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Endemism and taxonomy of *Chaptalia* (Asteraceae) in the Caribbean. I. Introduction and morphology

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The Caribbean contains a system of islands east of Central America with a high number of endemic taxa. Some of those taxa, such as the genus *Chaptalia* (Asteraceae) are taxonomically complex. Thirty-one species of *Chaptalia* were described for the Caribbean, 28 of them supposedly being endemic. In this first part of the revision, we present the background and discuss the morphological characters of the various species and the endemism in the Caribbean Islands.

Introduction

Based on endemicity, massive habitat loss, and species' vulnerability to extinction, the Caribbean Islands is one of the ten insular biodiversity hotspots. Asteraceae genera endemic to this area represent well-known examples of plant radiation. When compared with other island systems worldwide, the Caribbean Islands have the highest number of endemic genera (Francisco-Ortega *et al*. 2008).

Although the genus *Chaptalia* (Asteraceae, Mutisieae) is not endemic to the Caribbean, it has been thought to harbor a high number of species in the archipelago. The plants are perennial, rosulate herbs with the unusual feature of having three different types of florets in the capitulum: female marginal florets with ligulate or bilabiate corollas (with minute inner lips), female intermediate florets with filiform corollas, and bisexual central florets with bilabiate or tubular-bilabiate corollas (Katinas 2004, Katinas *et al*. 2008). The taxonomy of the genus has been complex and problematic.

The number of species assigned to *Chaptalia* is uncertain, probably because of the balance between sexual and asexual reproduction. The sexual reproduction concerns the typical chasmogamous capitula and in some species cleistogamous capitula. Asexual reproduction in the floral region (apomixis) occurs in *Chaptalia* (Solbrig 1963), and also in the vegetative region by means of rhizomes. Other factors contributing to the taxonomic difficulty are hybridization among species and polyploidy (Burkart 1944).

The genus currently comprises ca. 65 species distributed in the Americas, from southern United States to central Argentina. However, the number of species should be reduced to 20–35 because many of the species (e.g., *C. anisobasis*, *C. estribensis*, *C. meridensis*) deviate from the generic concept mainly by the presence of staminodes (Katinas *et al*. 2008). In addition, there are some species complexes in the genus

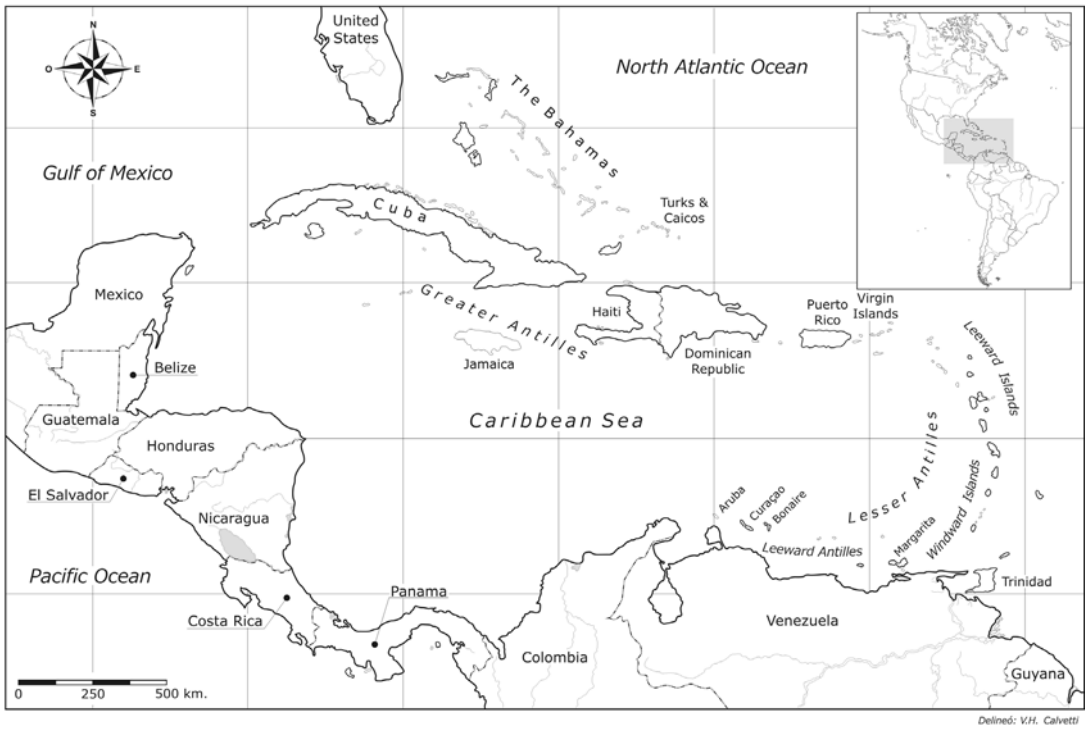

Fig. 1. Map of the Caribbean Islands showing the study area. It comprises the Antilles, with the Greater and the Lesser Antilles, and the Lucayan archipelago located north of the Antilles which comprises the Bahamas and the Turks and Caicos islands.

that are taxonomically unwieldy and require additional analysis. Such is the case with the Caribbean species with many specimens often difficult to identify to species because some of their characters are highly variable. Vegetative characters such as plant height, leaf size, shape, margin and indument, and fruit features were used to delineate the Caribbean species, but the reliability of such characters has not been evaluated.

The area considered in this study comprises a group of islands called in the past "West Indies", i.e., the Antilles and the Lucayan archipelago (Fig. 1), east of Central America. The Antilles are a group of islands located in the Caribbean Sea, traditionally divided into the Greater Antilles [Cuba, Hispaniola (Haiti and Dominican Republic), Jamaica, Puerto Rico, and Cayman Islands] and the Lesser Antilles located southeast of the former, comprising an arc of ca. 40 small islands including those located off the north coast of Venezuela (Fig. 2). The Lucayan archipelago is located north of the Antilles, in the North Atlantic Ocean, and comprises the Bahamas and the Turks and Caicos islands.

In all, 31 species of *Chaptalia* were described from the Caribbean (Table 1). Other than the original species descriptions, there have been some floristic studies involving *Chaptalia*, such as the floras of Bahamas (one species, Britton & Millspaugh 1920), Cuba (14 species, Liogier 1962), Haiti and Dominican Republic (nine species, Urban 1931; 14 species, Liogier 1996), Jamaica (three species, Moore & Rendle 1936, Adams 1972), Puerto Rico and adjacent islands (three species, Liogier 1997), and Trinidad and Tobago (one species, Cheesman *et al*. 1940). The relatively conservative floral structure across species in *Chaptalia* led the botanists to rely on other features to distinguish species. In some floristic studies, the species distinction is based mainly on leaf characters, and secondarily on floret and fruit size and pubescence (Appendix). There is, however, a high degree of polymorphism in the leaves. In addition, the key to the 14 species of *Chaptalia* accepted in

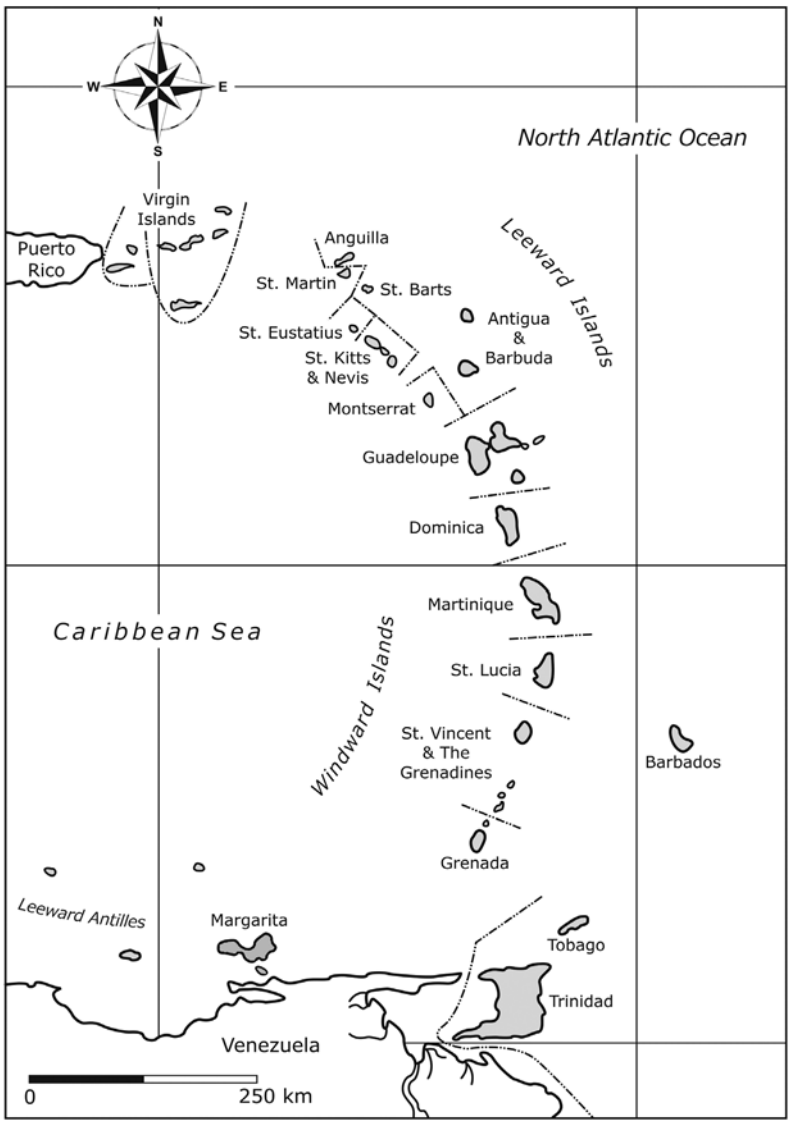

Fig. 2. Map of the Lesser Antilles, an arc of ca. small 40 islands at the southeast of the Greater Antilles, including those located off the north coast of Venezuela.

the *Flora of Hispaniola* (Liogier 1996), was developed using only the type specimens for most of the species. Our experience is that when other specimens are taken into consideration, species determination becomes difficult.

Some authors recognized morphological variation in Caribbean *Chaptalia* and synonymized many names. Britton and Millspaugh (1920), Moore and Rendle (1936), Burkart (1944), and Liogier (1962) considered *C. albicans* a synonym of *C. dentata*. On the other hand, Nesom (1984) considered the two species distinct by flower and fruit features. He included *C. primulacea* under the synonymy of *C. dentata*, and *C. crispula*, *C. fallax*, *C. leiocarpa* and *C. obovata* under *C. albicans*. Burkart (1944) included 23 Caribbean species in *Chaptalia* sect. *Microchaptalia* on the basis of reduced plant height and size of leaves and capitula. He placed the Caribbean *C. angustata*, *C. dentata*, *C. leiocarpa*, and *C. obovata* in his section *Lieberkhuna* suggesting that possibly *C. obovata* and *C. leiocarpa* might be taxonomic synonyms of *C. dentata*. Burkart (1944) commented that he did not analyze enough specimens to perform a profound study of the former group, and that

probably some Caribbean species might be reduced to synonymy. Burkart (1944) did not provide descriptions or illustrations for those species. Finally, Adams (1972), in his *Flora of Jamaica* found specimens of *C. pumila* intermediate between *C. dentata* and *C. crispata*.

We undertook the present study to elucidate the morphological variation within the Caribbean species of *Chaptalia* and to provide a workable species circumscription and classification. The second part of this revision (Katinas & Zavaro 2014) comprises the taxonomic treatment.

Material and methods

We conducted this study using type and non-type herbarium specimens, field observations, digital images, and photographs in herbaria (acronyms as in Holmgren *et al*. 1990). For microscopic examination, vegetative and reproductive parts were rehydrated, treated with a clearing process, stained with 2% safranin, and mounted on microscope slides. Plant organs were isolated and hand-cut transversely. We carried out observations and made drawings of the morphological and anatomical features on a Nikon Eclipse E200 light microscope equipped with a camera lucida.

Morphology

The Caribbean species of *Chaptalia* are

Table 1. Species of *Chaptalia* that have been originally described from the Antilles or mentioned to inhabit this area in floristic treatments. *Currently considered endemic to the Caribbean.

Species	Caribbean island mentioned in the protologue	Type of dubious location	Endemic to the Caribbean	Non-endemic to the Caribbean
C. albicans	Jamaica			X
C. angustata	Dominican Republic		X	
C. azuensis	Dominican Republic		X	
C. comptonioides	Cuba		X	
C. crassiuscula	Cuba		X	
C. crispata	Cuba		X	
C. dentata		"America"		X*
C. denticellata	Haiti		X	
C. dolichopoda	Cuba		X	
C. eggersii	Dominican Republic		X	
C. ekmanii	Cuba		X	
C. fallax	Cuba		X	
C. flavicans	Haiti		X	
C. latipes	Haiti		X	
C. leptophylla	Cuba		X	
C. media	Cuba		X	
C. membranacea	Dominican Republic		X	
C. montana	Cuba		X	
C. mornicola	Haiti		X	
C. nipensis	Cuba		X	
C. nutans		"America"		X
C. obovata	Cuba		X	
C. primulacea	Dominican Republic		X	
C. pumila	Jamaica		X	
C. rocana	Cuba		X	
C. shaferi	Cuba		X	
C. stenocephala	Cuba		X	
C. subcordata	"West Indies"		X	
C. turquinensis	Cuba		X	
C. undulata	Haiti		X	
C. vegaensis	Dominican Republic		X	

distinguished by a combination of characters, and some of those features differ only quantitatively. In the following text, we provide a description and discussion of the morphological characters with an emphasis on those that are useful for classification.

Vegetative characters

Height

Burkart (1944) considered plant height as one of the main features for establishing the Caribbean sect. *Microchaptalia*. The 23 species of this section were characterized as dwarf plants 6–28 cm tall, and the small size was considered to be due to an insular origin of these plants. The tendency of plants to become either smaller (dwarfism) or larger (gigantism) than in their mainland populations is a well-known feature of insular evolution (Filin & Ziv 2004). However, we emphasize that most of these populations grow on serpentine soils (*see* The Caribbean endemism, below), and the stature of serpentine-tolerant plants is usually significantly reduced relative to plants growing on non-serpentine soils (Brady *et al*. 2005). Since Burkart (1944) excluded from this section the Caribbean species *C. angustata*, *C. dentata*, *C. leiocarpa*, and *C. obovata* and included them in sect. *Lieberkhuna*, we explored if plant height has taxonomic value.

Our analysis of type specimens (Appendix) shows that some species of sect. *Microchaptalia* (*C. crassiuscula*, *C. nipensis*) exceed slightly the 28 cm height. The Cuban *C. turquinensis* which was described after Burkart's (1944) treatment is also taller, up to 31.5 cm. On the other hand, the height of the Caribbean *C. angustata*, *C. leiocarpa*, and *C. obovata* of sect. *Lieberkhuna* falls within the 6–28 cm range or is even less (*see* Appendix). The type of *C. dentata* was illustrated without scale or measurements in the original description; therefore, it is not possible to know the height of the type specimen. Despite the fact that there are dwarf specimens collected in Cuba, Jamaica, and to a lesser extent in the Dominican Republic, no gap in height from the smallest to the largest in our analysis of type and non-type specimens was found. Therefore, we consider that plant height has no taxonomic value within the Caribbean species of *Chaptalia*.

Leaves

Also the leaf features are highly variable and thus they were difficult to use for distinguishing species. Character states used to delimit the Caribbean species of *Chaptalia*, such as blade shape, size and margin (Fig. 3; *see* also Appendix) are continuous and overlapping, sometimes with variation within the same individual. For example, the type specimen of *C. leptophylla* (placed here under the synonymy of *C. dentata*) has the leaves pseudopetiolate and pinnatisect, or lyrate with many or few lateral lobes, or petiolate with an entire blade.

A typical lyrate leaf of *C. nutans*, with a well-developed upper lobe that is a very good character to distinguish this species from the mainland species of *Chaptalia*, overlaps with the leaf morphology of some Caribbean species, for example with *C. azuensis*, *C. flavicans*, *C. leptophylla*, *C. media*, *C. montana*, *C. rocana*, *C. shaferi* and *C. vegaensis*. Therefore, other features such as the type of cypsela pubescence, allow us to distinguish *C. nutans*.

Despite this leaf variation, the Dominican endemic *C. angustata* can be recognized by a unique combination of foliar characters: a long, narrowly oblanceolate blade, an acute apex, usually a retrorse-dentate and revolute margin, a coriaceous or sometimes bullate (with a puckered or blistered appearance) adaxial face of the blade, and a well demarcated nervation. A bullate adaxial surface is also present in leaves of *C. dentata*.

Leaf size changes in parallel with plant height, i.e., leaves are longer in taller plants and shorter in dwarf plants, and it does not allow us to separate species. The leaves of the type specimens of *C. crassiuscula*, for example, range from 9 to 29 cm; similar examples are the types of *C. crispata*, *C. flavicans*, *C. leptophylla*, *C. obovata*, *C. pumila*, and *C. stenocephala* (Appendix).

Finally, the color of the leaf indument is one of the features used to distinguish *C. albicans* (yellowish below) from *C. dentata* (white silvery

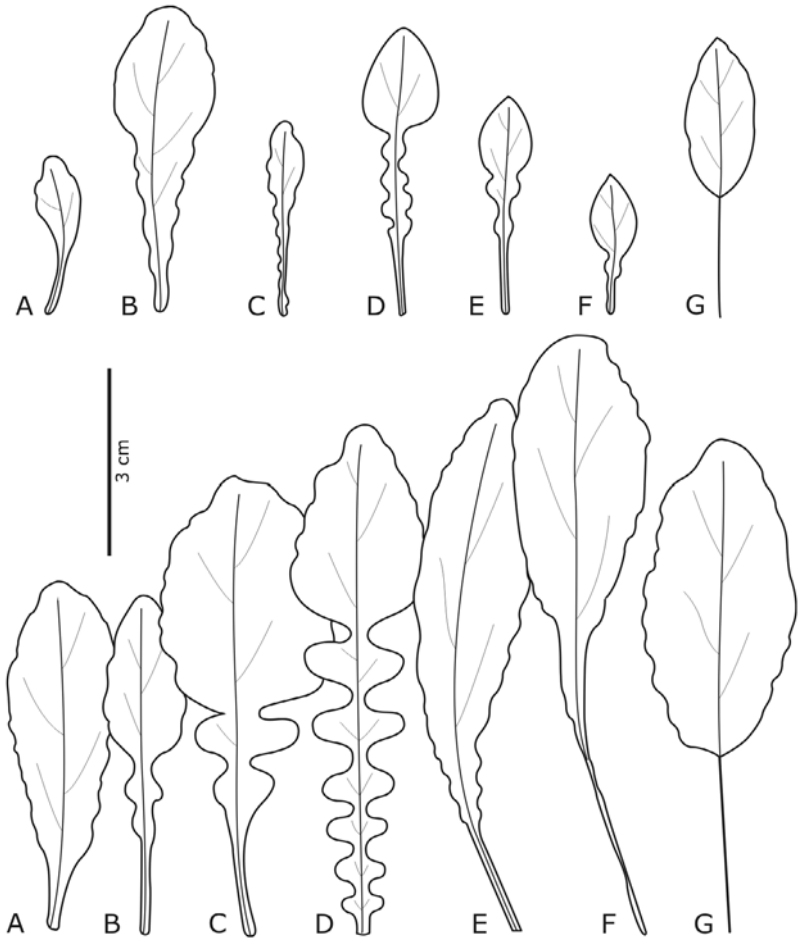

Fig. 3. Leaf variation in the Caribbean species of *Chaptalia*, drawn from type specimens. — First row: **A**: *C. denticellata* (*Ekman 5493*, S). — **B** and **C**: *C. stenocephala* (*Wright 2874*, MO). —**D** and **E**: *C. stenocephala* (without leg., SI). — **F** and **G**: *C. flavicans* (*Ekman 6903*, US). — Second row: **A**: *C. mornicola* (*Ekman 1413*, S). — **B**: *C. crispata* (*Ekman 8004a*, S). — **C**: *C. vegaensis* (*Ekman 11480*, S). — **D**: *C. media* (*Wright 332*, GH). — **E**: *C. angustata* (type of *Liabum oblanceolatum*, *Ekman 13827*, S). — **F**: *C. azuensis* (*Ekman 6305*, S). — **G**: *C. undulata* (*Ekman 4696*, S).

below) (Nesom 1984). Although in general this character allows separation, there are specimens of *C. dentata* with leaf pubescence that resembles *C. albicans* (*Britton & Millspaugh 2089*, F; *Leonard 3920*, GH; *Ekman 6874*, US) and vice versa (e.g., *van Hermann 857*, F; *Correll 50232*, MO, US; specimens from the Caribbean: *Henrich & Moreno 155*, MO; *Whiterfoord 2152*, MO; *Steyermark 31723, 51771*, F). In addition, the type specimens of *C. stenocephala* and *C. shaferi* have both types of leaf pubescence color.

Scape

Among the vegetative characters of *Chaptalia*, the scape is interesting. In some species the scape has approximately the same width from the base to its insertion to the receptaculum, whereas in other species it is widened in its distal part just below the capitulum. This trait is useful to separate some species, including the Caribbean *C. albicans* and *C. dentata*, although it is difficult to see in dwarf specimens. *Chaptalia angustata* is the only species in which this character varies.

Reproductive characters

Some reproductive characters used by authors in the past, such as capitulum and involucre size, phyllaries, and cypsela length, have a wide a morphological range without gaps to be useful for separating species (Appendix). On the other hand, the type of cypsela trichomes

and, to a lesser degree, the number of florets per capitulum are useful characters to separate some Caribbean *Chaptalia*.

Number of florets

The number of florets per capitulum, a character that is correlated with the capitulum size, is variable. In dwarf specimens, with capitula as small as 5–7 × 5–9 mm, there are 14–20 florets per head. Despite the fact that bigger capitula have 40–80 florets, there is no gap among specimens regarding the floret number. The type specimens of *C. flavicans* and *C. pumila*, for example, have capitula with 15–30 florets. *Chaptalia nutans* with ca. 165 florets per capitulum is the only species that may be distinguished by the floret number.

Cypselae

The cypselae of the Caribbean species of *Chaptalia* are cylindrical to elliptic, with a long and thin (filiform) rostrum usually longer than the seminal portion of the fruit. The cypsela is pubescent in all species and the type of pubescence is quite a good character to separate some Caribbean species. Three types of hairs occur (Fig. 4):

1. Short twin hairs (Fig. 4A): Twin hairs or *Zwillingshaare* (Hess 1938) are the typical fruit hairs in Asteraceae. They are basically formed of two triangular or rectangular, short, basal cells (one sometimes reduced), and two elongated, cylindrical hair cells, with thick walls, usually completely united with each other along their longitudinal walls. From this basic type a wide diversity exists (Freire & Katinas 1995). Short twin hairs are up to 30 μm long and have two rounded hair cells, obtuse at the apex. This type is exclusive of *C. nutans*.
2. Longer twin hairs (Fig. 4B–D): These are similar to the shorter ones but 70–145 μm long, with two cylindrical or elliptical hair cells, obtuse or acute at the apex. They are elliptical (Fig. 4B and C) or cylindrical (Fig. 4D). This type of hair is present in all fruits of the Caribbean species excepting *C. nutans* and *C. albicans*. A modification of these twin hairs are the "crenate hairs" (Freire & Katinas 1995) of *C. angustata*. These hairs have three or four cylindrical hair cells, sometimes septate, united with each other along their longitudinal walls.
3. Biseriate glandular hairs (Fig. 4E and F): These are cylindrical and have a biseriate body, with 3–8 cells in each row. This type is found in all the Caribbean species mixed with the other types, but *C. albicans* has exclusively glandular hairs in its fruits (Fig. 4F).

These descriptions correspond to observations under the light microscope. However, during specimen determination this character, although taxonomically very valuable, might be impractical. Under stereomicroscope observation: (a) the short twin hairs of *C. nutans* give the cypselae a papillose appearance, (b) the cypselae with longer twin hairs have a hispid or setuliferous aspect, and (c) the cypselae of *C. albicans*, with exclusively glandular hairs, seem almost glabrous at first sight but a careful observation reveals minute trichomes that give a dotted appearance to the fruits. If there is confusion between the small hairs of *C. nutans* and *C. albicans*, then the difference in the shape of the leaves and number of florets per capitulum allows separation.

The Caribbean endemism

Oceanic archipelagoes in general have endemic genera with a relatively high number of species that exploit different ecosystems (Acevedo-Rodríguez & Strong 2008, Maunder *et al.* 2011). The Caribbean islands have approximately 775 native species of Asteraceae with ca. 590 of them endemic to the islands. Most of the Caribbean Asteraceae endemic species belong to non-endemic genera, and some of them are regarded as having a relatively high number of species in the archipelago, such as *Chaptalia*, *Erigeron*, *Koanophyllum* and *Mikania* (Francisco-Ortega *et al.* 2008). Some taxa, however, constitute

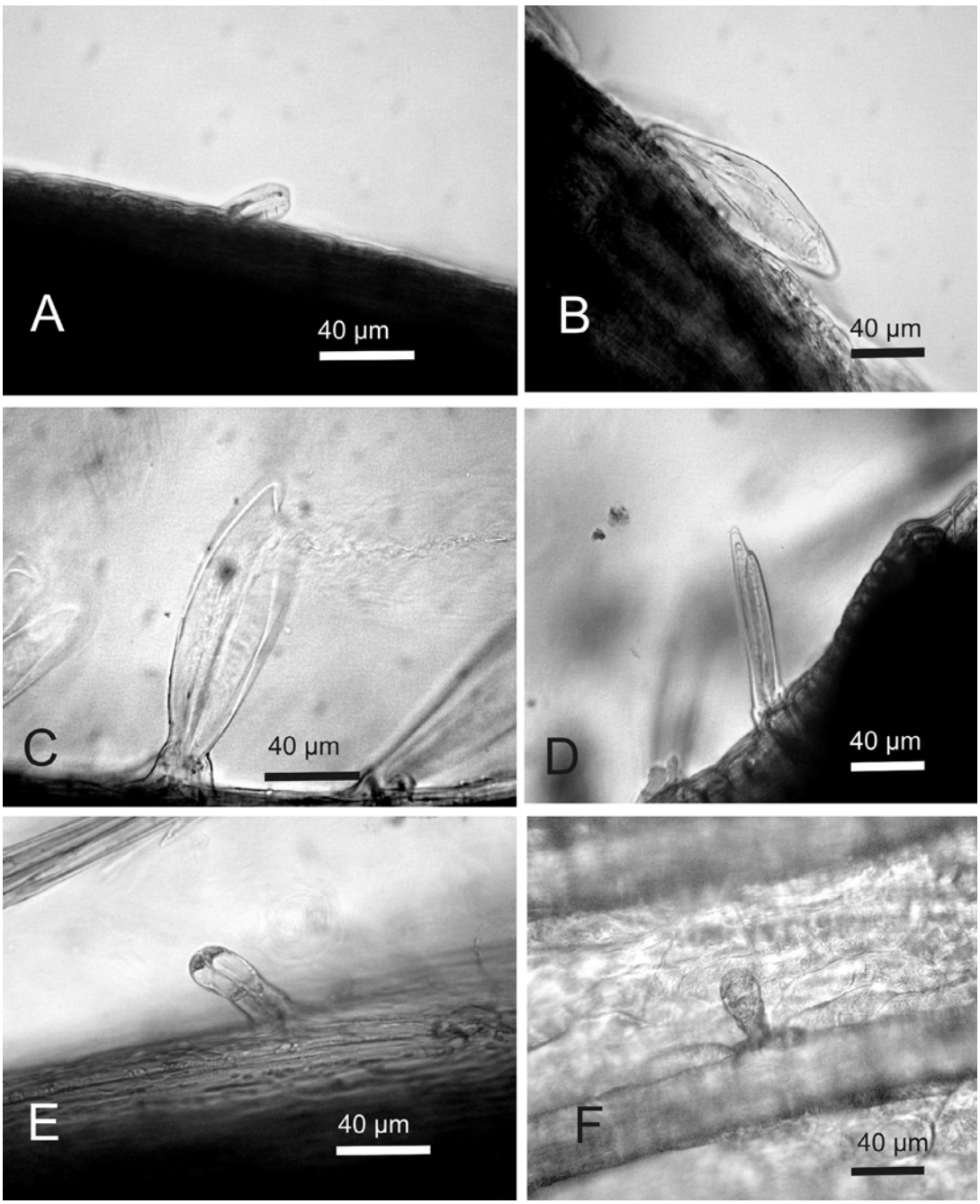

Fig. 4. Cypsela hairs in the Caribbean species of *Chaptalia* (**A** from *Wasum 2072*, WIS; **B** from *Wright 332*, MO; **C**–**E** from *von Türckheim 2908*, MO; **E** from *Wright s.n.*, MO). — **A**: Short twin hairs in *C. nutans*. — **B**–**D**: Longer twin hairs. — **B**: Elliptical twin hair in *C. dentata*. — **C**: Elliptical twin hair in *C. angustata*, releasing mucilage through hair apex. — **D**: Cylindrical twin hair in *C. angustata*. — **E**: Glandular hair in *C. angustata*. — **F**: Glandular hair in *C. albicans*.

morphological complexes with highly variable characters in which morphological gaps among species are not always very evident. With the advance of the taxonomic studies, the species

or variety numbers in some genera have decreased. Examples are *Liabum* (Asteraceae) with a supposed ca. 12 Caribbean species that were reduced to one by Gutiérrez and Katinas (2014). *Ernodea* (Rubiaceae) with nine species reduced to four (Negron-Ortiz & Hickey 1996), and *Vernonia* (Asteraceae) with a single, highly polymorphic species from the West Indies and Central and South America (Keeley 1982).

Most of the 31 species of *Chaptalia* described for the Caribbean are very close morphologically. The variable and particular habitats of the islands caused speciation and phenotypic plasticity that probably yielded this variation. Perhaps reproductive biology played a major role in the success of this species complex and in determining its polymorphism. The balance that many species of *Chaptalia* maintain between inbreeding and outbreeding is of major importance. Inbreeding allows seed formation even when there is only a single individual or genotype present. Also, it may help to fix a genotype that is successful by retaining the gene combination. Outbreeding, on the other hand, maintains a large gene pool and ensures that a wide range of genotypes is constantly exposed to selection. This enables the species to compete and adapt in a changing environment and to exploit new opportunities when they arise (Chinnappa & Morton 1984). Polyploidy, which is common in *Chaptalia*, also permits the formation of new genomes. In addition to a plastic genotype, phenotypic plasticity is a means of rapid adaptation of individuals and does not require immediate change of the genic composition of the population brought about by processes of reproduction and selection. To explain some local endemics in islands, the focus has changed from an emphasis on evolution in isolation to an understanding of the ecological determinants of the endemism. Edaphic specialization in locally endemic populations could well be the main reason for the endemism and great morphological variability in the Caribbean.

In Cuba, for example, 15 species of *Chaptalia* were regarded as local endemics. Examples are *C. ekmanii* from the pinelands of Cajálbana in western Cuba, *C. nipensis* from Sierra de Nipe in eastern Cuba, and *C. turquinensis* from Pico Turquino of Sierra Maestra in eastern Cuba. Most of the populations grow in specialized soils such as ferralitic (highly weathered and rich in iron and aluminum), serpentine or ultramafic (rich in magnesium and heavy metals and poor in macronutrients such as calcium), and "charrascales" (soils with very low fertility). Areas with serpentine soils are distributed along a longitudinal axis of the island, are patchily distributed, and are considered to have the highest number of endemics in Cuba (Berazaín 1997, Vázquez-Glaría *et al*. 2006). Ecotypic variation in plant populations is frequent where soil characteristics and water availability vary abruptly over short spatial scales. Studies performed in Asteraceae (Sambatti & Rice 2006) showed that local adaptation of serpentine ecotypes is evident despite the presence of a strong gene flow between populations. Cooke (1994) identified several traits in serpentine-tolerant races of *Achillea* and *Senecio* (Asteraceae) as pivotal to surviving on serpentine soils. In addition to physiological tolerance, Cooke found that the plants have a slower growth rate than non-serpentine species and they possess morphologies adapted to drought conditions. Populations of *Chaptalia* growing on specialized soils may be frequently differentiated from other populations, for instance by the low height of the plants or by leaf features, such as a bullate aspect of the adaxial face of leaves. However, when such populations are analyzed in the context of a relatively high number of specimens from Cuba and from other Caribbean islands, the alleged morphological gaps disappear.

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Appendix. Species characters taken from the original descriptions and used to distinguish Caribbean species of *Chaptalia* in floristic studies of the Caribbean or in taxonomic studies. In brackets: personal observations of type specimens when data is lacking in the original descriptions. * The type specimen lacks capitula.

Species	Plant height	Leaf shape, size and margin	Capitulum (C) or involucre (I) size and other features	Phyllaries	Cypsela length	Cypsela rostrum	Cypsela pubescence
C. albicans	18 cm	lanceolate to lanceolate ovate, [4–6 cm long]; retrorse- serrate	[C: 20 mm]	linear, acute	no data	no data	no data
C. angustata	10–22 cm	narrowly lanceolate to-lanceolate-linear, 6–10 cm long; lobulate-crenate	C: 15–17 mm	narrowly linear, acuminate, purplish, araneose	[4 mm]	(young) short	densely papillose
C. azuensis	16–26 cm	oblong to oblanceolate, 4–15 cm long; apically entire and basally lobate	C: 11 mm	linear, acute, green	3.3–3.7 mm	shorter than seminal part	shortly pilose
C. comptonioides	21 cm or less	spathulate-oblanceolate, 3–15 cm long; deeply	I: 9–11 mm	linear, acute, white-tomentulose	[5 mm]	as long as seminal part	minutely hispidulous pinnatifid
C. crassiuscula	9–29 cm	elliptic to oblong, 2–5 cm long; lobulate at base	C: 12 mm	linear, green, araneose	4–4.5 mm	shorter than seminal part	shortly papillose-pilose
C. crispata	11–26 cm	elliptic, oblong to obovate, 2–7 cm long; apically denticulate and basally lobate	C (young): 10 mm	linear, acuminate, tomentose, purplish	no data	[shorter than seminal part]	[papillose]
C. dentata (iconography)	no data [not dwarf]	lanceolate; emarginate dentate	no data	no data	no data	no data	no data
C. denticellata	21–28.5 cm	lanceolate to elliptic, 3–7 cm long; denticulate	C: 15 mm	linear, acuminate, tomentulose, green	2.5–3.5 mm	very short	papillose
**C. dolichopoda*	ca. 15 cm	narrowly ovate to elliptic-oblong, petiolate 2–6 cm long; denticulate to undulate- or retrorse-crenate	no data	acute, basally tomentose, purplish	no data	no data	no data
**C. eggersii*	8–16.5 cm	ovate, elliptic to obovate-elliptic, petiolate, 1–2.5 cm; entire	C: 10–12 mm	linear, acuminate, green and purplish, araneose	no data	very short glabrous	(immature)
C. ekmanii	21.5–26.5 cm	narrowly obovate to obovate-oblong, 2.5–6 cm long; entire to undulate-crenate	C: 15 mm	linear, acute to acuminate, araneose	6.5–7.5 mm	as long as the seminal part	shortly pilose

C. fallax	22–27 cm	oblanceolate to somewhat spathulate, 5–10 cm long; entire or faintly undulate or obscurely crenate	[C: 18 mm]	narrowly subulate, subulate-linear	5.5 mm]	no data	no data
C. flavicans	11–21 cm	ovate to elliptic, 1–3 cm long; entire to lobulate	C: 12 mm	linear, acute, tomentulose, green	3.5–5 mm	shorter than seminal part	shortly and sparcely pilose
C. latipes	11–14 cm	obovate, 2–3 cm long; denticulate	C: 10 mm	linear, acuminate, green, tomentulose	(young) 3 mm	very short	shortly papillose
C. leiocarpa	[3.5 cm]	oblong-lanceolate, 3.75–7.5 cm long, sub-entire	[C: 9–17 mm]	linear, subulate	[8 mm]	one third shorter than seminal part	glabrous
C. leptophylla	4.8–12.8 cm	terminal lobe ovate, 1–2 cm long; lobulate	C: 8 mm	linear, acute, green, subglabrous	3.5 mm	almost as long as seminal part	shortly and sparcely papillose
C. media	[14–27 cm]	terminal segment oblong, [5.5–16.5 cm long]; lyrate	I: 8.5 mm	linear, acute	[1.5 mm]	very short	[hispidulous-papillose]
C. membranacea	16.2 cm	elliptic to elliptic-oblong, 4–7 cm long; retrorse-denticulate	C: 120 mm	linear, purplish at apex, araneose	2–2.3 mm	as long as seminal part	shortly pilose
C. montana	16–26 cm	oblanceolate-spathulate, 4–7 cm long; lyrate-pinnatifid	I: 7 mm	linear, acuminate, lanate	5.5–6 mm	longer than seminal part	no data
C. mornicola	11.3–19.3 cm	obovate to oblong, 3–7 cm long; dentate at apex,undulate to lobate at base	C: 13 mm	linear, acuminate, purplish, tomentulose	(young) 5 mm	longer than seminal part	sparsely papillose
C. nipensis	31 cm	obovate-elliptic to oblong, 3–5 cm long; retrorse denticulate, rarely lobulated at base	C: 10 mm	linear, green, something villose at base	[2.5 mm]	(young) short	shortly pilose
C. nutans	[broken specimen]	[obovate; 17 cm long]; lyrate	[C: 12 mm]	no data	no data	no data	no data
C. obovata	[5.5–13 cm]	obovate to spathulate-oblong, [3–6 cm]; undulate to retrorse-dentate	[C: 11–15 mm]	linear-lanceolate, acute	[2–2.4]	[shorter than seminal part]	pilose
C. primulacea	13.5–21.5 cm	narrowly oblanceolate, 7.5–15 cm long; repand-crenate	[C: 12.5–14 mm]	subulate to linear, flocculent	[5–5.5 mm]	nearly as long	scabrous seminal part

continued

Appendix. Continued.

Species	Plant height	Leaf shape, size and margin	Capitulum (C) or involucre (I) size and other features	Phyllaries	Cypsela length	Cypsela rostrum	Cypsela pubescence
C. pumila	[8–16 cm]	[obovate to oblanceolate, 1–3 cm long]; lyrate, incise-denticulate	[6–10 mm]	[linear-oblong, green, tomentose]	[4.5 mm]	no data	no data
**C. rocana*	6–11 cm	spathulate-oblanceolate, 15 cm long; repand-pinnatifid, crenate	I: 6–7 mm	linear, acuminate, glabrate	no data	(young) less than 1/4 long of seminal part	minutely hispidulous
C. shaferi	20 cm	[oblanceolate to obovate, 2–6 cm long]; lyrate, lyrate-pinnatifid	I: 5 mm	linear, acute, glabrous	[2.5 mm]	half as long as seminal part	minutely hispidulous
C. stenocephala	[4–14.5 cm]	terminal segment elliptic, [2–6 cm long]; lyrate	[C: 10 mm]	linear, acute	[7.5 mm]	as long as seminal part or slightly longer	[minutely hispidulous]
C. subcordata	ca. 50 cm	large subcordate-oval terminal part, 12.5–20 cm long; lyrate	[C: 26 mm]	[linear, acute, tomentose, purplish]	[7.8 mm]	(young) short	no data
C. turquinensis	16.2–31.5 cm	oblong-oblanceolate to oblong-obovate, 5-11 cm long; undulate to crenulate-denticulate at apex, lobate at base	C: 12–15 mm	linear-lanceolate, acuminate to subulate, araneose	(young) 3 mm	as long as seminal part	glabrous to glabrescent
C. undulata	21 cm	narrowly ovate to elliptic, 3.5-6 cm long; undulate-crenate	I: 8 mm	narrowly linear, acute, tomentulose, purplish	3 mm	almost as long as seminal part	glabrous
C. vegaensis	16–26 cm	narrowly to widely ovate, 2.5–4 cm long;	C: 10 mm	Linear, slightly obtuse, green,	3.5–5 mm	shorter than seminal part	pilose lobulate, lobes scarcely tomentose, undulate-crenate