branches ca. 2 mm long. Disc florets ca. 25; corolla 5.5–7 mm long, tubular, tube 3–3.5 mm long, ca. 0.25 mm wide, gradually expanded into the limb, yellow, glabrescent or pubescent, limb 2.5–3.5 mm long, 0.7–0.8 mm wide, lobes 1.2–1.8 mm long, 0.25–0.3 mm wide, approximately equal to the throat, pubescent at the apex; anthers 2.2–3 mm long, apical appendage ca. 0.2 mm long, tails ca. 0.3 mm long; style 9–10 mm long, branches 2.5–3 mm long, papillae covering style branches and extending down the shaft of the style a distance less than the length of the branches. Cypselae ca. 1 mm long, 0.4 mm wide, cylindrical to ellipsoid. Pappus bristles pale yellow or yellowish orange, scabrous; outer series 0.9–1.4 mm long, sometimes absent; inner series 4.2–5.2 mm long. Chromosome number: $n = 19$ (Robinson et al. 1985). Fig. 25A–E.

Phenology. Plants with flowering capitula have been collected in March and April, and from July to September.

Distribution (Fig. 25F). Central and western Andes of Colombia; hillsides and

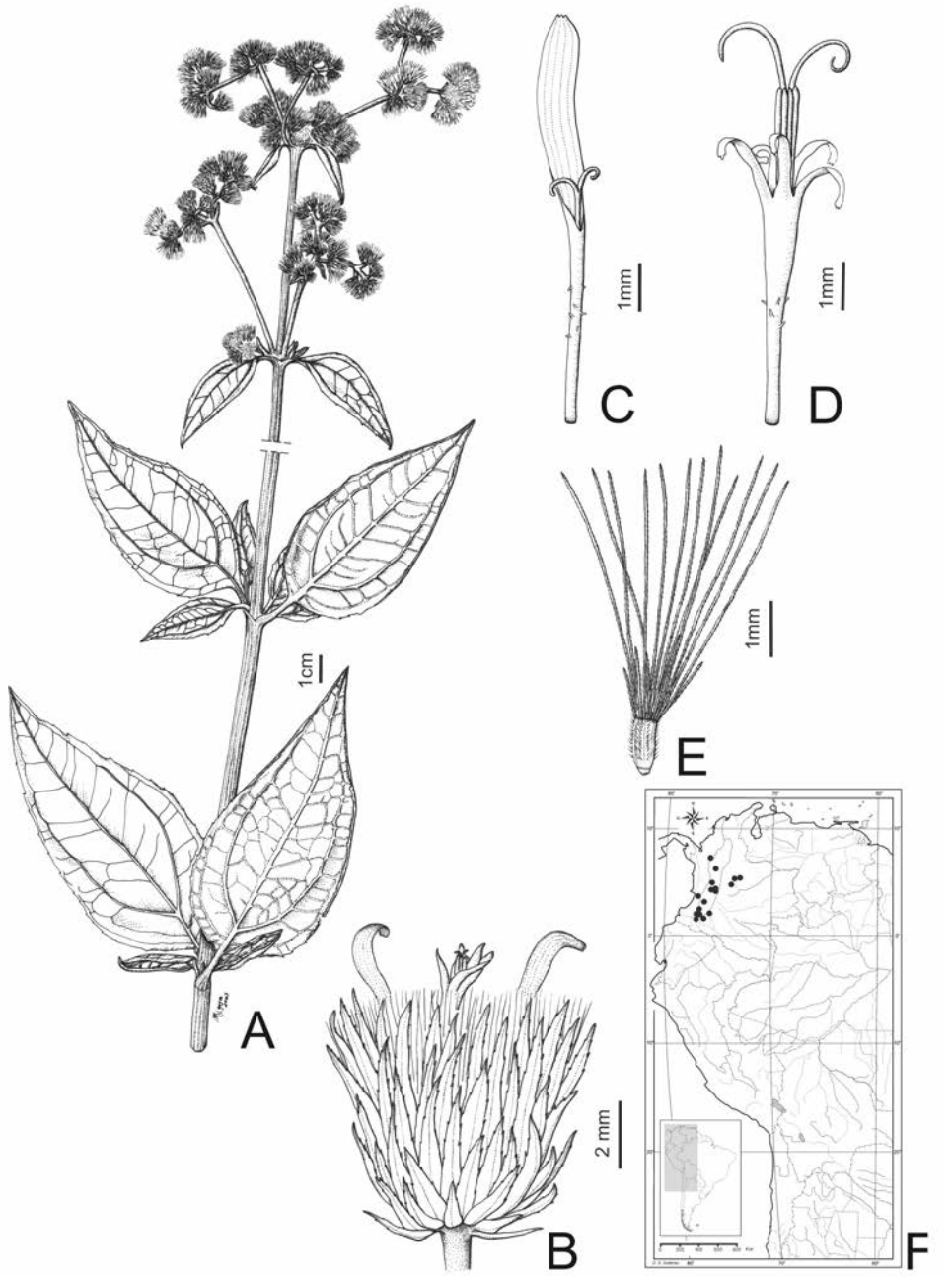

FIG. 25. *Liabum melastomoides* (Kunth) Less. A. Habit (branch). B. Capitulum (only some florets shown). C. Ray floret. D. Disc floret. E. Cypsela and pappus. F. Distribution. (Based on: A–B, *Holton s.n.*, NY; C–E, *Pennell 5854*, US.)

mountain slopes, margins of rivers and roads, grasslands and scrubby areas, sometimes becoming invasive (*Cabrera R. & Aragón 9000*); 700–1850 m.

Representative Specimens. **Colombia.** Antioquia: Mun. Fredonia, Corregimiento Marsella, *Fonnegra et al. 2725* (NY, US); de Medellín a Dabeiba, *Romero 2438* (F).—Cauca: Naranjo, *Andre K265* (F, MO, NY); cerca del Río Palo, *Espinal & Ramos 2620* (US).—Cundinamarca: Bogotá, Flora Neogranadina Bogotana, *Holton s.n.* in 1852 (GH, NY); 40 km NW of Bogotá, *Olsen & Escobar 602* (NY); 15 km NW of Villeta and 19 km SE of Guaduas, Bogotá to Manizales, *Stuessy & Funk 5664* (US).—Huila: E of Neiva, *Rusby & Pennell 466* (GH, NY, MO, US).—Quindio/Risaralda: Palmilla-Quindio, *Andre 2304* (NY).—Tolima: Ibagué, *Køie 5120* (US); Río Bermellón près de Ibagué, *Humbert et al. 26975* (LP, US); Ibagué, *Triana 1142* (MO, NY, US).—Valle del Cauca: Cali a Buenaventura, km 12–13, *Cabrera & Aragón 9000* (MO, US); Cali to Buenaventura, km 12–13, *Cabrera & Aragón s.n.* in 1985 (GH); hacienda Valparaíso, entre Zarzal y Bugalagrande, *Cuatrecasas & Pérez 6430* (F); Mun. de Buga, Río Guadalajara, *Cuatrecasas et al. 27575* (NY, US); entre La Uribe y Astenia, Bugalagrande-Sevilla, Vuelta de Violín, *Cuatrecasas & Cuadros 28932* (US); Mun. Bolívar, Bolívar-Primavera, Río Pescador, *Devia 967* (US); Loma Pelada, *Dryander 546* (US); near Mares, Cali to Buenaventura, *Killip et al. 39172* (F, LP); alrededores de La Buitrera, Palmira, *López Filgueiras 8028* (US); Yumbo, *Pennell 5854* (GH, US); Chuchila, E of Zarzal, *Pennell et al. 8547* (NY, US).—Without department: without locality, *Mutis 4780*, *5838* (US).

Liabum melastomoides resembles *L. solidagineum* in its general aspect, but differs by its glomerulose inflorescence with the capitula sessile or with peduncles up to 2.5 mm long and by its ovate leaves usually with an acute apex.

13. Liabum nigropilosum Hieronymus in Sodiro, Bot. Jahrb. Syst. 29: 59. 22 May 1900.—Types: Ecuador. Chimborazo/Tungurahua: Crescit cum varietate in silvis superioribus montium Atacazo et Chimborazo, *Sodiro 55/8* (holotype: B [destroyed], photo FM 18117!; lectotype here designated: F, digital image!); Ecuador. Pichincha: Steep schistic slopes 4 km E of Tandapi, above Río Naranjal, 00°27′S, 78°46′W, 5300 ft [1600 m], 3 Aug 1978, *Webster 22970* (epitype, here designated: US!).

Subshrubs or shrubs, 1–3 m tall; stems slightly to conspicuously costate, hexagonal in cross-section, densely and persistently white-tomentose; pseudostipules 0.5–1 cm long, without auricles, glabrous adaxially, densely white-tomentose abaxially. Leaves scattered along the main stem and branches; leaf blades 6.5–17.5 cm long, 4–11.5 cm wide, chartaceous, subtriangular, sometimes ovate, apex acute or shortly acuminate, base truncate or cordate, margin mucronate-serrate, venation acrodromous or actinodromous, with the pair of lateral veins exceeding the midpoint of the blade but not reaching the apex, surface smooth, glabrous or hirsute adaxially, densely white-tomentose abaxially; petioles 2–6 cm long, winged, wings 0.2–0.35 cm wide, continuous with the pseudostipules. Inflorescence not scapose, umbelliform or corymbiform, dense, with more than 50 capitula; capitula radiate, pedunculate, peduncles up to 4.5 mm long, densely white-tomentose. Involucre 5.5–6 mm long, 5–6 mm wide, campanulate; phyllaries 55–70 in 5–6 series, 1.3–5.5 mm long, 0.2–0.4 mm wide, greenish, outermost phyllaries ovate, apex acute, pubescence arachnoid, innermost phyllaries linear, apex attenuate, glabrescent; receptacle with chaff ca. 0.3 mm long. Ray florets 25–30; corolla 6.5–8.5 mm long, yellow, glabrescent or pubescent, tube 3–4 mm long, 0.3–0.4 mm wide, limb 3.5–4.5 mm long, 1–1.3 mm wide, obovate, 4-veined, apex 3-dentate; style 6–6.5 mm long, branches 2–3 mm long. Disc florets 20–30; corolla 5–6.5 mm long, tubular, tube 1.5–2.5 mm long, 0.2–0.3 mm wide, gradually expanded into the limb, yellow, pubescent, limb 3.5–4 mm long, ca. 1 mm wide,

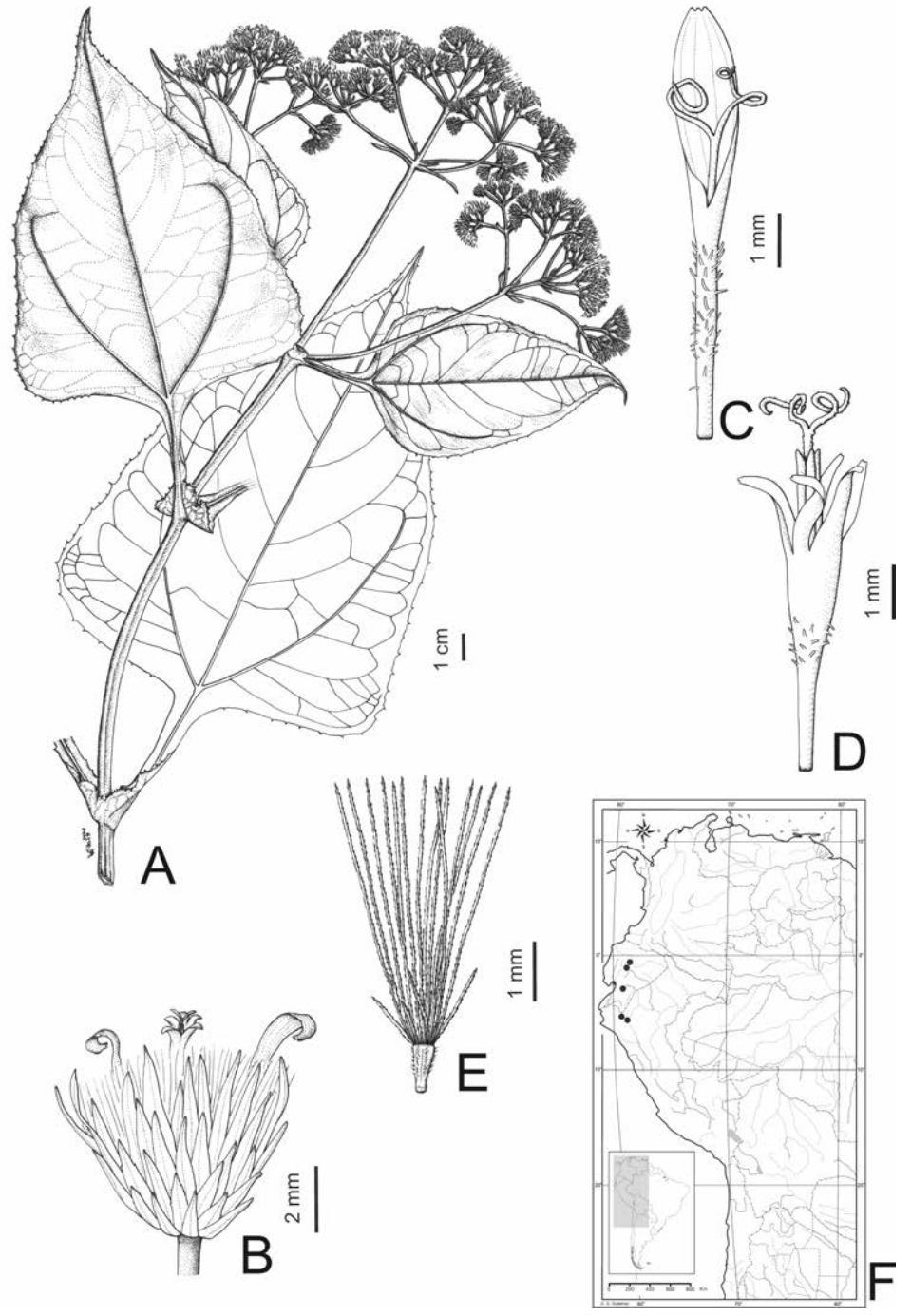

FIG. 26. *Liabum nigropilosum* Hieron. A. Habit (branch). B. Capitulum (only some florets shown). C. Ray floret. D. Disc floret. E. Cypsela and pappus. F. Distribution. (A–E based on *Webster 22970*, US.)

lobes 1.5–1.9 mm long, ca. 0.35 mm wide, shorter than the throat, pubescent at the apex; anthers ca. 1.8 mm long, apical appendage ca. 0.5 mm long, tails ca. 0.2 mm long; style 6–6.5 mm long, branches 1.8–2 mm long, papillae covering style branches and extending down the shaft of the style a distance less than the length of the branches. Cypselae 0.75–0.85 mm long, ca. 0.35 mm wide, obconical. Pappus bristles pale yellow, whitish yellow, or yellowish-orange, scabrous; outer series 1–1.5 mm long, sometimes absent; inner series up to 4.7 mm long. Chromosome number unknown. Fig. 26A–E.

Phenology. Plants with flowering capitula have been collected from July to September.

Distribution (Fig. 26F). Ecuador and northern Peru; slopes and montane forests, also in ditches; 750–900 m (Ecuador), 2200–2840 m (northern Peru).

Additional Specimens Examined. **Ecuador.** Cotopaxi: Tenefuerte, Río Pilalo, km 52–53, Quevedo-Latacunga, *Dodson & Embree 13365* (MO, US). **Peru.** Cajamarca: Prov. Cajamarca, Huacraruco, *Cabanillas et al. 39* (MO, US); Prov. Cajamarca, San Juan, *Sagástegui et al. 11995* (F, MO, NY).

According to Robinson (1978) and our own observations, the black "hairs" on the leaves, for which the species is named, is a fungus that is also found on other species of *Liabum*. *Liabum nigropilosum* resembles *L. floribundum* and *L. robinsonii*, but differs from them by the petiole wings that are continuous with the pseudostipules.

The holotype of *L. nigropilosum* kept at B was destroyed during World War II, and we therefore selected as lectotype the isotype deposited in F, since no other original material was found. This specimen at F, however, consisting of a capitulum and a fragment of a pseudostipule, does not allow a clear recognition of this species. For purposes of the precise application of the name of *L. nigropilosum*, an epitype is also designated here, following Article 9.7 of the ICN (McNeill et al. 2012). This specimen fits accurately with the diagnosis of *L. nigropilosum* and was collected in Tandapi (Pichincha Province, Ecuador), near the localities of Atacazo and Chimborazo cited in the protologue.

14. Liabum robinsonii D. G. Gutiérrez & Katinas, sp. nov.—Type: Ecuador. Loja: carretera Loja-Zamora, km 16–24, 15 Aug 1983, *Jaramillo & Winnerskjold 5776* (holotype: NY!).

Liabum robinsonii resembles *L. floribundum* and *L. nigropilosum* but is distinguished by its petiole winged only from the petiole midpoint to the blade, the wings ending in conspicuous lobes at the midpoint of the petiole.

Subshrubs to shrubs, 1–3 m tall; stems slightly to conspicuously costate, hexagonal in cross-section, densely and persistently white-tomentose, occasionally glabrescent; pseudostipules ca. 1 cm long, without auricles, glabrous adaxially, densely white-tomentose abaxially. Leaves scattered along the main stem and branches; leaf blades 5.5–17.5 cm long, 4–11.5 cm wide, chartaceous, subtriangular, apex acute or short-acuminate, base slightly truncate or cordate, margin mucronate-serrate, venation acrodromous or actinodromous, with the pair of lateral veins exceeding the midpoint of the blade but not reaching the apex, surface smooth, glabrous or hirsute adaxially, densely white-tomentose abaxially; petioles 3.5–8.5 cm long, winged from the midpoint of the petiole to the base of the blade, wings ca. 0.2 cm wide, lobulate at the base. Inflorescence not scapose, umbelliform or corymbiform, dense, with more than 35 capitula; capitula radiate, pedunculate, peduncles up to 5 mm long, densely white-tomentose. Involucre 5.5–8 mm long, 6–8 mm

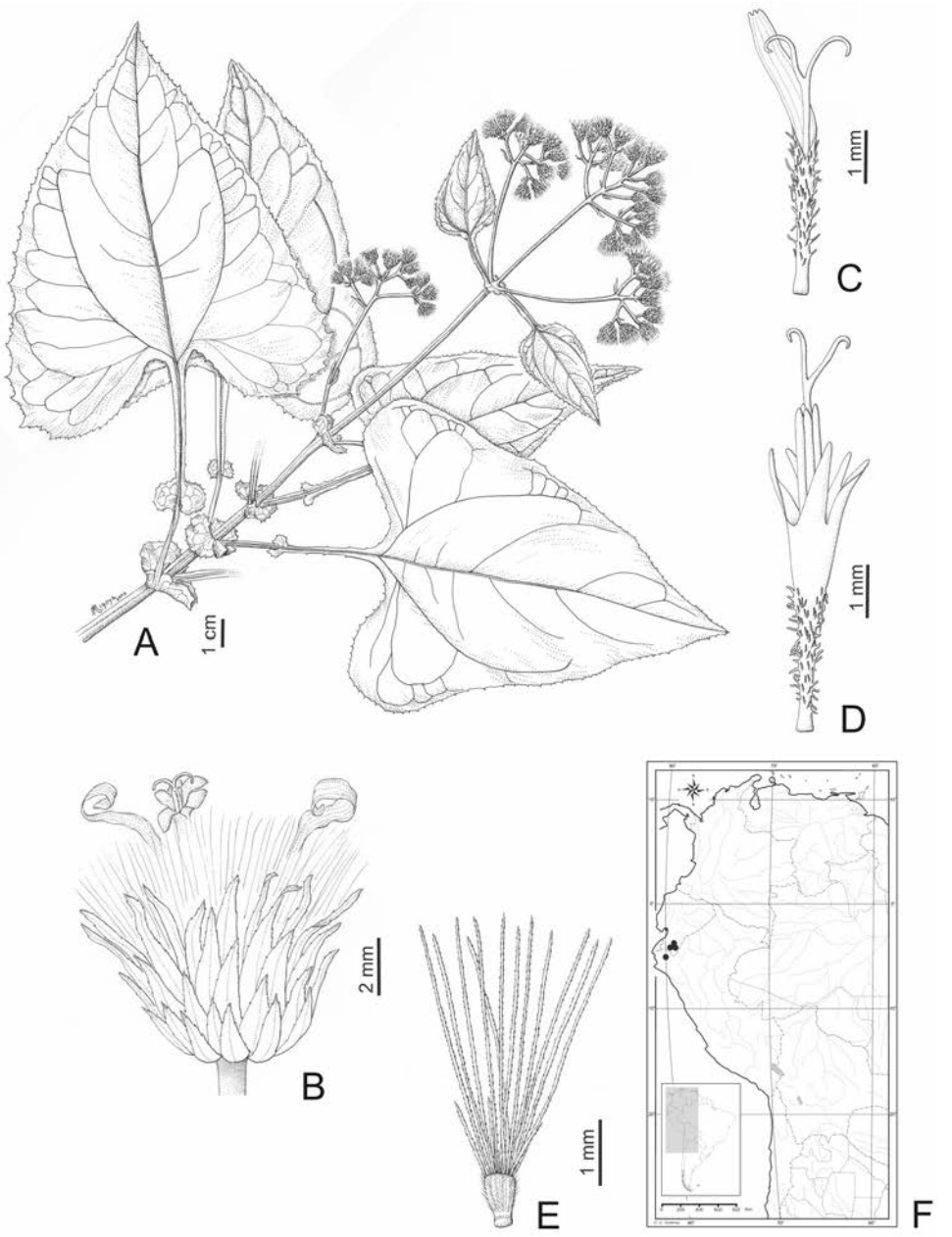

FIG. 27. *Liabum robinsonii* D. G. Gutiérrez & Katinas. A. Habit (branch). B. Capitulum (only some florets shown). C. Ray floret. D. Disc floret. E. Cypsela and pappus. F. Distribution. (A–E based on *Jaramillo & Winnerskjold 5776*, NY.)

wide, campanulate; phyllaries 50–60 in 5 series, 2.5–6 mm long, 0.35–0.8 mm wide, greenish, outermost phyllaries ovate, apex acute, pubescence arachnoid, innermost phyllaries linear, apex attenuate, glabrescent; receptacle with chaff ca. 0.2 mm long. Ray florets 25–30; corolla 5.5–6.5 mm long, yellow, pubescent, tube 2.5–3 mm long, ca. 0.25–0.3 mm wide, limb 3–3.5 mm long, 0.5–0.8 mm wide, elliptic to obovate, 4-veined, apex 3-dentate; style 6.3–7 mm long, branches 2.2–2.5 mm long. Disc florets 20–30; corolla 4.5–6.5 mm long, tubular, tube 1.5–2.5 mm long, ca. 0.25 mm wide, gradually expanded into the limb, yellow, pubescent, limb 3–4 mm long, 0.8–1 mm wide, lobes ca. 1.5 mm long, 0.35–0.4 mm wide, equal to or shorter than the throat, pubescent at the apex; anthers 2.5–2.8 mm long, apical appendage 0.4–0.5 mm long, tails 0.5–0.7 mm long; style 9–12 mm long, branches 2–3 mm long, papillae covering style branches and extending down the shaft of the style a distance equal to the length of the branches. Cypselae 0.75–0.85 mm long, ca. 0.4 mm wide, obconical. Pappus bristles pale yellow or yellowish orange, scabrous; outer series ca. 1.5 mm long, sometimes absent; inner series up to 4.5 mm long. Chromosome number unknown. Fig. 27A–E.

Phenology. Plants with flowering capitula have been collected from July to September.

Distribution (Fig. 27F). Southern Ecuador (Loja and Zamora-Chinchipe Provinces) to northern Peru (Piura Department); wet mountain forests, in clay or humus soils, and areas with cultivated eucalyptus trees; 1700–2800 (–3150) m.

Additional Specimens Examined. **Ecuador.** Loja: Yangana-Toledo, *Jaramillo et al. 8761* (NY, US).—Zamora-Chinchipe: 22.4 km E of Loja to Zamora, *Stuessy & Nesom 5892* (LP, SI). **Peru.** Piura: Prov. Huancabamba, puente Quebrada Seca, Canchaque-Huancabamba, *Sagástegui et al. 8149* (F, MO, US).

Liabum robinsonii is named in honor of Harold E. Robinson (born 1932), an eminent botanist from the United States of America at the Smithsonian Institution, specialist in Asteraceae who has provided major contributions to the systematics of the family and particularly to the systematics of the Liabeae.

Liabum robinsonii resembles *L. floribundum* and *L. nigropilosum* in its general aspect, but is easily distinguishable from these and all other species of *Liabum* by the unique wing structure of its petiole: the petiole is winged only from the blade down to the midpoint, where it ends in two conspicuous lobes (Figs. 4C, 27A). The wings are not continuous with the pseudostipules as in many other species of *Liabum*.

15. Liabum saloyense Domke in Diels, Beitr. Veg. Ecuador 168. 1937.—Types: Ecuador. Pichincha: West-Kordillere, Prov. Pichincha, Saloya-Tal, Saum des Bergwaldes, ca. 2600 m, 5 Sept 1933, *Diels 847* (holotype: B [destroyed]); Pichincha: valley of Río Saloya, El Cuello, 28 June 1939, *Asplund 7310* (neotype, here designated: GH!).

Liabum saloyense var. *punctulatum* Domke in Diels, Beitr. Veg. Ecuador 169. 1937.—Types: Ecuador. Pichincha: West-Kordillere, Saloya-Tal, 5 Sept 1933, *Diels 825* (holotype: B [destroyed]); Pichincha: Saloya, km 50–70, 1800 m, 11 Aug 1945, *Acosta Solís 10965* (neotype, here designated: F!).

Subshrubs to shrubs, sometimes climbing, 1–3 m tall; stems not costate, terete or slightly hexagonal in cross-section, persistently or deciduously white-tomentose; pseudostipules 0.5 cm long, with or without auricles, auricles divergent or convergent and overlapping, up to 1 cm, glabrous adaxially, densely white-tomentose abaxially. Leaves

scattered along the main stem and branches; leaf blades 7.5–15.5 cm long, 3.5–7 cm wide, chartaceous, ovate, apex acute or acuminate, base cuneate, margin mucronate-serrate, venation acrodromous, with the pair of lateral veins almost reaching the apex of the blade, surface smooth, hirsute adaxially, densely white-tomentose, with brownish hairs on main veins or mixed with the tomentum, abaxially, brownish hairs on main veins or mixed with the tomentum; petioles 1.6–2.8 cm long, not winged or slightly winged distally by decurrence of blade. Inflorescence not scapose, umbelliform or corymbiform, lax, with more than 50 capitula; capitula radiate, pedunculate, peduncles up to 8.5 mm long, densely white-tomentose. Involucre ca. 6 mm long, 6.5–8.5 mm wide, hemispherical; phyllaries 55–70 in 5 series, 1.5–6 mm long, ca. 0.5 mm wide, greenish, sometimes purplish toward the apex, outermost phyllaries ovate, apex acute, pubescence arachnoid, innermost phyllaries linear, glabrescent; receptacle with chaff ca. 2 mm long. Ray florets 20–30; corolla 9.5–13 mm long, yellow, pubescent, tube 4.5–6 mm long, ca. 0.25 mm wide, limb 5–7 mm long, 1–1.5 mm wide, elliptic or obovate, 4-veined, apex 3-dentate; style 7.5–9 mm long, branches 2.5–4 mm long. Disc florets ca. 30; corolla 7–9.5 mm long, tubular, tube 3.5–5.5 mm long, ca. 0.25 mm wide, abruptly expanded into the limb, yellow, pubescent, limb 3.5–4 mm long, ca. 1.5 mm wide, lobes ca. 2.5 mm long, 0.4 mm wide, much longer than the throat, pubescent at the apex; anthers 2.5–3.2 mm long, apical appendage ca. 0.25 mm long, tails ca. 0.25 mm long; style 10–12 mm long, branches ca. 4 mm long, papillae covering style branches and extending down the shaft of the style a distance equal to the length of the branches. Cypselae 1–1.5 mm long, 0.4–0.5 mm wide, ellipsoid to obconical. Pappus bristles yellowish orange, scabrous; outer series ca. 1.5 mm long, sometimes absent; inner series 5.5–6 mm long. Chromosome number unknown. Fig. 28A–E.

Phenology. Plants with flowering capitula have been collected from May to September and in December.

Distribution (Fig. 28F). Western Colombia to northern Ecuador; moist forests and disturbed areas such as roadsides; 600–2800 m.

Representative Specimens. **Colombia.** Nariño: Reserva Natural La Planada, 01°10′N, 77°58′W, *de Benavides 10202* (MO); La Planada, S of Ricaurte, 7 km from Tumaco-Pasto, 01°10′N, 77°15′W, *Gentry et al. 55128* (US).—Tolima: New Granada, Mariquita, *Triana 1135* (MO, NY, US).—Valle del Cauca: between San José del Palmar and Ansermanuevo, 04°47′N, 76°09′W, *Croat 56720* (F, MO). **Ecuador**. Esmeraldas: Lita to San Lorenzo, 00°58′N, 78°35′W, *Gentry et al. 69952* (US).—Napo: Sucumbíos-Santa Bárbara-La Alegría, *Jaramillo 9341* (NY).—Pichincha: km 51–53, Chiriboga-Quito-Santo Domingo, *Dodson et al. 14367* (MO); Santo Domingo-Quito, Cornejo Astorga, Tandapi, *Harling et al. 9402* (F, US); Reserva Florística-Ecológica Río Guajalito, km 59 Quito-Santo Domingo de los Colorados, 78°48′W, 00°13′S, *Jaramillo & Zak 7903* (F, MO, US); Reserva Florística-Ecológica Río Guajalito, km 49 Quito-Santo Domingo de los Colorados, 70°48′W, 00°13′S, *Jaramillo & Grijalva 13685* (NY); Monte Pichincha, *Mille 599* (MO, NY); 21 km N of Nono, 2–3 km N of Guarumos, *Stuessy et al. 4866* (MO); Quito-Nono-Tandayapa-Los Bancos, entre Tandayapa, Mindo y Los Bancos, *Zak 1162* (F, GH, MO, NY, US); Quito-San Juan-Chiriboga-empalme km 59, *Zak 1294* (CTES, GH, NY, US); Quito-Lloa-Mindo, hacienda El Pedregal, 00°03′S, 78°40′W, *Zak & Jaramillo 2143* (F, NY).

In its protologue, *Liabum saloyense* var. *punctulatum* was differentiated from *L. saloyense* var. *saloyense* by the abaxial leaf surface (glandular-punctate in *L. saloyense* var. *punctulatum* versus not punctate in *L. saloyense* var. *saloyense*) and the diameter of the pseudostipules (ca. 10 mm in *L. saloyense* var. *saloyense* versus 15 mm in *L. saloyense* var. *punctulatum*). However, we found these features to be so variable from one specimen to the next that *L. saloyense* var. *punctulatum* is proposed in this work as a synonym of *L. saloyense*.

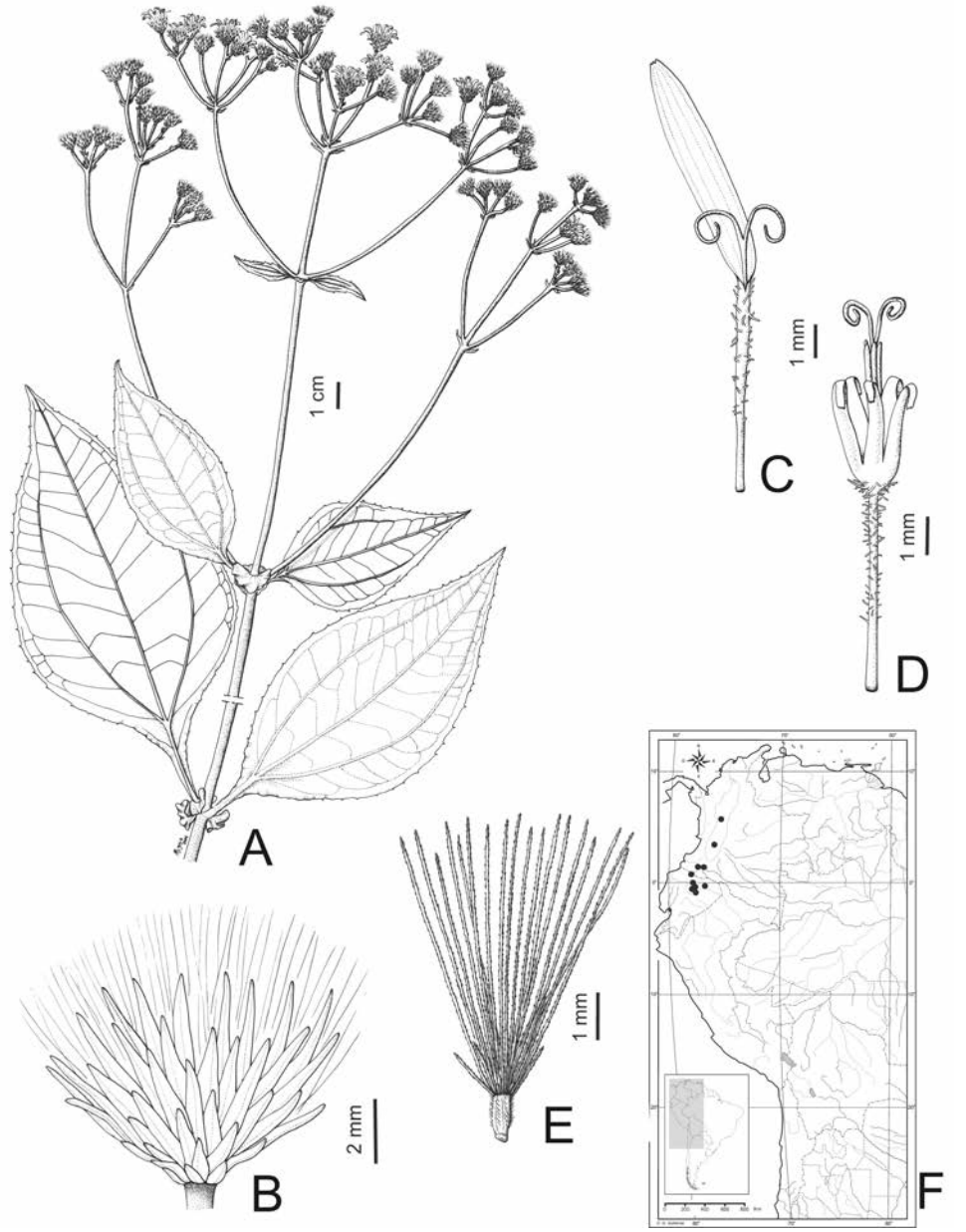

FIG. 28. *Liabum saloyense* Domke. A. Habit (branch). B. Capitulum (without florets). C. Ray floret. D. Disc floret. E. Cypsela and pappus. F. Distribution. (Based on: A–B, *Jaramillo & Zak 7903*, F; C–E, *Jaramillo & Zak 7903*, MO.)

16. Liabum saundersii H. Robinson, Phytologia 54: 62–63. 1983.—TYPE: PERU. Junín: Prov. Tarma, Dist. San Ramón, about 15 km from San Ramón towards Tarma, ca. 3400 ft [ca. 1000 m], 15 Aug 1960, *S. G. E. Saunders 559* (holotype: IJ, digital image! fragment US, digital image!).

Subshrubs or sometimes herbs, 0.5–2 m tall; stems not costate, terete or slightly hexagonal in cross-section, densely and persitently white-tomentose; pseudostipules 0.8–1.5 cm long, without auricles, glabrescent adaxially, densely white-tomentose abaxially. Leaves scattered along the main stem and branches, blade 5.5–10 cm long, 2–7 cm wide, ovate, chartaceous, apex acute, acuminate or attenuate, base rounded or cuneate, margin mucronate-serrate, acrodromous, with the pair of lateral veins reaching more than half of the blade, without reaching the apex, surface smooth, glabrous adaxially, white-tomentose abaxially; petiolate, petioles 1–3 cm long, winged, wings 0.25–0.4 cm, continuous with the pseudostipules. Inflorescence not scapose, umbelliform, lax, with 10–20 capitula; capitula radiate, pedunculate, peduncles up to 10 mm long, densely white-tomentose. Involucre 10–15 mm long, 9.5–11 mm wide, campanulate; phyllaries 110–140 in 5–7 series, 1.8–9 mm long, 0.4–0.7 mm wide, greenish, outermost phyllaries ovate, apex acute, pubescence arachnoid, innermost phyllaries linear, apex attenuate, glabrescent; receptacle with chaff ca. 0.5 mm long. Ray florets 30–40; corolla 9–12 mm long, orange-yellow to orange, pubescent, tube 3.5–5.5 mm long, 0.2–0.3 mm wide, limb 5.5–6.5 mm long, 1–1.5 mm wide, elliptic or obovate, 4-veined, apex 3-dentate; style 6.2–8 mm long, branches 3–3.3 mm long. Disc florets 90–110; corolla 7–10.5 mm long, tubular, tube 3–5 mm long, 0.3–0.4 mm wide, gradually expanded into the limb, yellow, pubescent, limb 4–5.5 mm long, 0.9–1 mm wide, lobes 1.5–2 mm long, ca. 0.25 mm wide, shorter than the throat, pubescent at the apex; anthers 2–3 mm long, apical appendage 0.5–0.8 mm long, tails 0.2–0.5 mm long; style 7.5–8 mm long, branches 2.5–3 mm long, papillae covering style branches and extending down the shaft of the style a distance less than the length of the branches. Cypselae 0.9–1.5 mm long, ca. 0.4 mm wide, cylindrical to ellipsoid. Pappus bristles pale yellow or yellowish orange, scabrous; outer series 1–1.5 mm long, sometimes absent; inner series 5.5–6.5 mm long. Chromosome number unknown. Fig. 29A–E.

Phenology. Plants with flowering capitula were collected in August.

Distribution (Fig. 29F). Peru (Department of Junín) and Bolivia (Department of La Paz); slopes and riversides; ca. 1000 m.

ADDITIONAL SPECIMEN EXAMINED. **Bolivia.** LA PAZ: Prov. Nor Yungas, Chuspipata 14 km hacia Yosola, 5 km Río Huarinillas, Río Elena, *Beck 13899* (SI, US).

Liabum saundersii resembles *L. grandiflorum* and *L. wurdackii* in its general aspect. However, *L. saundersii* differs from *L. grandiflorum* mainly by the rounded or cuneate base of its leaf blade, the blade white-tomentose without coarsely stiff hairs on the main veins abaxially, the ray floret corolla limb more than 5.5 mm long, the disc floret corolla limb more than 4 mm long, and the usually orange corollas. *Liabum saundersii* is easily distinguishable from *L. wurdackii* by its broadly winged petiole with the wings continuous with the pseudostipules.

The specimen *Beck 13899* provides the first record of *L. saundersii* in Bolivia.

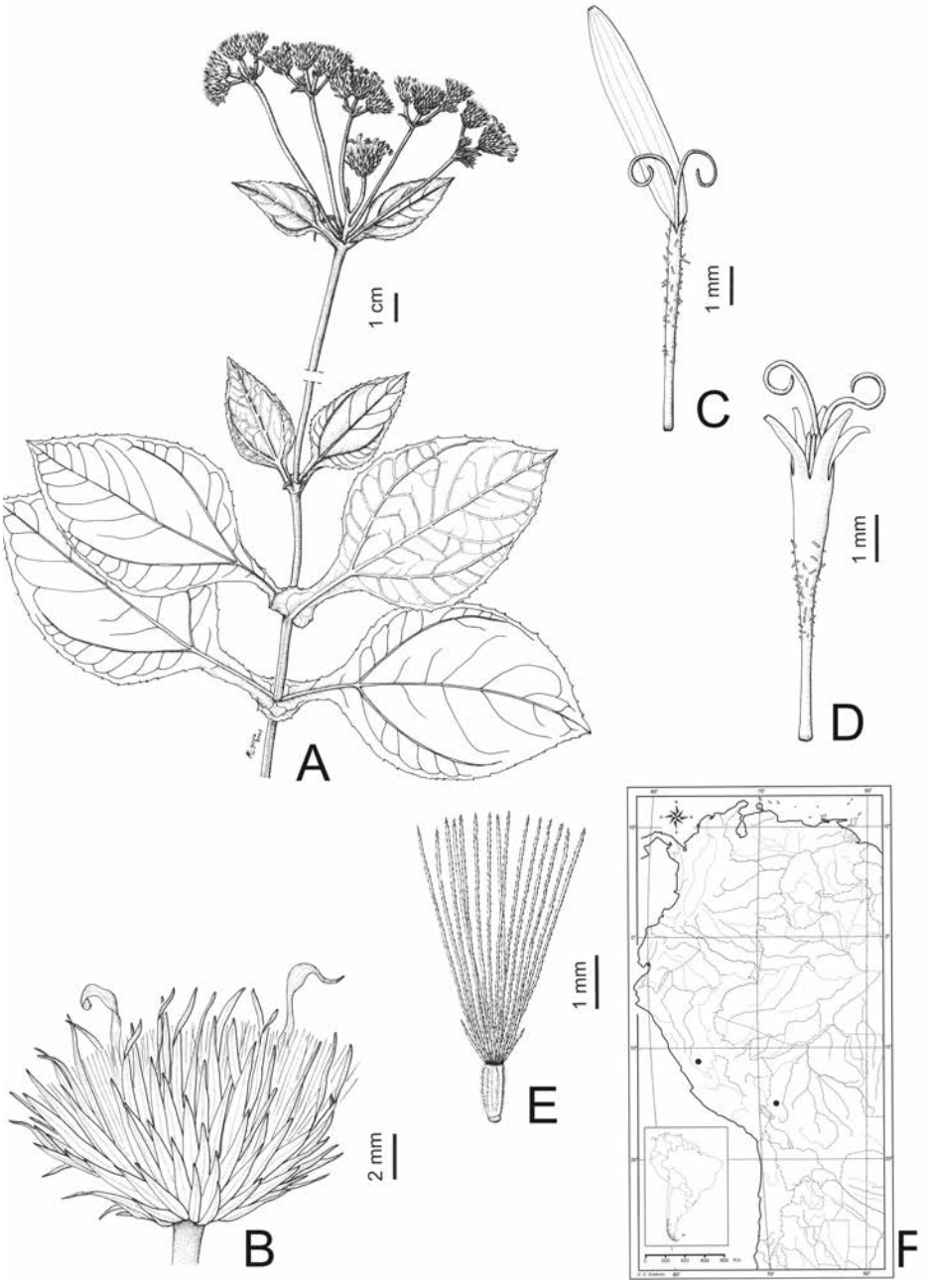

FIG. 29. *Liabum saundersii* H. Rob. A. Habit (branch). B. Capitulum (only some florets shown). C. Ray floret. D. Disc floret. E. Cypsela and pappus. F. Distribution. (A–E based on *Beck 13899*, SI.)

17. Liabum solidagineum (Kunth) Lessing, Linnaea 6: 700. 1831. *Andromachia solidaginea* Kunth in Humboldt, Bonpland & Kunth, Nov. Gen. Sp. [H.B.K.], ed. folio, 4: 78–79. 1818 ["1820"]. *Diplostephium solidagineum* (Kunth) Sprengel, Syst. Veg. (ed. 16) [Sprengel] 3: 544. 1826.—TYPE: PERU. Piura: Crescit in Andibus Peruvianorum inter Ayavaca et convallem fluminis Cutaco, alt. 1200 hex., ["Quito"], *Humboldt & Bonpland s.n.* (holotype: P, digital image!; isotype: B [destroyed], photo FM 18130!).

Liabum fulvotomentosum Kuntze, Revis. Gen. Pl. 3: 163. 1898.—TYPE: BOLIVIA. Without department: Río Juntas, 2000 m, April 1892, *Kuntze s.n.* (holotype: NY, digital image!, fragment US!; isotype: NY [without locality, 13–21 Apr 1892], digital image!).

Liabum acutifolium Cuatrecasas, Collect. Bot. (Barcelona) 3: 299–300. 1953.—TYPE: PERU. Junín: Carpapata (Provincia de Tarma), Aug 1947, *Soukup 3461* (holotype: F, digital image!; isotype: LP!).

Subshrubs, shrubs, or small trees, 2–6 m tall; stems not costate, terete or slightly hexagonal in cross-section, densely and persistently white- or ochraceous-tomentose; pseudostipules present or absent, ca. 0.5 cm long, with or without auricles, green, glabrous adaxially, densely white- or ochraceous-tomentose abaxially. Leaves scattered along the main stem and branches; leaf blades 11.5–23.5 cm long, 3.5–11 cm wide, coriaceous, ovate to narrowly ovate, apex attenuate, base rounded or truncate, occasionally cuneate, margin mucronate-serrate, venation acrodromous, with the pair of lateral veins reaching the midpoint of the blade, surface smooth, green, glabrous adaxially, densely white- or ochraceous-tomentose abaxially; petioles 1.5–4 cm long, not winged. Inflorescence not scapose, umbelliform or corymbiform, dense, with more than 50 capitula; capitula radiate, sessile or pedunculate, peduncles up to 5 (–10) mm long, densely white- or ochraceous-tomentose. Involucre 4.5–6 mm long, 3–5 mm wide, campanulate; phyllaries 50–60 in 5–6 series, 1.5–5.5 mm long, 0.4–0.8 mm wide, greenish, sometimes purplish toward the apex, outermost phyllaries ovate, apex acute, pubescence arachnoid, innermost phyllaries linear, apex attenuate, glabrescent; receptacle with chaff up to 1.5 mm long. Ray florets (15–) 20–25; corolla 6.5–9.5 mm long, yellow, pubescent, tube 3–5 mm long, ca. 0.2 mm wide, limb 3.5–4.5 mm long, 0.6–1 mm wide, obovate, 4-veined, apex 3-dentate; style 6–7 mm long, branches 2–3 mm long. Disc florets 20–25; corolla 5.5–7 mm long, tubular, tube 3–3.5 mm long, ca. 0.25 mm wide, gradually expanded into the limb, yellow, glabrescent or pubescent, limb 2.5–3.5 mm long, 0.6–0.8 mm wide, lobes 1.2–1.8 mm long, 0.25–0.35 mm wide, approximately equal in the length to the throat, pubescent at the apex; anthers ca. 2.5 mm long, apical appendage ca. 0.8 mm long, tails ca. 0.6 mm long; style 7–8 mm long, branches 1.8–2 mm long, papillae covering style branches and extending down the shaft of the style a distance less than the length of the branches. Cypselae 0.7–1.1 mm long, 0.3–0.5 mm wide, cylindrical to ellipsoid. Pappus bristles pale yellow or yellowish orange, scabrous; outer series 0.8–1.5 mm long, sometimes absent; inner series 4–4.7 mm long. Chromosome number unknown. Fig. 30A–E.

Phenology. Plants in flower have been collected throughout the year.

Distribution (Fig. 30F). Andes of Peru and in central and western Bolivia; wet or semi-cloud montane forests, sometimes with dry shrubby vegetation, stream margins, disturbed areas such as roadsides, and grazed and cultivated fields, in clay and rocky soils; (560–) 1700–3720 (–4600) m.

Local Names. Chote (*Cook & Gilbert 895*), hierba del espanto (*Rothschild 3037*), hoja

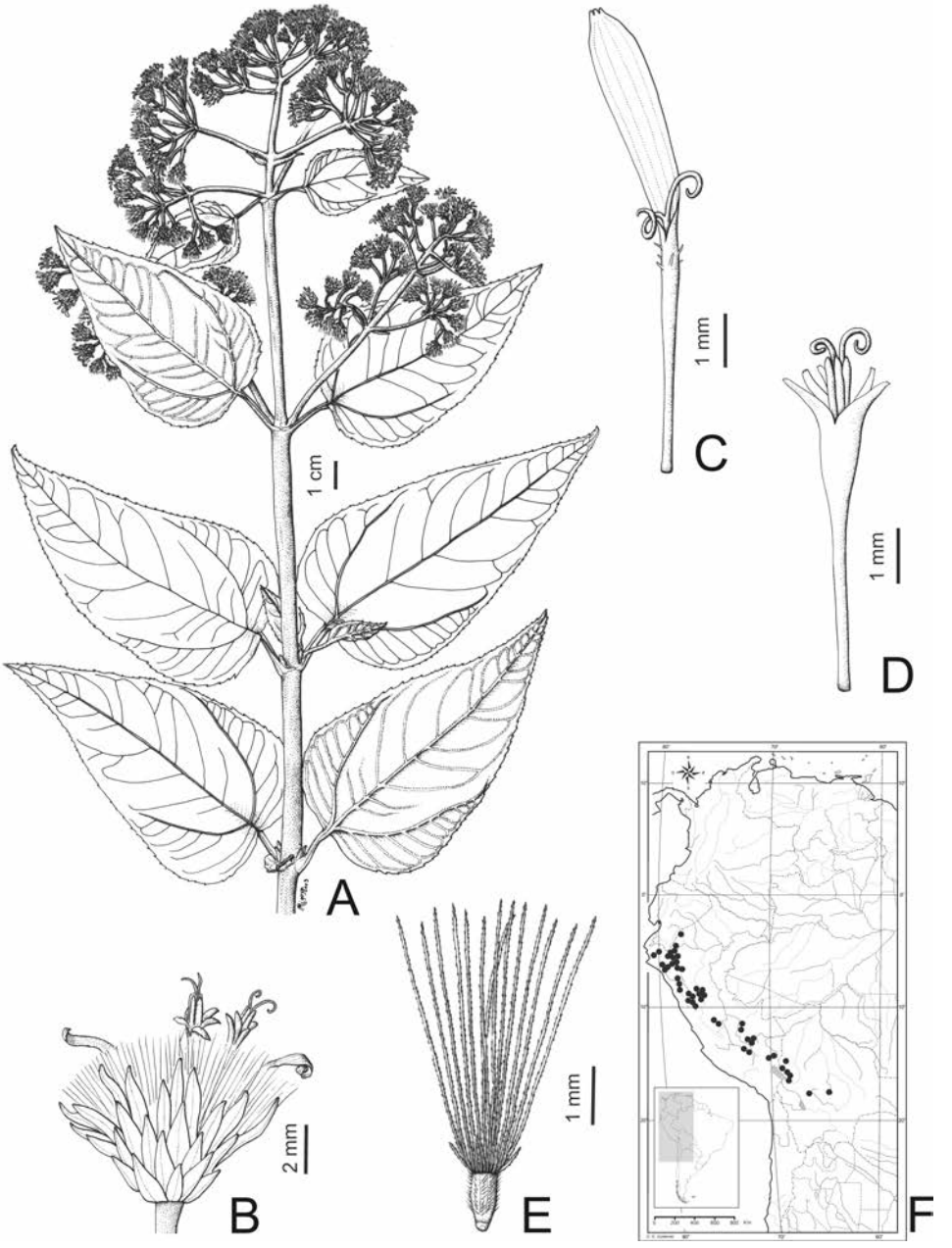

FIG. 30. *Liabum solidagineum* (Kunth) Less. A. Habit (branch). B. Capitulum (only some florets shown). C. Ray floret. D. Disc floret. E. Cypsela and pappus. F. Distribution. (Based on: A–B, *Smith 10501*, MO; C–E, *Cook & Gilbert 895*, US.)

blanca (*Leiva et al. 1347*), quisuar (*Smith & Blas 4867*), wakap haiyon (*Hutchison & Wright 4300*).

Representative Specimens. **Bolivia.** Cochabamba: Sailapata-Ayopaya, *Cárdenas 3276* (LIL).—La Paz: Prov. Nor Yungas, Unduavi, *Bang 2477* (NY); Prov. Inquisivi, Inquisivi 6 km hacia el N por Circuata, *Beck 4747* (SI); Prov. B. Saavedra, Charazani, 20 km hacia Apolo, *Beck 11387* (SI); Licoma 14 km hacia Miguillas, *Beck 22735* (US); Sorata, *Krapovickas & Fortunato 43939* (CTES); Abra de Alto Polea, between Alto Polea and Poqueloque, 16°42′S, 67°14′W, *Lewis 37368* (MO, US); Loma El Abra, ca. 5 km NW from Inquisivi, 16°52′S, 67°10′W, *Lewis 88902* (CTES, MO, NY, SI, US); without locality, *Mandon 236* (NY); Prov. Larecaja, vicinis Sorata, rivi Callasuyo, *Mandon 236* (NY); Prov. Larecaja, vicinis Sorata, monte Chilieca, *Mandon 236* (F, GH, NY); Yrupana [Irupana], *McCarty 124* (US); Prov. Sud Yungas, Yanacachi, 2.5 km hacia Chojlla, *Seibel & Vargas 1116* (SI, US); Prov. Murillo, Río Zongo, Río Jachcha Cruz, 16°07′S, 68°04′W, *Solomon 18740* (CTES, MO, NY); Sorata, *Williams 2379* (NY, US).—Santa Cruz: Prov. Caballero, Parque Nacional Amboró, Comarapa, 5–8 km N Río Arriba hacia Verdecillo, 17°50′S, 64°33′W, *Vargas et al. 2404* (NY, US). **Peru.** Amazonas: Balsas-Leimebamba, near Leimebamba, *Boeke 1776* (NY, US); Cordillera Calla-Calla, entre Leimebamba y Balsas, *Ferreyra 15310* (MO); cerca de Leimebamba, *Ferreyra 15541* (US); SE of Chachapoyas, *King & Bishop 9215* (MO, US); 3 km E of Florida, *King & Bishop 9236* (MO, US); El Tingo a Kuelap, 06°24′S, 77°56′W, *Sánchez & Dillon 9085* (F); entre Domila y Cohechán, *Soukup 4156* (US); Prov. Chachapoyas, SE of Chachapoyas, *Wurdack 466* (GH); Prov. Bongará, Shipasbamba-Pomacocha, *Wurdack 1114* (F, LP, NY).—Ancash: Cordillera Blanca, Río Marcará, Vicos, *Hutchison & Wright 4300* (F, MO, NY); Prov. Haylas, laguna Parón, *López et al. 7405* (LP); entre Yungay y Llanganuco, *Mostacero et al. 1378* (F, MO, NY); Prov. Carhuaz, cerca de Carhuaz, *Proaño 137* (US); Mancos to Río Santos, *Smith & Blas 4867* (F); Prov. Yungay, Huascarán National Park, Llanganuco, between guardpost and Chinancocha, 77°40′W, 09°05′S, *Smith 10501* (MO); Huascarán National Park, quebrada Parón, 77°03′W, 09°01′S, *Smith 10577* (F, US); Prov. Huaraz, Chancos, *Velarde 3184* (F, LP).—Apurimac: Abancay, *Marín 2254* (F, LIL); without locality, *Tupayachi & Gabino 2866* (US); Prov. Abancay, alrededores de Abancay, *Vargas 473* (F).—Cajamarca: Chetilla, a Llullapuquio, *Becker & Terrones 1200* (US); Prov. San Pablo, Distr. San Pablo, cerro San Pedro y San Pablo, *Cabanillas & Guevara 585*, *589* (F); Distr. San Juan, entre Yamagual y El Cruce, *Cabanillas & Guevara 686* (F); Distr. La Paccha, La Paccha-Chadin, *Cabanillas 772* (F); Prov. Hualgayoc, San Miguel, *Díaz s.n.* (US); below Las Palmas, ca. 24 km NE of Chota, 06°29′S, 78°37′W, *Dillon et al. 6402* (F); 4 km E of Celendín to Balsas, *Hutchison & Wright 5191* (F, MO, NY, US); Río Marañon above Balsas, 5 km to Celendín, *Hutchison & Wright 5355* (F, MO, NY); Prov. San Ignacio, San Martín, San Ignacio-Nueva Esperanza, *Leiva et al. 1347* (F); Mitopanga-Querocoto, *Leiva et al. 1460* (F, NY); Ushcundul, Niepos, *Llatas 1217* (SI); Miravalles Alto, Bolívar, *Llatas 3017* (F); Prov. Celendín, Celendín, *López & Sagástegui 3122* (LP); Prov. San Miguel, Distr. El Prado, Porvenir, 16.4 km NE of San Miguel, 07°02′S, 78°54′W, *Merello et al. 1115* (F); Cajabamba-Luchubamba, *Sagástegui et al. 11215* (NY); La Encañada, *Sagástegui et al. 12020* (MO, NY); Prov. Santa Cruz, arriba de Chorro Blanco, *Sagástegui et al. 12999* (F, NY); Prov. Contumazá, Bosque de Cachil, *Sagástegui et al. 15009* (F); Bosque Cachil, *Sagástegui et al. 15266* (F), *Sagástegui et al. 15318* (F, NY), *Sagástegui et al. 15804* (F); Prov. Cajamarca, km 156 Pacasmayo-Cajamarca, *Sánchez 2757* (F, SI); Distr. Namora, Río Llallumayo, *Sánchez & Ruiz 3622* (F); Yumagual, entre Cajamarca y San Juan, Paso Gavilán, *Sánchez 4762* (F); La Colpa de Namora, a Sondor, entre Namora y Matara, *Sánchez 4793* (F); Prov. Hualgayoc, Alán, a Huangamarca, E de Bambamarca, *Sánchez et al. 5730* (F); Distr. Baños del Inca, Otuzco, Carahuanga, *Sánchez 547* (F); próximo a Conchán, *Sánchez & Seminaio 778*, *789* (F); Pasacucho, hacia Paccha, *Sánchez 811* (F); Prov. Chota, Chota-Tacabamba, 10 km from Chota, 78°38′W, 06°30′S, *Smith & Vásquez 3532* (F); [Cerro] Huascaray, *Townsend A189* (F).—Cuzco: Prov. Urubamba, Machu Picchu, *Cabrera & Fabris 13551* (LP); a Huiñayhuayna, *Chávez 3423*, *3432* (MO); San Miguel, Urubamba valley, *Cook & Gilbert 895* (US); Paucartambo-Pilcopata, km 27.1 km below Pillahuata, *Gentry et al. 23520* (NY); Pilcopata, *Infantes 857* (US); Prov. Calca, Loaccay-Lares, *Marín 2158* (LIL, LP); Pamacahua, 95 km de Cuzco, km 95–107 ferrocarril Cuzco-Quillabamba, 13°18′S, 72°07′W, *Núñez & Bengoa 8563* (F, US); Prov. Quispicanchi, entre Abra Walla y Marcapata, 210 km de Cuzco, 13°25′S, 70°54′W, *Nuñez et al. 9089* (F, MO, NY); ca. 5 km N of Aguas Calientes, km 116, *Solomon 3184* (MO); Prov. La Convención, hacienda Amaibamba, Río Amaibamba, *Vargas 3444* (F, LP); Prov. Anta, Mollepata, *Vargas 8311* (LIL, US); Prov. Cuzco, Marcapata, *collector unknown 1336* (NY).—Huánuco: Prov. Huánuco, Mito, *Huapalla 3297* (US); Cordillera de Carpish, *Humbert 31002* (US); Huánuco to La Unión, km 5–31, Mito and surroundings, 09°55′S, 76°20′W, *Landrum 4616* (F. NY); Mito, *Macbride & Featherstone 1519* (F, GH, LP); Prov. Pachitea, arriba de Panao, *Meza 338* (US); 32 km from Huánuco, Huánuco-La Unión, 76°26′W, 09°53′S, *Smith et al. 2184* (MO, US). —Junín: Palca in Richtung La Merced, *Ellenberg 8827* (SI); Prov. Tarma, Río Huasahuasi, below Huasahuasi, *Hutchison 1129* (F, MO, NY, US); hacienda Hinari, Hinancuyo, *Infantes 563* (LIL); Carpapata, above Huacapistana, *Killip & Smith 24371* (F, NY, US).—La Libertad: Prov.

Huamachuco, Sartimbamba, *Infantes 3544b* (LIL); Prov. Huamachuco, Sartimbamba, *Infantes 4422*, *4449* (LIL); Prov. Sánchez Carrión, Huamachuco, Munmalca, hacienda Cochabamba, *López & Sagástegui 2806* (LP); Huamacucho, Pallar-Huaguil, a Tayabamba, *López & Sagástegui 8120* (GH, MO); Prov. Santiago de Chuco, cerro La Botica, Cachicadán, *Sagástegui et al. 11855* (F, MO, NY).—Lambayeque: Prov. Lambayeque, entre Huaratara y Colaya, *Llatas 1975* (F, SI); Abra de Porculla, Olmos to Pucará, km 45 E of Olmos, *Plowman et al. 14288* (F, MO, US); Prov. Ferreñafe, Bosque de Chiñama, *Valencia 2272* (US).—Lima: Prov. Lima, cultivated in Museo de Historia Natural Javier Prado, *Ferreyra 17157* (MO).—Piura: ca. 3 km E of Canchaque to Huancabamba, 05°24′S, 79°36′W, *Dillon & Sánchez 6253* (F); Prov. Huancabamba, Huancabamba, *Rothschild 3037* (SI).—Puno: Prov. Carabaya, Ollachaea to San Goban, N of Camatane, *Boeke & Boeke 3041* (MO, NY, US); Ollachea to San Gabon, *Dillon et al. 1117* (F). **Without country.** Andes, South America, *Herndon s.n.* (US).

The protologue of *Andromachia solidaginea* mentions the Peruvian Andes between Ayabaca and the Río Cutaco valley as the type locality. However, the label of the only specimen found of this species kept at P (Humboldt and Bonpland Herbarium) gives the locality as "Quito" (Ecuador), a location outside the known distribution of this species. Despite the discrepancy in the locality data on the specimen, this specimen is considered to be the holotype of *L. solidagineum*.

As in *L. barclayae* (see discussion under *L. barclayae*) and *L. igniarium*, the presence of capitulum galls in *L. solidagineum* is common (Fig. 7B). The plants are employed against viruga [sic] fever (*Smith & Blas 4867*), which probably refers to Carrión disease, also called Oroya fever or Peruvian wart, a disease endemic to Peru, Ecuador, and Colombia (Gonzáles R. et al. 2007).

The flowers are fragrant (*Macbride & Featherstone 1519*, *Smith et al. 2184*, *Smith 10577*) and visited by bumblebees of the genus *Bombus* (*Boeke 1776*).

18. Liabum steinbachii H. Robinson, Phytologia 35: 489–490. 1977.—Type: Bolivia. Santa Cruz: cerro Tres Cruces, 1400 m, 8 Oct 1928, *Steinbach 8152* (holotype: K, digital image! fragment US!; isotypes: G, digital image! GH! K fragment at US! LIL! MO! NY, S, digital images!).

Perennial caulescent erect herbs, ca. 0.5 m tall; stems slightly costate, terete or slightly hexagonal in cross-section, densely and persistently white-tomentose; pseudostipules 0.5–1 cm long, without auricles, glabrescent adaxially, white-tomentose abaxially. Leaves scattered along the main stem and branches; leaf blades 8–10.5 cm long, 4–7 cm wide, chartaceous, ovate, apex short-acuminate, base cuneate, margin mucronate-serrate, venation acrodromous, with the pair of lateral veins exceeding the midpoint of the blade but not reaching the apex, surface smooth, glabrous adaxially, densely white-tomentose abaxially; petiole 2–3.5 cm long, not winged or slightly winged distally by decurrence of blade. Inflorescence not scapose, umbelliform, lax, with 8–16 capitula; capitula radiate, pedunculate, peduncles up to 30 mm long, densely white-tomentose. Involucre 8.5–10.5 mm long, 10–13.5 mm wide, campanulate; phyllaries 85–100 in 5–6 series, 2–8.5 mm long, 0.6–1.2 mm wide, greenish, outermost phyllaries ovate, apex acute, pubescence arachnoid, innermost phyllaries linear, apex attenuate, glabrescent; receptacle with chaff ca. 1 mm long. Ray florets 40–50; corolla 15.5–20 mm long, yellow, pubescent, tube 6.5–9.5 mm long, ca. 0.35 mm wide, limb 9–10.5 mm long, 1.5–1.8 mm wide, elliptic or obovate, 4-veined, apex 3-dentate; style 10.5–12.5 mm long, branches 4–5 mm long. Disc florets 35–40; corolla 8–10 mm long, tubular, tube 4–5 mm long, ca. 0.25 mm wide, gradually expanded into the limb, yellow, pubescent, limb 4–5 mm long, ca. 1 mm wide, lobes ca. 1.5 mm long, 0.35 mm wide, shorter than the throat, pubescent at the apex; anthers 3–3.5 mm long, apical ap-

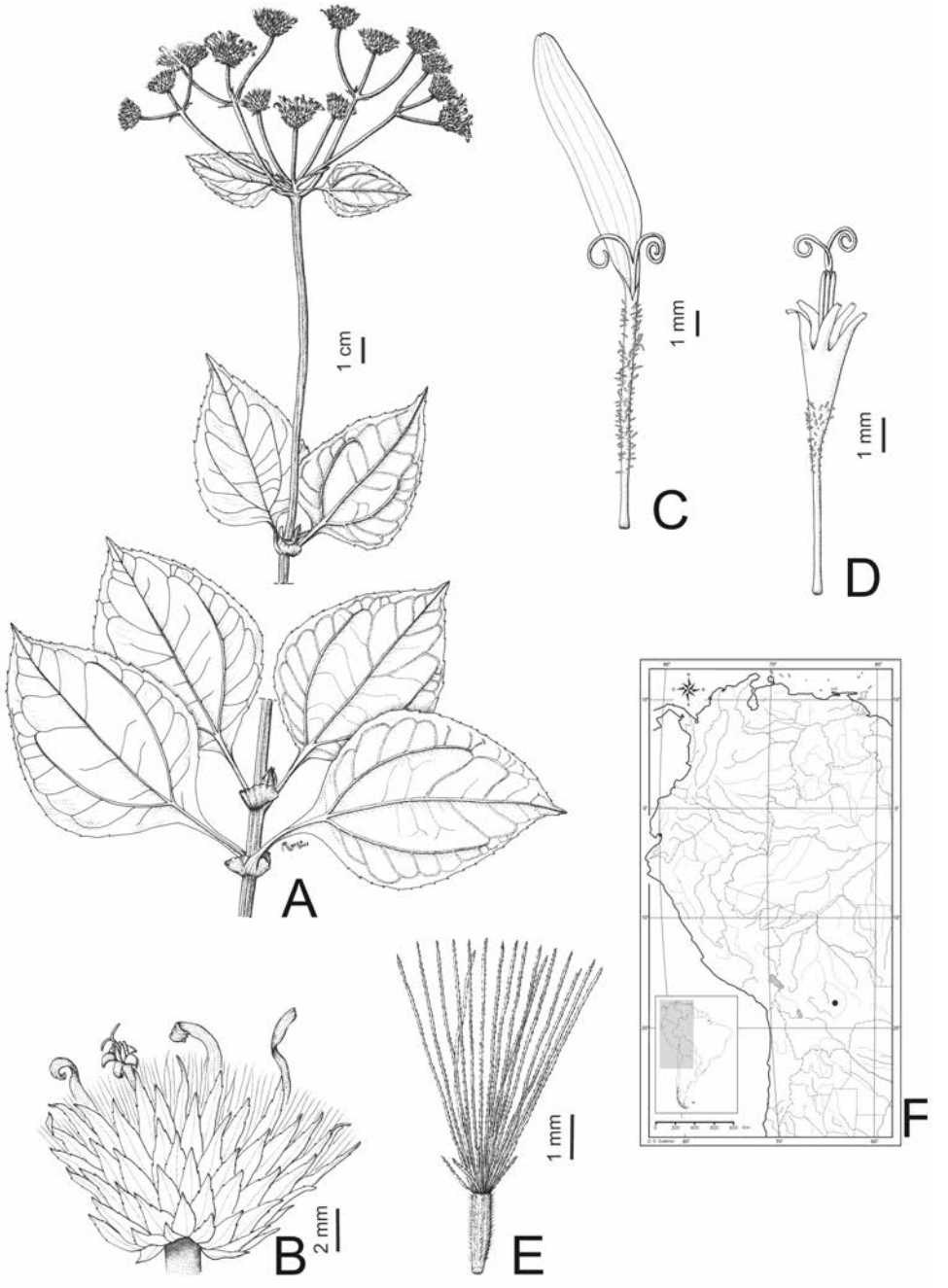

FIG. 31. *Liabum steinbachii* H. Rob. A. Habit (branch). B. Capitulum (only some florets shown). C. Ray floret. D. Disc floret. E. Cypsela and pappus. F. Distribution. (A–E based on *Steinbach 8152*, US.)

pendage 0.5–0.8 mm long, tails 0.5–0.6 mm long; style 11–15 mm long, branches 2.5–3 mm long, papillae covering style branches and extending down the shaft of the style a distance less than the length of the branches. Cypselae ca. 1.8 mm long, 0.5 mm wide, cylindrical to ellipsoid. Pappus bristles pale yellow or yellowish orange, scabrous; outer series ca. 1 mm long, sometimes absent; inner series up to 6 mm long. Chromosome number unknown. Fig. 31A–E.

Phenology. Plants with flowering capitula were collected in October.

Distribution (Fig. 31F). Department of Santa Cruz, Bolivia; montane areas; 1400–1800 m.

Additional Specimen Examined. **Bolivia.** Santa Cruz: Samaipata, cerro Tres Cruces, *Steinbach 8158* (LIL).

L. steinbachii differs from *L. igniarium* and *L. barclayae* mainly by its herbaceous habit and ray floret corollas more than 15.5 mm long.

19. Liabum stipulatum Rusby, Descr. S. Amer. Pl. 160–161. 1920.—Type: Colombia. Magdalena: Las Nubes, 4500 ft [1400 m], 7 Feb 1898 or 1899, *H. H. Smith 2001* (holotype: NY, digital image!; isotypes: BR, digital image! CM! E, F, digital image! GH! MO! PH, digital image! US!).

Subshrubs or shrubs, 1–3 m tall; stems slightly to conspicuously costate, hexagonal in cross-section, densely and persistently white-tomentose; pseudostipules ca. 1 cm long, without auricles, glabrous adaxially, white-tomentose abaxially. Leaves scattered along the main stem and branches; leaf blades 6.5–18.5 cm long, 4.5–14.5 cm wide, chartaceous, subtriangular, occasionally ovate, apex acute or shortly acuminate, base rounded or truncate, sometimes cuneate, margin mucronate-serrate, venation acrodromous or actinodromous, with the pair of lateral veins exceeding the midpoint of the blade but not reaching the apex (in larger leaves a second more basal pair of veins may be present), surface smooth, glabrous adaxially, densely white-tomentose abaxially; petioles 1.5–5 cm long, generally not winged, occasionally winged distally by decurrence of blade. Inflorescence not scapose, umbelliform or corymbiform, dense, with more than 50 capitula; capitula radiate, sessile or pedunculate, peduncles up to 5 mm long, densely white-tomentose. Involucre 5.5–6.5 mm long, 5–6 mm wide, campanulate; phyllaries 55–75 in 5–6 series, 1.5–5.5 mm long, 0.3–0.5 mm wide, greenish, sometimes purplish toward the apex, outermost phyllaries ovate, apex acute, pubescence arachnoid, innermost phyllaries linear, apex attenuate, glabrescent; receptacle with chaff ca. 0.3 mm long. Ray florets 25–30; corolla 6–7.5 mm long, yellow, pubescent, tube 2.5–3 mm long, 0.25–0.3 mm wide, limb 3.5–4.5 mm long, ca. 1 mm wide, obovate, 4-veined, apex 3-dentate; style 6–7.5 mm long, branches 3.3–4.5 mm long. Disc florets 20–25; corolla 5–6.5 mm long, tubular, tube 1.5–2.5 mm long, 0.25–0.35 mm wide, gradually expanded into the limb, yellow, glabrous or pubescent, limb 3.5–4 mm long, ca. 1 mm wide, lobes 1.8–2 mm long, 0.35–0.4 mm wide, approximately equal in length to the throat, pubescent at the apex; anthers 2.3–2.5 mm long, apical appendage 0.6–0.8 mm long, tails 0.3–0.5 mm long; style 7–7.5 mm long, branches 2–3 mm long, papillae covering style branches and extending down the shaft of the style a distance equal to or slightly less than the length of the branches. Cypselae 0.7–0.9 mm long, 0.3–0.4 mm wide, obconical. Pappus bristles pale yellow, whitish yellow, or yellow-

ish orange, scabrous; outer series 0.9–1.2 mm long, sometimes absent; inner series up to 5 mm long. Chromosome number unknown. Fig. 32A–E.

Phenology. Plants in flower have been collected throughout the year; flowering and fruiting capitula can occur on the same plant.

Distribution (Fig. 32F). Western Venezuela, Colombia, Ecuador, and northern Peru (Department of Cajamarca); montane and pre-montane humid forests, margins of streams, roadsides, mixed with the secondary vegetation; 0–2950 m.

Local Names. Santa María (*Cerón et al. 6897*), Santa María cordiforme (*Duque 1533*).

Representative Specimens. **Colombia.** Antioquia: 13 km E de Bolívar, *Araque & Barkley 19An041* (F, US); Angelópolis, *Gutiérrez & Barkley 17C681* (LIL, US); Heliconia, *Hermano Daniel 3991* (F); vicinity of Medellín, *Toro 193* (NY), *Toro 917* (NY).—Caldas: Manizales, *Aguirre 105* (F); Manizales, Monteleón, *de Fraume & Alvarez 63* (F).—Cauca: Río Cali, *Duque 1533* (F, US); Munchique, camino a la "Mina Tapada," *García-Barriga et al. 12979* (LIL); Popayán, *Lehmann 1147* (NY).—Cundinamarca: Sasaima, *Azolimar 192* (F); ca. 21 km NW of Facatativá, *King et al. 5931* (F, NY); Monte Redondo to Quetame, *Pennell 1864* (NY).—Huila: E of Neiva, *Rusby & Pennell 621* (GH, NY).—Magdalena: Sierra Nevada de Santa Marta, between cabecera de Huachaca-El Tagua, 11°06′N, 73°56′W, *Gentry 76331* (MO); Sierra Nevada de Santa Marta, *Romero 737* (US).—Nariño: Ricaurte, trayecto San Isidro-La Planada, 01°10′N, 77°58′W, *de Benavides 9140* (MO, NY, US).—Quindio: Mun. Génova, Vra. El Cedral, Génova-Pijao, a 5 km de Génova, *Arbelaez et al. 2612* (MO); La Palmira, E of Armenia, *Pennell 8628* (US); Río Quindio, above Armenia, *Pennell et al. 8700* (US).—Santander: vicinity of El Roble, *Killip & Smith 19362* (GH, NY, US).—Tolima: 3 km NE of Fresno, *King et al. 6013* (US); Líbano, *Pennell 3448* (NY).—Valle del Cauca: Río Cali, Río Pichindé, entre Los Cárpatos y El Olivo, *Cuatrecasas 21728* (F); quebrada del Tigre, entre Las Brisas y La Marina, *Cuatrecasas 22680* (F); Mercedes, *Dryander 2258* (US); arriba de La Habana, Buga, *Espinal 2003* (US); Buenaventura, 12.6 km E of Cali, *Hutchison & Idrobo 3049* (F, MO, NY, US); Miraflores, Palmira, *Killip 6117* (GH, NY, US); Mun. La Cumbre, La Herradura, entre Santa Inés y La Cumbre, ca. 3 km de La Cumbre, *Ramos 812* (MO). **Ecuador.** Carchi: Maldonado-Tobar Donoso, 3–4 km NW of Maldonado, *Harling & Andersson 12255* (MO); Peñas Blancas, 20 km below Maldonado, Río San Juan, *Madison et al. 4634* (F); km 2–6 Maldonado-Tulcán, *Werling & Leth-Nissen 54* (NY).—Cotopaxi: Quevedo-Latacunga, Río Pilaló, 00°53′S, 79°10′W, *Holm-Nielsen et al. 3071* (MO, NY); Cantón Pajili, hacienda Solento, near Santa Rosa, *Mexía 6686* (LP).—Esmeraldas: Lita-San Lorenzo, 10 km NW of Lita, 00°55′N, 78°35′W, *Gentry et al. 70177* (BAB, US); Esmeraldas-Coronel C. Concha, between Tabiazo and Coronel Concha, *Harling & Andersson 16749* (US).—Guayas: ca. 12 km SE of Vinces, *King & Garvey 7010* (F, MO, NY, US); Milagro, *Mille 1008* (F).—Imbabura: 0.5 km E of Lita, 00°50′N, 78°27′W, *Boom 2583* (MO, NY, US).—Loja: 23.5 km E of Catamayo to Loja, *Stuessy & Nesom 5885* (CTES).—Los Ríos: Cantón Vinces, Jauneche forest between Macachi and Palenque, estero Peñafiel, *Dodson et al. 7053* (MO, US).—Pichincha: Cantón Santo Domingo, parroquia Tandapi, 00°25′S, 78°45′W, *Cerón et al. 6897* (MO, US); alrededores de Santo Domingo de los Colorados, 79°08′W, 00°14′S, *Gavilanes 1007* (NY); Calacalí-Nieblí, hacienda El Cisne, *Jaramillo 9681* (F); Saloya, *Mille 598* (GH, MO).—Without province: Milagro, *Mille 1008* (F). **Peru.** Cajamarca: Prov. Hualgayoc, hacienda Taulis, vicinity Casa Hacienda, *Hutchison & von Bismarck 6337* (GH, MO, NY, US); Prov. Chota, a 4 km de Querocoto, entre Llama y Huambos, *Leiva et al. 1369* (F). **Venezuela.** Mérida: Mun. Jají, Distr. Campo Elías, La Chorrera, Río Las González, *Marcano B. 818* (MY).—Táchira: Distr. Junín, entre San Vicente de la Revancha y Río Chiquito, *A. Fernández 2042* (MY). **Country unknown.** Without locality, *Klatt s.n.* (GH).

The correct collector number of the type of *L. stipulatum*, as it appears on the specimen, is *Smith 2001* and not *Smith 200*, as it appears in the protologue (Ayers & Boufford 1988; corrected *in schedula* by D. E. Boufford in 1987).

The protologue of *L. stipulatum* gives "Las Nubes, 4500 ft" as the type locality. However, the label of the holotype in NY also reads "Santa Marta," the labels of the isotypes in GH and US indicate only "Santa Marta," and the label of the isotype at MO reads only "Colombia." There are also some differences in the date of collection, i.e., the protologue indicates "February 7" without the year of collection, and the labels of the type specimens

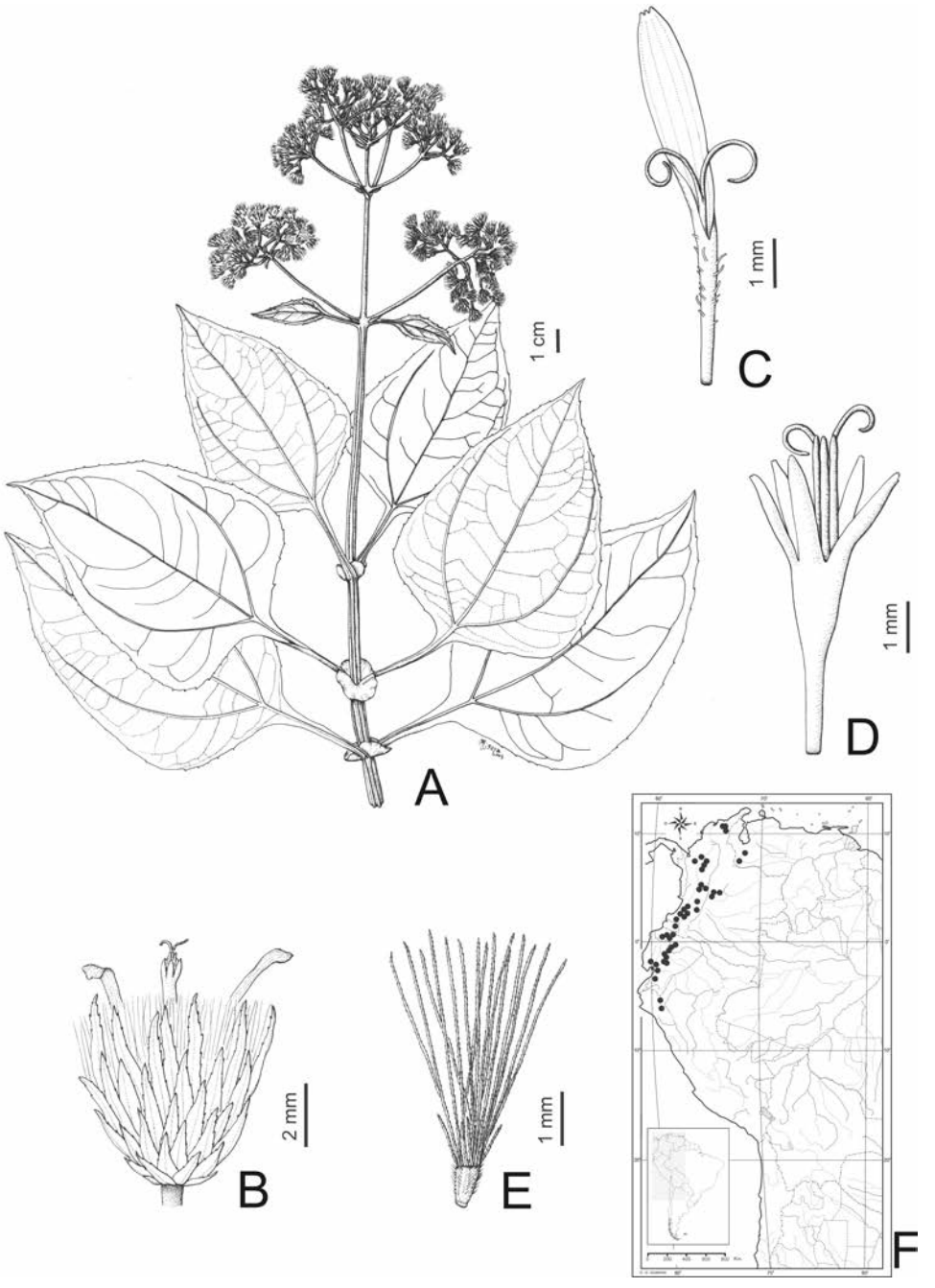

FIG. 32. *Liabum stipulatum* Rusby. A. Habit (branch). B. Capitulum (only some florets shown). C. Ray floret. D. Disc floret. E. Cypsela and pappus. F. Distribution. (A–E based on *Killip 6117*, NY.)

say "1898–1899" (GH, NY, US) and "1898–1901" (GH, MO). Despite the label differences, all of these specimens appear to represent the same gathering and are thus considered type material of this name. Similar typification problems were noted for *L. falcatum*, a synonym of *L. acuminatum*.

The label of the specimen *Cerón et al. 6897* mentions that it is used "para curar el espanto" (to cure fright). Use of plants in parts of Peru for ritual or magical aliments, such as "susto" or "espanto," a condition caused by fright brought on by a life event or the patient's environment, is reported to be common (Bussmann & Sharon 2006).

20. Liabum umbellatum (Linnaeus) Schultz Bipontinus, J. Bot. 1: 236. 1863. *Amellus umbellatus* Linnaeus, Syst. Nat., ed. 10, 2: 1225. 1759. *Starkea umbellata* (Linnaeus) Willdenow, Sp. Pl., ed. 4 [Willdenow] 3: 2216. 1803, nom. superfl.—TYPE: JAMAICA. Without locality: *Browne s.n.* (lectotype, designated by Moore (1936: 267): LINN 1023.3, digital image!).

Andromachia poiteaui Cassini, Bull. Soc. Philom. Paris 1817: 184. Nov 1817. *Liabum poiteaui* (Cassini) Urban, Ark. Bot. 23: 87. 1931.—TYPE: HAITI/DOMINICAN REPUBLIC. Saint-Domingue, *Poiteau s.n.* (herb. Desfontaines) (holotype: FI, digital image!).

Liabum wrightii Grisebach, Mem. Amer. Acad. Arts, n. s. 8: 515. 1863.—TYPE: CUBA. ["Cuba Orientali"] Holguín: In sylvis densis secus rivulos, prope Monte Verde, probably 21 Jun 1859 (but label dates vary, see below), *Wright 288* (holotype: GOET, digital image!; isotypes: BR, digital image! F! GH! GOET, HAC, K, digital images! MO! NY, P, PH, S, YU, digital images!).

Liabum crispum Schultz Bipontinus, J. Bot. 1: 236. 1863.—TYPE: CUBA. Holguín: Monte Verde, 1856–1857, *Wright 289* (holotype: K; isotypes: F! GH-2 sheets [one has date 13 Jan 1859]! MO!).

Liabum cubense Schultz Bipontinus, J. Bot. 1: 236–237. 1863.—TYPE: CUBA. Santiago: Grosse roche summit de la Sierra Maestra, alt. 5000′, July 1844, *Linden 2031* (holotype: P, digital image!; isotypes: G, K, P-2 sheets, W, digital images!).

Liabum subacaule Rydberg, N. Amer. Fl. 34(4): 290–291. 1927.—TYPE: HAITI. Nord: Between Petit Borgne and Mt. Casse, [about 610 m], 16 Aug 1903, *Nash 502* (holotype: NY, digital image!).

Liabum domingense Rydberg, N. Amer. Fl. 34(4): 291. 1927.—TYPE: DOMINICAN REPUBLIC. La Vega: prope Constanza, 1400 m, June 1910, *Türckheim 3113* (holotype: NY, digital image!; isotypes: F! GH! MO! US!).

Liabum longipes Urban, Feddes Repert. Spec. Nov. Regni Veg. 26: 115. 1929.—TYPE: CUBA. Santiago: Sierra Maestra, on the rocky edges of arroyo Bayajá at the famous cascade of Bayajá, 8 Aug 1922, *Ekman 14776* (holotype: S, digital image!; isotypes: F! G, NY, S, digital images! US!).

Liabum barahonense Urban, Ark. Bot. 23: 85. 1931.—TYPE: DOMINICAN REPUBLIC. Barahona: Paridis prope Barahona, in sylva frondosa rarissimum, 150 m, Dec 1909, *Türckheim 2785* (holotype: B [destroyed]; lectotype here designated: NY, digital image!).

Liabum selleanum Urban, Ark. Bot. 23: 86. 1931.—TYPE: HAITI. Sud-est: Massif de la Selle, [Pétiton-ville], Morne Cabaio, in pine forest on limestone silvis, 1900–2000 m, [20 Aug 1924], *Ekman H1548* (holotype: S, digital image!; isotypes: S, digital image! US!).

Liabum ovatifolium Urban, Ark. Bot. 23: 86. 1931.—Type: Dominican Republic. Espaillat: Cordillera Septentrional, Moca, Colonia de Jamao, rocky place, c. 900 m, 21 May 1929, *Ekman H12578* (holotype: S, digital image!; isotypes: GH! S, digital image! US!).

Liabum polycephalum Urban, Ark. Bot. 23: 88. 1931.—Type: Haiti. Sud: Massif de la Hotte, western group, Torbec, laterite ridge above La-Mare-Proux, 900 m, 8 Dec 1925, *Ekman H5346* (holotype: S, digital image!; isotypes: GH! S, digital image! US, digital image!).

Perennial caulescent, occasionally sub-acaulescent, erect herbs up to 80 cm tall; stems not costate, terete, densely and persistently white-tomentose; pseudostipules absent. Leaves clustered distally on shoot, rarely forming a basal rosette; leaf blades 1.6–14 cm long, 0.8–8.7 cm wide, chartaceous, elliptic, ovate, or broadly ovate, apex short-acuminate or acute, base rounded-cuneate, decurrent, margin mucronate-serrate, venation acrodromous with the pair of lateral veins exceeding the midpoint of the blade but not reaching the apex, surface smooth or slightly bullate, green, glabrous, hirsute, strigose, or with persistent arachnoid pubescence adaxially, densely white-tomentose abaxially; inconspicuously petiolate, petioles up to 15 cm long, minutely to widely mucronate-serrate, gradually or abruptly differentiated from the blade, winged, the wings 0.15–0.7 cm wide. Inflorescence long-scapose, umbelliform, lax or dense, capitula 3–60, sub-radiate, sessile or pedunculate, peduncles up to 10.5 cm long, up to 2 mm wide, white-tomentose. Involucre 5–14 mm long, 8–20 mm wide, campanulate; phyllaries 90–105 in 5–6 series, 1.5–18 mm long, 0.4–1 mm wide, greenish, outermost phyllaries ovate, apex acute, pubescence arachnoid, innermost phyllaries linear, apex attenuate, erect or twisted, glabrescent; receptacle with chaff up to 6 mm long. Ray florets 10–60; corolla 5.4–17.5 mm long, yellow, glabrous or slightly pubescent, tube 4–7 mm long, 0.08–0.16 mm wide, limb 1.1–11 mm long, 0.17–0.45 mm wide, linear, 1–3-veined, apex entire or slightly dentate; style 6–10 mm long, branches 1.5–4 mm long. Disc florets 15–30; corolla 6.3–11.4 mm long, tubular, tube 3–4.8 mm long, 0.11–0.26 mm wide, gradually expanded into the limb, yellow, glabrous or pubescent, limb 1.7–3.8 mm long, 0.4–0.9 mm wide, lobes 1–2.5 mm long, 0.18–0.37 mm wide, longer than the throat, pubescent or glabrous at the apex; anthers 1.6–3.3 mm long, apical appendage 0.3–0.8 mm long, tails 0.2–0.8 mm long; style 5.5–12.5 mm long, branches 1.5–4 mm long, papillae covering style branches and extending down the shaft of the style a distance equal to or less than the length of the branches. Cypselae 0.8–2.4 mm long, 0.17–0.54 mm wide, cylindrical to ellipsoid. Pappus bristles yellowish orange, scabrous; outer series 1–2.6 mm long, sometimes absent; inner series up to 8.3 mm long. Chromosome number: $n = 18$ (Torres & Liogier 1970). Fig. 33A–E.

Phenology. Plants with flowering capitula have been collected mainly from February to October, but also in December.

Distribution (Fig. 33F). West Indies: central and eastern Jamaica, eastern Cuba, and Hispaniola; near waterfalls or rivers, slopes of rain or cloud forests, open areas on the summit of mountains and common in open forests of *Pinus occidentalis* Sw., and along roadsides or other disturbed areas, in calcareous or rocky soils; 150–1980 (–2250) m.

Local Names. Cura nacido (Hispaniola: *Liogier 11533*), chupa nacío, voladora (Hispaniola: Liogier 1996), wound worth (Jamaica: *Yuncker 18202*; Browne 1756).

Representative Specimens. **Cuba.** Granma: Sierra Maestra, arroyo Corojo, a tributary of Yara, near Nagua, *Ekman 14745* (F); Sierra Maestra, en el arroyo próximo al campamento El Cojo, *Ventosa et al. s.n.* in

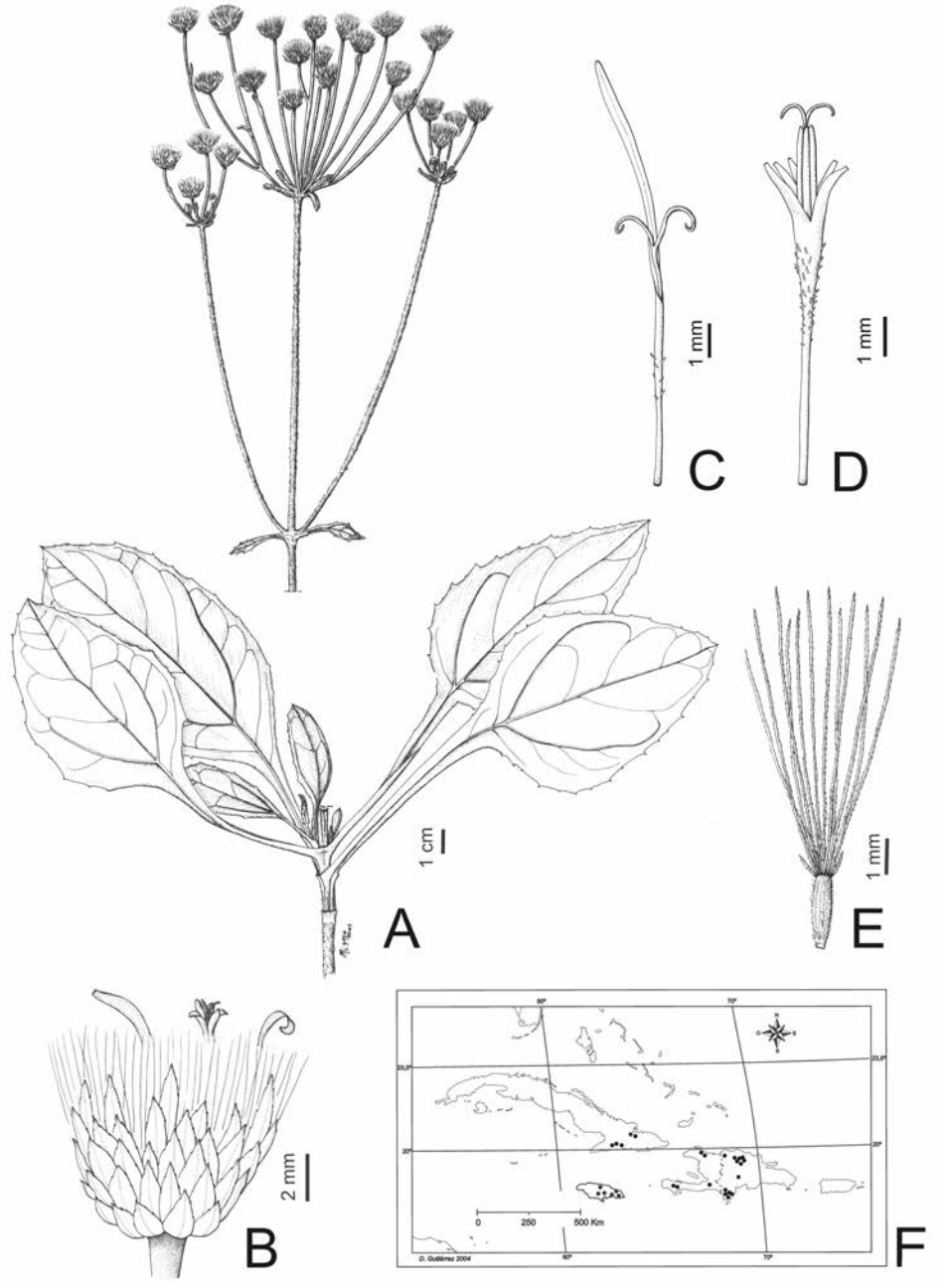

FIG. 33. *Liabum umbellatum* (L.) Sch. Bip. A. Habit. B. Capitulum (only some florets shown). C. Ray floret. D. Disc floret. E. Cypsela and pappus. F. Distribution. (Based on: A–B, *Crosby et al. 535*, GH; C–E, *Crosby et al. 535*, F.)

2008 (HAC 42552); Sierra Maestra, campamento El Cojo hacia Santo Domingo, *Ventosa et al. s.n.* in 2008 (HAC 42554).—Guantánamo: sur de la región de Baracoa, arroyo Frío, *León 12145* (HAC); yunque de Baracoa, *Ventosa et al. s.n.* in 2008 (HAC 42553).—Santiago de Cuba: Loma del Gato, Señora del Cobre, *Acuña 9905* (HAC); Loma del Gato, *Clemente 1857* (HAC); márgen río Peladero, Alto Valenzuela, Sierra Maestra, *Lopez Figueras 2339* (HAC); Pico Suecia, Pico Turquino, *Samek 26060* (HAC).—Province uncertain: Cuba Orientali, *Wright 185* (S); *Wright 2871* (GH 9727). **Dominican Republic.** Barahona: without locality, *Fuertes 959b* (GH); between Pedernales y Aceitial, *Howard & Howard 8158* (GH); between Palo Mino and Montasse to Polo, *Howard 12087* (GH); Sierra de Bahoruco, 1–2 km south of Polo along DR Carretera Ramal 533 to Cabral, 18–19 km south of Cabral, 18°07′N, 71°16′W, *Pruski & Ortíz 4061* (JBSD, LP); Sierra de Bahoruco, arroyo La Travesia, carretera de Barahona-Paraíso, 16°07′N, 71°07.5′W, *Zanoni et al. 43619* (JBSD).—Elías Piña: municipio Hondo Valle, Sierra de Neiba, desde Aniceto Martínez, 1 km antes del puesto militar 204, 18°41′27.5″N, 71°46′42.1″W, *Clase & Alvarez Fuentes 5114* (JBSD).—La Vega: prope Jarabacoa, *Fuertes 1635b* (GH); La Ciénaga, *Gastony et al. 394* (GH); Valle Nuevo, *Lavastre 964* (GH); arroyo de la Sal, above Jimenoa dam, *Liogier 11754* (F); 10.7 km W to Arroyo Prieto and El Río, 19°01′N, 70°31′W, *Mejía & Zanoni 4975* (MO); Cordillera Central, along DR Carretera secundaria 12, ca. 5 km east of El Río on the road to Arroyo Prieto, ca. 25 km east of Constanza, 19°01′N, 70°30′W, *Pruski et al. 4028* (LP); Cordillera Central, ladera del N de La Lona de La Sal, frente al valle de Jarabacoa, 19°05′N, 70°35′W, *Zanoni et al. 36408* (JBSD).—Monte Cristi-Santiago Rodríguez: Monción near Tomás, *Ekman H13012* (F, GH).—Pedernales: Sierra de Baoruco, along road to El Aceitillar, 18°07.332′N, 71°35.972′W, *Acevedo-Rodríguez et al. 12967* (JBSD); Sierra de Bahoruco, a 26 km al nordeste de Pedernales, carretera a la Estación Forestal Aceitillar, 17°54′N, 71°32′W, *González & McDowell 619A* (JBSD); between Pedernales and Aceitial, *R. Howard & E. Howard 8166*, *8179* (GH); S of Aceitillar along "Alcoa Aluminum Co. Road" in the Sierra de Baoruco, *Judd 1481* (GH); between Las Mercedes and Aceitillar, Sierra de Bahoruco, *Liogier 14130* (GH); Sierra de Baoruco, en Los Arroyos, 4 km suroeste de Polo, 18°04′N, 71°18′W, *Mejía & Pimentel 18488* (MO).—Peravia: Cordillera Central, camino desde La Yayita a Cañaveral, 18°24′N, 70°20′W, *Jiménez & Polanco 1032* (JBSD); 27 km north of San José de Ocoa on the road to Constanza, 18°30′N, 71°30′W, *Watson & Mejía 984* (JBSD).—Puerto Plata: Cordillera de Yaroa, *Liogier 11063* (GH).—San José de Ocoa: Firme de Benilejo, Piedra Blanca, *Liogier 19903* (F).—Santiago: Loma de Oro, about 5 mi S of Mata Grande, *Liogier 11533* (GH); Distr. San José de las Matas, Jicomé, *Valeur 56* (F, GH, MO); Loma Diego de Ocampo, 13 km NO [NW] de Santiago, 19°35′N, 70°44.5′W, *Zanoni et al. 42442* (MO). **Jamaica.** Clarendon: Leicesterfield, upper Clarendon, *Harris 10844* (F).—Portland: Hardwar Gap, *Crosby et al. 535* (F, GH); Nannypot I, Blue Mountains, *Morley & Whitefoord 717* (MO); Morce's Gap, *Nicholson 25* (F, GH, MO).—Portland-Saint Andrew-Saint Thomas: near New Haven Gap, Blue Mountains, *Philipson 1118* (MO).—Saint Andrew: Forest Reserve area W of Hardwar Gap, *Anderson & Sternberg 3113* (GH, MO); West slope of Mt. Horeb, near Hardwar Gap, Port Royal Mountains, *Barkley & Proctor 22J271* (LIL); Newcastle, at Hardwar Gap above, *West & Arnold 119* (GH).—Saint Ann: Mount Diablo, *Alexander s.n.* in 1850 (GH); near Bamboo, *Hunnewell & Griscom 14406* (GH); Camperdown school, 1.5 mi SW of Gibraltar, *Stearn 566* (GH); near Hollymount, *Yuncker 18202* (F).—Saint Catherine: Resource, *Adams 10803* (MO).—Saint Thomas: between Blue Mountain Peak and Portland Gap, *Crosby et al. 859* (F, GH, MO); Cuna Cuna, above Mattis River, *Maxon & Killip 194* (F).—Without parish: without locality, *Bertero s.n.* (MO). **Haiti.** Nord-Ouest: vicinity of Saint-Louis-du-Nord, *E. Leonard & G. Leonard 14518* (GH).—Sud: Massif de la Hotte, Jérémie between Lopineau and Morne Pain-de-Sucré, *Ekman H10392* (F, GH).—Sud-est: Massif de la Selle, Morne Brouet, *Ekman H1870* (GH).

According to our morphological analyses (see section *Liabum* in the Caribbean), we propose the names *Liabum crispum* Sch. Bip., *L. cubense* Sch. Bip., *L. longipes* Urb., and *L. wrightii* Griseb. as synonyms of *L. umbellatum.*

According to Greuter et al. (1993), the type species of *Liabum* was not designated. Adanson (1763), however, had designated *L. umbellatum* as the type species in equating his new genus with *Amellus umbellatus* described by Linnaeus in 1759. Rydberg (1927) was the first to identify *L. umbellatum* as the type species of *Liabum*. Cassini (1823) created the illegitimate name *Liabum brownei* for *Liabum umbellatum*, and the former has been sometimes erroneously named as the type species of *Liabum* (e.g., Cabrera 1947; Robinson & Brettell 1974; Robinson 1983).

Some workers have cited *Plantarum Jamaicensium Pugillus* (Linnaeus 1759b) as the original place of publication of the name *Amellus umbellatus*, but this work was published

(28 November 1759) after the *Systema Naturae* (7 June 1759), where the species was first described.

According to Turner (1996), the type specimen of *Andromachia poiteaui* was kept at P; however, this type is deposited in FI.

Duplicates of the specimen *Wright 288*, the type of *L. wrightii* Griseb., were distributed with many different dates: the sheets at BR, F, G, GOET, MO, PH, and NY give the date as 1856–1857, one sheet at GH bears the date 21 June 1859 and a second the date 17 July 1856/1857, a second sheet at MO indicates Sep 1859–Jan 1860, one at K Jan–July 1859, and sheets at HAC, P, and S 1860–1864. Despite this variation in dates all specimens appear to represent the same gathering and are here considered types.

Browne (1756) commented that *L. umbellatum* was used in Jamaica for healing wounds and that, because it has a taste that is acerbic, the leaves are sweet upon the palate.

21. Liabum vargasii H. Robinson, Phytologia 34: 292–293. 1976.—Type: Peru. Cuzco: Prov. Urubamba, Machupycchu, 2000 m, 28 July 1951, *Vargas 10182* (holotype: US!).

Subshrubs or shrubs, 2–3 m tall; stems slightly costate, hexagonal in cross-section, densely and persistently white-tomentose; pseudostipules 0.5–0.8 cm long, without auricles, glabrous adaxially, white-tomentose abaxially. Leaves scattered along the main stem and branches leaf blades 7.5–16.5 cm long, 4.5–7 cm wide, chartaceous, ovate, apex attenuate, base cuneate, margin mucronate-serrate, venation acrodromous, with the pair of lateral veins exceeding the midpoint of the blade but not reaching the apex, surface smooth, glabrous adaxially, densely white-tomentose abaxially; petioles 1.2–2.7 cm long, not winged. Inflorescence not scapose, umbelliform or corymbiform, lax, with more than 50 capitula; capitula radiate, pedunculate, peduncles up to 10 mm long, densely white-tomentose. Involucre 5–6.5 mm long, 5.5–6 mm wide, campanulate; phyllaries 65–75 in 5–6-series, 1.5–5 mm long, 0.4–0.7 mm wide, greenish, outermost phyllaries ovate, apex acute, pubescence arachnoid, innermost phyllaries linear, apex attenuate, glabrescent; receptacle with chaff ca. 2 mm long. Ray florets 25–35; corolla 8.5–9.5 mm long, yellow, pubescent, tube 3.5–4 mm long, ca. 0.25 mm wide, limb 5–5.5 mm long, 1–1.5 mm wide, obovate, 4-veined, apex 3-dentate; style 6.2–7.5 mm long, branches 2–2.5 mm long. Disc florets 30–40; corolla 5.5–7 mm long, tubular, tube 2.5–3 mm long, ca. 0.3 mm wide, gradually expanded into the limb, yellow, pubescent, limb 3–4 mm long, ca. 1 mm wide, lobes 1.5–2 mm long, ca. 0.4 mm wide, equal in length to the throat, pubescent at the apex; anthers 2.8–3 mm long, apical appendage 0.3–0.5 mm long, tails 0.5–0.8 mm long; style 9–12.2 mm long, branches ca. 2 mm long, papillae covering style branches and extending down the shaft of the style a distance equal to the length of the branches. Cypselae 0.8–1 mm long, 0.4–0.5 mm wide, ellipsoid to obconical. Pappus bristles pale yellow or yellowish orange, scabrous; outer series 0.7–2.5 mm long, sometimes absent; inner series ca. 4.5 mm long. Chromosome number unknown. Fig. 34A–E.

Phenology. Plants with flowering capitula have been collected from July to November.

Distribution (Fig. 34F). Department of Cuzco, Peru; evergreen montane forests, the montane "ceja," lower subtropical forests associated with herbaceous vegetation, and along rivers; 2000–2400 m.

Additional Specimens Examined. **Peru.** Cuzco: Prov. Cuzco, Río Urubamba, *Angulo 1774* (LP); Prov. Urubamba, Machu Picchu, *Ferreyra 2691* (US), *Ferreyra 9910* (MO, US), *Vargas 2114* (F), *Vargas 2186* (NY).

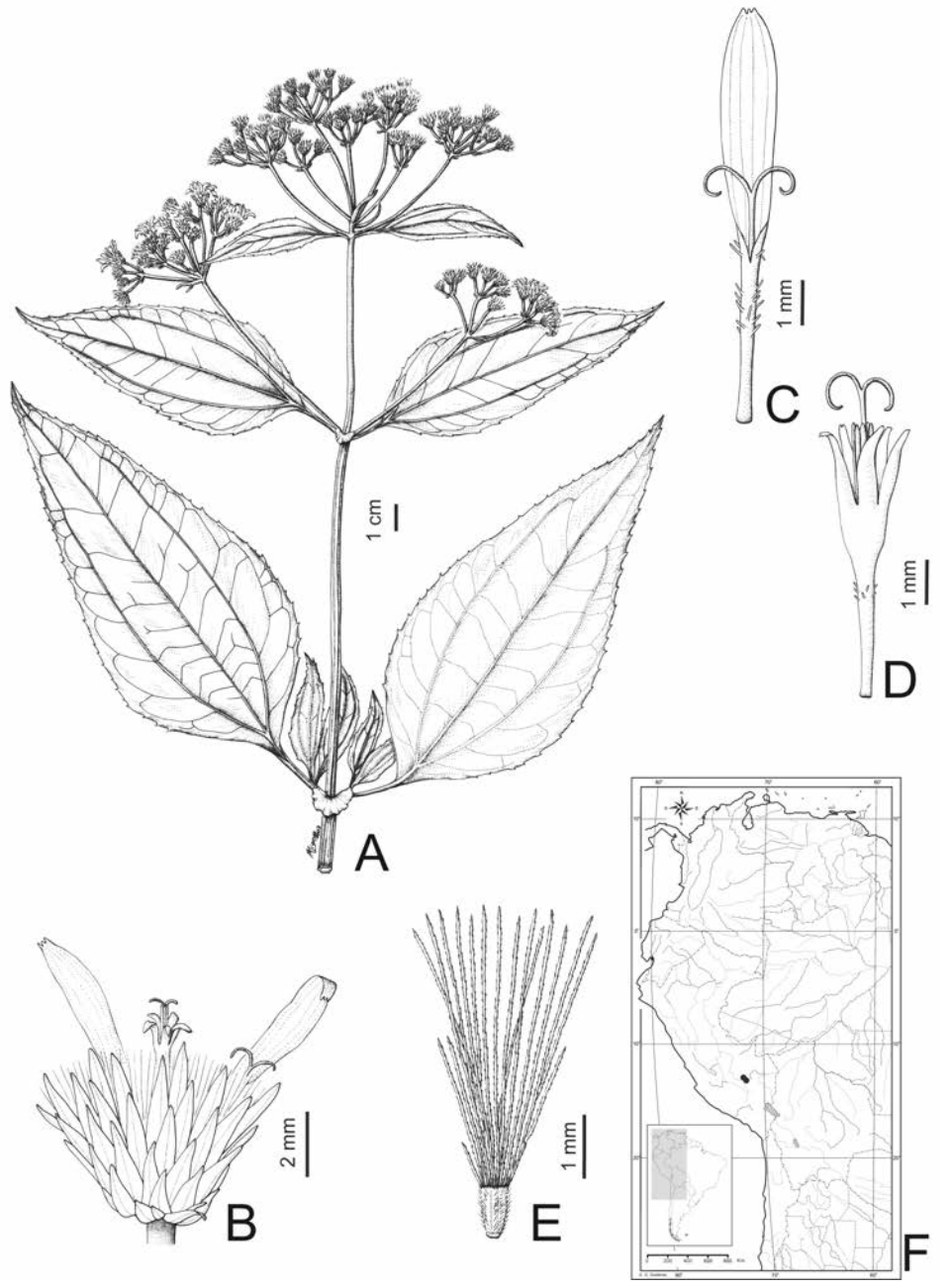

FIG. 34. *Liabum vargasii* H. Rob. A. Habit. B. Capitulum (only some florets shown). C. Ray floret. D. Disc floret. E. Cypsela and pappus. F. Distribution. (A–E based on *Vargas 10182*, US.)

Liabum vargasii resembles *L. macbridei* and *L. wurdackii* in its general aspect. However, *L. vargasii* differs from *L. macbridei* by its ovate leaf blade up to 7 cm wide with an attenuate apex, inflorescence with more than 50 capitula, involucre up to 6.5 mm long, and ray floret corolla limb up to 6.5 mm long. It is easily distinguishable from *L. wurdackii* by its fewer than 40 ray florets per capitulum and yellow ray corollas.

22. Liabum wurdackii Ferreyra, Publ. Mus. Hist. Nat. "Javier Prado," Ser. B, Bot. 20: 1. 1965.—Type: Peru. Amazonas: Prov. Bagua, entre Bagua Grande y Chachapoyas, 1200–1300 m, 17 May 1962, *Ferreyra 14423* (holotype: USM, digital image!).

Subshrubs or shrubs, sometimes climbing, 0.5–4 m tall; stems not costate, terete or slightly hexagonal in cross-section, with dense persistent to deciduous white-tomentose pubescence; pseudostipules 0.8–1.5 cm long, without auricles, green, glabrescent adaxially, white-tomentose abaxially. Leaves scattered along the main stem and branches; leaf blades 5.5–13.5 cm long, 2–6.5 cm wide, chartaceous, ovate, apex acute, acuminate or attenuate, base rounded or truncate, sometimes cuneate or decurrent, margin mucronate-serrate, venation acrodromous, with the pair of lateral veins exceeding the midpoint of the blade but not reaching the apex, surface smooth, green, and glabrous adaxially, densely white-tomentose abaxially; petioles 0.5–3.5 cm long, not winged or sometimes slightly winged distally. Inflorescence not scapose, umbelliform, lax, with (4–7) 25 to more than 50 capitula; capitula radiate, pedunculate, peduncles up to 15 mm long, densely white-tomentose. Involucre 7.5–10 mm long, 7–9.5 mm wide, campanulate; phyllaries 80–90 in 5–6 series, 1.8–8.5 mm long, 0.5–0.8 mm wide, greenish, occasionally purplish toward the apex, outermost phyllaries ovate, apex acute, usually covered with arachnoid pubescence, sometimes densely white-tomentose or glabrous, innermost phyllaries linear, apex attenuate, glabrescent; receptacle with chaff ca. 0.7 mm long. Ray florets 40–50; corolla 9–11.5 mm long, orange or orange-yellow, glabrescent or pubescent, tube 4–5 mm long, 0.3–0.4 mm wide, limb 5–6.5 mm long, 1–1.5 mm wide, obovate, 4-veined, apex 3-dentate; style 8.5–9.5 mm long, branches 3–4 mm long. Disc florets 60–80; corolla 6–8.5 mm long, tubular, tube 3.5–5 mm long, 0.3–0.5 mm wide, gradually or sometimes abruptly expanded into the limb, yellow, glabrescent or pubescent, limb 2.5–3.5 mm long, 0.7–1 mm wide, lobes 1.5–2 mm long, ca. 0.25 mm wide, longer than the throat, pubescent at the apex; anthers 2.8–3 mm long, apical appendage ca. 0.4 mm long, tails 0.4–0.8 mm long; style 8–9.5 mm long, branches ca. 3 mm long, papillae covering style branches and extending down the shaft of the style a distance less than the length of the branches. Cypselae 0.8–1.3 mm long, 0.3–0.5 mm wide, cylindrical to ellipsoid. Pappus bristles yellow or whitish yellow, scabrous; outer series ca. 1.5 mm long, sometimes absent; inner series up to 6 mm long. Chromosome number unknown. Fig. 35A–E.

Phenology. Collected in flower from May to January.

Distribution (Fig. 35F). Andean ranges of northern Peru; slopes, margin of rivers, roadsides, and arid to semiarid scrub, on clay and rocky soils; 660–2800 m (one collection at 300–350 m).

Representative Specimens. **Peru.** Amazonas: Chomza, ca. 5 km of La Peca, *Barbour 4304* (US); entre Bagua Grande y Jazán, *Ferreyra 20590* (US); 48 km NW of Chachapoyas to Bagua, Río Utcubamba, *Gentry et al. 23212* (F, NY); Prov. Bagua, Río Utcubamba, cerro Tapur, hacienda Misqui ca. 40 km S of Bagua Grande, *Hutchison 1460* (F); Río Utcubamba, 60 km N of Leimebamba, 11 km S of Caclic, *Hutchison & Wright 5850* (F, GH, NY); 34 km from Chachapoyas N to Florida, *King & Bishop 9226* (MO, US); El Tingo, entre Bagua e Ingenio, *López et al. 4240* (LP); Roca San Lorenzo, entre Bagua e Ingenio, *López et al. 4246* (LP); Chachapoyas,

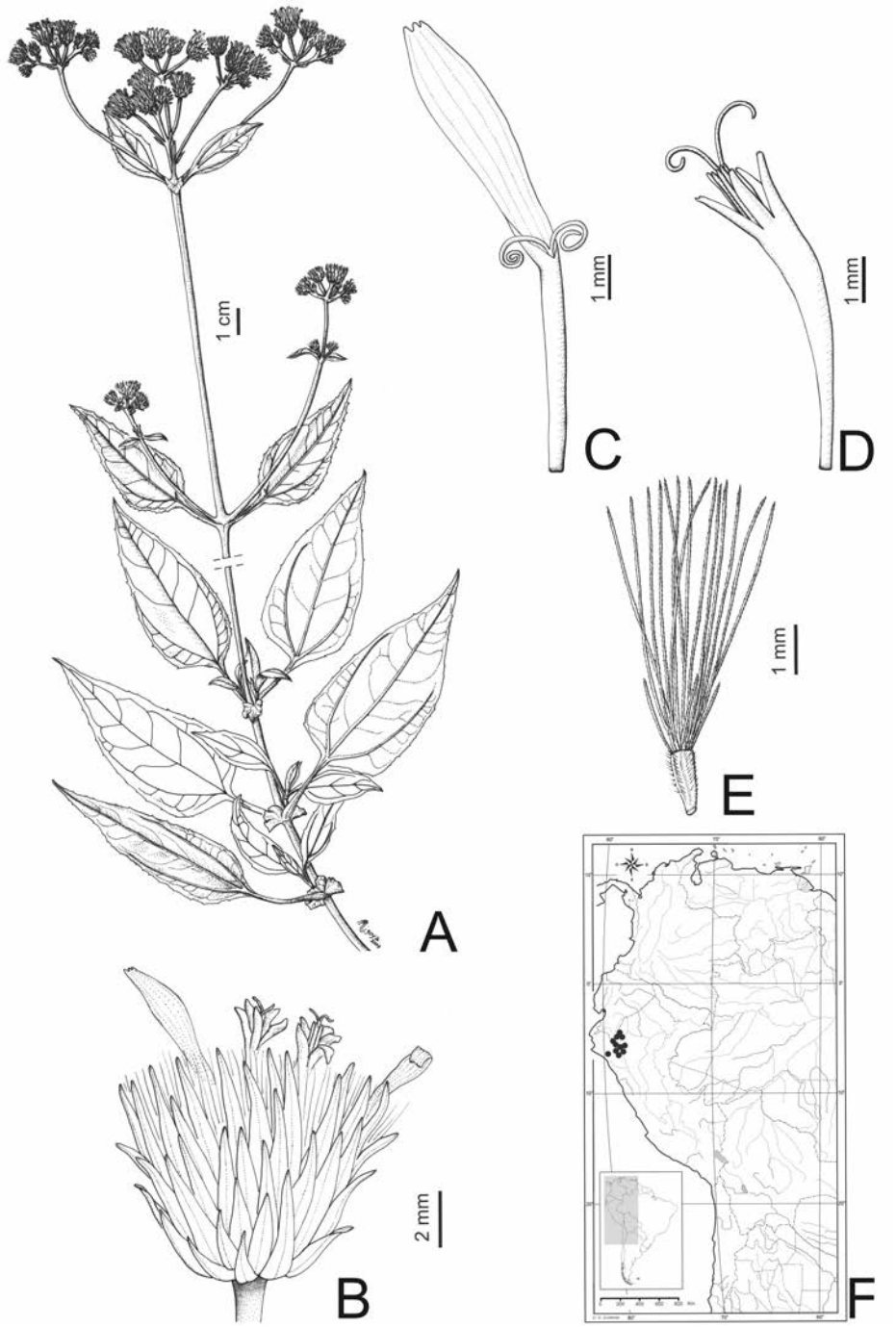

FIG. 35. *Liabum wurdackii* Ferreyra. A. Habit (branch). B. Capitulum (only some florets shown). C. Ray floret. D. Disc floret. E. Cypsela and pappus. F. Distribution. (Based on: A–B, *Sánchez & Dillon 8010*; C–E, *Gentry et al. 74613*, MO.)

Mathews s.n. in 1862 (US); Prov. Chachapoyas, entre Cacle y Pedro Ruiz, 21 km al S de Pedro Ruiz, *Sánchez & Dillon 8010* (F); Pedro Ruiz, 6 km a Pomacochas, *Sánchez & Dillon 9094* (F); Río Sonche near Sonche, *Wurdack 1531* (GH, LP, NY, US).—CAJAMARCA: Prov. Chota, Distr. La Paccha, entre La Paccha y Río Llaucano, *Cabanillas 788* (F); San Ignacio, San José de Lourdes, Crucero, 05°45′S, 78°56′W, *Campos 6151* (LP); San Ignacio, San Martín del Chinchipe, 05°19′16″S, 78°41′05″W, *Flores et al. 128* (LP); 13 km N of Leimbamba, Río Utcubamba, *Gentry et al. 23202* (F); 1 km S of Socota, Río Cutervo, 24 km NE of Cutervo, 06°15′S, 78°45′W, *Gentry et al. 74613* (MO, US); Prov. Jaén, Pucará, Río Huancabamba, km 127 E of Olmos, *Hutchison & Wright 3571* (F, LIL, NY, US); 7 km SE of San Ignacio to Jaén, *King & Bishop 9298* (MO, US); alrededores de Huahuaya, a Tabaconas, *Leiva et al. 1212* (F); Huahuaya-Tabaconas, *Leiva et al. 1293* (F); Pucará to Chamaya, km 27 E of Pucará, Río Huancabamba, Chiple, *Plowman et al. 14263* (F, US); Jaén, *Sánchez 85* (F, LP); Prov. Cutervo, Río Sucse, W of Socota, *Stork & Horton 10114* (F).—LAMBAYEQUE: Prov. Ferreñafe, La Llorona, Atumpampa, *Llatas 2528* (F).—WITHOUT DEPARTMENT OR LOCALITY: *Mathews s.n.* (NY); *Mathews 3059* (GH, NY).

Liabum wurdackii resembles *L. saundersii* but differs from it in having the petioles usually not winged or winged only on the distal portion of the petiole.

DOUBTFUL AND EXCLUDED NAMES

Amellus floribundus Willdenow in Lessing, Linnaea 6: 702. 1831, pro syn.

Andromachia sect. *Chrysactinia* Kunth in Humboldt, Bonpland & Kunth, Nov. Gen. Sp. [H.B.K.], ed. folio, 4: 77. 1818 [“1820”]. = *Chrysactinia* (Kunth) Weddell.

Andromachia sect. *Oligactis* Kunth in Humboldt, Bonpland & Kunth, Nov. Gen. Sp. [H.B.K.], ed. folio, 4: 79. 1818 [“1820”]. = *Oligactis* (Kunth) Cassini in F. Cuvier.

Andromachia alternifolia Kunze ex Steudel, Nomencl. Bot. [Steudel], ed. 2, 1: 87. 1840, nomen nudum.

Andromachia maronii André, Rev. Hort. 21: 496. 1887.—TYPE: probably BOLIVIA. Without department and locality, Feb 1887, *André 1331* (holotype: K, digital image!). = *Munnozia maronii* (André) H. Robinson, Phytologia 35: 200. 1977 (Robinson 1983).

Liabum sect. *Chrysactinium* (Kunth) Lessing, Linnaea 6: 696. 1831. = *Chrysactinium* (Kunth) Weddell.

Liabum sect. *Erato* (Candolle) Bentham & Hooker f., Gen. Pl. [Bentham & Hooker f.] 2(1): 436. 1873. = *Erato* Candolle.

Liabum sect. *Kastnera* (Schultz Bipontinus) Bentham & Hooker f., Gen. Pl. [Bentham & Hooker f.] 2(1): 436. 1873. = *Munnozia* Ruiz & Pavón.

Liabum sect. *Liabopsis* Kuntze, Revis. Gen. Pl. 3: 163. 1898. = *Munnozia* Ruiz & Pavón.

Liabum sect. *Munnozia* (Ruiz & Pavón) Bentham & Hooker f., Gen. Pl. [Bentham & Hooker f.] 2(1): 436. 1873. = *Munnozia* Ruiz & Pavón.

Liabum sect. *Oligactis* (Kunth) Lessing, Linnaea 6: 703. 1831. = *Oligactis* (Kunth) Cassini in F. Cuvier.

Liabum sect. *Paranephelium* (Poeppig) Bentham & Hooker f., Gen. Pl. [Bentham & Hooker f.] 2(1): 436. 1873. = *Paranephelius* Poeppig.

Liabum sect. *Platylepis* Lessing, Linnaea 6: 704. 1831. *Liabum* sect. *Platylepidea* Lessing in Candolle, Prodr. [A. P. de Candolle] 7: 265. 1838, orthographic variant. = *Sinclairia* Hooker & Arnott.

Liabum sect. *Sinclairia* (Hooker & Arnott) Bentham & Hooker f., Gen. Pl. [Bentham & Hooker f.] 2(1): 436. 1873. = *Sinclairia* Hooker & Arnott.

Liabum sect. *Stenophyllum* Lessing, Linnaea 6: 704. 1831. = *Diplostephium* Kunth in Humboldt, Bonpland & Kunth.

Liabum subgenus *Chrysastrum* [‘*Chryartrum*’] Willdenow ex Schultz Bipontinus, Flora 36: 37. 1853. = *Munnozia* Ruiz & Pavón.

Liabum acaule (Kunth) Lessing, Linnaea 6: 696. 1831. *Andromachia acaulis* Kunth in Humboldt, Bonpland & Kunth, Nov. Gen. Sp. [H.B.K.], ed. folio, 4: 77 + tab. 336. 1818 [“1820”].—Type: Ecuador. Azuay: Crescit in montibus Quitensibus (El Assuaye) inter Los Paredones et villam Turche, 1700 hex., 2–3 July 1802, *Humboldt & Bonpland 3262* (holotype: P, digital image! photos LP! SI!; isotypes: P). = *Chrysactinium acaule* (Kunth) Weddell, Chlor. And. 1(7): 212. 1857 (Funk & Zermoglio 1999). Funk and Zermoglio selected a lectotype for *A. acaulis* Kunth because they considered the holotype to have been at B and thus destroyed. However, Kunth based his descriptions on the specimens of Humboldt and Bonpland kept at P (Stafleu & Cowan 1979), and the holotype of this name is therefore the specimen deposited in P (Hind & Jeffrey 2001).

Liabum acostae Chung, Phytologia 14: 323. 1967.—Type: Ecuador. Pichincha: Entre Oya Cachi y Comenia, Cordillera Oriental, *Acosta Solís 11175* (holotype: F, digital image!). = *Munnozia acostae* (Chung) H. Robinson & Brettell, Phytologia 28: 54. 1974 (Robinson 1983).

Liabum adenotrichum Greenman, Publ. Field Mus. Nat. Hist., Bot. Ser. 2: 349. 1912.—Type: Mexico. Oaxaca: Distrito del Centro, cerro de Frujano, 1700 m, 15 Nov 1908, *Conzatti 2316* (syntypes: F-239615, digital image! F-246875, MEXU, digital image!). = *Sinclairia adenotricha* (Greenman) Rydberg, N. Amer. Fl. 34: 300. 1927 (Robinson 1983) or *Sinclairia liebmannii* (Klatt) Schultz Bipontinus ex Rydberg (Turner 1989).

Liabum affine S. F. Blake, J. Wash. Acad. Sci. 17: 301–302. 1927.—Type: Peru. Huánuco: Muña, trail to Tambo de Vaca, 2440 m, 5–7 June 1923, *Macbride 4337* (holotype: F, digital image!; isotype: US, digital image!). = *Munnozia affinis* (S. F. Blake) H. Robinson & Brettell, Phytologia 28: 54. 1974 (Robinson 1983).

Liabum alibum Hieronymus, Bot. Jahrb. Syst. 28: 627. 1901, nom. superfl. (*Alibum liaboides* Lessing, Syn. Gen. Compos. 152. 1832, cited as synonym).—Type: Ecuador. Chimborazo: In Pomalacte [Pomallacta] Americae aequinoctialis, *Humboldt s.n.* (Herbarium Kunth) (holotype: B [destroyed], photo FM 18112!, fragment GH, digital image!; isotype: K, photo LP!). = *Munnozia liaboides* (Lessing) H. Robinson (Robinson 1983).

Liabum amphothrix S. F. Blake, J. Wash. Acad. Sci. 17: 290–291. 1927.—Type: Peru. Huánuco: Mito, 2745 m, 8–22 July 1922, *Macbride & Featherstone 1665* (holotype: F, digital image!; isotypes: GH, US, digital images!). = *Chrysactinium amphothrix* (S. F. Blake) H. Robinson & Brettell, Phytologia 28: 49. 1974 (Funk & Zermoglio 1999).

Liabum anatinum Benoist, Bull. Soc. Bot. France 84: 633. 1938.—Type: Ecuador. Imbabura-Pichincha: Au-dessus de San José de Minas, 3 Mar 1931, *Benoist 3962* (holotype: P, digital image!). = *Erato vulcanica* (Klatt) H. Robinson (Moran & Funk 2006).

Liabum andrieuxii (de Candolle) Bentham & Hooker f. ex Hemsley, Biol. Centr.-Amer., Bot. 2: 231. 1881. *Vernonia andrieuxii* Candolle, Prodr. [A. P. de Candolle] 5: 16. 1836.—Type: Mexico. Oaxaca or Veracruz: Inter Tehuantepec et flum. Guaracoalcos [Coatzacoalcos], Sept 1834, *Andrieux 269* (holotype: G; isotypes: K-2 sheets!). = *Sinclairia andrieuxii* (de Candolle) H. Robinson & Brettell, Phytologia 28: 60. 1974 (Robinson 1983, Turner 1989).

Liabum andromachioides (Lessing) Bentham & Hooker f. ex Hemsley, Biol. Cent.-Amer., Bot. 2: 231. 1881. *Vernonia andromachioides* Lessing, Linnaea 6: 397–398. 1831.—

TYPE: MEXICO. Veracruz: In sylvis Misantlae, *Schiede 1234* (holotype: B [destroyed], photo FM 18087!). = *Sinclairia andromachioides* (Lessing) Schultz Bipontinus ex Rydberg, N. Amer. Fl. 34: 298. 1927 (Robinson 1983, Turner 1989).

Liabum angustissimum A. Gray, Proc. Amer. Acad. Arts 22: 432. 1887.—TYPE: MEXICO. Jalisco: Guadalajara, Río Blanco, July 1886, *Palmer 215* (holotype: GH, digital image!; isotypes: K, NY, PH, US, YU, digital images!). = *Liabellum angustissimum* (A. Gray) Rydberg, N. Amer. Fl. 34: 295. 1927 (Robinson 1983) or *Sinclairia angustissima* (A. Gray) B. L. Turner, Phytologia 67: 205. 1989.

Liabum angustum S. F. Blake, J. Wash. Acad. Sci. 17: 295–296. 1927.—TYPE: PERU. Huánuco: Villcabamba, an hacienda on Río Chinchao, 1830 m, 17–26 July 1923, *Macbride 5198* (holotype: F, digital image!; isotype: US, digital image!). = *Munnozia angusta* (S. F. Blake) H. Robinson & Brettell, Phytologia 28: 54. 1974 (Robinson 1983).

Liabum annuum Muschler, Bot. Jahrb. Syst. 50(2/3), Beibl. 111: 84–85. 1913.—TYPE: PERU. Cajamarca: Prov. Cajamarca, infra San Pablo, 2200–2400 m, 29 Apr 1904, *Weberbauer 3876* (holotype: B [destroyed], photo FM 18088!). = *Munnozia annua* (Muschler) H. Robinson & Brettell, Phytologia 28: 57. 1974 (Robinson 1983).

Liabum arthrothrix S. F. Blake, J. Wash. Acad. Sci. 17: 288–289. 1927.—TYPE: ECUADOR. Azuay: Páramo, between Oña and Cuenca, 2700–3300 m, 9–10 Sept 1923, *Hitchcock 21645* (holotype: US, digital image!; isotype: NY, digital image!). = *Chrysactinium acaule* (Kunth) Weddell (Funk & Zermoglio 1999).

Liabum asperifolium Muschler, Bot. Jahrb. Syst. 50(2/3), Beibl. 111: 78. 1913.—TYPE: BOLIVIA. Without department: Calderillo, 22 Mar 1904, *Fiebrig 3538* (syntype: B [destroyed], photo FM 18091!; isosyntypes: G, GH, K, US, digital images!); Calderillo, in declivibus, 3000–3500 m, 23 Mar 1904, *Fiebrig 3163* (syntype: probably B). = *Paranephelius asperifolius* (Muschler) H. Robinson & Brettell, Phytologia 28: 59. 1974 (Robinson 1983).

Liabum auriculatum Grisebach, Symb. Fl. Argent. 202–203. 1879.—TYPE: ARGENTINA. Córdoba: Sierra de Achala, al norte de Cuesta de Copina, *Hieronymus 641* (holotype: GOET, digital image!; isotype: CORD!). = *Microliabum candidum* (Grisebach) H. Robinson (Robinson 1990, pers. obs.).

Liabum biattenuatum Rusby, Descr. S. Amer. Pl. 159. 1920.—TYPE: COLOMBIA. Magdalena: Sierra del Líbano, (near) Santa Marta, 5500 ft, 19 Jan 1898 or 1899, *Smith 2013* (holotype: NY, digital image!; isotypes: BR, F, GH, digital images, P photos LP!, SI! MO, MPU, digital images!, P photos LP!, SI! S, US, WIS, digital images!). = *Oligactis sessiliflora* (Kunth) H. Robinson & Brettell (Gutiérrez 2008).

Liabum bicolor S. F. Blake, J. Wash. Acad. Sci. 17: 290. 1927.—TYPE: ECUADOR. Loja: mountains, Sept 1864, *Jameson s.n.* (holotype: US, digital image!). = *Chrysactinium caulescens* (Hieronymus) H. Robinson & Brettell (Funk & Zermoglio 1999).

Liabum bolivianum Klatt, Ann. K. K. Naturhist. Hofmus. 9: 362. 1894.—TYPE: BOLIVIA. Without department and locality: *Cuming s.n.* (holotype: GH, digital image!). = *Gynoxys boliviana* (Klatt) S. F. Blake, Contr. Gray Herb. 53: 28. 1918 (Robinson 1983).

Liabum bonplandii Cassini in F. Cuvier, Dict. Sci. Nat., ed. 2 [F. Cuvier] 26: 206. 1823, nom. illeg. = *Liabum igniarium* (Humboldt & Bonpland) Lessing.

Liabum boyacense Cuatrecasas, Notas Fl. Colombia 6: 36. 30 Mar 1944.—TYPE: COLOMBIA. Boyacá: Cordillera Oriental, entre Moniquirá y Arcabuco, 2150 m, 25 Feb 1940, *Pérez Arbeláez & Cuatrecasas 8164* (holotype: COL, digital image!; isotypes: BC, F,

NY, US, digital images!). = *Oligactis sessiliflora* (Kunth) H. Robinson & Brettell (Gutiérrez 2008).

Liabum brachypus (Rydberg) S. F. Blake, J. Wash. Acad. Sci. 22: 386. 1932. *Sinclairia brachypus* Rydberg, N. Amer. Fl. 34(4): 299. 1927.—TYPE: GUATEMALA. Jutiapa: Volcán Ipala, Jan 1907, *Pittier 1886* (holotype: US, digital image!; isotypes: F, NY fragment, digital images!). = *Sinclairia brachypus* Rydberg (Robinson 1983) or *S. sublobata* (B. L. Robinson) Rydberg (Turner 1989).

Liabum brownei Cassini in F. Cuvier, Dict. Sci. Nat., ed. 2 [F. Cuvier] 26: 203. 1823, nom. superfl. See explanation under *Liabum umbellatum*.

Liabum bullatum (Weddell) Hieronymus, Bot. Jahrb. Syst. 36: 500. 1905.—TYPE: PERU. Without department and locality: *Pavón s.n*. (holotype: P). = *Paranephelius bullatus* Weddell, Chlor. And. 1(7): 214. 1857 (Robinson 1983).

Liabum caducifolium B. L. Robinson & Bartlett, Proc. Amer. Acad. Arts 43: 59–60. 1907.—TYPE: MEXICO. Guerrero: Near Acapulco, Oct 1894–Mar 1895, *Palmer 245* (holotype: GH, digital image!; isotypes: BM, F, K, MICH, NY, US, digital images!). = *Sinclairia caducifolia* (B. L. Robinson & Bartlett) Rydberg, N. Amer. Fl. 34: 299. 1927 (Robinson 1983) or *S. liebmannii* (Klatt) Schultz Bipontinus ex Rydberg (Turner 1989).

Liabum canarense Cuatrecasas, Brittonia 8: 46. 1954.—TYPE: ECUADOR. Cañar: Cañar, North rim of the valley of the Río Cañar, *Giler E-2836* (holotype: NY, digital image!; isotypes: K, photos LP!, SI! US, digital image!). = *Munnozia canarensis* (Cuatrecasas) H. Robinson & Brettell, Phytologia 28: 54. 1974 (Robinson 1983).

Liabum candidum Grisebach, Symb. Fl. Argent. 203. 1879.—TYPE: ARGENTINA. Córdoba: in rupibus prope Santa María, *Hieronymus 280* (holotype: GOET, digital image!; isotypes: CORD-2 sheets! F-2 sheets, one a fragment of G, digital images! G, photo SI!). = *Microliabum candidum* (Grisebach) H. Robinson, Syst. Bot. 15: 743. 1990 (Robinson 1990).

Liabum candidum var. *glanduliferum* Cabrera, Bol. Soc. Argent. Bot. 2: 96. 1947.—TYPE: ARGENTINA. San Luis: Estancia Grande, 16 Jan 1911, *Pastore 124* (holotype: LP!). = *Microliabum glanduliferum* (Cabrera) H. Robinson, Syst. Bot. 15: 744. 1990 (Robinson 1990).

Liabum cardenasii Cabrera, Notas Mus. La Plata, Bot. 14: 191. 1949.—TYPE: BOLIVIA. Cochabamba: Road to Chimoré-Cochabamba, 2200 m, Mar 1940, *Cárdenas 784* (holotype: LP!). = *Munnozia cardenasii* (Cabrera) H. Robinson & Brettell, Phytologia 28: 54. 1974 (Robinson 1983).

Liabum caulescens Hieronymus, Bot. Jahrb. Syst. 36: 500–501. 1905.—TYPE: PERU. Cajamarca: Crescit inter Chota et Cutervo, June 1879, *Jelski 727* (holotype: B [destroyed], photo FM 18094!; lectotype, designated by Funk and Zermoglio (1999: 333): KRA). = *Chrysactinium caulescens* (Hieronymus) H. Robinson & Brettell, Phytologia 28: 50. 1974 (Funk & Zermoglio 1999).

Liabum cervinum B. L. Robinson, Proc. Amer. Acad. Arts 29: 317. 1894.—TYPE: MEXICO. Jalisco: San Marcos, 9 June 1893, *Pringle 4398* (holotype: GH, digital image!; isotypes: AC, BR, E, F, GOET, ISC, JE, K, MEXU, MIN, MO, MSC, MU, NDG, NY, PH, S, TEX, US, digital images!). = *Liabellum cervinum* (B. L. Robinson) Rydberg, N. Amer. Fl. 34: 294. 1927 (Robinson 1983) or *Sinclairia cervina* (B. L. Robinson) B. L. Turner, Phytologia 67: 204. 1989.

Liabum columbianum Klatt, Bot. Jahrb. Syst. 8: 47. 1887.—TYPE: COLOMBIA. Cauca: in silvis densis ad latera montis Paramo de Moras, 2800–3400 m, Mar 1884, *Lehmann*

3783 (holotype: GH, digital image!; isotypes: K, US, digital images!). = *Gynoxys columbiana* (Klatt) Hieronymus, Bot. Jahrb. Syst. 28: 631. 1901 (Robinson 1983).

Liabum convencionense Cuatrecasas, Collect. Bot. (Barcelona) 3: 300–301. 1953.—TYPE: PERU. Cuzco: Prov. Convención, entre Janamanche y Quellomayo, 3600–3800 m, 25 July 1944, *Vargas 4446* (holotype: F, digital image!). = *Munnozia convencionensis* (Cuatrecasas) H. Robinson & Brettell, Phytologia 28: 54. 1974 (Robinson 1983).

Liabum coriaceum Hieronymus in Sodiro, Bot. Jahrb. Syst. 29: 58. 1900.—TYPE: ECUADOR. Without province and locality: Crescit in fruticetis silvisque subandinis, *Sodiro 55/5 partim* (holotype: B [destroyed], photo FM 18096!). = *Sampera coriacea* (Hieronymus) V. A. Funk & H. Robinson, Proc. Biol. Soc. Washington 122: 158. 2009.

Liabum coriaceum f. *subcordatum* Domke in Diels, Beitr. Veg. Ecuador 169. 1937.—TYPE: ECUADOR. Pichincha: Saloya, 3200 m, 4 Aug 1933, *Diels 445* (holotype: B, destroyed). = *Oligactis coriacea* (Hieronymus) H. Robinson & Brettell (Robinson 1999), now *Sampera coriacea* (Hieronymus) V. A. Funk & H. Robinson.

Liabum corymbosum (Ruiz & Pavón) Schultz Bipontinus, Flora 36: 34. 1853.—TYPE: PERU. Huánuco: In Pillao circuitu et versuris, 1787, *Ruiz & Pavón s.n.* (holotype: MA-3 sheets, digital images!; isotypes: B-2 sheets, one a fragment ex MA, digital images! BC, digital image! P, photos LP!, SI! US-2 sheets, one fragment ex MA, the other probably ex P, digital images!). = *Munnozia corymbosa* Ruiz & Pavón, Syst. Veg. Fl. Peruv. Chil. 195. 1798 (Robinson 1983).

Liabum corymbosum Schultz Bipontinus ex Klatt, Ann. K. K. Naturhist. Hofmus. 9: 363. 1894, non *L. corymbosum* (Ruiz & Pavon) Schultz Bipontinus, 1853.—TYPE: BOLIVIA. La Paz: Viciniis Sorata, 2700–3000 m, Jan/Nov 1852, *Mandon 240* (holotype: GH, digital image!; isotypes: F, GOET, K, NY, RB, US, digital images!). = *Munnozia maronii* (André) H. Robinson (Robinson 1983).

Liabum cusalaguense Hieronymus in Sodiro, Bot. Jahrb. Syst. 29: 55–56. 1900.—TYPE: ECUADOR. Without province: Crescit prope Sacha Piguil del Río Cusalagua, 2599 m, *Sodiro 55/4* (holotype: B [destroyed], photo FM 18097!). = *Sampera cusalaguensis* (Hieronymus) V. A. Funk & H. Robinson, Proc. Biol. Soc. Washington 122: 158. 2009.

Liabum deamii B. L. Robinson & Bartlett, Proc. Amer. Acad. Arts 43: 60. 1907.—TYPE: GUATEMALA. Zacapa: Gualán, 420 ft, Jan 1905, *Deam 194* (holotype: GH, digital image!; isotypes: F, MICH, MO, NY, US, digital images!). = *Sinclairia deamii* (B. L. Robinson & Bartlett) Rydberg, N. Amer. Fl. 34: 299. 1927 (Robinson 1983, Turner 1989).

Liabum deppeanum (Lessing) Lessing, Linnaea 6: 704, 1831. *Andromachia deppeana* Lessing, Linnaea 6: 401–402. 1831.—TYPE: MEXICO. Veracruz: Cuesta grande del Jacingo, Dec 1819, *Schiede 1239* (holotype: B [destroyed], photo FM 18098!; isotypes: HAL-2 sheets! [one gives collector as *Deppe & Schiede 1239*]). = *Sinclairia deppeana* (Lessing) Rydberg, N. Amer. Fl. 34: 300. 1927 (Robinson 1983, Turner 1989).

Liabum diehlii H. Robinson, Phytologia 46: 99–100. 1980.—TYPE. PERU. Cuzco: Quellouno, 750 m, 22 May 1930, *Bues 923* (holotype: F!). = *Inkaliabum diehlii* (H. Robinson) D. G. Gutiérrez, Bol. Soc. Argent. Bot. 45: 363–372. 2010.

Liabum dimidium S. F. Blake, J. Wash. Acad. Sci. 22: 385–386. 1932.—TYPE: GUATEMALA. Petén: Tikal, 12–15 Apr 1931, *Bartlett 12602* (holotype: US, digital image!; isotypes: F, GH-2 sheets, LL-2 sheets, MICH, MO, TEX, digital images!). = *Sinclairia polyantha* (Klatt) Rydberg (Turner 1989).

Liabum discolor (Hooker & Arnott) Bentham & Hooker f. ex Hemsley, Biol. Cent.-Amer.,

Bot. 2: 232. 1881. *Sinclairia discolor* Hooker & Arnott, Bot. Beechey Voy. 433. 1841.—Type: Nicaragua. Chinandega: [El] Realejo, *Sinclair s.n*. (holotype: K, digital image!, fragment US, digital image!). = *Sinclairia discolor* Hooker & Arnott (Robinson 1983, Turner 1989).

Liabum ecuadoriense Hieronymus, Bot. Jahrb. Syst. 19: 60. 1895.—Type: Ecuador. Azuay: Crescit in fruticetis densis prope Chagal et Molleturo, Andium occidentalium, 2200–2800 m, Aug, *Lehmann 4897* (holotype: B [destroyed], photo FM 18099!; isotypes: K, digital images!, fragment US, digital image!). = *Sampera ecuadoriensis* (Hieronymus) V. A. Funk & H. Robinson, Proc. Biol. Soc. Washington 122: 158. 2009.

Liabum eremophilum Cabrera, Bol. Soc. Argent. Bot. 2: 96. 1947.—Type: Argentina. Salta: Sierra del Cajón, el alisal, 2800 m, 17 Jan 1914, *Rodríguez 1294* (holotype: LP!; isotypes: BAB! CORD, digital image! LIL! LP-2 sheets! SI!). = *Microliabum eremophilum* (Cabrera) H. Robinson, Syst. Bot. 15: 744. 1990.

Liabum ericoides (Lamarck) Lessing, Linnaea 6: 704. 1831. *Conyza ericoides* Lamarck, Encycl. [J. Lamarck & al.] 2: 92. 1786.—Type: Peru. Without department and locality: *Jussieu s.n*. (holotype: P; isotype: P). = *Diplostephium ericoides* (Lamarck) Cabrera, Bol. Soc. Argent. Bot. 7: 238. 1959.

Liabum erigeroides Bentham, Pl. Hartw. [Bentham] 206. 1845.—Type: Ecuador. Napo: Prope hacienda de Antisana [Antizana], *Hartweg s.n.* (holotype: K, digital image!). = *Oritrophium peruvianum* (Lamarck) Cuatrecasas (Robinson 1983).

Liabum eriocalyx S. F. Blake, J. Wash. Acad. Sci. 17: 297. 1927.—Type: Peru. Junín: Hacienda Schunke, La Merced, 1220 m, 27 Aug–1 Sept 1923, *Macbride 5783* (holotype: F, digital image!; isotype: US, digital image!). = *Munnozia corymbosa* Ruiz & Pavón (Robinson 1983).

Liabum eupatorioides Muschler, Bot. Jahrb. Syst. 50(2/3), Beibl. 111: 83–84. 1913.—Type: Peru. Cajamarca: Chugur, 2700–2900 m, 21 May 1904, *Weberbauer 4084* (holotype: B [destroyed], photo FM 18101!, fragment US, digital image!). = *Schistocarpha sinforosi* Cuatrecasas, Trab. Mus. Nac. Ci. Nat., Ser. Bot. 29: 43. 1935, non *Schistocarpha eupatorioides* (Fenzl) Kuntze, Revis. Gen. Pl. 3: 170. 1898 (Robinson 1983).

Liabum excelsum (Poeppig) S. F. Blake, J. Wash. Acad. Sci. 17: 293. 1927. *Andromachia excelsa* Poeppig, Nov. Gen. Sp. Pl. (Poeppig & Endlicher) 3: 44. 1843.—Type: Peru. Huánuco: Crescit in montium calcareorum lateribus aridioribus Peruviae subandinae versus Cassapi et Cuchero, Sept 1829, *Poeppig s.n. [D.1314]* (holotype: W-3 sheets [two labeled Cuchero and one labeled Cassapi], digital images!; isotype: B [Peruvia subandina, destroyed], photo FM 18102! F fragment ex B). = *Ferreyranthus excelsus* (Poeppig) H. Robinson & Brettell, Phytologia 28: 51. 1974 (Dillon & Sagástegui Alva 1994).

Liabum ferreyri H. Robinson, Phytologia 34: 287–288. 1976.—Type: Peru. Huánuco: Prov. Huánuco, Carpish entre Huánuco y Tingo María, 2700–2800 m, 1 Oct 1950, *Ferreyra 8074* (holotype: US!; isotypes: MO, USM, digital images!). This species is excluded here from *Liabum* because it has several morphological features such as a sheath at the stem nodes, an areolate receptacle, and densely glandular cypselae, all of which deviate from the characters of this genus. *Liabum ferreyri* is currently under study in order to determine its taxonomic position (Gutiérrez, in prep.).

Liabum foliosum (Rusby) Ferreyra, Bol. Soc. Peruana Bot. 1: 18. 1948. *Munnozia foliosa* Rusby, Bull. Torrey Bot. Club 54: 312. 1927. *Liabum foliosum* (Rusby) Cabrera, Notas Mus. La Plata, Bot. 14: 193. 1950, nom. superfl.—Type: Bolivia. Cochabamba: Near

Cochabamba, 1891, *Bang 1195* (holotype: NY, digital image!; isotypes: A, GH, K, NY-2 sheets, PH, US, digital images!). = *Munnozia foliosa* Rusby (Robinson 1983).

Liabum fruticosum Muschler, Bot. Jahrb. Syst. 50(2/3), Beibl. 111: 81–82. 1913.—TYPE: PERU. Cajamarca: inter Balsas et Celendín, 2000 m, 23 June 1904, *Weberbauer 4257* (holotype: B [destroyed], photo FM 18103!). = *Ferreyranthus fruticosus* (Muschler) H. Robinson & Brettell, Phytologia 51: 169. 1982 (Dillon & Sagástegui Alva 1994).

Liabum giganteum Rusby, Bull. New York Bot. Gard. 4: 391. 1907.—TYPE: BOLIVIA. La Paz: Sacramento, Yungas, 14 Aug 1894, *Bang 2379* (holotype: NY-3 sheets, digital images!; isotypes: CORD, E, F, GH, K, M, MIN, MO, NY, PH, PUL, US, WIS, digital images!). = *Munnozia gigantea* (Rusby) Rusby, Bull. Torrey Bot. Club 54: 312. 1927 (Robinson 1983).

Liabum glabrum Hemsley, Biol. Cent.-Amer., Bot. 2: 232. 1881.—TYPE: MEXICO. Morelos: Cuernavaca, Iturbide, 1865, *Bourgeau 1401* (holotype: K, digital image!, fragment US, digital image!; isotypes: BR, F, digital images!, G, photo FM 28808! GH, L, MSC fragment ex L, digital image!, P, S, US fragment ex K, digital images!). = *Sinclairia glabra* (Hemsley) Rydberg, N. Amer. Fl. 34: 297. 1927 (Robinson 1983, Turner 1989).

Liabum glabrum var. *hypoleucum* Greenman, Proc. Amer. Acad. Arts 32: 294. 1897.—TYPE: MEXICO. Jalisco: In cañons near Guadalajara, 8 Dec 1888, *Pringle 2169* (lectotype, designated by McVaugh (1984: 579): GH, digital image!). = *Sinclairia glabra* (Hemsley) Rydberg (Robinson 1983) or *Sinclairia glabra* (Hemsley) Rydberg var. *hypoleuca* (Greenman) B. L. Turner, Phytologia 67: 180. 1989.

Liabum glandulosum Kuntze, Revis. Gen. Pl. 3: 163. 1898.—TYPE: BOLIVIA. Without department: Río Juntas, 1000 m, 13/21 Apr 1892, *Kuntze s.n.* (holotype: NY, digital image! fragment, US, digital image!; isotype: B [destroyed], photo FM 18104! US fragment ex NY, digital image!). = *Munnozia glandulosa* (Kuntze) Rusby, Bull. Torrey Bot. Club 54: 312. 1927 (Robinson 1983).

Liabum granatense Cuatrecasas, Feddes Repert. Spec. Nov. Regni Veg. 55: 128. 1953.—TYPE: COLOMBIA. Putumayo: Comisaría del Putumayo, alto de la Cordillera entre el valle de Sibundoy y Mocoa, El Portachuelo, 2600 m, 30 Dec 1940, *Cuatrecasas 11490* (holotype: US, digital image!; isotypes: BC, COL, F, digital images!). = *Sampera coriacea* (Hieronymus) V. A. Funk & H. Robinson.

Liabum hallii Hieronymus in Sodiro, Bot. Jahrb. Syst. 29: 57–58. 22 May 1900.—TYPES: ECUADOR. Pichincha: Crescit in monte Pichincha, c. 3300 m, 1833, *Francis Hall s.n.* (syntype: B [destroyed], photo FM 18106!); in fruticetis silvisque subandinis, *Sodiro 55/5 partim* (syntype: B [destroyed]). = *Sampera pichinchensis* (Hieronymus) V. A. Funk & H. Robinson. According to the protologue, one part of the specimen *Sodiro 55/5* is a syntype of *Liabum hallii*, and other part is the type of *L. coriaceum* Hieron. (see under that name above). This sheet was destroyed during World War II. However, the photo kept at F (FM 18096) shows only one reproductive branch on the sheet, with the name *L. coriaceum* next to it on the label written by Hieronymus.

Liabum hastatum Britton, Bull. Torrey Bot. Club 19: 263. 1892, nom. nov. pro *Munnozia sagittata* Willdenow ex Weddell, Chlor. And. 1(7): 211. 1857 non *Liabum sagittatum* Schultz Bipontinus.—TYPES: ECUADOR. Probably Pichincha: In Andibus quitensibus, 3000 m, 21 Jan 1856, *Jameson 392* (syntype: K, digital image!, US fragment ex K, digital image!); COLOMBIA. Probably Cundinamarca and Norte de Santander: in Prov. Bogota et Pamplona, *Humboldt & Bonpland s.n.* (syntypes: probably P, PC), 1844, *Goudot s.n.* (syntypes: K, digital image! P, photo LP!) and *Funck & Schlimm 129*

(syntype: probably P, PC). = *Munnozia senecionidis* Bentham (Robinson 1983). The type specimens *Humboldt & Bonpland s.n.* and *Funck & Schlimm 129* used by Weddell for describing *Munnozia sagittata* are probably kept at P or PC (Stafleu & Cowan 1988). Britton, in proposing the new name *Liabum hastatum*, referred to Weddell's name as *Munnozia hastata* rather than *M. sagittata*, but cited the correct page reference in *Chloris Andina*.

Liabum hastifolium Poeppig, Nov. Gen. Sp. Pl. (Poeppig & Endlicher) 3: 43–44. 1843.—Type: Peru. San Martín: Crescit in versuris cultorum cum praecedente, nec non in fruticetis circum Missionem Tocache, Jul/Aug, Poeppig 1220 (holotype: W-3 sheets, digital images!; isotypes: B [destroyed], photo FM 18107! F, NY, digital images!). = *Munnozia hastifolia* (Poeppig) H. Robinson & Brettell, Phytologia 28: 55. 1974 (Robinson 1983).

Liabum herrerae Cabrera, Revista Univ. (Cuzco) 33(87): 119 + tab. 19. 1945.—Type: Peru. Cuzco: Prov. Urubamba, entre Yuncaipata y Puyupatamarca, 3200 m, 29 Mar 1942, *Vargas 2761* (holotype: LP!; isotype: F, digital image!). = *Munnozia foliosa* Rusby (Robinson 1983).

Liabum hexagonum S. F. Blake, J. Wash. Acad. Sci. 17: 300–301. 4 Jun 1927, nom. superfl.—Type: Bolivia. La Paz: North Yungas, Unduavi, 3300 m, Nov 1910, *Buchtien 3079* (holotype: US, digital image!; isotype: NY, digital image!). = *Munnozia longifolia* Rusby, Bull. Torrey Bot. Club 54: 313. 1927 (Robinson 1983). Blake described *Liabum hexagonum* on the basis of *Buchtien 3079*, unaware that this same collection had just been made the type of *Munnozia longifolia* Rusby (see *Liabum longifolium*).

Liabum hieracioides (Kunth) Lessing, Linnaea 6: 699. 1831. *Andromachia hieracioides* Kunth in Humboldt, Bonpland & Kunth, Nov. Gen. Sp. [H.B.K.], ed. folio, 4: 77. 1818 ["1820"].—Type: Ecuador. Loja: Crescit locis siccis temperatis prope Loxa Quitensium, 1060 hex., 23–28 July 1802, *Bonpland 3329* (holotype: P, digital image!). = *Chrysactinium hieracioides* (Kunth) H. Robinson & Brettell, Phytologia 28: 58. 1974 (Funk & Zermoglio 1999). See observation under *L. acaule*.

Liabum hirtum Kuntze, Revis. Gen. Pl. 3: 163. 1898.—Type: Bolivia. Without department: Río Juntas, 1800 m., 13/20 Apr 1892, *Kuntze s.n.* (holotype: NY, digital image! US fragment, digital image!). = *Munnozia hirta* (Kuntze) Rusby, Bull. Torrey Bot. Club 54: 312. 1927 (Robinson 1983).

Liabum homogamum Hieronymus, Bot. Jahrb. Syst. 28: 626. 1901.—Type: Colombia. Cauca: Crescit in silvis densis prope La Conga in declivibus Andium occidentalium regionis urbis Popayán, 1800–2400 m, Mar, *Lehmann 5972* (holotype: B [destroyed], photo FM 18108!, GH fragment ex B, digital image!; isotypes: F, GH, K, US fragment ex K, digital images!). = *Neomirandea homogama* (Hieronymus) H. Robinson & Brettell, Phytologia 28: 62. 1974 (Robinson 1983).

Liabum hypochlorum S. F. Blake, Contr. Gray Herb. 53: 27–28. 1918.—Type: Guatemala. Retalhuleu: San Felipe, 13 Jan 1917, *Holway 703* (holotype: GH, digital image!). = *Sinclairia hypochlora* (S. F. Blake) Rydberg, N. Amer. Fl. 34: 301. 1927 (Robinson 1983, Turner 1989).

Liabum hypoleucum (Candolle) S. F. Blake, Proc. Biol. Soc. Washington 39: 144. 1926. *Vernonia hypoleuca* Candolle, Prodr. [A. P. de Candolle] 5: 27. 1836.—Type: Mexico. Between Acapulco and Mexico City, Nov 1790–Dec 1791, *Haenke s.n.* (lectotype, designated by Turner (1989: 194): G). = *Sinclairia blakei* H. Robinson & Brettell (Robinson 1983) or *S. liebmannii* (Klatt) Schultz Bipontinus ex Rydberg (Turner 1989).

Liabum insigne V. M. Badillo, Bol. Soc. Venez. Ci. Nat. 10: 313. 1946.—Type: Venezuela. Mérida: Los Quebraditos, arriba de Jají, 2590 m, 21 Apr 1944, *Steyermark 55981* (holotype: VEN, digital image!; isotypes: F-2 sheets, digital images!). = *Erato vulcanica* (Klatt) H. Robinson (Moran & Funk 2006).

Liabum isodontum S. F. Blake, J. Wash. Acad. Sci. 17: 298. 1927.—Type: Bolivia. La Paz: Unduavi, North Yungas, 3300 m, Nov 1910, *Buchtien 4808* (holotype: US, digital image!). = *Munnozia senecionidis* Bentham (Robinson 1983).

Liabum jelskii Hieronymus, Bot. Jahrb. Syst. 36: 499–500. 1905.—Type: Peru. Cajamarca: Crescit prope Cutervo, May 1879, *Jelski 716* (holotype: B [destroyed], photo FM 18110!). = *Paranephelius jelskii* (Hieronymus) H. Robinson & Brettell, Phytologia 28: 59. 1974 (Robinson 1983).

Liabum jussieui (Cassini) Cassini in F. Cuvier, Dict. Sci. Nat., ed. 2. [F. Cuvier] 26: 205. 1823, as '*Liabum jussiei*.' *Andromachia jussieui* Cassini, Bull. Soc. Philom. Paris 1817: 184. 1817.—Type: Peru. "*Conyza stipulata* Vahl," without department and locality: *Jussieu s.n*. (holotype: P). = *Munnozia jussieui* (Cassini) H. Robinson & Brettell, Phytologia 28: 55. 1974 (Robinson 1983).

Liabum klattii B. L. Robinson & Greenman, Amer. J. Sci. Arts, ser. 3, 50: 156. 1895.—Type: Mexico. Oaxaca: Monte Alban, 6000 ft, 24 Nov 1894, *Pringle 6059* (holotype: GH, digital image!; isotypes: A, AC, BKL, BR, E, GOET, JE, K, M, MEXU-2 sheets, MIN, MSC, NDG, NY, PH, S, TEX, US-2 sheets, digital images!). = *Sinclairia klattii* (B. L. Robinson & Greenman) H. Robinson & Brettell, Phytologia 28: 61. 1974 (Turner 1989) or *Sinclairiopsis klattii* (B. L. Robinson & Greenman) Rydberg, N. Amer. Fl. 34(4): 293. 1927 (Dillon et al. 2009).

Liabum lanatum Ferreyra, Bol. Soc. Peruana Bot. 1: 17. 1948, nom. nov. pro *Onoseris discolor* Muschler, Bot. Jahrb. Syst. 50(2/3), Beibl. 111: 94–95. 1913, non *Liabum discolor* (Hooker & Arnott) Hemsley.—Type: Peru. Puno: Inter Sandia et Cuyocuyo ad rupes, 2600–2800 m, 1 May 1902, *Weberbauer 883* (holotype: B [destroyed], photo FM 15889!). = *Pseudonoseris discolor* (Muschler) H. Robinson & Brettell, Phytologia 28: 60. 1974 (Robinson 1983).

Liabum lanceolatum (Ruiz & Pavón) Schultz Bipontinus, Flora 36: 34. 1853. *Munnozia lanceolata* Ruiz & Pavón, Syst. Veg. Fl. Peruv. Chil. 196. 1798.—Type: Peru. Huánuco: In altis frigidis Muña, ad Tambo nuevo et Sarriapata tractus, June/Aug, *Ruiz & Pavón s.n.* (holotype: MA, digital image!, fragment US, digital image!; isotypes: BC (probable), digital image! FI). = *Munnozia lanceolata* Ruiz & Pavon (Robinson 1983).

Liabum laticiferum V. M. Badillo, Bol. Soc. Venez. Ci. Nat. 10: 312. 1946.—Type: Venezuela. Mérida: Cerca de El Gritadero, Torondoy, 1400 m, 20 May 1944, *Badillo 896* (holotype: VEN, digital image!). = *Munnozia hastifolia* (Poeppig) H. Robinson & Brettell, Phytologia 28: 55. 1974 (Robinson 1983).

Liabum latifolium (Hieronymus) Cuatrecasas, Feddes Repert. Spec. Nov. Regni Veg. 55: 129. 1953. *Liabum volubile* var. *latifolium* Hieronymus, Bot. Jahrb. Syst. 28: 622. 1901.—Type: Colombia. Cauca: Crescit in fruticetis declivium supra urbem Popayan, 1700–2200 m, Feb, *Lehmann 5227* (holotype: B [destroyed], fragment LP!; isotypes: F, digital image! GH, digital image! K, photo SI!, US-2 sheets, one a fragment ex K, digital images!). = *Oligactis latifolia* (Hieronymus) H. Robinson & Brettell, Phytologia 28: 57. 1974 (Robinson 1983, Gutiérrez 2008).

Liabum lechleri Schultz Bipontinus, Bonplandia 3: 236. 1855.—Type: Peru. Puno: Prov. Carabaya, near Sachapata, Andes of Peru, Aug 1854, *Lechler 2517* (holotype: G; isotypes: BR, F, GOET, NY, P-3 sheets, S, US fragment ex P-733169, digital images!). =

Diplostephium lechleri (Schultz Bipontinus) Weddell, Chlor. And. 1(7): 204. 1857 (Robinson & Brettell 1974).

Liabum liaboides (Lessing) Hieronymus, Bot. Jahrb. Syst. 19: 63. 1895. *Alibum liaboides* Lessing, Syn. Gen. Compos. 152. 1832.—TYPE: probably ECUADOR. Chimborazo: Pomalacte [Pomallacta], *Humboldt s.n.* (holotype: B [destroyed], photo FM 18112!, GH fragment, digital image!). = *Munnozia liaboides* (Lessing) H. Robinson, Phytologia 35: 38. 1976 (Robinson 1983).

Liabum liebmannii Klatt, Leopoldina 23: 146. 1887.—TYPE: MEXICO. Oaxaca: San Bartolo, 1842, *Liebmann 357* (holotype: C, fragment US, digital images!; probable isotype: GH fragment, digital image!). = *Sinclairia liebmannii* (Klatt) Schultz Bipontinus ex Rydberg, N. Amer. Fl. 34: 300. 1927 (Robinson 1983, Turner 1989).

Liabum longifolium (Rusby) S. F. Blake, J. Wash. Acad. Sci. 25: 322. 1935. *Munnozia longifolia* Rusby, Bull. Torrey Bot. Club 54: 313. 16 May 1927.—TYPE: BOLIVIA. La Paz: Unduavi, 3300 m, Nov 1910, *Buchtien 3079* (holotype: NY, digital image!; isotype: US, digital image!). = *Munnozia longifolia* Rusby (Robinson 1983).

Liabum longiradiatum Hieronymus, Bot. Jahrb. Syst. 21: 352–353. 6 Aug 1895.—TYPES: ECUADOR. Imbabura: Crescit in monte Imbabura, 4000 m, Mar [1870], *Stübel 62* (holotype: B [destroyed], photo FM 18113!); Pichincha: pass west of Quito-Santo Domingo road, 3900 m, 21 Apr 1942, *Haught 3261* (neotype, designated by Funk and Zermoglio (1999: 325): US, digital image!; isoneotypes: F, digital image!, P). = *Chrysactinium acaule* (Kunth) Weddell (Funk & Zermoglio 1999).

Liabum lyratum A. Gray, Proc. Amer. Acad. Arts 5: 115. 1861.—TYPES: PERU: [Amazonas, Chachapoyas, 1840], *Mathews 3057* (syntype: GH, digital image!; isosyntypes: K-three sheets [one mounted with *Mathews 762]*, digital images!); Lima: Obrajillo, 1838–1842, *United States Exploring Expedition s.n.* (syntype: US, digital image!). = *Munnozia lyrata* (A. Gray) H. Robinson & Brettell, Phytologia 28: 55. 1974 (Robinson 1983).

Liabum megacephalum Schultz Bipontinus, Flora 36: 38. 1853.—TYPES: VENEZUELA. Mérida: Jají, 7500 ped., Nov 1846, *Funk & Schlimm 1201* (syntype: P, US fragment, digital images!); Mérida: Colonia Tobar, in sylvis umbrosis ad viam La bictor in summis montibus, June/July, *Moritz 837* (syntypes: B [destroyed], photo FM 18114! K, digital image!). = *Munnozia senecionidis* Bentham (Robinson 1983).

Liabum meridense V. M. Badillo, Bol. Soc. Venez. Ci. Nat. 10: 314. 1946.—TYPE: VENEZUELA. Mérida: Tabay, selva de la Isla y El Rincón, 2500–2700 m, 8 Sept 1930, *Gehriger 427* (holotype: VEN, digital image!; isotypes: F, US, digital images!). = *Oligactis sessiliflora* (Kunth) Candolle (Gutiérrez 2008).

Liabum mikanioides S. F. Blake, J. Wash. Acad. Sci. 17: 294. 1927.—TYPE: COLOMBIA. Caldas: Alaska, above Salento, Cordillera Central, 3000–3400 m, 10–13 Aug 1922, *Pennell 9706* (holotype: US, digital image!; isotype: NY, digital image!). = *Oligactis mikanioides* (S. F. Blake) H. Robinson & Brettell, Phytologia 28: 57. 1974 (Robinson 1983).

Liabum moorei H. Robinson & Brettell, Phytologia 27: 252–253. 1973.—TYPE: MEXICO. Guerrero: 36–38 km from Iguala on road to Teloloapan, streamsides and slopes by Río de los Sabinos near Los Sabinos, 5 Nov 1949, *Moore 5518* (holotype: US, digital image!; isotypes: GH, MEXU, NY, TEX, digital images!). = *Sinclairia moorei* (H. Robinson & Brettell) H. Robinson & Brettell, Phytologia 28: 61. 1974 (Robinson 1983, Turner 1989).

Liabum mulgediifolium Muschler, Bot. Jahrb. Syst. 50(2/3), Beibl. 111: 85. 1913.—TYPE:

Bolivia. Tarija: Camacho, *Fiebrig 2870* (holotype: B [destroyed], photo FM 18116! US fragment, digital image!; lectotype, designated by Robinson (1990: 743): K, digital image!). = *Microliabum mulgediifolium* (Muschler) H. Robinson, Syst. Bot. 15: 743. 1990.

Liabum niveum Hieronymus, Bot. Jahrb. Syst. 19: 62. 1895.—Type: Colombia. Cauca: Crescit locis umbrosis, humidis in declivibus superioribus orientalibus prope Páramo de Guanacas, 2600–3000 m, Mar, *Lehmann 4775* (holotype: B [destroyed], photo FM 18118!; isotypes: K-2 sheets, digital images!, US fragment ex K, digital image!). = *Munnozia nivea* (Hieronymus) H. Robinson & Brettell, Phytologia 28: 57. 1974 (Robinson 1983).

Liabum nonoense Hieronymus in Sodiro, Bot. Jahrb. Syst. 29: 59–60. 1900.—Type: Ecuador. Pichincha: Crescit in silvis subandinis prope Nono et Tablahuasi, *Sodiro 55/6* (holotype: B [destroyed], photo FM 18119! F fragment, digital image!). = *Munnozia jussieui* (Cassini) H. Robinson & Brettell (Robinson 1983).

Liabum nonoense var. *microcephalum* Hieronymus, Bot. Jahrb. Syst. 28: 625. 1901.—Type: Colombia. Cauca: Crescit in silvis densis declivium orientalium Andium centralium ditionis urbis Popayán, 2800–3400 m, Dec–Jan, *Lehmann 8450* (holotype: B [destroyed], photo SI!; isotypes: F, K-2 sheets, US fragment ex K, digital images!). = *Munnozia jussieui* (Cassini) H. Robinson & Brettell (Robinson 1983).

Liabum nubigenum (Kunth) Lessing, Linnaea 6: 704. 1831. *Andromachia nubigena* Kunth in Humboldt, Bonpland & Kunth, Nov. Gen. Sp. [H.B.K.], ed. folio, 4: 79–80. 1818 ["1820"].—Type: Ecuador. Chimborazo: Crescit in excelsis montis Chimborazo, 1800 hex., June, *Humboldt & Bonpland s.n.* (holotype: P, digital image!). = *Oligactis nubigena* (Kunth) Cassini in F. Cuvier (ed.), Dict. Sci. Nat., ed. 2. [F. Cuvier] 36: 17. 1825 (Robinson 1983).

Liabum oblanceolatum Urban & Ekman, Ark. Bot. 23A: 89. 1931.—Type: Dominican Republic. La Vega: In scopulosis umbrosis Valle Nuevo ad rivulum, Cordillera Central, 2400 m, 17 Oct 1929, *Ekman H13827* (holotype: S, digital image!; isotypes: G, digital image! GH! S, digital image!). = *Chaptalia angustata* Urban (Gutiérrez & Katinas 2006; Katinas & Zavaro 2014).

Liabum ochraceum Cuatrecasas, Collect. Bot. (Barcelona) 3: 302–303. 1953.—Type: Peru. Cajamarca-Piura: Huascaray, 6500–7500 ft, 10 Sept 1911, *C. H. T. Townsend A-193* (holotype: F, digital image!). = *Sampera ochracea* (Cuatrecasas) V. A. Funk & H. Robinson, Proc. Biol. Soc. Washington 122: 158. 2009 (Funk & Robinson 2009).

Liabum olearioides Muschler, Bot. Jahrb. Syst. 50(2/3), Beibl. 111: 82–83. 1913.—Types: Peru. Amazonas: Prope Chachapoyas, inter Tambo Ventillas et Piscohuañuma, 2800–2900 m, 19 July 1904, *Weberbauer 4417* (syntype: B [destroyed], photo FM 18120! fragment US, digital image!); San Martín: inter Pacasmayo et Moyobamba, 3100 m, *Stübel 20a* (syntype: probably B). = *Munnozia olearioides* (Muschler) H. Robinson & Brettell, Phytologia 28: 55. 1974 (Robinson 1983).

Liabum onoserifolium S. Díaz & Rodríguez-Cabeza, Revista Acad. Colomb. Ci. Exact. 36: 502. 2012.—Type: Colombia. Boyacá: Municipio de Santa María, vereda La Almenara, 04°53′17″N, 73°15′01″W, 1200 m, 9 Oct 2000, *Jiménez 359* (holotype: COL 519097, digital image!). This species is here excluded from *Liabum* because it has several morphological features not typical of the genus, such as broadly ovate outer phyllaries, phyllaries with many conspicuous veins, disc florets with short stigmatic branches, and sweeping hairs that extend below the stigmatic branch bifurcation point to a greater distance than the length of the branches. On the other hand, the main traits

of the leaves, capitula, type of phyllaries, type of disc and ray florets, style branches, cypsela, and pappus of *Liabum onoserifolium* are those found in species of *Munnozia* (see Robinson, 1983). Some traits, however, such as the number of disc florets (120–174) and the number of series of phyllaries (5–6) deviate from this genus. Because there is not a complete systematic treatment of *Munnozia*, we prefer to transfer *Liabum onoserifolium* to *Munnozia* as a distinct species. Thus, the new combination **Munnozia onoserifolia (S. Díaz & Rodríguez-Cabeza) D. G. Gutiérrez & Katinas** is proposed here.

Liabum ovatum (Weddell) J. Ball, J. Linn. Soc., Bot. 22: 46. 1885. *Paranephelius ovatus* Weddell, Chlor. And. 1(7): 214 + pl. 37B. 1857.—Types: Peru. Cuzco, Lima and Puno: Without locality, Cordilléres, 4000 m, *Gay s.n.*, *Dombey s.n*., *Pavón s.n.* (probable isosyntype: MA-2 sheets, digital images!), *Weddell s.n*.; Bolivia. Chuquisaca: punas de la province de Cinti, *Weddell s.n.* (syntypes: probably in P; isosyntype: K, photos in LP!, SI!). = *Paranephelius ovatus* Weddell (Robinson 1983). The correct author of the name of *Paranephelius ovatus* is H. A. Weddell and not A. Gray, as was attributed by J. Ball in his combination. The name *Paranephelius ovatifolius* A. Gray, mentioned in the protologue of *P. ovatus*, is a nomen nudum.

Liabum ovatum (Weddell) Britton, Bull. Torrey Bot. Club 19: 263. 1892, non *Liabum ovatum* (Weddell) J. Ball, 1885. = *Paranephelius ovatus* Weddell, Chlor. And. 1(7): 214 + pl. 37B. 1857. See observation under *Liabum ovatum* (Weddell) J. Ball.

Liabum ovatum var. *hirtum* Perkins, Bot. Jahrb. Syst. 49: 229. 1913.—Type: Bolivia. La Paz: Palca-La Paz, 4600 m, Dec 1907, *K. Pflanz 218* (holotype: probably B, duplicates not found). This variety is excluded from *Liabum* because it has characters that deviate from the genus. This variety probably belongs to *Paranephelius*, which is characterized by its acaulescent herbaceous habit with leaves in a rosette, latex present, and pinnate venation of the leaves. According to Perkins (1913), this taxon is a variety of *Paranephelius ovatus* Weddell.

Liabum oxyphyllum Cuatrecasas, Collect. Bot. (Barcelona) 3: 303. 1953.—Type: Peru. Huánuco: Pillao, 2700 m, *Woytkowski 34165* (holotype: F, digital image!; isotype: G, digital image!). = *Munnozia oxyphylla* (Cuatrecasas) H. Robinson & Brettell, Phytologia 28: 55. 1974 (Robinson 1983).

Liabum pallatangense Hieronymus in Sodiro, Bot. Jahrb. Syst. 29: 60–61. 1900.—Type: Ecuador. Chimborazo: Crescit in valle Pallatanga et fluminis Pilotón, *Sodiro 55/12* (holotype: B [destroyed], photo FM 18121!; probable isotypes: BAF-2 sheets (*Sodiro s.n.*), digital images!). = *Erato polymnioides* de Candolle (Moran & Funk 2006).

Liabum palmeri A. Gray, Proc. Amer. Acad. Arts 22: 432. 1887.—Type. Mexico. Jalisco: Río Blanco, [June–Oct] 1886, *Palmer 586* (holotype: GH, digital image!; isotypes: K, MEXU, NY-2 sheets, US, YU, digital images!). = *Liabellum palmeri* (A. Gray) Rydberg, N. Amer. Fl. 34: 295. 1927 (Robinson 1983) or *Sinclairia palmeri* (A. Gray) B. L. Turner, Phytologia 67: 203. 1989. One isotype sheet at NY and the isotype at PH include a second specimen that is not type material: México, Jalisco, dry rocky hills near Guadalajara, 14 Oct 1889, *Pringle 2328*.

Liabum pastoense Cuatrecasas, Notas Fl. Colombia 6: 36. 1944.—Type: Colombia. Nariño: Entre El Encanto y Pasto, vertiente occidental de la cordillera, entre Páramo del Tábano y La Laguna, 2700–2900 m, 11 Jan 1941, *Cuatrecasas 11949* (holotype: COL, digital image!; isotypes: fragment BC, F, US, digital images!). = *Sampera pastoensis* (Cuatrecasas) V. A. Funk & H. Robinson, Proc. Biol. Soc. Washington 122: 158. 2009.

Liabum perfoliatum S. F. Blake, J. Wash. Acad. Sci. 17: 291–292. 1927.—Type: Colombia. Cauca: La Gallera, Micay Valley, Cordillera Occidental, 2000–2200 m, 1 Jul 1922, *Killip 7952* (holotype: US, digital image!; isotypes: GH, K, NY, PH, S, US, digital images!). = *Dillandia perfoliata* (S. F. Blake) V. A. Funk & H. Robinson, Syst. Bot. 26: 219. 2001.

Liabum peruense Cuatrecasas, Collect. Bot. (Barcelona) 3: 304–306. 1953.—Type: Peru. Huánuco: Torre-huasi, puna and below till 3500–4100 m, *Woytkowski 34275* (holotype: F, digital image!). = *Munnozia peruensis* (Cuatrecasas) H. Robinson & Brettell, Phytologia 28: 56. 1974 (Robinson 1983).

Liabum pichinchense Hieronymus in Sodiro, Bot. Jahrb. Syst. 29: 56–57. 1900.—Type: Ecuador. Pichincha: Crescit in silvis subandinis montium Pichincha et Corazón, *Sodiro 55/3* (holotype: B [destroyed], photo FM 18122!; isotype: F [*Sodiro s.n.*], digital image!). = *Sampera pichinchensis* (Hieronymus) V. A. Funk & H. Robinson, Proc. Biol. Soc. Washington 122: 158. 2009.

Liabum pinnatipartitum Hieronymus in Sodiro, Bot. Jahrb. Syst. 29: 62–63. 1900.—Type: Ecuador. Pichincha: Crescit ad rivulos, etc. in regione subtropica prope San Nicolás, *Sodiro 55/10* (holotype: B [destroyed], photo FM 18123!). = *Munnozia pinnatipartita* (Hieronymus) H. Robinson & Brettell, Phytologia 28: 57. 1974 (Robinson 1983).

Liabum pinnulosum Kuntze, Revis. Gen. Pl. 3: 163–164. 1898.—Type: Bolivia. Probably Cochabamba: Zwischen La Seja [La Ceja] und Santa Rosa, 2600 m, Jan–Apr 1892, *Kuntze s.n.* (holotype: NY, digital image!; isotypes: B [destroyed], photo FM 18124! K, digital image! US, digital images!). = *Munnozia pinnulosa* (Kuntze) H. Robinson & Brettell, Phytologia 28: 56. 1974 (Robinson 1983).

Liabum platylepis Schultz Bipontinus ex Klatt, Leopoldina 23: 146. 1887.—Type: Mexico. Veracruz: Mirador, *Sartorius s.n.* (*Linden 1236*) (lectotype, designated by Turner (1989: 175): GH, digital image!; isotype: K, photo LP!). = *Sinclairia platylepis* (Schultz Bipontinus ex Klatt) Rydberg, N. Amer. Fl. 34: 296. 1927 (Robinson 1983) or *S. discolor* Hooker & Arnott (Turner 1989).

Liabum polyanthum Klatt, Bull. Soc. Roy. Bot. Belgique 31: 209–210. 1893.—Type: Costa Rica. San José: Forêt à Général, Jan 1891, *Pittier 3419* (holotype: C; isotypes: BR-2 sheets, F, GH, digital images!). = *Sinclairia polyantha* (Klatt) Rydberg, N. Amer. Fl. 34: 299. 1927 (Robinson 1983, Turner 1989).

Liabum polymnioides R. E. Fries, Ark. Bot. 5(13): 24–25 + pl. 1, figs 10–11. 1906.—Type: Argentina. Jujuy: Quinta, in nemore Citri raro, 2 June 1901, *Fries 74* (holotype: S!). = *Microliabum polymnioides* (R. E. Fries) H. Robinson, Syst. Bot. 15: 743. 1990.

Liabum pringlei B. L. Robinson & Greenman, Proc. Amer. Acad. Arts 32(1): 49. 1896.—Type: Mexico. Jalisco: Rocky slopes, mountains near Lake Chapala, 7000 ft, 18 Oct 1895, *Pringle 6214* (holotype: GH, digital image!; isotypes: AC, BR, CAS, CM, E, F, GOET, ISC, JE, digital images! K photos LP! SI! M, MEXU-2 sheets, MIN, MSC, NY, PH, S, TEX, US-2 sheets, digital images!). = *Sinclairia pringlei* (B. L. Robinson & Greenman) H. Robinson & Brettell, Phytologia 28: 61. 1974 (Robinson 1983, Turner 1989). The collection number is erroneously cited as *Pringle 6215* in the protologue of *Liabum pringlei* (Turner, 1989).

Liabum pseudosalviifolium Hieronymus, Bot. Jahrb. Syst. 36: 502. 1905.—Type: Peru. Without department: Crescit prope Callacate, May 1879, *Jelski 753* (holotype: B [destroyed], photo FM 18125!; isotype: K, photo SI!). = *Ferreyranthus verbascifolius* (Kunth) H. Robinson & Brettell (Dillon & Sagástegui Alva 1994).

Liabum pulchrum S. F. Blake, J. Wash. Acad. Sci. 17: 299. 1927.—Type: Peru. Huánuco:

Muña, trail to Tambo de Vaca, 2440 m, 5–7 June 1923, *Macbride 4312* (holotype: F, digital image!; isotype: US, digital image!). = *Munnozia venosissima* Ruiz & Pavón (Robinson 1983).

Liabum rosulatum Hieronymus, Bot. Jahrb. Syst. 36: 501–502. 1905.—Types: Peru. Cajamarca: Crescit prope Cutervo, Feb 1879, *Jelski 722* (holotype: B [destroyed], photo FM 18126!; Ancash: Yungay Prov., Huascarán National Park, Quebrada Ranincuray, 3900–4100 m, 17 Apr 1985, *Smith et al. 10377* (neotype, designated by Funk and Zermoglio (1999: 325): US, digital image!; isoneotypes: F, MO, digital images!). = *Chrysactinium acaule* (Kunth) Weddell (Funk & Zermoglio 1999).

Liabum rugosum Ferreyra, Publ. Mus. Hist. Nat. "Javier Prado," Ser. B, Bot. 20: 3. 1965.—Type: Peru. Amazonas: Prov. Chachapoyas, 1 km al sudoeste de Chachapoyas, 2300 m, 22 May 1962, *Wurdack 469* (holotype: USM, photo LP!; isotypes: F, GH, NY, TEX, UC, US, digital images!). = *Ferreyranthus rugosus* (Ferreyra) H. Robinson & Brettell, Phytologia 28: 51. 1974 (Dillon & Sagástegui Alva 1994).

Liabum rusbyi Britton, Bull. Torrey Bot. Club 19: 263. 1892.—Type: Bolivia. La Paz: Mapiri, 10,000 ft, Apr/May 1886, *Rusby 1745* (holotype: NY-3 sheets, digital images!; isotypes: GH, K, NY, PH, US, digital images!). = *Munnozia rusbyi* (Britton) Rusby, Bull. Torrey Bot. Club 54: 312. 1927 (Robinson 1983).

Liabum sagittatum Schultz Bipontinus, Flora 36: 37–38. 1853.—Types: Colombia. Santander: Prov. Pamplona, La Baja, 8000 ped., Dec 1846, *Funk & Schlimm 1293* (syntype: P-2 sheets, digital images!); Nova Granada, Prov. Bogotá, salto de Tequendama, 7200–7800 ped., Dec 1842, *Linden 805* (syntype: P-2 sheets, digital images!); Peru. Without department and locality: Peruviae calidis, *Humboldt s.n.* (herb. Willdenow 16525) (syntype: B digital image!, photo FM 18127!). = *Munnozia senecionidis* Bentham (Robinson 1983).

Liabum salviifolium Hieronymus, Bot. Jahrb. Syst. 28: 622–623. 1901.—Type: Ecuador. Azuay: Crescit frequenter in fruticetis prope Chagal et Molleturo in Andibus occidentalibus cuencanis, 2300–2800 m, Sept, *Lehmann 7958* (holotype: B [destroyed], photo FM 18128!, G fragment, digital image!; isotypes: F, K, digital image!). = *Ferreyranthus verbascifolius* (Kunth) H. Robinson & Brettell (Dillon & Sagástegui Alva 1994).

Liabum sandemanii H. Robinson, Phytologia 35: 488–489. 1977.—Type: Peru. Junín: Huacapistana, 5600 ft, Oct 1943, *Sandeman 4420* (holotype: K, digital image! fragment US!). This species is here excluded from *Liabum* because it has morphological features such as a sheath at the stem nodes, an areolate receptacle, and densely glandular cypselae that do not fit the traits of *Liabum*. *Liabum sandemanii* is being studied in order to determine its taxonomic position (Gutiérrez, in prep.).

Liabum scandens Domke in Diels, Beitr. Veg. Ecuador: 167–168. 1937.—Type: Ecuador. Chimborazo: Nördlich von Typococha, ca. 3200 m, 19 Aug 1933, *Diels 636* (holotype: B, destroyed). = *Sampera coriacea* (Hieronymus) V. A. Funk & H. Robinson (Funk & Robinson 2009).

Liabum sericolepis Hemsley, Biol. Cent.-Amer., Bot. 2: 232. 1881.—Type: Mexico. Veracruz: Valley of Cordova, 10 Mar 1865/10 Mar 1866, *Bourgeau 2177* (holotype: K, digital image! fragment US, digital image!; isotypes: F, digital image! G, photo FM 28810! P, photo FM 38034!). = *Sinclairia sericolepis* (Hemsley) Rydberg, N. Amer. Fl. 34: 301. 1927 (Robinson 1983, Turner 1989).

Liabum sessiliflorum (Kunth) Lessing, Linnaea 6: 703. 1831. *Andromachia sessiliflora* Kunth in Humboldt, Bonpland & Kunth, Nov. Gen. Sp. [H.B.K.], ed. folio, 4: 80 + tab. 338. 1818 ["1820"].—Type: probably Colombia. Without department and locality:

Crescit in Regno Peruviano?, *Humboldt & Bonpland s.n.* (holotype: P, digital image!; isotypes: B [destroyed], photo FM 18129!, F, fragment US, digital images!). = *Oligactis sessiliflora* (Kunth) Candolle, Prodr. [A. P. de Candolle] 5: 96. 1836 (Robinson 1983, Gutiérrez 2008).

Liabum silphioides (Poeppig) S. F. Blake, J. Wash. Acad. Sci. 17: 301. 1927. *Prionolepis silphioides* Poeppig, Nov. Gen. Sp. Pl. (Poeppig & Endlicher) 3: 55 + tab. 261. 1845.—Type: Peru. Huánuco: Crescit in montibus herbidis Peruviae subandinae versus Cuchero, Jan 1830, *Poeppig 1702* (holotype: W-2 sheets, digital images!; isotype: NY, digital image!). = *Munnozia silphioides* (Poeppig) H. Robinson & Brettell, Phytologia 28: 56. 1974 (Robinson 1983).

Liabum simile McVaugh, Contr. Univ. Michigan Herb. 9: 468–470. 1972.—Type: Mexico. Nayarit: Volcán Ceboruco, ca. 6 mi NW of Ahuacatlán, 3200 ft, 4 Oct 1962, *Cronquist 9602* (holotype: MICH, digital image!; isotypes: MEXU, MSC, TEX, digital images!). = *Sinclairia similis* (McVaugh) H. Robinson & Brettell, Phytologia 28: 62. 1974 (Robinson 1983, Turner 1989).

Liabum sodiroi Hieronymus in Sodiro, Bot. Jahrb. Syst. 29: 61–62. 1900.—Type: Ecuador. Without province: Crescit in regione subtropica prope San Florencio, Pallatanga, etc., *Sodiro 55/11* (holotype: B [destroyed], photo FM 18131!; lectotype, designated by Moran and Funk (2006): QPLS; probable isolectotype: BAF [*Sodiro s.n.*], digital image!). = *Erato sodiroi* (Hieronymus) H. Robinson, Phytologia 34: 379. 1976 (Moran & Funk 2006).

Liabum stenolepis S. F. Blake, J. Wash. Acad. Sci. 17: 302–303. 1927.—Type: Peru. Huánuco: Muña, trail to Tambo de Vaca, 2440 m, 5/7 June 1923, *Macbride 4338* (holotype: F, digital image!; isotype: US, digital image!). = *Erato stenolepis* (S. F. Blake) H. Robinson, Phytologia 34: 379. 1976 (Moran & Funk 2006).

Liabum stipulatum Vahl ex Schultz Bipontinus, J. Bot. 1: 237. 1863, not validly published. *Conyza stipulata* Vahl was listed by Candolle (1836: 97) as a synonym of *Liabum jussieui* and is thus a nomen nudum. In publishing the name *L. stipulatum*, Schultz Bipontinus based it on Vahl's name but cited it as a synonym of *L. jussieui*, an earlier name. The combination is therefore not validly published and has no nomenclatural standing, i.e., it has no priority over *Liabum stipulatum* Rusby. = *Munnozia jussieui* (Cassini) H. Robinson & Brettell.

Liabum striatum Cuatrecasas, Collect. Bot. (Barcelona) 3: 306–307. 1953.—Type: Peru. Lambayeque: Prov. Lambayeque, above Olmos, 1800–1900 m, May 1915, *Weberbauer 7107* (holotype: F, digital image!). = *Pseudonoseris striata* (Cuatrecasas) H. Robinson & Brettell, Phytologia 28: 60. 1974 (Robinson 1983).

Liabum stuebelii Hieronymus, Bot. Jahrb. Syst. 21(3): 353. 1895.—Type: Ecuador. Chimborazo: Crescit prope Campamento Utañag in valle fluminis Rio Chambo, 3045 m, Nov, *Stübel 280* (holotype: B [destroyed], photo FM 18132!). = *Munnozia nivea* (Hieronymus) H. Robinson & Brettell (Robinson 1983).

Liabum subcirrhosum S. F. Blake, J. Wash. Acad. Sci. 17: 293. 1927. *Liabum candidum* var. *subcirrhosum* (S. F. Blake) Cabrera, Bol. Soc. Argent. Bot. 2: 95. 1947.—Type: Argentina. Catamarca: Depto. Andagalá, La Playa, 12 Feb 1917, *Jörgensen 1673* (holotype: US, digital image!; isotypes: GH! SI!). = *Microliabum candidum* (Grisebach) H. Robinson.

Liabum subglandulare S. F. Blake, Contr. U.S. Natl. Herb. 24: 31. 1922.—Type: Honduras. Copán: Hacienda La Zumbadora between El Paraíso and La Florida, 13

May 1919, *Blake 7386* (holotype: US, digital image!). = *Sinclairia deamii* (B. L. Robinson & Bartlett) Rydberg (Robinson 1983, Turner 1989).

Liabum sublobatum B. L. Robinson, Proc. Amer. Acad. Arts 51: 539. 1916.—Type: Guatemala. Sololá: San Lucas Toliman, 1665 m, 2 Feb 1915, *Holway 179* (holotype: GH, digital image!). = *Sinclairia sublobata* (B. L. Robinson) Rydberg, N. Amer. Fl. 34: 297. 1927 (Robinson 1983, Turner 1989).

Liabum subviride S. F. Blake, J. Wash. Acad. Sci. 17: 294–295. 1927.—Type: Peru. Cuzco: Lucumayo Valley, not far from Ollantaytambo, 1800–3600 m, 19 June 1915, *Cook & Gilbert 1365* (holotype: US, digital image!). = *Munnozia subviridis* (S. F. Blake) H. Robinson & Brettell, Phytologia 28: 56. 1974 (Robinson 1983).

Liabum szyszylowiczii Hieronymus, Bot. Jahrb. Syst. 36: 503–504. 1905.—Type: Peru. Cajamarca: Crescit prope Callacate, May 1879, *Jelski 718* (holotype: B [destroyed], photo FM 18133!). = *Pseudonoseris szyszylowiczii* (Hieronymus) H. Robinson & Brettell, Phytologia 28: 60. 1974 (Robinson 1983).

Liabum tabanense Cuatrecasas, Caldasia 3: 425. 1945.—Type: Colombia. Nariño: Páramo del Tábano, alto de la cordillera entre Pasto y El Encano, vertiente occidental, 3200 m, 11 Jan 1941, *Cuatrecasas 11904* (holotype: COL, digital image!; isotypes: F, US, digital images!). = *Munnozia jussieui* (Cassini) H. Robinson & Brettell (Robinson 1983).

Liabum taeniotrichum S. F. Blake, J. Wash. Acad. Sci. 17: 298–299. 1927.—Type: Peru. Amazonas: Prov. Chachapoyas, [1836], *Mathews s.n.* (holotype: K-504110, digital image! fragment US, digital image!; isotype: K [*Mathews 104*], digital image!). = *Munnozia senecionidis* Bentham (Robinson 1983).

Liabum tajumulcense Standley & Steyermark, Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 27. 1943.—Type: Guatemala. San Marcos: Barrancos southwest of Tajumulco, northwestern slopes of Volcán de Tajumulco, 2300–2500 m, Feb 1940, *Steyermark 36543* (holotype: F, digital image!). = *Sinclairia tajumulcensis* (Standley & Steyermark) H. Robinson & Brettell, Phytologia 28: 62. 1974 (Robinson 1983, Turner 1989).

Liabum tenerum (Schultz Bipontinus) S. F. Blake, J. Wash. Acad. Sci. 17: 303. 1927. *Kastnera tenera* Schultz Bipontinus, Flora 36: 38. 1853.—Type: Colombia. Cauca: Prope Quindiu Paramilla, 10500 ped., Feb 1843, *Linden 1136* (holotype: probably P). = *Munnozia tenera* (Schultz Bipontinus) H. Robinson & Brettell, Phytologia 28: 57. 1974 (Robinson 1983).

Liabum tenuius S. F. Blake [‘*tenuior*’], J. Wash. Acad. Sci. 17: 289. 1927.—Type: Ecuador. Pichincha: Casitagua, May 1903, *Rivet 478* (holotype: P, digital image!, fragment US, digital image!). = *Chrysactinium acaule* (Kunth) Weddell (Funk & Zermoglio 1999).

Liabum tonduzii B. L. Robinson, Proc. Boston Soc. Nat. Hist. 31: 270. 1904.—Type: Costa Rica. San José: Banks of Río Virilla, San José, 1100 m, Jan 1896, *Tonduz 9859* [*Donnell Smith 7064*] (lectotype, designated by Turner (1989: 187): GH, digital image!; isolectotypes: F, K, M, MO, NY, US-2 sheets, digital images!). = *Sinclairia polyantha* (Klatt) Rydberg (Robinson 1983, Turner 1989).

Liabum tovarense V. M. Badillo, Bol. Soc. Venez. Ci. Nat. 10: 314. 1946.—Type: Venezuela. Aragua: Colonia Tovar, [1800–2000 m], Dec 1942, *Allart 370* (holotype: VEN, digital image!; isotype: US, digital image!). = *Oligactis sessiliflora* (Kunth) Candolle (Robinson 1983, Gutiérrez 2008).

Liabum tovari Cabrera, Bol. Soc. Argent. Bot. 10: 29. 1962.—Type: Peru. Huancavelica: Prov. Huancavelica, mejorada entre Izcuchaca y Acoria, valle del Mantaro, 2900 m, 7

Apr 1952, *Tovar 998* (holotype: LP!; isotype: USM). = *Ferreyranthus vernonioides* (Muschler) H. Robinson & Brettell (Dillon & Sagástegui Alva 1994).

Liabum trinerve (Ruiz & Pavón) Schultz Bipontinus, Flora 36: 34. 1853. *Munnozia trinervis* Ruiz & Pavón, Syst. Veg. Fl. Peruv. Chil. 195. 1798.—Type: Peru. Junín-Lima: In Peruviae praeruptis et segetibus versus Picoy et Huassahuassi vicos, Nov/Dec, *Ruiz & Pavón s.n.* (holotype: MA, fragment US, digital images!). = *Munnozia trinervis* Ruiz & Pavón (Robinson 1983).

Liabum uniflorum (Poeppig) Schultz Bipontinus, Flora 36: 34. 1853. *Paranephelius uniflorus* Poeppig, Nov. Gen. Sp. Pl. (Poeppig & Endlicher) 3: 42 + tab. 248A. 1843.—Type: Peru. Without department: Crescit locis frigidissimis glareosis Andium peruvianorum, Sierra la Viuda, 15200 ped., June, *Poeppig s.n*. (holotype: W, digital image!). = *Paranephelius uniflorus* Poeppig (Robinson 1983).

Liabum vagans S. F. Blake, Brittonia 2: 354. 1937.—Type: Guatemala. Quiché: In thicket on mountainside, along Nebaj-Aguacatán trail, 2470 m, 12 Dec 1934, *Skutch 1913* (holotype: A, digital image!; isotypes: F, LL, NY, US, digital images!). = *Sinclairia vagans* (S. F. Blake) H. Robinson & Brettell, Phytologia 28: 62. 1974 (Robinson 1983, Turner 1989).

Liabum vaginans Muschler, Bot. Jahrb. Syst. 50(2/3), Beibl. 111: 79–80. 1913.—Type: Peru. Apurimac: Prov. Andahuaylas, in valle Rio Pincos fluvii secundarii Rio Pampas fluminis, 2400–2500 m, June 1911, *Weberbauer 5868* (holotype: B [destroyed]; isotypes: F, US, digital images!). = *Ferreyranthus vaginans* (Muschler) H. Robinson & Brettell, Phytologia 28: 51. 1974 (Dillon & Sagástegui Alva 1994).

Liabum valeri Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1490. 1938, as "*valerii*."—Type: Costa Rica. San José: Near Finca La Cima, above Los Lotes, North of Copey, 2100–2400 m, 21–22 Dec 1925, *Standley 42555* (holotype: F, digital image!; isotype: US, digital image!). = *Oligactis sessiliflora* (Kunth) Candolle (Gutiérrez 2008).

Liabum venosissimum (Ruiz & Pavón) Schultz Bipontinus, Flora 36: 34. 1853. *Munnozia venosissima* Ruiz & Pavón, Syst. Veg. Fl. Peruv. Chil. 195. 1798.—Type: Peru. Huánuco: In Peruviae montibus silvaticis versus Pillao vicum, Aug–Sept, *Ruiz & Pavón s.n.* (holotype: MA, fragment US, digital images!; isotype: P ["Herb. Pavón s.n., donné per Boissier, Peruvia"], photos LP! SI!). = *Munnozia venosissima* Ruiz & Pavón (Robinson 1983).

Liabum verbascifolium (Kunth) Lessing, Linnaea 6: 700. 1831. *Andromachia verbascifolia* Kunth in Humboldt, Bonpland & Kunth, Nov. Gen. Sp. [H.B.K.], ed. folio, 4: 79. 1818 ["1820"].—Type: Ecuador. Loja: Crescit in montibus Quitensium cum Cinchona inter Malacates et Gonzanama, 1060 hex., Aug, *Humboldt & Bonpland s.n.* (holotype: P ["*3414*, Gonzanama", fide V. A. Funk in Hind & Jeffrey 2001], digital image!). = *Ferreyranthus verbascifolius* (Kunth) H. Robinson & Brettell, Phytologia 28: 51. 1974 (Dillon & Sagástegui Alva 1994).

Liabum vernonioides Muschler, Bot. Jahrb. Syst. 50(2/3), Beibl. 111: 80–81. 1913.—Type: Peru. Apurimac: Prov. Andahuaylas, in valle secundario Pampas fluminis prope Haciendam Cotahuacho, 2900–3000 m, 10 June 1911, *Weberbauer 5854* (holotype: B [destroyed], fragment US, digital image!; isotype: F, digital image!). = *Ferreyranthus vernonioides* (Muschler) H. Robinson & Brettell, Phytologia 28: 51. 1974 (Dillon & Sagástegui Alva 1994).

Liabum volubile (Kunth) Lessing, Linnaea 6: 704. 1831. *Andromachia volubilis* Kunth in Humboldt, Bonpland & Kunth, Nov. Gen. Sp. [H.B.K.], ed. folio, 4: 80–81. 1818

["1820"].—TYPE: probably COLOMBIA. Without department and locality: Crescit in monte Antisana [Antizana] Quitensium?, *Humboldt & Bonpland s.n.* (holotype: P, digital image!). = *Oligactis volubilis* (Kunth) Cassini in F. Cuvier, Dict. Sci. Nat., ed. 2. [F. Cuvier] 36: 17. 1825 (Gutiérrez 2008). Colombia, not Ecuador, is probably the country where the type specimen was collected (Gutiérrez 2008).

Liabum volubile var. *latifolium* Hieronymus, Bot. Jahrb. Syst. 28: 622. 1901.—TYPE: COLOMBIA. Cauca: Crescit in fruticetis declivium supra urbem Popayan, 1700–2200 m, Feb, *Lehmann 5227* (holotype: B [destroyed], fragment LP!; isotypes: F, GH, digital images! K, photos SI! US! US-2 sheets, one fragment ex K, digital images!). = *Oligactis latifolia* (Hieronymus) H. Robinson & Brettell, Phytologia 28: 57. 1974 (Robinson 1983).

Liabum vulcanicum Klatt, Bot. Jahrb. Syst. 8: 47. 1887.—TYPE: COLOMBIA. Cauca: Ad latera occident. Montis ignivomi, Puracé, 2600–3200 m, Jan 1884, *Lehmann 3504* (holotype: B [destroyed], photo FM 18135!; lectotype, designated by Moran and Funk (2006): US, digital image!; isolectotypes: GH, K, digital images!). = *Erato vulcanica* (Klatt) H. Robinson, Phytologia 34: 379. 1976 (Moran & Funk 2006).

Solidago villosa P. Browne ex Lessing, Linnaea 4: 319. 1829, pro syn. of *Liabum umbellatum* (Linnaeus) Schultz Bipontinus.

Starkea pinnata Nuttall, Gen. N. Amer. Pl. [Nuttall] 2: 169. 1818. = *Xanthisma spinulosum* (Pursh) D. R. Morgan & R. L. Hartm.

Starkia Jussieu in Steudel, Nom. Bot. 2 (2): 632. 1841, pro syn. of *Liabum* Adanson. An orthographic variant of the name *Starkea* Willdenow.

Viviania Willdenow ex Lessing, Linnaea 4: 318. 1829. Nomen nudum, pro syn. of *Andromachia* Humboldt & Bonpland.

Viviania bicolor Willdenow ex Lessing, Linnaea 4: 318. 1829, nomen nudum, pro syn. of *Liabum melastomoides* (Kunth) Lessing.

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APPENDIX

Species and particular specimens (collector, collector number, and herbarium) analyzed micromorphologically, anatomically, and palynologically (*) in this study.

L. acuminatum Rusby: *Beck 12711* (SI); *Nee 38833* (SI)*; *Nee 38923* (MO)*; *Vargas & Seibel 2021* (US), *D. Williams 990* (NY).
L. amplexicaule Poepp.: *Ferreyra 4358* (US)*; *Schunke 4881* (NY)*; *Schunke 9755* (MO); *Schunke 12512* (US).
L. asclepiadeum Sch. Bip.: *Bunting 4993* (NY)*; *Clark 282* (NY); *Croat 13302* (MO); *Hammel et al. 6875* (F); *King et al. 10546* (US)*.
L. barclayae H. Rob.: *Barclay & Juajibioy 8316* (US)*.
L. dillonii D. G. Gut. & Katinas: *Jaramillo & Winnerskjold 5770* (F)*.
L. eriocaulon Poepp.: *Dillon 2687* (F, MO)*.
L. floribundum Less.: *Hutchison & von Bismarck 6337* (US), *Játiva & Epling 24* (NY); *King 6541* (MO)*; *Mille 1995* (MO)*; *Schunke 9432* (MO).
L. grandiflorum (Kunth) Less.: *Cabanillas & Guevara 433* (F); *Camp E3123* (F)*; *Hitchcock 21452* (NY)*; *Sagástegui 12746* (MO); *I. Sánchez 463* (LP).
L. igniarium (Humb. & Bonpl.) Less.: *Flora Ecuatoriana 1093* (GH); *Funk 11458* (US); *Jaramillo 9660* (NY)*; *Mexia 7389* (F); *Peñafiel & Ortiz 249* (MO)*; *Zak & Jaramillo 2058* (NY).
L. kingii H. Rob.: *King 6563* (US); *King et al. 6006* (US); *Øllgaard et al. 35517* (MO); *Panero & Clark 2969* (NY); *Stuessy & Nesom 5808* (LP)*.
L. macbridei H. Rob.: *Macbride 4224* (US)*.
L. melastomoides (Kunth) Less.: *Cabrera & Aragón 9000* (MO)*; *Cabrera & Aragón s.n.* (GH)*; *Dryander 546* (US); *Pennell 5854* (US); *Holton s.n.* (NY).
L. nigropilosum Hieron.: *Webster 22970* (US)*.
L. robinsonii D. G. Gut. & Katinas: *Jaramillo & Winnerskjold 5776* (NY)*; *Stuessy & Nesom 5892* (LP).
L. saloyense Domke: *Jaramillo & Zak 7903* (F, MO)*; *Stuessy et al. 4866* (MO); *Zak 1162* (MO).
L. saundersii H. Rob.: *Beck 13899* (SI, US)*.
L. solidagineum (Kunth) Less.: *Cook & Gilbert 895* (US); *Ferreyra 15541* (US); *Lewis 88902* (MO); *López & Sagástegui 8120* (GH)*; *Smith 10501* (MO).
L. steinbachii H. Rob.: *Steinbach 8152* (MO, US)*.
L. stipulatum Rusby: *Aguirre 105* (F)*; *Gutiérrez & Barkley 17C681* (US); *Harling & Andersson 12255* (MO); *Killip 6117* (NY)*; *H. Smith 2001* (US).
L. umbellatum (L.) Sch. Bip.: *Crosby et al. 535* (F, GH)*; *Crosby et al. 859* (F)*; *Ekman 1548* (US)*, *5346* (GH)*, *12578* (GH)*; *Howard 12087* (GH); *Liogier 11533* (GH)*; *Wright 288* (F, GH)*.
L. vargasii H. Rob.: *Angulo 1774* (LP); *Vargas 10182* (US)*.
L. wurdackii Ferreyra: *Gentry el al. 74613* (MO); *Llatas 2528* (F)*; *López et al. 4246* (LP); *Plowman et al. 14263* (F)*; *Sánchez & Dillon 8010* (F).

NUMERICAL LIST OF SPECIES

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3. Liabum asclepiadeum
4. Liabum barclayae
5. Liabum dillonii
6. Liabum eriocaulon
7. Liabum floribundum
8. Liabum grandiflorum
9. Liabum igniarium
10. Liabum kingii
11. Liabum macbridei
12. Liabum melastomoides
13. Liabum nigropilosum
14. Liabum robinsonii
15. Liabum saloyense
16. Liabum saundersii
17. Liabum solidagineum
18. Liabum steinbachii
19. Liabum stipulatum
20. Liabum umbellatum
21. Liabum vargasii
22. Liabum wurdackii

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