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To which genus of Asteraceae does *Liabum oblanceolatum* belong? Vegetative characters have the answer

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The West Indian species *Liabum oblanceolatum* Urb. & Ekman was established on the basis of sterile young specimens represented by acaulescent herbs with rosulate leaves. However, these specimens have important traits that do not correspond to *Liabum* Adans. More than 90 genera of Asteraceae occur in Hispaniola (= Santo Domingo), but only 14 of them include species represented by acaulescent herbs with rosulate or grouped leaves at the base of the stem. From these genera, *Chaptalia* Vent. and *Liabum* are the most similar to the types of *L. oblanceolatum*. Habit, leaf arrangement, lamina shape, leaf margin, leaf surface, leaf margin intrasection, leaf venation, leaf pubescence, leaf trichomes, stomata and upper surface leaf cuticle were analysed in the type specimens of *L. oblanceolatum* and in species of *Chaptalia* and *Liabum* of Hispaniola. The vegetative trichomes are described in detail. The analysis reveals that the type specimens of *L. oblanceolatum* fit with all the vegetative traits of *Chaptalia angustata* Urb.

ADDITIONAL KEYWORDS: *Chaptalia* – *C. angustata* – Hispaniola – Liabeae – microcharacters – Mutisieae.

INTRODUCTION

During the preparation of a revision of the genus *Liabum* Adans. (Asteraceae, Liabeae) (Gutiérrez, 2004) the first author found that some characters of the type specimen of *L. oblanceolatum* Urb. & Ekman do not correspond to the typical characters of *Liabum*. The Neotropical genus *Liabum s.s.* includes *c.* 30 species (Gutiérrez, 2004) and is distributed from southeastern Mexico, through Central America to the Andes of South America, where it ranges from Venezuela to the boundary of Argentina and Bolivia (Gutiérrez, 2003). In addition, this genus is also represented in the West Indies, especially in Cuba, Jamaica and Hispaniola (= Santo Domingo) in moist forests associated with limestone areas (Funk, Robinson & Dillon, 1996). Five species of *Liabum* occur on Hispaniola, among them *L. oblanceolatum*.

Liabum oblanceolatum was established by Urban and Ekman (Urban, 1931) on the basis of young specimens collected by Ekman on Hispaniola, represented by acaulescent herbs with rosulate leaves without capitula (Fig. 1). Some traits that are not common in *Liabum* were described in the protologue of the new species (e.g. oblanceolate shape of the lamina, pinnate venation and entire margin bearing glandular hairs). However, other characteristics in these type materials are common to the Caribbean species of *Liabum*, such as grouped leaves sometimes in subacaulescent or acaulescent rosettes, upper surface of leaves with arachnoid and evanescent pubescence, and lower surface with tomentose pubescence.

Later, Moscoso (1943) recorded eight species of *Liabum* from Hispaniola: *L. barahonense* Urb., *L. ovatifolium* Urb., *L. poiteaui* (Cass.) Urb., *L. polycephalum* Urb., *L. selleanum* Urb., *L. subacaule* Rydb., *L. umbellatum* (L.) Sch. Bip. and *L. oblanceolatum*. Moscoso mentioned that *L. oblanceolatum* had yellow florets, but he did not indicate voucher specimens. No additional specimens determined as *L. oblanceolatum* are kept at the Dominican herbarium JBSD (D. Castillo, pers. comm.), and Moscoso's personal herbarium was destroyed by fire (Stafleu & Cowan, 1981). Furthermore, after searching in other herbaria, only sterile young type specimens of *L. oblanceolatum* were found; there were no additional specimens with capitula features. It is possible that

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Figure 1. Holotype of *Liabum oblanceolatum* conserved in S.

Moscoso associated *L. oblanceolatum* with other species of *Liabum* only by leaf resemblance but without seeing florets.

Robinson & Brettell (1974) and then Robinson (1983) included *L. oblanceolatum* under *Liabum s.s.* According to Turner (1996), all the Dominican and Haitian species of *Liabum* appear to be the highly variable species *Liabum poiteaui*. However, Liogier (1996) indicated seven species of *Liabum* in Hispaniola and differentiated *L. oblanceolatum* based on its oblanceolate leaves with entire or slightly glandular-dentate margin. Moreover, Funk & Skalsky (unpublished: http://www.nmnh.si.edu/rtp/students/1997/skalsky.htm) recognized several species of *Liabum* in the island on the basis of the size of the plants, leaves and florets, the presence of corolla hairs and leaf pubescence.

A detailed study of the type specimens of *L. oblanceolatum* shows that many characters such as oblanceolate laminae, pinnate venation and entire margin bearing glandular hairs do not correspond to the genus *Liabum*. There are two alternatives: to consider *L. oblanceolatum* as a dubious species under the genus *Liabum*, or to try to determine if the type specimens of *L. oblanceolatum* correspond to another genus on the basis of vegetative characters. The latter was chosen here.

MATERIAL AND METHODS

The selection of genera and species analysed in this work follows Moscoso (1943) and Liogier (1996). This study is also based on herbarium specimens kept at F, GH, JBSD, K, LINN, LP, M, MO, NY, S, SI, US (Holmgren, Holmgren & Barnett, 1990).

For microscopic examination, leaves were treated with a clearing process (Dizeo de Strittmatter, 1973) and stained with 2% safranin. Drawings were made by the authors using an Olympus CH2 microscope with camera-lucida. For scanning electron microscopy (SEM) studies, dried material was placed directly on the stubs and coated with gold. The samples were scanned and photographed in a Jeol JSM-T 100 scanning electron microscope. The following specimens were analysed: *Chaptalia angustata* Urb.: Dominican Republic. La Vega: Santo Domingo prope Constanza, 1250 m, ii.1910, *Türkheim 2908* (SI, fragment of B); *Chaptalia nutans* (L.) Pol.: Dominican Republic. Santiago: El Rubio, 17.iv.1946, *Jiménez 1101* (LP); *Liabum oblanceolatum* Urb. & Ekman: Dominican Republic. La Vega: Valle Nuevo, shaded cliff at a brook, *c.* 2400 m, 17.x.1929, *Ekman H 13827* (GH); *Liabum subacaule* Rydb.: Dominican Republic. Santiago: Loma de Oro, about 5 miles S of Mata Grande, 4.vi.1968, *Liogier 11533* (GH); and *Liabum umbellatum* (L.) Sch. Bip.: Jamaica. Saint Thomas: between Blue Mountain Peak and Portland Gap, 24.vii.1963, *Crosby et al. 859* (F).

We follow Christensen & Hansen (1998) for terms of leaf epidermal patterns of cuticle, Harris & Woolf Harris (1994) and Hickey (1973) for architecture of leaves and pubescence, and Ramayya (1962) for vegetative trichomes.

RESULTS AND DISCUSSION

To which genus of Asteraceae does *L. oblanceolatum* belong?

According to Moscoso (1943) and Liogier (1996), more than 90 genera of Asteraceae occur on Hispaniola, but only 14 of them (i.e. *Chaptalia* Vent., *Elephantopus* L., *Emilia* Cass., *Erigeron* L., *Hieracium* L., *Lactuca* L., *Launaea* Cass., *Leontodon* L., *Liabum* Adans., *Orthopappus* Gleason, *Sachsia* Griseb., *Sonchus* L., *Taraxacum* Weber ex F. H. Wigg. and *Youngia* Cass.) include species represented by acaulescent herbs with rosu-

late leaves, caulescent herbs with rosulate leaves (at least in the basal part of the stem) or herbs sometimes with densely grouped leaves at the base of the stem. From these genera, *Taraxacum*, *Erigeron*, *Launaea*, *Sonchus* and *Lactuca* are very different from the types of *L. oblanceolatum* based on their glabrous or glabrescent lower surface of leaves. *Elephantopus*, *Emilia*, *Hieracium*, *Leontodon*, *Orthopappus*, *Sachsia* and *Youngia* are also distinct because of their densely or slightly hirsute leaf lower surfaces (not tomentose). Thus, *Chaptalia* and *Liabum* are most similar to each other with regard to their leaf pubescence, especially the tomentose lower surface, which is similar to that of the specimens of *L. oblanceolatum*.

The genus *Chaptalia*, which is being revised by the second author, belongs within the tribe Mutisieae. It is an American genus with *c.* 35 species distributed in the southern USA, Mexico, Central America and South America, reaching central Chile and Argentina (Burkart, 1944; Nesom, 1995; Katinas, 1998). Within this range, the West Indies contain many endemic species of *Chaptalia* (Burkart, 1944). This genus is distinguished from other genera of Mutisieae by its scapose habit, rosulate leaves, outer ray corollas ligulate or with a scarcely developed inner lip, filiform and reduced inner ray corollas, bilabiate or tubulose disc corollas, absence of staminodes in the ray florets and rostrate cypselas (Katinas, 1998, 2004).

We analysed the following macrocharacters and microcharacters in Haitian and Dominican species of *Chaptalia* and *Liabum*, and the type specimens of *L. oblanceolatum*: habit, leaf arrangement, lamina shape, leaf margin, leaf margin intrasection, leaf venation, leaf surface, leaf pubescence, leaf trichomes, stomata and upper surface leaf cuticle (Table 1). Leaf trichomes (Fig. 2) and upper surface leaf cuticle (Fig. 3) resulted in fundamental traits in the analysis. A detailed description of the leaf trichomes is given in Appendix 1. Table 1 and Appendix 1 show that there is a correspondence between the above mentioned characters in *L. oblanceolatum* and *Chaptalia*: acaulescent herbs, alternate and rosulate leaf arrangement, oblanceolate laminae, leaf margin with several simple biseriate glandular hairs, revolute leaf margin intrasection, pinnate leaf venation, oblique-septate-flagellate leaf hairs, simple biseriate glandular hairs with head with thick walls and striate upper surface leaf cuticle.

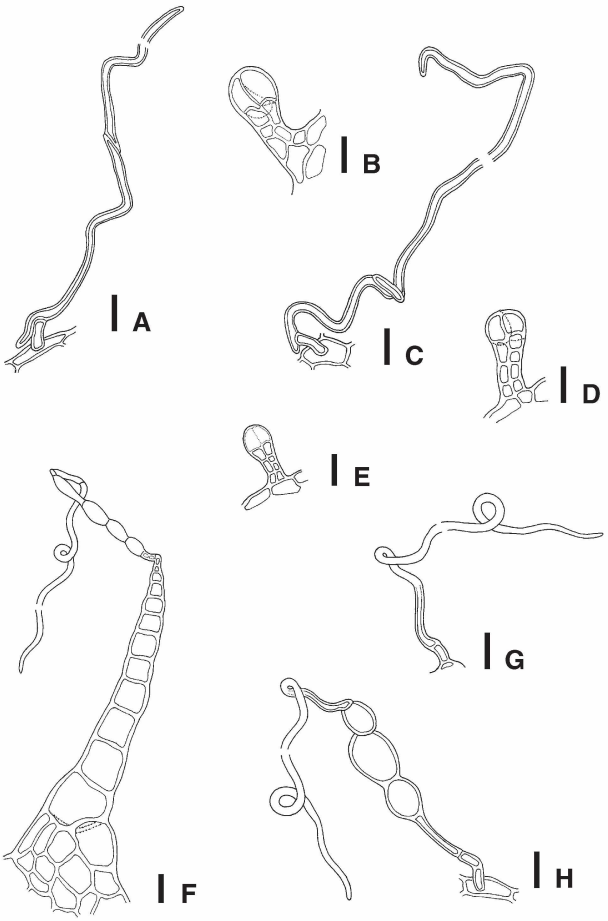

Figure 2. Vegetative leaf trichomes in *Chaptalia* and *Liabum*. Scale bars = 2.5 μm. A, oblique-septate-flagellate hair. *Liabum oblanceolatum*. Coll. Ekman H 13827 (GH). B, simple biseriate glandular hair. *Liabum oblanceolatum*. Coll. Ekman H 13827 (GH). C, oblique-septate-flagellate hair. *Chaptalia angustata.* Coll. Türkheim 2908 (SI). D, simple biseriate glandular hair. *Chaptalia angustata.* Coll. Türkheim 2908 (SI). E, simple biseriate glandular hair. *Liabum subacaule*. Coll. Liogier 11533 (GH). F, bulbiferous flagellate hair with compound foot. *Liabum subacaule*. Coll. Liogier 11533 (GH). G, bulbiferous flagellate hair with single foot. *Liabum subacaule*. Coll. Liogier 11533 (GH). H, aseptate-flagellate hair. *Liabum subacaule*. Coll. Liogier 11533 (GH).

IS *L. OBLANCEOLATUM* SIMILAR TO ANY *CHAPTALIA* SPECIES?

From the 15 species of *Chaptalia* from Hispaniola described by Liogier (1996), *C. tomentosa* Vent. should be excluded. *Chaptalia tomentosa* grows typically in the south-eastern USA, and does not reach the Caribbean. The specimens studied by Liogier under *C. tomentosa* (i.e. *Ekman 6305*, *11862* and *14181*) correspond to the types of *Chaptalia azuensis* Urb. & Ekman, which is cited by Liogier as a synonym of *C. tomentosa*. However, *C. azuensis* is a very different species found exclusively on Hispaniola. For the remaining 14 species, the types of all of them (Appendix 2) along with extensive additional specimens were analysed.

Table 1. Vegetative characters in *Liabum oblanceolatum*, West Indian species of *Liabum* and *Chaptalia*

Character	*L. oblanceolatum*	*Liabum*	*Chaptalia*
Habit	Acaulescent herbs	Caulescent herbs, sometimes acaulescent herbs	Acaulescent herbs
Leaf arrangement	Inconspicuous alternate and rosulate	Decussate and grouped or rosulate	Alternate and rosulate
Lamina shape	Obovate (oblanceolate)	Ovate	Elliptical, obovate (oblanceolate), ovate (lanceolate)
Leaf margin	Entire or slightly crenate, some mucronulate with several biseriate glandular hairs	Mucronate serrulate, serrate, or dentate, without biseriate glandular hairs	Lyrate, runcinate, crenate, or entire, some mucronulate with several biseriate glandular hairs
Leaf margin intrasection	Revolute	Planate	Planate or revolute
Leaf venation	Pinnate (eucamptodromous)	Slightly triplinerved (imperfect suprabasal acrodromous)	Pinnate (eucamptodromous) or uninervate (hyphodromous)
Leaf surface	Bullate	Smooth or bullate	Smooth or bullate
Leaf pubescence			
a. Upper surface	Glabrous, glabrescent or arachnoid	Glabrous, glabrescent or sometimes arachnoid, hirsute or strigose	Glabrous, glabrescent or arachnoid
b. Lower surface	Densely tomentose with coarse wavy hairs usually entangled	Densely tomentose with coiled or curly hairs usually interwoven	Densely tomentose with coarse, wavy or curly hairs usually entangled or interwoven
Leaves trichomes			
a. Clothing hairs	Oblique-septate-flagellate (Fig. 2A)	Aseptate-flagellate and bulbiferous flagellate (Fig. 2F–H)	Oblique-septate-flagellate (Fig. 2C)
b. Glandular hairs	Simple biseriate: head with thick walls (Fig. 2B)	Simple biseriate: head with thin walls (Fig. 2E)	Simple biseriate: head with thick walls (Fig. 2D)
Stomata	Anomocytic	Anomocytic	Anomocytic or anisocytic
Upper surface leaf cuticle	Striate (Fig. 3A,B)	Smooth (Fig. 3C,D)	Striate (Fig. 3E,F)

The analysis revealed that the type specimens of *L. oblanceolatum* are strikingly similar to the types and the additional material analysed of *Chaptalia angustata*. The specimens of both taxa share the following combination of characters: blades entire and oblanceolate, slightly crenate margin, conspicuously bullate surface, yellowish pubescence on lower surface. This set of features is not present in the other species of *Chaptalia*. Thus, *L. oblanceolatum* is proposed as a synonym of *C. angustata*.

Chaptalia angustata Urb., Symb. antill. 7: 432. 1912. Type: Dominican Republic. La Vega: 'prope Constanza, in pineto, 1250 m, ii.1910, *H. von Türckheim 2908*' (syntypes US!, F!, GH!, M!, MO!, SI! [fragment of B]; K, photo in GH!, LP!, MO!, SI!, US!). Dominican Republic: Santo Domingo, prope Maniel (*sic*) de Ocoa, 300 m alt., in declivibus saxosis, xi, *H. von Türckheim 3708* (syntype not located).

= *Liabum oblanceolatum* Urb. & Ekman, Ark. Bot. 23A: 89.1931 nov. syn. Type: Dominican Republic. La Vega: 'in scopulosis umbrosis Valle Nuevo ad ribulum, Cordillera Central, 2400 m, 17.x.1929, *E. L. Ekman H 13827*' (holotype S, photo in LP!; isotype GH!; isotype S, photo in LP!).

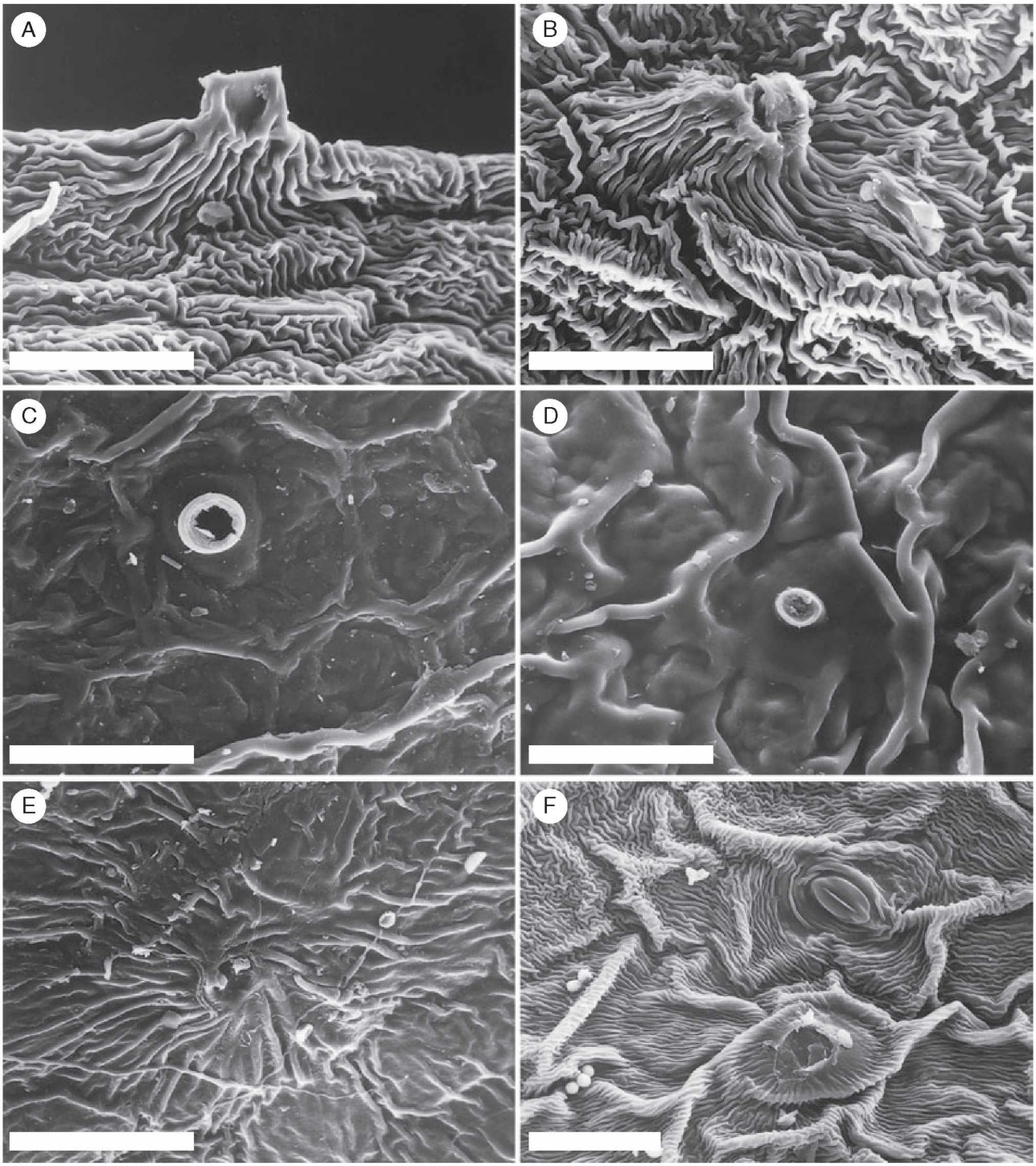

Figure 3. Upper surface leaf cuticle in *Chaptalia* and *Liabum*. Scale bars = 5 μm. A–B, striate cuticle. *Liabum oblanceolatum*. Coll. Ekman H 13827 (GH). C, smooth cuticle. *Liabum subacaule*. Coll. Liogier 11533 (GH). D, smooth cuticle. *Liabum umbellatum*. Coll. Crosby *et al*. 859 (F). E, striate cuticle. *Chaptalia angustata*. Coll. Türkheim 2908 (SI). F, striate cuticle. *Chaptalia nutans*. Coll. Jiménez 1101 (LP).

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APPENDIX 1

Vegetative trichomes in *Liabum oblanceolatum*, West Indian species of *Liabum*, and *Chaptalia*.

Chaptalia

Oblique-septate-flagellate hair (Fig. 2C). Foot: simple. Body: uniseriate. Stalk: 1(–3)-celled, cylindrical. Cells growing longer above, but the basal cell usually longer than broad or as long as broad. Cross walls thick. Head: usually 2-celled, tapering to a pointed tip. Cells longer than broad, usually basal cell slightly to strongly protruded. Cross walls oblique and thick. Location: mainly lower surface producing a tomentose pubescence, and sometimes on upper surface producing an arachnoid pubescence.

Simple biseriate glandular hair (Fig. 2D). Thick walls and distinct cells of the head. Foot: 2-celled. Body: biseriate, rarely 3-seriate. Stalk: 3–4-celled in each row. Inner and outer walls thick. Head: 1–2-celled in each row, demarcated from the stalk or continuous with it. Inner and outer walls thick. Location: margins, usually evident under stereo microscopy, and lower surface below clothing hairs.

Liabum

Aseptate-flagellate hair (Fig. 2G). Foot: simple. Body: uniseriate. Stalk: 1(–2)-celled, cylindrical or slightly tapering below. Cells usually longer than broad. Cross and lateral walls thin. Head: 1-celled, very long, coiled, flagellate, tubular, sharply delimited from the stalk remaining intact. Lateral wall thin. Swollen in basal sept, apex acute. Location: mainly lower surface producing a tomentose pubescence, and sometimes on upper surface producing an arachnoid pubescence.

Bulbiferous flagellate hair with simple foot (Fig. 2H). Foot: simple. Body: uniseriate. Stalk: 1–4-celled, cylindrical. Cells usually growing longer than broad. Terminal cells swollen, spherical or oblong in shape, collapsing early. Cross and lateral walls thin. Head: 1-celled, very long, coiled, tubular, flagellate, slightly narrower than the basal cells of the stalk, collapsing early or not collapsing. Basal and lateral walls thick, tapering above. Location: lower surface, usually on main veins.

Bulbiferous flagellate hair with compound foot (Fig. 2F). Foot: compound. Body: uniseriate to basally biseriate or multiseriate. Stalk: 1 to usually many cells, conical. Cells of various types, shape and lengths; usually basal cells isodiametric or slightly longer than broad, middle cells isodiametric tapering above, subterminal cells collapsing early. Cross and lateral walls thick. Terminal cells swollen, spherical or oblong in shape, collapsing early. Cross and lateral walls thin. Head: 1-celled, very long, coiled, tubular, flagellate, narrower than the basal cells of the stalk, collapsing early. Basal and lateral walls thick, tapering above. Location: upper surface, in some specimens producing a strigose or hirsute pubescence.

Simple biseriate glandular hair (Fig. 2E). Thin walls and no distinct or slightly distinct cells of the head like a vesicle. Foot: 1–2-celled. Body: biseriate. Stalk: 1–3-celled in each row. Inner and outer walls thin. Head: 1–2-celled in each row, demarcated from the stalk or continuous with it, and two terminal cells not distinct or slightly distinct like a vesicle. Inner and outer walls thin. Location: lower surface covered by clothing hairs.

Liabum oblanceolatum

Oblique-septate-flagellate hair (Fig. 2A). This type of hair and its location are the same as in *Chaptalia*.

Simple biseriate glandular hair (Fig. 2B). This type of glandular hair and its location are the same as in *Chaptalia*.

APPENDIX 2

Type specimens analysed of the species of *Chaptalia* found on Hispaniola.

Chaptalia albicans (Sw.) Vent. ex Steud., Nomencl. bot. ed. 2, 1: 344. 1840. ≡ *Tussilago albicans* Sw., Fl. Ind. occid. 3: 1348. 1806. Types: Jamaica. 'Habitat in Jamaica' (Lectotype LINN 953.16, microfiche 537, designated by Nesom, 1984).

Chaptalia angustata Urb., Symb. antill. 7: 432. 1912. Types: Dominican Republic. 'Prope Constanza, in pineto, 1250 m, ii.1910, *H. von Türckheim 2908*' (isosyntypes F!, GH!, M!, MO!, SI! [fragment of B]; K, photos in GH!, LP!, MO!, SI!, US!). Dominican Republic. 'Santo Domingo, prope Maniel (*sic*) de Ocoa, 300 m alt., in declivibus saxosis, xi, *H. von Türckheim 3708*' (syntype not located).

Chaptalia azuensis Urb. & Ekman, Ark. Bot. 23A (11): 95. 1931. Types: Dominican Republic. 'Cordillera Central, prov. de Azua, Loma Nalga de Maco, 16–1800 m, 9.vi.1926, *E. L. Ekman H 6305*' (isosyntypes US!; K, photo in LP!). Dominican Republic. 'Sierra de Ocoa, prov. de Azua, San José de Ocoa, Bejucal, in forest, steep slope, shaded place, *c.* 1300 m, 10.iii.1929, *E. L. Ekman H 11862*' (isosyntype GH!). Dominican Republic. 'Cordillera Central, prov. de La Vega, Jarabacoa, at the falls of Río Jimenoa, steep cliffs, *c.* 800 m, 18.xi.1929, *E. L. Ekman H 14181*' (isosyntype US!).

Chaptalia crispata Urb. & Ekman, Ark. Bot. 23A (11): 97. 1931. Types: Haiti. 'Massif de la Selle, Marigot, near Rivière Chotard, *c.* 1900 m, limestone rocks, 12.iv.1927, *E. L. Ekman 8004b*' (isosyntypes GH!, MO!).

Chaptalia dentata (L.) Cass., in F. Cuvier (ed.), Dict. sci. nat. 26: 104. 1823. ≡ *Tussilago dentata* L., Sp. pl. ed. 2: 1213. 1763. Types: Unknown country. 'Habitat in America' (Lectotype: iconography in Plumier. Pl. Amer. 2: tab. 40, fig. 2. 1755, designated by Nesom, 1984 as holotype).

Chaptalia denticellata Urb. & Ekman, Ark. Bot. 23A (11): 98. 1931. Types: Haiti. 'Massif de la Selle, Port au Prince, steep hillsides near Bassin-Laval, 250 m, 2.ii.1926, *E. L. Ekman H 5493*' (holotype S!; isotype GH!).

Chaptalia dolichopoda Urb. & Ekman, Ark. Bot. 23A (11): 99. 1931. Types: Haiti. 'Massif de la Selle, Croix-des-Bouquets, Badeau, ravine between Morne Mérillon and Morne Badeau, steep cliffs, *c.* 2000 m, 7.iii.1927, *E. L. Ekman 7796a*' (isotype GH!).

Chaptalia eggersii Urb., Symb. antill. 3: 418. 1903. Types: Dominican Republic. 'In graminosis juxta rivulum in Valle Nuevo, 2270 m alt., *H. F. A. Eggers 2220*' (isotype SI! [fragment of B: 'Haiti, Santo Domingo, *Eggers 2220*']).

Chaptalia flavicans Urb. & Ekman, Ark. Bot. 23A (11): 101. 1931. Types: Haiti. 'Massif de la Selle, gr. M. Commissaires, Gd. Gosier, Morne des Commissaires, *c.* 1450 m, 4.ix.1926, *E. L. Ekman H 6903*' (isotype US!).

Chaptalia latipes Urb. & Ekman, Ark. Bot. 23A (11): 99. 1931. Types: Haiti. 'Massif du Nord, Gros-Morne, Morne Belanse, open grassy and stony slopes, scarce, 1000 m, 26.ix.1925, *E. L. Ekman H 4921*' (holotype S!).

Chaptalia membranacea Urb., Symb. antill. 3: 418. 1903. Types: Dominican Republic. 'Prope Puerto Plata in saxis montis Loma Isabel de la Torre inter muscos humidos, 670 m alt., *H. F. A. Eggers 1582*' (isotype SI! [fragment of B: 'Haiti, Santo Domingo, *Eggers 1582*']).

Chaptalia mornicola Urb. & Ekman, Ark. Bot. 23A (11): 97. 1931. Types: Haiti. 'Massif de la Selle, Nouvelle Touraine, Chapelle Faure, in earth-slopes, 10.viii.1924, *E. L. Ekman H 1413*' (holotype S!).

Chaptalia nutans (L.) Pol., Linnaea 41: 582. 1877. ≡ *Tussilago nutans* L., Syst. nat. ed. 10, 2: 1214. 1759. Types: Unknown country. 'America' (Lectotype LINN 995.5 designated by Nesom, 1995).

Chaptalia pumila (Sw.) Urb., Symb. antill. 3: 420. 1903. ≡ *Tussilago pumila* Sw., Prodr. 113. 1788. Types: 'Jamaica, *Swartz*' (isotype M! 3455).