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Authors: Greuter, Werner, and Rodríguez, Rosa Rankin

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WERNER GREUTER[1*] & ROSA RANKIN RODRÍGUEZ[2]

# Revision of the Caribbean endemics currently placed in *Nashia* (*Verbenaceae*)

**Abstract:** The seven species currently placed in the genus *Nashia* are revised, based on the near totality of the (scant) material found in the world's herbaria. A morphological analysis of, in particular, the calyx and fruit reveals the heterogeneity of that genus. As a result, *Nashia* is reduced to its single original species, *N. inaguensis*, described from Great Inagua, Bahamas (where it is here considered to have been introduced by man), and recently found on Puerto Rico and the Virgin Islands (St Croix). *Nashia spinifera*, of Hispaniola, is placed in *Isidroa*, a monotypic new genus. The five Cuban endemics, plus two newly described here, make up the new genus *Diphyllocalyx*, formerly *Lippia* sect. *Diphyllocalyx* of Grisebach. The formal treatment of all nine taxa comprises synonymy, type citation, detailed descriptions, specimen citation, distribution maps, and a key for identification. Possible evolutionary scenarios as well as conservation status are discussed.

**Key words:** Bahamas, Caribbean, Cuba, *Diphyllocalyx*, fruit morphology, Hispaniola, *Isidroa*, key, *Lantana*, *Lippia*, monograph, *Nashia*, new genus, Puerto Rico, *Verbenaceae*, Virgin Islands

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## Introduction

The genus *Nashia* as currently understood belongs to *Verbenaceae* sensu stricto; it is confined to the Caribbean islands and consists of only seven species. They are all very rare, each known from a single, or a few widely scattered, localities. In the first part of this paper, the name *Nashia* is used for that genus, our own assessment notwithstanding.

The first *Nashia* species to be discovered was described by Grisebach (1866) in the genus *Lippia* L., as *L. myrtifolia*, but was considered sufficiently distinctive to be placed in a newly described, monotypic section, *L.* sect. *Diphyllocalyx*. Millspaugh (1906) used the second species to become known, *N. inaguensis*, as the basis and single member of his new genus *Nashia*. Urban (1912) challenged the distinctness of *Nashia* and reduced it to synonymy under *Lippia*. Having, he believed, demonstrated his point conclusively, he (Urban 1922) castigated Britton (1915) for nevertheless describing in *Nashia* the third species detected, *N. cayensis*. Accordingly, Urban (1922, 1924) described species numbers four to seven in *Lippia*, but even though no one undertook to dispute his rationale, he eventually lost the contest. Moldenke (1941), without comment, transferred the species described under *Lippia* to *Nashia*. Later he (Moldenke 1980) explained: "I feel that this small group of extremely closely related taxa are so manifestly distinct from those of the very large and variable genus *Lippia* that they deserve generic rank". No one protested, and *Nashia* to date stands unchallenged.

When Moldenke (1980) wrote his "Notes" – a surrogate for the planned monograph that never materialized –

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[1] Botanischer Garten und Botanisches Museum Berlin, Freie Universität Berlin, Königin-Luise-Str. 6–8, 14195 Berlin, Germany; *e-mail: w.greuter@bgbm.org (author for correspondence).
[2] Jardín Botánico Nacional, Universidad de la Habana, carretera "El Rocío", km 3.5, Calabazar, Boyeros, La Habana, Cuba; e-mail: rosarankin@fbio.uh.cu

the known species of *Nashia* were still seven in number, each known from a single locality and natural population, and five of them collected only once. Since then, twelve additional localities of *Nashia* have been discovered, ten of which were accounted for by Méndez (2003), Peguero & al. (2001), or Cedeño & O'Reilly (1996). The newest and last was spotted by the two of us in May 2015. By the initial difficulties we had in placing it correctly, it triggered our interest in *Nashia*. We found enough new data and old contradictions to warrant the present revision.

## Material and methods

The present monographic revision is based on the study of herbarium material with the aid of a binocular dissecting microscope Wild M5A at up to 100× magnification. Inflorescences, flowers and fruits were soaked in tap water and boiled to be mollified. Specimens were studied at, or obtained on loan from, the following herbaria (abbreviated in conformity with Thiers 2015+): B, GH, GOET, HAC, HAJB, HAJU, HIPC, JE, NY, PAL-Gr, S and US. From JBSD and K we obtained photographs of whole specimens and close-up views of details. Digital images available via the Internet were also studied: they included additional material from F, G, GH, P and YU. The sample at our disposal included specimens (mostly physical) from every single known population, but flowers and/or fruits were not available in all cases. Some of the species are but incompletely known to date.

## Features, delimitation and affinities of *Nashia*

In his seminal revision of the *Verbenaceae* (sensu lato), Briquet (1895) failed to mention *Lippia* sect. *Diphyllocalyx* and *L. myrtifolia*, the only *Nashia* species then known – a surprising omission when one considers Briquet's legendary thoroughness plus the fact that specimens were present at Geneva in the Candolle and Boissier herbaria (both still in private hands at the time). The most likely explanation is that Briquet did not know where to place that plant, as its fruit was (and is) unknown and the calyx features do not match any of the subdivisions of *Lippia* recognized by him. When *Nashia* was published, Pilger & Krause (1915) placed it between *Lantana* L. and *Lippia*, in tribe *Lantaneae*, a position it still holds to date. The placement of *Nashia* among the core genera of the tribe *Lantaneae*, as amended by Briquet (1895) to include *Lippieae*, has been confirmed by subsequent studies of gynaecium anatomy (Junell 1934). It is consistent with pollen morphology (Raj 1983) and has been upheld by Atkins (2004) in her recent family survey. Recent studies of the classification of the family, using DNA sequence data (Marx & al. 2010; O'Leary & al. 2012), corroborate this position.

The following is an overview of the taxonomically important features encountered in *Nashia*, their variation, and, mostly based on a study of the literature, their comparison with those found in the most closely related genera, *Lippia* and *Lantana*.

*Habit* — All species are shrubby, and most are spiny. Presence or absence of spines has been used as a principal key feature for species by Moldenke (1980) and Méndez (2003), but – apart from the fact that both keys are flawed – it is not such a clear-cut character as one might believe. The only unequivocally spineless species is in fact *Nashia inaguensis.* A second species, *N. nipensis*, does not form true spines but has hardening side branches, which toward the tip are usually fragile and break off, but may on occasion become subspinescent. The type specimen of *N. cayensis* has only a few inconspicuous, minute axillary spines, not mentioned in the original description, but spines can be seen on the duplicates, and plants from two nearby localities are decidedly if sparingly spiny.

In two species, *Nashia myrtifolia* and *N. spinifera*, the spines, when present, all arise as short axillary branches with 0 or 1(or 2) leaf pairs, of similar length and ± evenly distributed along the twigs, which are not themselves spiny and have been described as virgate. In the other pungent species side branches of varying length terminate in spines, and major branches may again be spiny, the branching pattern being ± pyramidal.

According to label and literature data (Méndez 2003), *Nashia* shrubs are aromatic. Millspaugh (1906) compared the smell of *N. inaguensis* to that of "citronelle" (presumably lemon verbena, *Aloysia citrodora* Paláu) and mentioned that it is used for brewing a medicinal tea.

*Indumentum* — The hairs are unicellular and unbranched, and are of two types. Those of the upper leaf surface, termed bristles hereafter, are stiff, straight or forward-curved, conspicuously widened toward the base. When well developed, they arise from the centre of a crown of specialized cells, most often eight, which when mature are ± bulging and usually become white or whitish. They can be observed in all *Nashia* species (and with varying frequency in many other *Lantaneae* genera, e.g. *Lantana*: see Méndez 1998: fig. 4H, J, L). It is not equally pronounced in all species, nor in all seasons and developmental stages. The nature and function of these "pedestal cells" is unknown to us, but might be secretory rather than mechanical. The pedestal may be bulging or flat and may extend to cells outside the initial circle to form roughly circular white blotches that, when as pronounced as in *N. nipensis*, have at times (Moldenke 1980; Méndez 1998) been misinterpreted as "scales" – which they are definitely not.

Hairs on the lower leaf surface (and along the midvein above), petiole, axes, and flower parts are slender, short, ± straight or more often forward-curved, at times forming a half-circle. They may be so dense as to obscure the surface, or sparse, and in some species (*Nashia myrtifolia*, *N. nipensis*, *N. spinifera*) they may be absent from the abaxial leaf surface. Similar hairs also exist in other *Lantaneae* genera, e.g. *Lantana* (see Méndez 1998: fig. 4F, I, K).

Sessile, globular, shiny yellow glands occur in all species. They are particularly numerous on the abaxial leaf surface, axes, and dorsally on corolla lobes. In the three species with glabrous lower leaf surface they are sparser and perhaps slightly smaller than in the others, and in *Nashia spinifera* they appear to be ephemeral and, on the abaxial leaf epidermis, partly sunk in depressions.

*Leaves* — The leaves are opposite (whorls of three are seen occasionally, e.g. in some specimens of *Nashia myrtifolia*), shortly petiolate to subsessile, rather firm, and relatively small. The lamina is ovate to elliptical or lanceolate, rarely obovate, with entire or sparsely and shallowly crenate margin – a feature that, in some taxa or even populations, may be quite variable. The margin is ± strongly revolute in some species (*N. armata*, *N. inaguensis*, *N. nipensis*), flat to narrowly recurved in others. In *N. inaguensis* the leaf tip is characteristically downward-curved so that the leaf, consistently acute, often appears blunt when seen from above.

Venation, at least the midvein, is sunk adaxially and raised abaxially. The lateral veins are few in number, mostly in 3–6 pairs, and may be scarcely visible, as are the veins of higher order (with the notable exception of a population in W Cuba).

*Inflorescence* — As in all true *Verbenaceae*, the inflorescence in *Nashia* is of the racemose type. Using Troll's (1964, 1969) terminology, the "synflorescences" are "homothetic pleiobotrya", meaning that all "florescences" arise laterally in the leaf axils – which is the normal condition in *Lantaneae* (Múlgura & al. 1998, 2002; O'Leary & al. 2012). The flowers are sessile or almost so and arranged in either of two patterns. In *Nashia inaguensis* and *N. spinifera* they form few-flowered, sessile glomerules of definite growth, ending in a bud-like cluster of minute, sterile bracts; the lower floriferous bracts are either early deciduous (in *N. inaguensis*) or rather inconspicuous (in *N. spinifera*). In the other species the inflorescence (when known) is a shortly pedunculate, dense spike, initially hemispherical but elongating as anthesis and maturation proceed, to become globose then cylindrical, with densely packed, long persistent, ± tetrastichous, broadly ovate or suborbicular to obovate-spatulate, herbaceous bracts. In these species, inflorescence size – which has sometimes been used as a diagnostic criterion – is largely an expression of the phenological state of the plant, inflorescence development being apparently stopped by summer drought, which, if setting in early, may leave no time for fruits to develop, or only permits a few scattered fruits to mature in an otherwise barren spike.

*Calyx* — Calyx features are of prime importance for generic and sectional classification in *Lantaneae.* One of the reasons that led Urban (1912) to sink *Nashia* was that, contrary to Millspaugh's original description of a reduced, ring-like calyx, he had observed two free, ± linear lateral sepals in *N. inaguensis*.

It so happens that both authors were partly right. As observed by Urban, two minute, membranous, early deciduous sepals are sometimes present on either side of the *Nashia inaguensis* flower, but they are often unequally developed, and mostly one or both are lacking. The ring-like structure observed by Millspaugh does not pertain to the calyx: it was either (more likely) the prominent, long and densely ciliate rim on the outside of the scar left by the bract, thus belonging to the inflorescence axis; or else, the margin of the disk, inside the corolla. When the sepals are absent or have been shed, the place of the calyx is held by a crown of short hairs at the corolla base, usually hidden beneath the disk.

The calyx of *Nashia spinifera* is very different. It is a subtruncate, shallowly bilobate, ovoid structure encircling the corolla, membranous at the base but foliaceous distally, which enlarges markedly as the fruit develops, being distended by it and enveloping it completely except for a small area at the tip. Each of the shallow, laterally placed calyx lobes has two well-spaced, parallel veins, whereas no ventral or dorsal vein is developed. Similar calyces have been described for representatives of *Lippia*.

The other species of *Nashia* (all Cuban representatives of which the flowers are known, except *N. armata* in which there is no trace of a calyx) have a calyx consisting of two linear to narrowly spatulate, free sepals, emulating bracteoles by their aspect and position. Considering these structures as sepals rather than bracteoles is in line with their past interpretation in the literature, and is consistent with the fact that in no case were two different organs (bracteoles and sepals) seen to be present simultaneously. The presence of bracteoles in *Verbenaceae* is mentioned occasionally, e.g. by Briquet (1895) where it mostly refers to genera now placed in *Labiatae*; few genuine examples are known in *Verbenaceae* sensu stricto – one such exception being *Bouchea* Cham. (Troncoso 1974: 348, fig. 13). Use of the term bracteoles, or "bractlets", in describing *Lantaneae* species is widespread in the work of Alain (1957, 1994) and Moldenke (e.g. 1980) but is an error for bracts.

Urban (1912) considered a calyx of two free, narrow, laterally placed sepals to be the normal condition in *Lippia*, but Briquet (1895) and other authors described the *Lippia* calyx as shortly tubular and 2–4-dentate. We found that, in the Caribbean in particular, *Lippia* species with 2(–4) free, linear sepals do exist, e.g. *L. flavida* Urb. and *L. domingensis* Moldenke; how this fact might reflect on the generic delimitation of *Nashia* against *Lippia* we will consider further on.

*Flower* — The corolla in *Nashia* is small, white to yellowish or greenish (in *N. spinifera* it is said to be violet), broadly funnel-shaped to hypocrateriform, only slightly zygomorphic, with four short, ± spreading, subequal lobes. Atkins (2004) misleadingly describes it as "campanulate" and uses that shape as a key character. In the species we studied the corolla tube is glabrous or subglabrous outside, as is the margin of the lobes; inside the distal half of the tube, up to the throat, it is hairy; the outside and base of the lobes is densely covered with short hairs, or sessile glands, or (usually) a mixture of both; inside, the lobes are finely velvety-papillose. *N. spinifera* differs in having a corolla tube that is glabrous both outside and within.

Millspaugh (1906) mistakenly described the corolla lobes of *Nashia inaguensis* as valvate in bud, a condition not found in *Verbenaceae.* That error was stigmatized by Urban (1912) and spuriously used by him as an argument to sink *Nashia.* In fact the lobes are imbricate; the coverage between the lobes appears to vary.

The four stamens are inserted in the distal part of the corolla tube, on about the same level or on two superposed levels. The anthers are almost sessile, and often partly or totally exserted, especially those of the distal pair of stamens.

The short, included style is terminal to the ovary and, at or just below its tip, bears the elliptic, oblique or lateral stigmatic area on its ventral side, sometimes shortly overtopped by the sterile, conical apex of the style. This is the general condition found in all taxa examined, with one exception: in *Nashia spinifera* the stigma is terminal to the apically thickened, truncate style.

*Fruit* — Same as calyx morphology, fruit morphology is a major feature used to define and differentiate *Lantaneae* genera. The tribe as a whole is characterized by 2-seeded fruits formed from a single carpel. In Briquet's (1895) system, *Lantana* is set off against *Lippia* (sensu lato) for possessing fleshy, pink to violet drupes with a hard stone (pyrene) rather than a dry schizocarp split lengthwise into two 1-seeded halves (mericarps) at maturity. Within *Lantana*, Briquet distinguished between those in which the pyrene is split into unilocular halves coherent only at the base and those in which it is one bilocular unit, the former condition characterizing *L.* sect. *Lantana* (as *L.* sect. *Camara* Cham.). Our own, limited observations coincide with those of Méndez (1993: fig. 1.6–1.7; 1998: fig. 12H), who found the pyrene halves in *L.* sect. *Lantana* to be fused all around into a single unit, even though they are internally separated by a longitudinal cavity (which he interprets as a third "sterile locule"; Atkins 2004, more appropriately, speaks of a "central weakness zone").

In *Nashia*, Méndez (1993: fig. 1.4; 1998: fig. 12F; species not indicated) found a different type of fruit: a drupe with two free, unilocular pyrenes closely contiguous along their flat median face. The fleshy mesocarp does not separate easily from the stony endocarp (contrary to what he observed in *Lantana*), and, together with the tough exocarp, holds the two pyrenes together even after full maturation; but when the exocarp is removed, even a slight pressure suffices to pry them apart. This feature is used by Méndez (2003), followed by Atkins (2004), to key out *Nashia* against *Lantana*.

We can confirm Méndez's findings for all Cuban *Nashia* species of which fruits are known (*N. cayensis*, *N. nipensis*, *N. variifolia*). But the story does not end here: the two non-Cuban species, upon examination, show significantly different fruits.

In *Nashia inaguensis* the fruit is a yellow to orange drupe with a single, bilocular pyrene without a "central weakness zone". Except for colour, it resembles the fruits described for *Lantana* sect. *Callioreas* Cham. (Méndez 1998). The pyrene, when freed from the strongly adhering mesocarp, shows irregular longitudinal ridges and furrows; its osseous shell is brittle and breaks apart irregularly when subjected to strong pressure. A comparative anatomical survey may or may not reveal structural differences with respect to the situation in *Lantana*.

The fruit of *Nashia spinifera* is a dry, indehiscent nut of dark green colour turning brown at maturity, hidden within the calyx, the corolla being promptly shed at the end of anthesis. The outer fruit layers are thin and adhere closely to the strongly hardened, smooth, globular endocarp that encloses two 1-seeded locules. To the best of our knowledge, no similar fruit has so far been described for any representative of *Lantaneae*.

*Delimitation and affinities* — The species currently assigned to *Nashia* show an original mix of features believed to characterize *Lippia* (sensu stricto) with others of *Lantana*, and some found in neither. Taken together and projected on the chessboard of nature, the *Nashia* species appear to be scattered over a space between these large, traditional genera. They may not be united with either without jeopardizing their mutual independence. Unless and until it can be demonstrated that, in phylogenetic terms, the *Nashia* species are unequivocally nested within one or the other of their putative closest relatives, a move toward more widely defined genera, however circumscribed, seems unreasonable.

Our work on *Nashia* species also casts doubt on the coherence of the genus they are supposed to constitute, because they form three groups that differ in characters traditionally used in *Verbenaceae* to define genera. Their overall similarity is undisputed, but features such as spiny habit, microphylly, and spinosity are well known to have arisen repeatedly by convergent evolution in constraining habitats such as the Caribbean scrub communities in which *Nashia* species are found, known in Cuba as "manigua costera" (on coastal limestone) and "charrascales" (on ultramafic substrates). Therefore, it is by no means unlikely that taxa of similar appearance but differing in fundamental characters have arisen independently. Similar convergent evolution of habit features has recently been revealed by a phylogenetic study of the *Acantholippia-Aloysia* complex and has led to the transfer to *Aloysia* of a number of species formerly included in *Acantholippia* Griseb. (Lu-Irving & al. 2014).

*Nashia inaguensis*, which provides the type of the generic name, has fruits of the same type as *Lantana.* It differs from representatives of that genus, among other things, by its calyx (absent or reduced to two minute, free sepals, as in some *Lippia* species) and the sessile, few-flowered inflorescence of determinate growth. Even though its evolution from within *Lantana* is not unlikely, nothing would be gained by proposing to sink it on the basis of the presently known facts.

The Cuban species of *Nashia* differ from both *Lippia* and *Lantana* by their dipyrenous drupe. Most have a calyx of two free lateral sepals emulating bracteoles (absent in *N. armata*), thereby resembling some *Lippia* species. Atkins (2004) referred to the fruit as a "fleshy schizocarp" (although the term schizocarp, functionally at least, is inappropriate); within *Lantaneae*, according to her, such fruits are only known from two other genera: *Diostea* Miers (monotypic) and *Lampayo* Murillo (two or three species), both from the highlands of C and S South America, which have flowers in terminal spikes, with a 5-lobed tubular calyx and 5-lobed corolla, and are therefore obviously unrelated to the Cuban taxa. If not themselves an old evolutionary lineage, the Cuban *Nashia* species may with equal justification be considered as derived from *Lantana* (by a sagittal split of the latter's pyrene into two free halves) or *Lippia* (by transformation of its dry schizocarp into a fleshy, coloured dispersal unit), whereas postulating a direct link with *N. inaguensis* with its deviating inflorescence and other significant differences is, we believe, a less convincing hypothesis. The best solution, at present, is to consider the Cuban species complex as a separate genus, for which the epithet of *Lippia* sect. *Diphyllocalyx* is available as name.

Last, *Nashia spinifera* is the most puzzling and most strongly deviating of the lot. It differs from the other species studied here in fruit type, calyx, and indumentum; and from the Cuban species in inflorescence structure. It appears to have been placed in *Nashia* primarily on the basis of its spiny habit, which, as explained above, is a very unsatisfactory criterion. We consider its direct relationship with either *Nashia* proper or *Diphyllocalyx* as unlikely. We also do not see a clear affinity with either *Lippia* or *Lantana*, and we therefore consider its position within *Lantaneae* as isolated and unresolved. We take pleasure in dedicating what we consider an excellent new genus to our friend, and specialist of Cuban *Verbenaceae* and *Labiatae*, Isidro Méndez Santos of Camagüey.

## Systematic treatment

**1. *Nashia*** Millsp. in Publ. Field Columbian Mus., Bot. Ser. 2: 176. 1906. – Type: *Nashia inaguensis* Millsp. (*Lippia inaguensis* (Millsp.) Urb.).

Spineless shrub. *Bark* compact, often fissured longitudinally but not peeling off in fibres. *Indumentum* of bristles (stiff unicellular hairs placed on a pedestal of radially disposed specialized cells; confined to adaxial leaf surface), simple unicellular hairs, and sessile, globular glands. *Leaves* subsessile to shortly petiolate, small, firm, apparently evergreen, with entire, strongly revolute margin. *Inflorescence*: few-flowered, sessile axillary clusters of definite growth, ending in a bud-like assemblage of minute, sterile bracts. *Bracts* ± sheathing flower, herbaceous, deciduous, leaving an outwardly long-ciliate, platform-like scar. *Calyx* usually nil (or reduced to a circle of short hairs), sometimes present as (1 or)2 minute, linear, membranous free lateral sepals. *Corolla* early deciduous, broadly funnel-shaped, with 4 somewhat unequal lobes and oblique mouth; tube thinly pubescent outside and within. *Stamens* 4; anthers subsessile. *Style* terminal, short, included, apically curved and with stigma laterally on its ventral, concave side. *Fruit* an orange drupe; exocarp tough, fleshy mesocarp strongly adhering to osseous endocarp; stone single, osseous, breaking up irregularly under strong pressure, with two 1-seeded cells.

**1.1. *Nashia inaguensis*** Millsp. in Publ. Field Columbian Mus., Bot. Ser. 2: 177. 1906 ≡ *Lippia inaguensis* (Millsp.) Urb. in Symb. Antill. 7: 353. 1912. – Lectotype (Moldenke 1980: 176): *Nash & Taylor 1006* (NY!; isolectotypes: F [photo!], F [fragm., photo!]).

Shrub 1–3 m tall. *Twigs* obtusely quadrangular. *Bristles* stout to slender, forward-curved, their pedestal distinctly raised, ± conical, 100–200 µm across, of a single ring of 4–8 cells not usually becoming white (or if so, white colour spreading to surrounding epidermal cells). *Hairs* straight to ± curved, patent to antrorse, forming a dense, villous indumentum covering abaxial leaf surface (extending to adaxial one along proximal portion of midvein), petioles, stems, and inflorescence axes. *Glands* scattered all over plant, visible on adaxial leaf surface but elsewhere hidden by indumentum. *Leaves* in opposite pairs and axillary fascicles on current year's shoots, crowded at end of basally defoliated brachyblasts at nodes of older branches; petiole 0–1 mm long; lamina ovate to (mostly) lanceolate, 6–8(–12) × 2–3(–6) mm, with ± rounded base, consistently pointed (often appearing blunt from above, as tip bends downward); venation pinnate, midvein and to a lesser degree 3–5 pairs of lateral veins, or even some cross-veins, sunk adaxially and raised abaxially. *Flowers* mostly in 2 functional pairs per cluster, in axil of distal leaf pairs of twigs and lateral branches, sometimes appearing subterminal. *Bracts* broadly obovate or suborbicular, outer ones obtuse with outward-curved tip, inner ones rounded, hairy outside and apically within, with 7–9 faint, colourless (translucent) longitudinal veins. *Corolla* c. 3 mm long, with white limb and yellowish or greenish tube, lobes densely hairy and glandular dorsally and at their junction. *Stamens* didynamous, adaxial pair inserted in distal third of tube, abaxial pair near throat; anthers yellow, adaxial partly exserted, abaxial wholly exserted. *Drupe* subglobular with a faint ventral groove, c. 4 mm in diam.

*Specimens seen* — Bahamas: "Great Inagua", 4 Dec 1890, *Rothrock 383* (NY #1367523); "Inagua, Mathew Town. Shrub 3–5 ft.", 13 Oct 1904, *Nash & Taylor 1006* (F #74418F, F #74419F [fragm.], NY #111293 [lectotype]); "Scrub, Mathew Town. Shrub 3–4 ft. (wood section), 'Moujean Tea'", 5 Oct 1904, *Nash & Taylor 1454* (NY #1367522); "Cult. from Inagua", 14 Oct 1904, *Brace* (NY #1367524); "Great Inagua. Fruits smooth, shiny, spherical, translucent pale yellow and shallowly, longitudinally grooved, drupe-like", 30 Jan 1963, *Dunbar 187* (GH #571217); "Scrublands around Matthewtown, Inagua", 7 May 1970, *Hill 502* (GH #571218); "Inagua, Matthewtown, along roadside. Aromatic shrub c. 1 m tall; corolla cream, berries orange", 12 Feb 1973, *Proctor & Gillis 33240* (B #668819, GH #571216); "Great Inagua: in coppice on south east edge of Matthew Town on road to Lighthouse. Shrub to 2 m tall, with spreading-arched branches", 1 Mar 1974, *Correll 41660* (NY #1367525); "Inagua, Matthew Town, old fields and roadsides in village. Flowers white; foliage resinous-fragrant. Used to make tea with flavour of Earl Grey Tea. 'Tea-bush'", 7 Jun 1974, *Gillis & Proctor 12178* (B #668818); "Great Inagua: shrub along rock wall in north-east part of Matthew Town. Fruits orange-color", 19 Aug 1975, *Correll 46036* (NY #1367526). — Puerto Rico: "Peñuelas: Bo. Encarnación, hill N of Rt 2 just W of Ponce border, 17°59.12'N, 66°43.3'W. Dry scrub forest. Shrub (1.5 m). White fl. Locally common", elevation 50–100 m, 20 Mar 1995, *Axelrod & Cedeño 8846* (NY #1367521); id., "Orange, globose fr.", *Axelrod & Cedeño 8845* (NY #1367520); "Peñuelas: Bo. Encarnación, urb. El Peñón, E of Peñón de Ponce, N of hwy 2, 17°59'14"N, 66°42'12". Dense brushland, 2–3 m high (cut in past) with scattered trees, 4–5 m high on low, dry coastal limestone hills. Shrubs, 1–3 m high; flw buds creamy; open flws with white lobes, creamy-yellow tube; stamens yellow; frt bright orange, mature, flesh thin", elevation 40–50 m, 21 Mar 1995, *Breckon & Cedeño 4518* (NY #1367527); "Municipio de Peñuelas, Barrio Encarnación: hills SE. of Tallaboa, c. 0.4 km NW of Peñón de Ponce, arid scrubland over Miocene limestone. Shrub 1.5 m tall, locally frequent: flowers greenish-cream, very inconspicuous; fruits orange", elevation 50–70 m, 29 May 1995, *Proctor*, *Haneke & Hernández 50008* (US #739206); "Peñuelas: Bo. Encarnación, N of Rd. 2, c. 600 m W of Peñón de Ponce. Shrub 1–1.2 m tall, with numerous lateral branches; fruits depressed-globose, orange", elevation 40–50 m, 16 Jan 1996, *Acevedo*, *Cedeño & Vázquez 7775* (NY #842715, US #520815); "Peñuela, municipio Encarnación. Matorral xeromorpho costero y subcostero", 22 Mar 1997, *Méndez & Urquiola HPC 8719* (HIPC); "Ponce, Bo. El Peñon. W of town of Ponce, between Ponce and Guayanillas. On hill, N side of Hwy 2 near km 2158, c. 17°59.362'N, 66°42.621'W. Dry forest. Small shrub; leaves scabrous; plant with strong smell", elevation c. 24 m, 11 Feb 2003, *Stevens*, *González & Christopher 253* (NY #210702). — Virgin Islands: "St. Croix, Jacks Bay", Oct 1990, *Hayes* (US #739208); Goat Hills, Jurisdiction of Christiansted, Estate Jacks Bay, St Croix; trasladada a las colecciones vivas de la Universidad de VI. Planta cultivada", Oct 1997, *O'Reilly HPC 2967* (HIPC). — Hawai'i: "Cultivated at Bishop Museum", undated, *Wong* (K #634941 [photos!]).

*Note* — Acevedo & Strong (2012) mentioned the occurrence of *Nashia inaguensis* on St Thomas in addition to St Croix, Virgin Islands. We saw no specimen, nor is there any information in Acevedo & Strong's cited sources that would substantiate such a claim, which we dismiss as erroneous.

**2. *Diphyllocalyx*** (Griseb.) Greuter & R. Rankin, **stat. nov.** ≡ *Lippia* sect. *Diphyllocalyx* Griseb., Cat. Pl. Cub.: 215. 1866. – Type: *Lippia myrtifolia* Griseb. (*Diphyllocalyx myrtifolius* (Griseb.) Greuter & R. Rankin, *Nashia myrtifolia* (Griseb.) Moldenke).

Spiny or rarely ± spineless shrubs. *Bark* tending to peel off in fibres that correspond to angles of twigs. *Spines*, when developed, either all axillary, of similar length, distributed along virgate long twigs; or terminating side branches of varying length of twigs with a pyramidal branching pattern. *Indumentum* of bristles (stiff unicellular hairs placed on a pedestal of radially disposed specialized cells; confined to adaxial leaf surface), simple unicellular hairs (on axes, petioles, leaves and bracts, but absent or confined to midrib on adaxial leaf surface), and sessile, globular glands (on all parts). *Leaves* firm or herbaceous, opposite (occasionally in whorls of 3), small to medium-sized; petiole short or nil; lamina ovate, elliptical or obovate, with entire or shallowly crenate, flat to revolute margin; venation pinnate, at least midvein sunk adaxially and raised abaxially. *Inflorescence*: axillary, shortly pedunculate, dense spikes of indefinite growth, first hemispherical, later elongating and becoming ± cylindrical. *Bracts* ± sheathing flower, densely imbricate, herbaceous, persistent. *Calyx* (rarely absent) of 2 free, linear to narrowly spatulate lateral sepals pubescent dorsally, glabrous ventrally. *Corolla* funnel-shaped; proximal part of tube glabrous, extended by ovary after anthesis, split lengthwise by ripening fruit, corolla eventually shed; lobes 4, subequal, ± spreading, imbricate in bud. *Stamens* 4. *Style* terminal, included, with an oblique to lateral stigmatic area ventrally near its tip. *Fruit* an orange drupe; exocarp tough, fleshy mesocarp strongly adhering to osseous endocarp; stone of 2 distinct, unilocular, 1-seeded halves that are closely contiguous along their flat median face but are easily parted.

**2.1. *Diphyllocalyx armatus*** (Urb.) Greuter & R. Rankin, **comb. nov.** ≡ *Lippia armata* Urb. in Repert. Spec. Nov. Regni Veg. 18: 194. 1922 ≡ *Nashia armata* (Urb.) Moldenke in Phytologia 2: 53. 1941. – Lectotype (Moldenke 1980: 174–175): *Ekman 9220* (S!; isolectotypes: NY [fragm.!], S!).

Shrub with dense, pyramidal branching and bluntly quadrangular twigs. *Spines* both terminal to twigs or branches and axillary, numerous, strong, those on older branches often compound. *Bristles* well developed, patent and slightly forward-curved, their pedestal somewhat bulging, 200–300 µm across, of (6–)8–16 cells in a ring, becoming white with age. *Hairs* patent, dense and flexuous abaxially on leaves, short, markedly forward-curved on stems, antrorsely appressed on bracts. *Glands* scarce on adaxial leaf surface, moderately dense elsewhere. *Leaves* apparently deciduous in dry season, in opposite pairs and axillary fascicles, firm, sessile or with a petiole of ≤ 0.5 mm long; lamina revolute, narrowly elliptical (c. 3× as long as broad), 4–10 × 1–3.5 mm, with rounded base, margin (not visible) appearing entire, and rounded to obtuse tip; adaxially shiny and with distinct cell pattern between bristle pedestals, abaxially shortly villous; lateral veins in 2 or 3 pairs, forming an acute angle with midvein, sunk adaxially and raised abaxially, higher-level (reticulate) venation obsolete; narrowly conical, hollow, glabrous excrescences (pathological or teratological?) frequent on adaxial surface of young leaves. *Inflorescence* peduncle (remains from old spike) c. 2 mm long; inflorescence buds axillary, globular, subsessile. *Bracts* (outer ones of buds) suborbicular, 1.7 × 1.7 mm, obtuse, not patent distally, appressed-hairy and glandular dorsally. *Flowers* (in bud) devoid of calyx. *Corolla* tube glabrous; lobes 4, suborbicular, densely glandular dorsally and hairy at base. Open flowers and fruit unknown.

*Specimens seen* — Cuba, prov. Santiago de Cuba: “Prov. Oriente: prope Santiago de Cuba ad ostium Aguadores in collibus calcareis. Frutex”, 14 Jun 1918, *Ekman 9220* (NY #111296 [fragm.], S #3-128 [lectotype], S #8-14132). – Only known from the type gathering.

*Note* — The type locality is situated in the area in which the airport of Santiago de Cuba has been built. It is now likely covered by the runway. Should some plants have survived they are out of reach for botanists. Other populations assigned to *Nashia armata* (Méndez 2003) belong in fact to *Diphyllocalyx cayensis* subsp. *variifolius*.

**2.2.** ***Diphyllocalyx cayensis*** (Britton) Greuter & R. Rankin, **comb. nov.** ≡ *Nashia cayensis* Britton in Bull. Torrey Bot. Club 42: 517. 1915 ≡ *Lippia cayensis* (Britton) Urb. in Repert. Spec. Nov. Regni Veg. 18: 195. 1922. – Lectotype (Moldenke 1980: 175): *Shafer 2450* (NY!; isolectotypes: F [photo!], HAC!, US [photo!]).

Shrub with quadrangular, ± 4-ribbed twigs. *Spines* both terminal to twigs or branches and axillary (corresponding to side branches with 0 or 1 leaf pairs, mostly shorter than subtending leaf). *Bristles* usually slender, patent, slightly forward-curved, their pedestal conically raised. *Hairs* patent at least basally, straight to markedly forward-curved, especially on stem, of varying length, very sparse to dense but not obscuring glands. *Leaves* deciduous in dry season, in opposite pairs (axillary or nodal leaf fascicles reduced or lacking), higher-level (reticulate) venation obsolete; narrowly conical, solid, hairy galls often present on lower leaf surface. *Inflorescence* peduncle longer than subtending petiole, 1–4(–7) mm long, spike often becoming long-cylindrical. *Bracts* concave, spatulate-orbicular, c. 2 × 2 mm, hairy and glandular dorsally, truncate and with a short triangular, non-divergent tooth apically, with 3–5 thin, inconspicuous longitudinal veins. *Sepals* narrowly navicular to spatulate-linear, usually inward-curved, accumbent to corolla tube, 1.5–2.5 mm long, slightly shorter or longer than subtending bract, hairy and glandular dorsally. *Corolla* 2.5–3 mm long, with tube hairy outside in distal half, hairy inside below stamen insertion, hairy and glandular dorsally on short (0.5–0.8 mm long), suborbicular lobes. *Stamens* didynamous, inserted at or just below corolla throat, with anthers of at least distal pair exserted.

**2.2A.** ***Diphyllocalyx cayensis*** (Britton) Greuter & R. Rankin subsp. ***cayensis***

Branching loose; twigs pendent, ± virgate. *Spines* few, often weak, axillary ones often lacking or short, those persistent on older branches simple. *Bristle* pedestal ≤ 400 µm across, of (4–)8–16 cells in a ring, becoming white with age, white colour often extending to a peripheral ring of smaller, less regularly arranged cells. *Leaves* herbaceous; lamina ± elliptical, (8–)12–20 × (3–)4–9 mm, with narrowed to obtuse base, flat to narrowly recurved, entire (rarely distally 1- or 2-crenate) margin and rounded to acute tip; lateral veins in 4–6 pairs, weakly to distinctly sunk adaxially and raised abaxially. *Flowers* greenish.

*Specimens seen* — Cuba, prov. Camagüey: “Vicinity of Pueblo Romano, Cayo Romano, Camaguey. Dense shrub, branches pendant, fls. greenish, fruit orange-red”, 8–9 Oct 1909, *Shafer 2450* (F #74417F, HAC, NY #111292 [lectotype], US #118884); “Esmeralda. Cayo Romano, camino de El Molino a Sabanita del Burro”, 17 May 1976, *Areces*, *Bisse*, *Berazaín*, *Díaz*, *González & Lippold HFC 31701* (B #381109, HAJB #401, JE, PAL-Gr #66249); “Sola [by error; correctly: Mun. Esmeralda: Cayo Romano], maniguas y montes de la Silla de Cayo Romano, caliza”, 21 Feb 1981, *Álvarez*, *Bisse*, *Beurton & Gutiérrez HFC 43756* (B #412535, HAJB #411, HAJB ##488–489, JE [2×], PAL-Gr #66248).

*Note* — The figure of *Nashia cayensis* in Méndez (2003: 58) is a mixture: fig. 7.1 shows a branch of *Diphyllocalyx cayensis* subsp. *cayensis*, although with some “introgression" from *N. inaguensis* with respect to the inflorescences; fig. 7.2, however, is a faithful copy of the illustration of *N. inaguensis* in Correll & Correll (1982: fig. 532c). The deed, unfortunately not detected in good time, was committed by the artist, Julio Figueroa, responsible for several other plagiarisms in his work as botanical illustrator. Beware!

**2.2B. *Diphyllocalyx cayensis*** subsp. ***variifolius*** (Urb.) Greuter & R. Rankin, **comb. & stat. nov.** ≡ *Lippia variifolia* Urb. in Repert. Spec. Nov. Regni Veg. 20: 344. 1924 ≡ *Nashia variifolia* (Urb.) Moldenke in Phytologia 2: 54. 1941. – Lectotype (Moldenke 1980: 180): *Ekman 15542* (S!; isolectotypes: F [n.v.], NY!, S!).

Branching dense, intricate, pyramidal. *Spines* numerous, usually strong, axillary ones very short or, proximally, grading into short side branches, those persistent on older branches often compound. *Bristle* pedestal ≤ 300 µm across, of (4–)8 cells in a ring becoming white with age. *Leaves* firm; lamina ovate to ± broadly elliptical, 5–10(–12) × 3–6 mm, with subcordate to cuneate base, almost flat to recurved, entire or crenate margin (with veins ending in notches) and obtuse to acute tip; lateral veins in 2–5 pairs, deeply sunk adaxially and prominently raised abaxially.

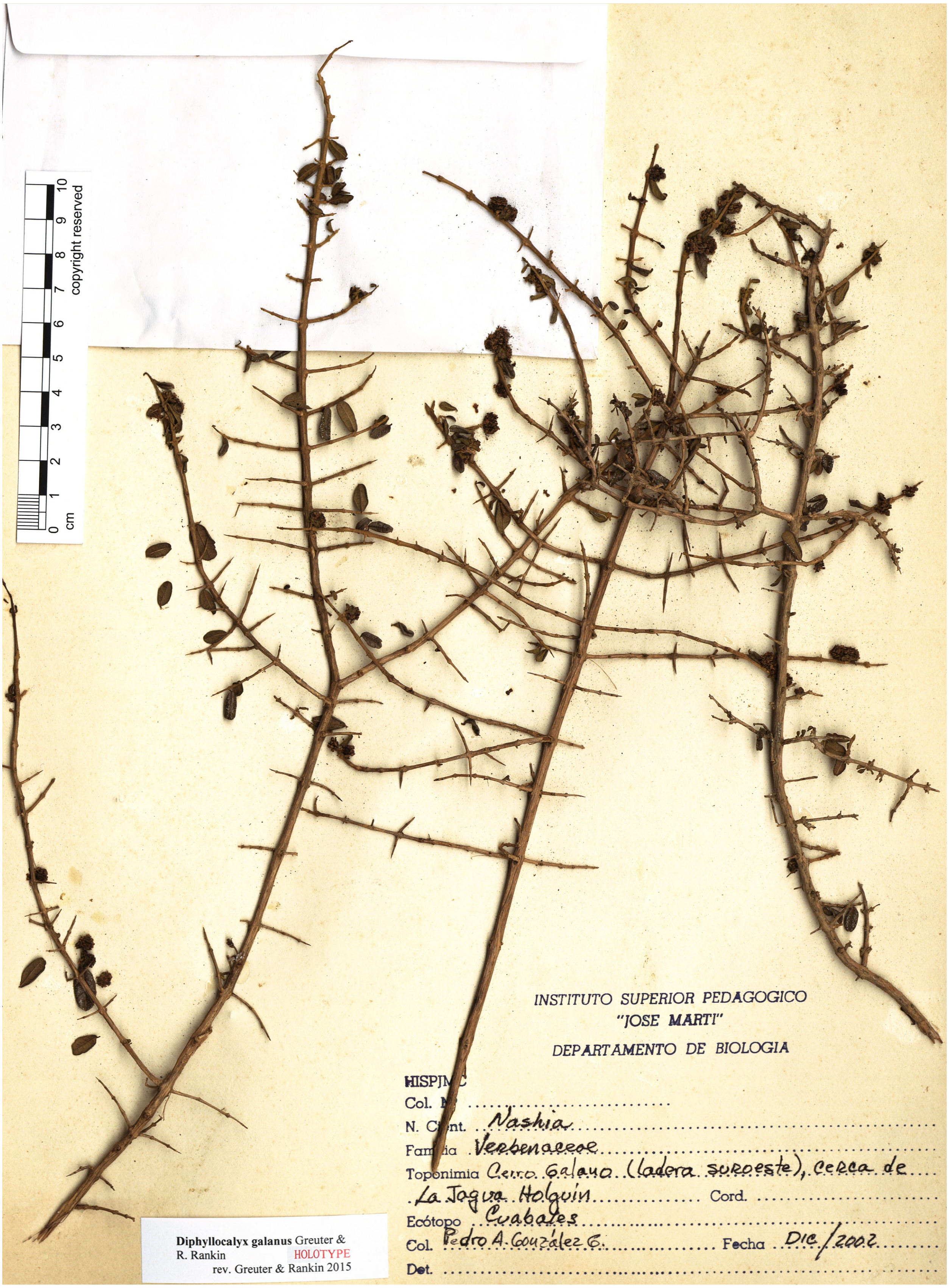
*Specimens seen* — Cuba, Prov. Camagüey: "Pastelillo, in loose limestone rocks", 19 Oct 1922, *Ekman 15542* (NY #111295 [fragm.!], S #3-129, S #8-14150 [lectotype]). – Cuba, prov. Holguín: "Los Cocos de Gibara, carretera de Gibara a Caletones, km 2, matorral xeromorfo costero y subcostero", 27 Mar 1990, *Méndez HPC 5888* (HIPC). – Cuba, Prov. Guantánamo: "Monte seco de Baitiquirí por el camino a la mina de Yeso", May 1968, *Bisse & Köhler HFC 7891* (B #376914, HAJB #412, JE); "Lomas de Minas de Yeso, 10 km de Baitiquirí. Matorral xeromorfo costero y subcostero", 19 May 1998, *Romano HPC 10122* (HIPC); Baitiquirí, en el camino a la mina de Yeso, monte seco", 19 Aug 1971, *Bisse HFC 20041* (HAJB #408, HAJB ##490–492, PAL-Gr #66252); Baitiquirí, en el camino a la mina de Yeso, monte seco", 11 Apr 1972, *Bisse & Berazaín HFC 21793* (HAJB #407, JE, PAL-Gr #66250); "Maisí, entre Cueva del Agua y El Canto, Punta de Maisí, bosque siempreverde microfilo y matorral xeromorfo subespinoso costero, suelo esquelético (rendzina roja)", 24 Apr 1986, *Genes*, *Gutiérrez*, *Oviedo*, *Rankin & Stohr HFC 59218* (B #412534, HAJB #409, HAJB #493, JE [2×], PAL-Gr #66251); "El Canto, al este de la Cueva del Agua, Maisí", 21 Mar 1989, *Oviedo & al.* (HAC #39162 [2×]); "Los Azules, Noroeste de Punta de Maisí, matorral xeromorfo costero y subcostero", *Méndez & Barbatillo HPC 7076* (HIPC), "Prov. Oriente; Imías. Yacambo [Yacabo], loma de Yacambo", 9 Feb 1976, *Areces*, *Bisse*, *Catasús*, *Gutiérrez & Manitz HFC 29838* (B #386058, HAC #34118, HAJB #410, JE, PAL-Gr #66253).

*Note* — Leaf crenation and inflorescence length have been used by previous authors to distinguish between *Nashia cayensis* and *N. variifolia.* Neither character is useful when phenological and intra-populational variation is taken into account. The plants from Cayo Romano have peculiarities of spinosity, leaf size etc. that justify their maintenance as distinct subspecies; but the differences are partly bridged by the Yacabo population, which by habit and leaf dimensions is intermediate between the taxa here described and is assigned to the second principally on the basis of geography. In Méndez (2003) the Yacabo population has been erroneously assigned to *N. nipensis*, and the two other ones from Guantánamo Province (Baitiquirí and Maisí), to *N. armata*.

**2.3. *Diphyllocalyx galanus*** Greuter & R. Rankin, **sp. nov.** – Holotype: *González Gutiérrez* (HIPC!). – Fig. 1.

Shrub with quadrangular, ± 4-ribbed twigs. *Spines* both terminal to twigs or branches and axillary, numerous, strong, axillary ones very short or, proximally, grading into short side branches, those persistent on older branches often compound. *Bristles* short to almost nil, patent, their pedestal flat, 200–300 µm across, of 4–8 cells in a ring, becoming white with age, white colour extending to a peripheral ring of smaller, less regularly arranged cells. *Hairs* absent from petioles and midvein, elsewhere short (c. 0.1 mm long), those on adaxial leaf surface appressed, those on axes and bracts few, markedly forward-curved, none exceeding glands. *Glands* everywhere dense, indumentum on young leaves, abaxially, drowned in their exudate. *Leaves* deciduous in dry season, in opposite pairs (axillary or nodal leaf fascicles lacking), firm, sessile or with a petiole of ≤ 1 mm long; lamina elliptical, 5–12 × 3–6 mm, with truncate-cuneate base, narrowly recurved, entire or distally 1-crenate margin and rounded to subacute tip, shiny above and with distinct cell pattern between bristle pedestals; lateral veins in 3 or 4 pairs, barely sunk adaxially or raised abaxially, higher-level (reticulate) venation obsolete. *Inflorescence* peduncle longer than subtending petiole, 1–2 mm long. *Bracts* broadly rhombic-elliptical, c. 2 × 2 mm, narrowed into a triangular, outward-curved tip, with inconspicuous venation. *Sepals* linear, inward-curved, often unequal, c. 1 mm long, about as long as ovary, hairy and glandular dorsally. *Corolla* 2–2.5 mm long, tube hairy outside at throat level, hairy inside from above base up to throat, glandular dorsally on ≤ 1 mm long, suborbicular to ovate lobes. *Stamens* scarcely didynamous, inserted at corolla throat, smallish anthers exserted.

*Specimens seen* — Cuba, prov. Holguín: "Cerro Galano (ladera suroeste), cerca de La Jagua; cuabales", Dec 2002, *González G.* (holotype, HIPC). – Only known from the type gathering, which according to the collector (pers. comm.), stems from a single, isolated shrub.



**Diphyllocalyx galanus** Greuter &
R. Rankin HOLOTYPE
rev. Greuter & Rankin 2015

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HISPJM C
Col. N ..........................
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Toponimia Cerro Galano (ladera suroeste), cerca de
La Jagua Holguin .............. Cord. ..........................
Ecótopo Cuabales ..........................
Col. Pedro A. González G. .............. Fecha Dic/2002
Det. ..........................

Fig. 1. Holotype specimen of *Diphyllocalyx galanus* (HIPC). Scan by the second author, reproduced by kind permission of Isidro Méndez, Instituto Pedagógico de Camagüey.

**2.4. *Diphyllocalyx urquiolae*** Greuter & R. Rankin, **sp. nov.** – Holotype: *Urquiola & al. HPR 7894* (HIPC!; isotypes: HAJB #494!, HAJU!). – Fig. 2.

Shrub c. 1 m tall, with bluntly quadrangular twigs. *Spines* both terminal to twigs or branches and axillary, numerous, strong, those persistent on older branches often compound. *Bristles* weak, dense, patent, only largest ones with an indistinct, concolorous pedestal c. 100 µm across. *Hairs* absent from adaxial leaf surface except along midvein, long, dense and flexuous on abaxial leaf surface, scattered, short and ± straight elsewhere. *Glands* dense on leaves and axes. *Leaves* herbaceous, deciduous, in opposite pairs (axillary or nodal leaf fascicles lacking), with a petiole of 1–2 mm long; lamina 6–13 × 4–8 mm, broadly obovate to broadly elliptical (c. 1.5× as long as broad), with cuneate base, entire or shallowly crenate, flat or barely recurved margin, and rounded, often minutely apiculate tip; adaxial face dull, with indistinct cellular pattern, appearing bullate due to sunk midvein, lateral veins, and cross veins, densely villous abaxial surface, conversely, appearing areolate; lateral veins in 3 or 4 pairs. Flowers and fruits unknown.

*Specimens seen* — CUBA, PROV. PINAR DEL RÍO: “Vegetación sobre costa rocosa, El Resguardo, en el borde del farallón, Guanahac., Sandino”, elevation 8 m, 18 Mar 1995, *Urquiola*, *Iglesias*, *Figueroa & Martínez HPR 7894* (HAJB #494, HAJU [isotypes], HIPC [holotype]). – Only known from the type gathering.

*Note* — In Méndez (2003) the Guanahacabibes population has been erroneously assigned to *Nashia myrtifolia*, under which name a photograph has been published in Urquiola & al. (2010). Whereas that illustration indeed shows *Diphyllocalyx urquiolae*, the associated description of the flower is taken from Méndez’s treatment and refers to *D. myrtifolius*.

**2.5. *Diphyllocalyx nipensis*** (Urb.) Greuter & R. Rankin, **comb. nov.** ≡ *Lippia nipensis* Urb. in Repert. Spec. Nov. Regni Veg. 20: 344. 1924 ≡ *Nashia nipensis* (Urb.) Moldenke in Phytologia 2: 54. 1941. – Lectotype (Moldenke 1980: 178): *Ekman 15044* (S!; isolectotypes: G [photo!], HAC!, HAJB!, K [photos!], NY!, S [2×!], US [photo!]).

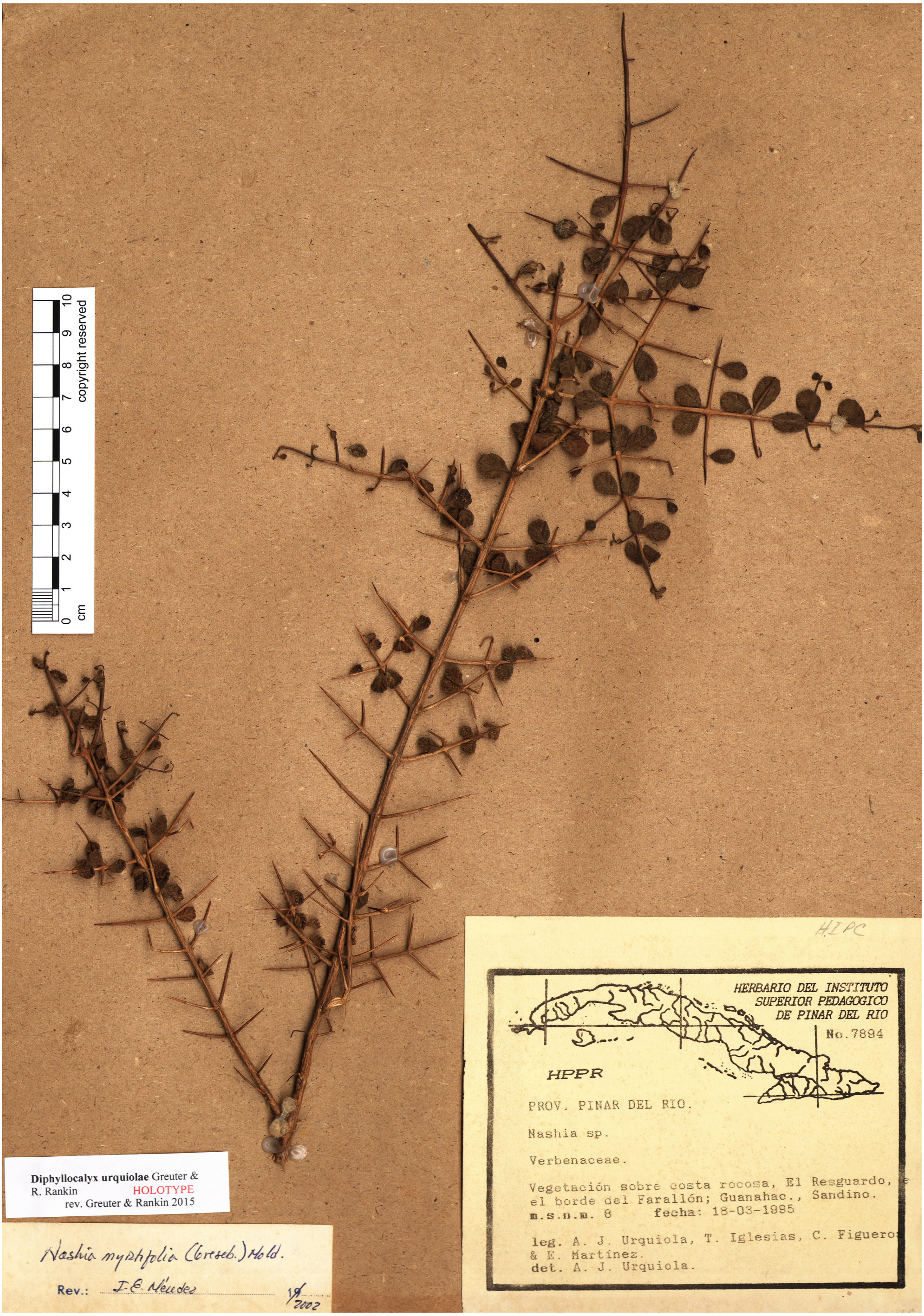
Shrub to 2 m tall, with pyramidal branching and quadrangular, ± 4-ribbed twigs, *Spines* lacking; side branches short, divaricate, leaf scars crowded toward their scarcely tapering apex. *Bristles* antrorse, slender to stout and conical, sometimes completely reduced, arising from a flat pedestal 200–400 µm across, of 8–16 cells in a ring or fewer and surrounded by a second ring of smaller, irregularly arranged cells, usually becoming white with age and set off sharply against surrounding, dark green tissue. *Hairs* short, antrorse, those of leaves straight, confined to midrib, those of pedicels and stems strongly curved. *Glands* small, absent from leaves adaxially, abundant elsewhere. *Leaves* eventually deciduous, spaced in opposite pairs along stem and proximal part of side branches, on which they are crowded distally; petiole 0.5–1.5 mm long; lamina firm, convex, ovate to elliptical, 3–13 × 3–8 mm, with subcordate to broadly cuneate base, entire, tightly recurved to narrowly revolute margin, and obtuse to acute tip; adaxially shiny and with distinct cell pattern between bristle pedestals, abaxially glandular; lateral veins in 2–4 pairs, slightly or barely sunk adaxially or raised abaxially, reticulum of cross-veins sometimes darker and visible from below but not raised. *Inflorescence* peduncle 0.5–3 mm long, equalling or exceeding subtending petiole; mature spikes longer than leaves. *Bracts* appressed-hairy and glandular dorsally, suborbicular to broadly ovate, c. 3 × 3 mm, tip truncate and straight or with an outward-curved acumen, with 5(–7) thin, inconspicuous longitudinal veins. *Sepals* linear to linear-spatulate, narrowly navicular and falcate, mostly equalling or slightly exceeding bracts. *Corolla* (yellowish?) 2–3 mm long, tube glabrous outside, villous inside in its distal half up to oblique throat; lobes c. 0.5 mm long, glandular dorsally and in places pubescent. *Stamens* didynamous, proximal (adaxial) pair inserted inside corolla tube, its anthers ± included, distal pair placed in corolla throat and exserted. *Stigma* oblique.

*Specimens seen* — CUBA, PROV. HOLGUÍN: “Prov. Oriente: Sierra de Nipe, pinelands on the edge of Río Piloto; fl. yellowish, a shrub”, elevation c. 350 m, 8 Sep 1922, *Ekman 15044* (G #366479, HAC, HAJB #395, K #470802, NY #111294, S #3-134 [lectotype], S #8-14146, S #8-14147, US #118852); “Sagua de Tánamo: loma cerca de Yirimía. Charrascal sobre serpentina”, elevation 360 m, 20°28'06"N, 75°18'52"W, 1 May 2015, *Greuter & Rankin 28719* (B #645763, HAJB, JE, PAL-Gr #63240, US).

*Note* — As Mendez’s (2003) record of *Nashia nipensis* from Yacabo is an error for *Diphyllocalyx cayensis* subsp. *variifolius*, our recent find constitutes the rediscovery of a species not seen in nature for almost a century. It confirms *D. nipensis* as a member of the “charrascales” scrub communities covering the dry serpentine areas of NE Cuba.

**2.6. *Diphyllocalyx myrtifolius*** (Griseb.) Greuter & R. Rankin, **comb. nov.** ≡ *Lippia myrtifolia* Griseb., Cat. Pl. Cub.: 215. 1866 ≡ *Nashia myrtifolia* (Griseb.) Moldenke in Phytologia 2: 53. 1941. – Holotype: *Wright 118 = 3160* (GOET!); probable isotypes: G [2×, photos!], GH [photo!], HAC [3×!], K [photo!], NY [fragm.!], P [photo!], YU [photo!]).

Shrub to 3 m tall, with virgate branching and quadrangular, ± 4-ribbed twigs. *Spines* axillary only, mostly shorter than or equalling leaves, with 0 or 1 leaf pair. *Bristles* short and stout, conical, antrorse, ± appressed, arising



HERBARIO DEL INSTITUTO
SUPERIOR PEDAGOGICO
DE PINAR DEL RIO
No.7894

HPPR

PROV. PINAR DEL RIO.

Nashia sp.

Verbenaceae.

Vegetación sobre costa rocosa, El Resguardo, e
el borde del Farallón; Guanahac., Sandino.
m.s.n.m. 8 fecha: 18-03-1995

leg. A. J. Urquiola, T. Iglesias, C. Figuero
& E. Martínez.
det. A. J. Urquiola.

**Diphyllocalyx urquiolae** Greuter &
R. Rankin HOLOTYPE
rev. Greuter & Rankin 2015

Nashia myrtifolia (Griseb.) Mold.

Rev.: I. E. Méndez 19/2002

Fig. 2. Holotype specimen of *Diphyllocalyx urquiolae* (HIPC). Scan by the second author, reproduced by kind permission of Isidro Méndez, Instituto Pedagógico de Camagüey.

from a slightly raised, disciform pedestal 200–400 μm across, of 5–8 cells in a ring, becoming white with age. *Hairs* confined to leaf midrib adaxially, stem nodes and inflorescences, absent from abaxial leaf surface, petioles and stem internodes. *Glands* small, abundant on all parts of plant. *Leaves* apparently deciduous, spaced along stem in opposite pairs and sometimes whorls of 3, not in axillary fascicles; petiole c. 1 mm long, glandular; lamina thin, flat, ovate, 10–18 × 4–10 mm, with rounded base, entire, recurved margin, and obtuse to subacute and often mucronulate tip; adaxially with distinct cell pattern between bristle pedestals, abaxially glabrous and minutely glandular; lateral veins in 3–5 pairs, somewhat sunk adaxially and raised abaxially, reticulum of cross-veins visible as a dark pattern from below but not raised. *Inflorescence* peduncle c. 1 mm long, equalling subtending petiole; young spikes ± globular, much shorter than leaves. *Bracts* appressed-hairy and glandular dorsally, lowermost broadly ovate, c. 2.4 × 1.8 mm, subacute, with outward-curving tip, following ones suborbicular, c. 1.8 mm across, rounded, appressed, with 3(–5) thin, inconspicuous longitudinal veins. *Sepals* narrowly spatulate, c. 1.2 mm long, obtuse, glandular and pubescent dorsally. *Corolla* white, c. 2.5 mm long; tube glabrous outside, shortly villous inside from above base up to throat; lobes c. 0.5 mm long, glandular and pubescent dorsally and at base. *Stamens* didynamous, inserted at or just below corolla throat, anthers of distal pair exserted. *Stigma* oblique.

*Specimens seen* — CUBA, PROV. GUANTÁNAMO: “in Cuba orientali”, 1861, *Wright 118 = 3160* (GOET #11524 [holotype]); “Potosí Monte Toro; fruticose 10 [feet], slender with long pendent branches, Fl. white”, 11 Oct [1861], *Wright 3160* (GH #95249); without locality, 1860–1864, *Wright 3160* (G #366482, G #366551, GH #95249, HAC [3×!], K #470803 [photos!], NY #111299, P #713619, YU #1918). – Only known from the type gathering.

*Note* — The record from W Cuba, Guanahacabibes peninsula (Méndez 2003), being an error for *Diphyllocalyx urquiolae*, the locus classicus, “Potosí Monte Toro”, remains the single known locality to date – but has not been identified with certainty. In Latin America, potosí usually refers to a mining site, and indeed there appear to be some laterite deposits in the Monte Toro area, where past mining is not unlikely. Samek (1973: 60), for nearby Monte Cristo, reports a mosaic of serpentinite, laterite and limestone bedrock. Searching for the species in serpentine and laterite enclaves, usually less degraded than the surrounding limestone zones, bears promise.

**3.** ***Isidroa*** Greuter & R. Rankin, **gen. nov.** – Type: *Isidroa spinifera* (Urb.) Greuter & R. Rankin (*Lippia spinifera* Urb., *Nashia spinifera* (Urb.) Moldenke).

Spiny shrub or small tree. *Bark* compact, eventually fissured longitudinally, not peeling off in fibres. *Spines*, when present, of similar length, axillary, formed on current year’s twigs not themselves ending in a spine. *Indumentum* of bristles (stiff unicellular hairs placed on a pedestal of radially disposed specialized cells; confined to adaxial leaf surface), simple unicellular hairs, and sessile, globular glands. *Leaves* small, firm, apparently evergreen, with entire margin. *Inflorescence*: few-flowered, sessile axillary clusters of definite growth, ending in a bud-like assemblage of minute, sterile bracts. *Bracts* herbaceous, blunt, not enlarged during maturation. *Calyx* ovoid-tubular, encircling corolla, shallowly bilobed, later much enlarged and sheathing fruit. *Corolla* readily shed after anthesis, with 4 subequal lobes; tube glabrous outside and within. *Stamens* 4. *Style* terminal, short, included, apically thickened and truncate, with terminal stigma. *Fruit* a dry, indehiscent, globular nut, its thin outer layers adhering to hard, smooth endocarp forming a single pyrene with two 1-seeded locules.

**3.1.** ***Isidroa spinifera*** (Urb.) Greuter & R. Rankin, **comb. nov.** ≡ *Lippia spinifera* Urb. in Repert. Spec. Nov. Regni Veg. 18: 195. 1922 ≡ *Nashia spinifera* (Urb.) Moldenke in Phytologia 2: 54. 1941. – Holotype: Hispaniola, Haiti, Morne Tranchant, *Buch 1994* (B†). – **Neotype (designated here):** *Ekman H 1166b* (S!; isoneotype: K #634940 [photos!], NY!; presumed isoneotype: *Ekman H 1166a* (S!). – Fig. 3.

Shrub growing into a small tree, to 4 m tall. Young twigs quadrangular. *Spines* (often not present on all branches) 1–2× as long as subtending leaf, leafless except for 1 sub-basal leaf pair. *Bristles* short, antrorse, their pedestal slightly raised, c. 150 μm across, of a single ring of 5–8 cells soon becoming white (white spots widening and becoming ± confluent on older leaves). *Hairs* short, straight and stiff, antrorse on petioles, leaf midvein abaxially, and dorsally on bracts and calyx; ± patent on axes. *Glands* scattered over most of plant but absent from adaxial leaf surface, often ephemeral. *Leaves* opposite on young twigs, in lateral clusters at nodes of previous year’s growth; petiole 0.5–1 mm long; lamina ± elliptic, 6–10 × 3–4.5 mm, obtuse at both ends, flat with a slightly revolute margin; dark and shiny above between bristle pedestals, surface appearing lacquered with cell limits obscured, paler and densely pitted below, with minute glands partly immersed in pits; midvein sunk adaxially, raised abaxially; lateral veins in 2 or 3 pairs, barely visible. *Flowers* in 1 or 2 functional pairs per axillary cluster, only half developing into fruits. *Bracts* suborbicular, concave, initially at least as long as calyx, dark striate by parallel longitudinal, somewhat anastomosing veins. *Calyx* subtruncate, with inconspicuous, broadly rounded lateral lobes each fed by 2 well-spaced, parallel veins; no dorsal or ventral vein present. *Corolla* pale when dry (violet according to label information), c. 2.5 mm long, glabrous but with a densely glandular zone outside at level of throat, densely papillose inside; lobes suborbicu-

Fig. 3. Neotype specimen of *Isidroa spinifera* (S). Scan by the second author, reproduced by kind permission of the Swedish Museum of Natural History, Stockholm.

lar, c. 1 mm across, concave. *Anthers* subsessile, inserted in distal third of corolla tube and barely attaining level of throat. *Nut* smooth to irregularly wrinkled, dark green turning brown, globose, c. 4 mm in diam.

*Specimens seen* — HISPANIOLA, HAITI: “Massif de la Selle, Morne Tranchant, in thickets on the eruptive slopes”, elevation 1700 m, 28 Jul 1924, *Ekman H 1166b* (K #634940; NY #1367528, S #3-131 [neotype]) and *H 1166a* (S #3-130). – HISPANIOLA, DOMINICAN REPUBLIC, PROV. SAN JUAN DE LA MAGUANA: “Sierra de Neiba, Municipio El Cercado, Paraje Pinal Grande, Sabana del Silencio en la Loma de Los Magüeyes, bosque nublado, latifoliado con *Brunellia*, *Podocarpus*, *Juniperus*, *Meliosma*, etc.; arbolito de 4 m, con flores moradas y frutos verdes”, elevation 1920 m, 3 Dec 2000, *Clase*, *Santana & Montilla 2358* (JBSD [photo!]); id., “arbolito de 3,5 m, con botones y flores moradas”, elevation 1920 m, 3 Dec 2000, *Clase*, *Santana & Montilla 2469* (JBSD [photo!]); id., “bosque nublado; arbusto de 3 m, con botones”, elevation 1920 m, 1 Nov 2004, *Clase*, *Nuñez*, *Rawling & Young 3809* (JBSD [photo!]); “Sierra de Neyba, entre los límites de la Provincia de San Juan y Bahoruco, Sabana del Silencio, en los alrededores del Valle, sobre suelo con abundante materia orgánica; bosque nublado con predominancia de *Baccharis myrsinites*, *Garrya fadyenii* y *Myrsine coriacea*; arbusto de 2 m; frutos secos, abiertos”, 18°39'05"N, 71°33'23"W, elevación 1985 m, 27 Feb 2001, *Veloz*, *Santana*, *Hierro*, *Dominici*, *Perdomo & De Los Santos 2506* (JBSD [photo!]).

*Note* — We consider *Ekman H 1166a* and *H 1166b* as part of a single gathering as defined in the *Code* (McNeill & al. 2012: Art. 8.2 and footnote 2) since they belong to the same taxon and were collected simultaneously by the same collector in the same place. According to T. Clase (pers. comm.) all specimens in JBSD were collected in exactly the same locality, where only two adult individuals of the species are known to exist.

## Key for species identification

1. Flowers few, in sessile axillary clusters of definite growth; leaf margin entire; fruit fleshy or dry, containing a single osseous stone with two 1-seeded locules (not in Cuba) . . . . . . . . . . . . . . . . . . . . . . . . **2**

– Flowers in axillary, shortly pedunculate, dense spikes of indefinite growth; leaf margin entire or crenate; fruit fleshy, containing twin osseous stones, each with a 1-seeded locule (Cuba) . . . . . . . . . . . . . . . . . . . . **3**

2. Spineless shrub; fruit fleshy, yellow or orange; calyx nil or of (1 or)2 minute, linear sepals; leaves acute with downward-turned tip, villous beneath (not in Hispaniola) . . . . . . . . . . . . **1.1. *Nashia inaguensis***

– Spiny shrub; fruit dry, dark green turning brown; calyx ovoid-tubular, strongly enlarged to sheathe fruit; leaves obtuse, glabrous or subglabrous beneath (Hispaniola) . . . . . . . . . . . . . . . . . **3.1. *Isidroa spinifera***

3. Leaves ovate or some elliptical, glabrous beneath; spines absent or axillary, simple (E Cuba) . . . . . . **4**

– Leaves elliptical to obovate, puberulent to villous beneath; twigs and their branches mostly ending in spines . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **5**

4. Twigs elongate, ± virgate, with regular axillary spines; leaf lamina flat, glandular on both surfaces . . . . . . . . . . . . . . . . . . . . . . . **2.6. *Diphyllocalyx myrtifolius***

– Branching ± pyramidal, twigs with divaricate, non-spiny side branches; leaf lamina convex, glandular only abaxially . . . . . . . . ***2.5. Diphyllocalyx nipensis***

5. Leaves dull and with indistinct cellular pattern adaxially, appearing bullate due to sunk lateral veins and cross veins; only largest bristles with an ill differentiated, concolorous pedestal; abaxial leaf surface long-villous (W Cuba) . . . . . . . . . **2.4. *Diphyllocalyx urquiolae***

– Leaves shiny and with distinct cellular pattern adaxially, with scarcely visible, not sunk cross-veins; most or all bristles with a distinctive pedestal turning white; abaxial leaf surface variously hairy (C and E Cuba) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **6**

6. Leaves abaxially with short, appressed hairs, adaxially with flat bristle pedestals; leaf lamina 5–12 × 3–6 mm, lateral veins barely sunk adaxially and raised abaxially; bract tip outward-curved . . . . . . . . . . . . . . . . . . . . . . . . . . . **2.3. *Diphyllocalyx galanus***

– Leaves abaxially with hairs patent at least basally, adaxially with ± raised bristle pedestals; lateral veins of leaf lamina deeply sunk adaxially and prominently raised abaxially (or, if only weakly sunk, leaves larger); bract tip not divergent . . . . . . . . . . . . . . . . . . . **7**

7. Calyx nil; leaves narrow (c. 3× as long as wide), strongly revolute . . . . . . **2.1. *Diphyllocalyx armatus***

– Calyx of two free, lateral, linear-spatulate sepals; leaves broader (mostly 1.5–2× as long as wide), flat except for ± recurved margin . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . (**2.2. *Diphyllocalyx cayensis***) **8**

8. Twigs ± virgate; spines few, old ones usually simple; leaf lamina (8–)12–20 × (3–)4–9 mm, veins adaxially sunk but not in deep grooves . . . . . . . . . . . . . . . . . . . **2.2A. *Diphyllocalyx cayensis*** subsp. ***cayensis***

– Branching intricate, pyramidal; spines many, old ones often branched; leaf lamina 5–10(–12) × 3–6 mm, grooved adaxially by deeply sunk veins . . . . . . . . . . . . **2.2B. *Diphyllocalyx cayensis*** subsp. ***variifolius***

## Discussion and conclusions

*Evolution* — As is the general rule, our study of the *Nashia* group, while answering some questions, opens new ones. The evolutionary pathways in *Lantaneae* are even less evident now than they were before. We feel unable to formulate a sound hypothesis as to how taxa and their characters have evolved in this tribe. Is the

*Isidroa* fruit a *Lantana*-type drupe gone dry or a *Lippia*-type schizocarp in which the mericarps became fused, or perhaps even the archetype from which both types have evolved? Does the twin pyrene of *Diphyllocalyx* derive from a *Lantana* drupe by fission of the bilocular stone or from a *Lippia* schizocarp gone coloured and fleshy? Is *Nashia* proper an ancestral lineage within *Lantaneae* or a new offspring nested within *Lantana*? For one, our results do not support the distinction, proposed by Caro (1982), of two tribes entirely based on drupaceous vs schizocarpic fruits: *Lantaneae* s. str. and *Lippieae*.

Molecular phylogenetic studies would be helpful in answering these questions, and also to resolve the position of *Lippia* species with a calyx of two free sepals, such as *L. flavida* and *L. domingensis*. Concerning the latter: the *Verbenaceae* specialist, Moldenke, appears to have been at daggers drawn with calyx morphology. On one hand, to justify the generic status of *Nashia*, he (Moldenke 1980: 173) claimed that "the '2 free sepals' … are not seen in *Lippia*". On the other hand, he (Moldenke 1965: 159) wrote: "Urban's description of the calyx of *L. flavida* being composed of 2 or 3 free [separate] sepals is curious. It is more probable that the calyx is merely deeply and irregularly split". Finally, he (l.c.: 146) did not mention at all the calyx of his own species, *L. domingensis*, otherwise described at length – but in an isotype specimen (*Howard & Howard 8118*, B #668820) we found a calyx corresponding exactly to Urban's description of *L. flavida*. Unfortunately, fruits of neither of these two very local endemics of S Hispaniola have so far been described, nor are any available to us.

Generally speaking, the phylogeny of the whole *Lantana-Lippia* complex of genera is not yet adequately understood. Lu-Irving & Olmstead (2013) have recently conducted a DNA sequence analysis of multiple nuclear and plastid loci in the *Lantaneae*, including 38 species of the *Lantana-Lippia* clade. They did not recover either *Lantana* or *Lippia* as natural units; instead, they found largely incongruent gene trees, pointing to frequent reticulation events. In such conditions, and with a still inadequate sampling of perhaps 10 % of the known species, they wisely refrained from drawing far-reaching taxonomic conclusions.

Including as many as possible of the critical taxa mentioned above in the analysis would clearly be desirable, but obtaining suitable material will not be easy when most of them are extremely rare – some have not been collected for over a century and are perhaps extinct. Meanwhile, morphological analyses are the best we can hope for, and we see the present paper as a contribution to such studies.

*Biogeography* — The distribution of the taxa recognized here falls into a plausible pattern. The seven *Diphyllocalyx* taxa are all Cuban endemics, with non-overlapping areas (Fig. 4), and are specialists of either "charrascales" communities growing on ultramafic substrates (*D. galanus*, *D. nipensis* and probably *D. myrtifolius*) or of the "monte seco" typical of dry coastal limestone areas (other taxa). *Isidroa* (Fig. 5) is only known from two mountains in Hispaniola, where it grows in high-altitude scrub or forest communities. Only the distribution of *Nashia* proper (Fig. 5) is somewhat unusual. The species is known from three very local populations on Inagua (Bahamas), Puerto Rico, and St Croix in the Virgin Islands, thus skipping Hispaniola and Cuba. This slightly anomalous, disjunct area has, we believe, a plausible explanation.

As stated by Cedeño & O'Reilly (1996), the two *Nashia* populations of St Croix and Puerto Rico, first reported by them, grow in natural or semi-natural coastal thorn-scrub communities. We found subtle differences in leaf venation between plants of the two populations (the veins are more deeply sunk adaxially in the former than in the latter), too tiny to warrant formal taxonomic recognition but sufficient to ascribe any specimen seen by us to one or the other origin. On the other hand, Proctor (quoted by Cedeño & O'Reilly) stated that on Great Inagua *Nashia* "occurs on roadsides and in disturbed or

Fig. 4. Map of the total known distribution of *Diphyllocalyx*. – ●, *D. armatus*; ▲, *D. cayensis* subsp. *cayensis*; ▼, *D. cayensis* subsp. *variifolius*; ○, *D. galanus*; ■, *D. urquiolae*; △, *D. nipensis*; □, *D. myrtifolius*. – Solid symbols denote coastal taxa growing on limestone, outline symbols correspond to inland taxa assumed to be specialists of ultramafic substrates.

inhabited sites", which is confirmed by collector's notes on various labels; and leaf morphology of the Bahamas plants is exactly the same as in those from the Virgin Islands. We therefore postulate that the Bahamas population was introduced to Matthew Town from St Croix by man, presumably by some early settlers or their slaves, who used the plant for brewing their "moujean tea" (Correll & Correll 1982).

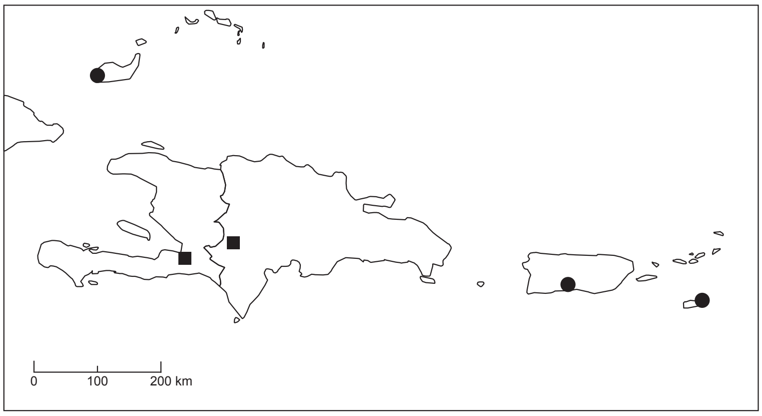


Fig. 5. Map of the total known distribution of *Nashia* (*N. inaguensis*, ●) and *Isidroa* (*I. spinifera*, ■).

*Conservation status* — Méndez (1997) made tentative conservation assessments for the five Cuban species then placed in *Nashia*, based on recent collections made by Cuban botanists, including himself. He considered two to be rare, two to be threatened, and one to be extinct. Based essentially on the same information, apposite workshops of Cuban botanists assessed first *N. nipensis* (Peña & al. 1998: 315–318), then the remaining four species (Lazcano & al. 2004: 119–122), as critically endangered (CR), an assessment confirmed for all of them by Berazaín & al. (2005: 48), and for *N. nipensis* by González-Oliva & al. (2014: 295). The problem is that, of all plant populations on which this analysis was based, only those of *N. cayensis* had been correctly named, all others were misidentified. A reappraisal is therefore necessary. To ease the task of the competent Cuban specialist group, the following suggestions are made. These are preliminary suggestions only, not full evaluations based on IUCN (2012) criteria.

*Diphyllocalyx armatus* has not been collected again since its discovery by Ekman in 1918. The vegetation at the locus classicus, now inaccessible, has been largely destroyed. The species might be considered as data deficient (DD) but is most likely extinct (EX).

*Diphyllocalyx cayensis* subsp. *cayensis* has been collected in three neighbouring localities at the south-eastern end of the island Cayo Romano. It likely forms a single population, with stands scattered over an area of at most 25 km$^2$. No concrete threat to the habitat is apparent, but based on the small occupancy area and depending on a census of individuals present, the taxon is either endangered (EN) or critically endangered (CR).

*Diphyllocalyx cayensis* subsp. *variifolius* has, of all the taxa treated here, the widest total range and highest number of known populations. Even so, depending on the results of a renewed survey, it might qualify as endangered (EN) rather than near threatened (NT).

*Diphyllocalyx galanus* is known from a single locality, where only one shrub has been observed. Efforts should be made to find out whether it still exists (as CR) or has become extinct (EX).

*Diphyllocalyx myrtifolius* has not been seen since its discovery over 150 years ago. We consider that the possibility of its being rediscovered is real and would therefore prefer to assign it to the data deficient (DD) rather than extinct (EX) category.

*Diphyllocalyx nipensis* would be in the same situation as *D. myrtifolius*, had it not been rediscovered in 2015 in a second locality, at a distance of c. 50 km from the locus classicus. We estimate the number of observed shrubs, all in a single clump, to be between 10 and 20. It is of course not unlikely that, in the future, further populations and localities of *D. nipensis* will be found, as there are still considerable unexplored areas of suitable "charrascal" vegetation in the foothills between Mayarí and Moa, Holguín province. Yet based on what is currently known, critically endangered (CR) status seems appropriate.

*Diphyllocalyx urquiolae* has been considered as critically endangered (CR) by Urquiola & al. (2010) based on their first-hand knowledge of the single known population of that species, then misnamed *Nashia myrtifolia.* We cannot but agree.

Cedeño & O'Reilly (1996) reported the occurrence on St Croix of 50–100 individuals of *Nashia inaguensis*, scattered over an area of less than 50 ha; and of c. 100 individuals on Puerto Rico, also confined to a limited area. They recommend prompt conservation measures, considering the species to be endangered.

Finally, the situation of *Isidroa* is obviously critical due to the fact that it is only known from two localities. The first, in Haiti, is a mountain top situated in an area affected to some degree by human settlement, between the villages of Kenscoff and Furcy; as nothing is known about population size and possible concrete threat, for Haiti data deficient (DD) appears to be the appropriate category. A second population was recently discovered in the Dominican Republic, at a distance of 80 km as the crow flies. Although the cloud forest in which the plant grows appears to be unspoilt, the fact that only two individuals have been found obviously means that *I. spinifera* in the Dominican Republic is critically endangered (CR). Appropriate conservation measures, both in situ and ex situ, should be enacted as a matter of urgency.

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