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Taxonomic studies in the Miconieae (Melastomataceae). XIII. Systematics of *Miconia subcompressa*, a Hispaniolan endemic comprised of three eco-geographic subspecies

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Abstract

The pattern of morphological variation in *Miconia subcompressa,* a species endemic to the mountains of southern Hispaniola, is assessed by a consideration of numerous herbarium specimens (many collected by the authors) and a phenetic (Principal Components) analysis of 14 vegetative characters, and morphological entities are compared with a phylogenetic hypothesis based on nrDNA-sequence variation (ITS, ETS) including several accessions of this species (from across its geographic and elevational range) as well as related species of *Miconia* sect. *Chaenopleura*, especially those of the Massif de la Hotte, Haiti. Our morphological data, incorporating recently collected herbarium material, indicate that the populations of *M. subcompressa* from the Monteada Nueva region (= Loma Trocha de Pey) are diagnosable morphologically from those of the Massif de la Selle and Massif de la Hotte, and these plants are described here as *Miconia subcompressa* subsp. *beverlyana*. Additionally, this study supports the recognition of the populations from moist pine forest/cloud forest habitats of the Massif de la Hotte, occurring mainly from 1450–2300 m, as *M. subcompressa* subsp. *plumieri* (= *M. plumerii,* sic). Finally, *Miconia subcompressa* may be paraphyletic, as preliminary molecular evidence suggests that *M. xenotricha* may have arisen within its phylogenetic structure.

Resumen

El patrón de variación morfológica en *Miconia subcompressa*, una especie endémica de las montañas del sur de la Española, está revisado considerando numerosos especímenes de herbario (muchos colectados por los autores), un análisis fenético (Componentes Principales) de 14 caracteres vegetativos y las entidades morfológicas están comparadas con una hipótesis filogenética basada en datos moleculares (ITS, ETS) que incluye varias accesiones de *M. subcompressa* (de todo su rango geográfico y de elevación) y otras especies de *Miconia* sect. *Chaenopleura*, especialmente las especies del macizo de la Hotte, Haití. Nuestros datos morfológicos, los cuales incorporan colecciones recientes, indican que las poblaciones de *M. subcompressa* de la región Monteada Nueva (=Loma Trocha del Pey) son reconocibles morfológicamente de las poblaciones del macizo de la Selle y del macizo de la Hotte, y aquí están descritas como *Miconia subcompressa* subsp. *beverlyana*. Adicionalmente, este estudio apoya el reconocimiento de las poblaciones de los hábitats del bosque de pino húmedo/nuboso del macizo de la Hotte, que ocurre mayormente de 1450–2300 m, como *M. sucompressa* subsp. *plumieri* (=*M. plumerii*, sic). Finalmente, es probable que la especie *Miconia subcompressa* es parafilético, dado que evidencia preliminar de datos moleculares sugiere que *M. xenotricha* se originó adentro de la estructura filogenética de *M. subcompressa*.

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Introduction

During recent fieldwork on Hispaniola in the Massif de la Hotte, Massif de la Selle, and the Sierra de Bahoruco, on Hispaniola, in conjunction with a phylogenetic and revisionary study of *Miconia* Ruiz & Pavón (1794: 60) s. lat. (Goldenberg *et al.* 2008, Michelangeli *et al.* 2008, 2013, Majure *et al.* 2013a), the authors (and also J.D. Skean, Jr. and J. Timyan) collected additional specimens of *Miconia subcompressa* Urban (1921b: 45), a member of *Miconia* sect. *Chaenopleura* (L.C. Richard ex de Candolle 1828: 197) J.D. Hooker (1867: 764) (Judd & Beaman 1988, Judd 2007) that highlighted some potential problems in our understanding of the systematics of this species, which is endemic to the mountains of southern Hispaniola (i.e., Massif de la Hotte and Massif de la Selle, in Haiti, and the Sierra de Bahoruco, the extension of the latter in the Dominican Republic). Therefore, the pattern of morphological variation within this species has been reassessed by comparing numerous herbarium specimens and the results of a phenetic (Principal Components; Sneath & Sokal 1973) analysis of 14 vegetative characters, in conjunction with a DNA-sequence based phylogenetic analysis including several accessions of *Miconia subcompressa* from across its geographical and elevational range along with several related species of *Miconia* sect. *Chaenopleura*, especially those occurring in the Massif de la Hotte.

Although *Miconia* has been shown to be an extremely polyphyletic genus (Goldenberg *et al.* 2008, Martin *et al.* 2008, Michelangeli *et al.* 2008, 2013), the species of *Miconia* sect. *Chaenopleura* occurring in the Greater Antilles form a clade that is supported by both morphological (Judd 2007) and DNA-sequence data (Judd 2007, Goldenberg *et al.* 2008, Michelangeli *et al.* 2008, 2013), following the circumscription of this clade presented in Judd (2007) with the addition of a few species previously treated in sect. *Cremanium* (D. Don 1823: 310) J.D. Hooker (1867: 764), e.g., *Miconia desportesii* Urban (1921a: 496) and *M. sphagnicola* Urban & Ekman (1931: 19; see Judd & Penneys 2004) and *M. alloeotricha* (Urban 1929: 64) Judd, Penneys & Skean (2004: 160). Members of the Antillean clade of *Miconia* sect. *Chaenopleura* are morphologically distinctive and easily distinguished from other *Miconia* species. They are united by their actinomorphic androecium (i.e., the stamens arranged in a radially symmetrical pattern around the style) of white stamens with erectly held, obovate anthers that open more or less by longitudinal slits, which expose the contents of the four locules (Figs. 2F, G, 4F). The presence of a radially symmetrical androecium of usually white anthers is shared with sect. *Cremanium*, but the other androecial features are likely synapomorphic for the Antillean clade of sect. *Chaenopleura*. Pale blue berries (Fig. 5) and more or less smooth seeds may also be synapomorphies of this clade (Judd 2007).

Phylogenetic relationships of the species within the Antillean clade of *Miconia* sect. *Chaenopleura* based on morphology (Judd 2007) and the recently published, DNA-based (i.e., nrITS and *ndhF* sequences), tribal-wide phylogenies that include numerous members of this clade (Goldenberg *et al.* 2008, Michelangeli *et al.* 2008) show little resolution within Antillean sect. *Chaenopleura*. It is likely that the Antillean species of sect. *Chaenopleura* represent a rapid radiation, following a single dispersal event into the Caribbean region (Judd 2007, Michelangeli *et al.* 2008). Phylogenetic analysis of morphological data suggests that *M. subcompressa* is most closely related to *M. septentrionalis* Judd & R. Beaman (1988: 383) and *M. jimenezii* Judd & R. Beaman (1988: 386), of mountains in the northern part of Hispaniola (Judd & Beaman 1988), *M. hypiodes* Urban & Ekman (1929: 38), of high elevations in the Massif de la Hotte (Judd 2007), and *M. rufa* (Grisebach 1866: 102) Triana (1871: 130), of the mountains of eastern Cuba (Judd 2007), on the basis of their abaxial leaf surfaces with dense, more or less ferrugineous, straight-armed, stellate hairs (Figs. 2E, 4B, E) and the large size of their berries (Figs. 2H, 5). However, this "densely-stellate clade" (Judd 2007) was not statistically supported and was evident only in some of the most parsimonious trees. *Miconia septentrionalis* and *M. jimenezii* differ from *M. subcompressa* in their 2- to 4-ridged twigs; in contrast, the twigs of *M. subcompressa* are terete (± elliptical in cross section, sometimes sulcate) (Figs. 2C, 4C). These two species also differ from *M. subcompressa* in having tertiary veins that are separated by composite-intertertiary veins, while the tertiary veins of *M. subcompressa* are connected by quaternaries (Fig. 4B, E; Judd & Beaman 1988, Judd 2007). *Miconia hypiodes* can be distinguished readily from *M. subcompressa* (and also *M. septentrionalis*, *M. jimenezii*) by its smaller leaves and flowers with a 3-loculate (vs. 5-loculate) ovary. Finally, *M. rufa* is separable from all of its putative relatives by the form of the hairs on the abaxial leaf surface, i.e., elongate-branched to globular-stellate vs. consistently globular-stellate (Judd 2007). Of these species, only *M. hypiodes* occurs sympatrically with *M. subcompressa*—in the high elevation, cloud forests/moist pine forests of the Massif de la Hotte.

Measurements, terminology, methods and species/subspecies concepts

About 190 specimens were examined for this study, a robust sampling given the limited distribution of these plants and their occurrence primarily in Haiti, which has been poorly collected. The authors (together) have made 30 collections

(86 specimens) from across the geographical and elevational range of this species, during the course of 11 field trips to Hispaniola between April 1976 and January 2013. The remaining specimens are from the herbaria listed in the Acknowledgments [abbreviations follow Thiers (2012)]. One hundred and thirty-two different characteristics were measured or observed within *M. subcompressa* (see Judd 2007 for terminology and methodology details).

All measurements included in the key and descriptions were taken from dried herbarium material, with the exception of plant height, color of the adaxial leaf surface, and flower and fruit color, which were assessed from information given on specimen labels, field observations, or from photographs. Extent of impression of veins on the adaxial leaf surface was assessed in the field, by using photographs, and also using herbarium material (although pressing distorts this character, making it harder to observe in dried material). The angle of the leaf apex (to the midvein) of fully mature leaves was measured using a protractor, placing the line at the zero degree mark over the midvein, and drawing a parallel line 1.5 cm away from the line covering the midvein; the intersection of the leaf margin with the line 1.5 cm away was marked, and a line was drawn from this intersection to the leaf apex; the angle between this line and the midvein line was then recorded. Terminology and measurement methodology, other than leaf angle, follows Judd (2007) except that the outgrowths of the abaxial surface of the calyx lobes are here termed calyx teeth rather than "external calyx lobes" and the sterile extension of the ovary apex, which surrounds the base of the style, is referred to in this publication as a collar. The characteristic branched hairs of these species ("dendritic hairs with a short axis" in Wurdack 1986, see fig. 151) are here referred to as globular-stellate.

In addition to subjectively assessing morphological variation through observations of herbarium material, a quantitative phenetic analysis (i.e., Principal Components Analysis) was conducted using M.V.S.P. (Kovach 2010). This analysis employed 14 continuously varying, "count" or qualitative multistate characters assessed on 66 individual leaves from 48 specimens of *Miconia subcompressa* (i.e., those indicated with an asterisk in the specimens examined). These characters are 1) stem indumentum (coded as 0 = hairs erect, dendritic to globular stellate; 1 = hairs intermediate, erect to appressed; 2 = hairs appressed, globular-stellate), 2) development of adaxial bullate-ridge on adaxial leaf surface (0 = such ridge absent, 1 = ridge slightly developed, 3 = ridge well developed); 3) color of abaxial leaf surface (0 = white, 1 = pale ferrugineous, 2 = orange, 3 = deep orange to reddish-brown); 4) lamina length/distance from base of lamina to point along midvein corresponding to where lamina is widest; 5) length of largest marginal serration on lamina; 6) angle of leaf apex (measured as indicated above); 7) number of secondary veins in lamina; 8) length/width quotient of lamina; 9) shape of leaf base (0 = acute, 1 = obtuse, 2 = rounded, 3 = slightly cordate); 10) leaf width; 11) petiole length; 12) distance from innermost secondary vein to leaf margin, at widest point of lamina; 13) distance between tertiary veins, taken as average of two measurements per leaf); 14) shape of leaf apex (0 = ± acute, 1 = ± acuminate or slightly so, 3 = shortly acuminate, 4 = obtuse or obtuse-mucronate). The analysis was first run with all OTUs, and then run a second time with the more phenetically divergent phenetic cluster (i.e., OTUs of *M. subcompressa* subsp. *beverlyana*) removed, in order to increase the separation between the remaining OTUs. The data were centered before each analysis was run.

The majority of leaf material was preserved in the field in silica gel (Chase and Hills 1991), however, several leaf samples were taken directly from herbarium specimens. Genomic DNA was extracted using a modified cetyl trimethylammonium bromide (CTAB) technique (Doyle & Doyle 1987), scaled to a 1-ml volume reaction. Approximately 10 mg of dried tissue were ground in 1-ml of CTAB 2X buffer and 10 µl of proteinase-K. Some total DNAs were then cleaned with Qiagen QIAquick PCR purification columns to remove any inhibitory secondary compounds. We sampled the nuclear ribosomal ITS and ETS regions.

Amplifications were performed using an Eppendorf Mastercycler EP Gradient S thermocycler and Sigma brand reagents in ~25-µl volumes with the following reaction components for ITS and ETS: 1 µl template DNA (~10–100 ng), 11 µl water, 7 µl 5M betaine, 2.5 µl 10X buffer, 2.5 µl $MgCl_2$ (25 mM), 0.5 µl of 10 µM dNTPs, 0.5 µl each of 10 µM primers, and 0.5 units (0.2 µl) *Taq*.

The nuclear loci ITS (Internal Transcribed Spacer, including ITS 1 + 5.8S rDNA+ ITS 2) and ETS (External Transcribed Spacer) were amplified using a protocol using the parameters 99°C, 2 min; 35X (94°C, 20 s; 55°C, 20 s; 72°C, 1 min); 72°C, 2 min with the primers F (TAG AGG AAG GAG AAG TCG TAA CAA) and R (CCC GCC TGA CCT GGG GTC GC) from Hoshi *et al.* (2008) for ITS and primers ETSF (GTA CGG GTT GCA TTT CGA TCC TCC GG; Majure *et al.* submitted), and NY320 (AGA CAA GCA TAT GAC TAC TGG CAG G) from Michelangeli *et al.* (unpubl. data). Alternatively, for very low quality DNAs, ITS was amplified in two pieces that have partial overlap using primers designed for general angiosperms (ITS-A + ITS-C and ITS-D + ITS-B, Blattner 1999), and omitting betaine with that volume replaced by water (Neubig 2005).

GenBank accession numbers for sequences are given in Appendix 1.

Sequences were edited using Sequencher 4.2.2 (Gene Codes, Ann Arbor, Michigan, USA) and manually aligned in SeAl v. 2.0 (Rambaut 2007). We analyzed our combined data set (including both ETS and ITS) using Maximum Parsimony (MP) and Maximum Likelihood (ML). Maximum Parsimony analysis was carried out in PAUP* (Swofford 2002) by conducting 1000 random addition sequence replicates, and clade support was evaluated by running 1000 nonparametric bootstrap (BS) pseudoreplicates, each with 10 addition sequence replicates. Maximum Likelihood analysis was carried out in RAxML (Stamatakis 2006) using the GTR + Γ model of molecular evolution under 25 rate categories. Clade support was evaluated by running 1000 nonparametric BS pseudoreplicates, as in MP. *Miconia howardiana* Judd, Salzman & Skean (1995: 416) was used as an outgroup based on previous phylogenetic analyses (Goldenberg *et al.* 2008, Michelangeli *et al.* 2008, Michelangeli *et al.*, unpubl. data, Majure *et al.* unpubl. data).

Species delimitations are based on the morphological-phenetic species concept (Judd 2007), i.e., species are morphologically cohesive entities that are separated from others by consistent morphological gaps, in conjunction with the diagnostic species concept (Davis & Nixon 1992, Wheeler & Platnick 2000). This morphological information was considered along with the phylogenetic insights provided by the DNA-based phylogenetic analysis, keeping in mind the phylogenetic species approach (Donoghue 1985, Mishler & Brandon 1987, Mishler & Theriot 2000). However, some speciation mechanisms (e.g., peripheral isolation, parapatric speciation) frequently lead to species non-monophyly (see extensive discussion in Rieseberg & Brouillet 1994, Olmstead 1995, Crisp & Chandler 1996, Vanderpoorten & Shaw 2010) and thus we acknowledge that evidence for paraphyly does not necessarily provide strong evidence for combining paraphyletic and nested species. Subspecies are considered to be entities evolutionarily comparable to species, but phenetically more similar, showing incomplete differentiation, and thus not as easily diagnosed. The pattern of variation characteristic of subspecies is often strongly correlated with geography (Mayr & Ashlock 1991, Winston 1999), with infraspecific entities exhibiting more or less allopatric or ecologically divergent distributional patterns. We follow the recommendations of Ellison *et al.* (2014) in using the rank of subspecies for such entities.

Results

The cladogram (Fig. 1) resulting from our analyses of DNA sequence data shows little resolution, supporting the results of earlier molecular analyses that suggest a rapid radiation of Antillean species of *Miconia* sect. *Chaenopleura*. Additionally, it suggests that the rate of morphological change is often greater than that of sequence evolution since accessions representing morphologically divergent species, e.g., *M. dielsiana* Urban (1931: 22), *M. ferruginea* (Desrousseaux 1797: 42) de Candolle (1828: 182), *M. samanensis* Urban (1929: 46), and *M. selleana* Urban & Ekman (1926: 27), are unresolved, represented by short branches in a polytomy (see also Judd 2007); however, a few morphologically divergent species, i.e., *M. hypiodes* and *M. foveolata* Cogniaux (1886b: 281), show a larger number of putative DNA sequence apomorphies. The high elevation Massif de la Hotte endemics *Miconia hypiodes* and *M. barkeri* are supported as sister species, a placement at odds with the earlier morphology-based hypothesis (Judd 2007) that considered *M. hypiodes* to be most closely related to *M. subcompressa* (based on the density and form of the hairs on the abaxial leaf surface). Finally, our molecular analyses suggest that *M. subcompressa* may not be monophyletic, since several populations from the Massif de la Hotte (i.e., *Ionta 2036, Majure 4276,* and *Timyan 29*) form a clade with *M. xenotricha* Urban & Ekman (1929: 32). Interestingly, these populations are morphologically undiagnosable from other populations of *M. subcompressa* not allied with *M. xenotricha* in our molecular analyses, e.g., *Timyan 18* (from Tete Boeuf, in the Massif de la Hotte) and *Judd 8116* (from Sierra de Bahoruco). However, the cladogram topology is not well supported, and *M. subcompressa* would be monophyletic (discounting the position of *M. xenotricha*) if the populations represented by *Judd 8116* and *Majure 4362* were moved to a basal branch on the clade comprising the other accessions of *M. subcompressa*. (Such a placement is not rejected by our tree topology and is strongly supported by morphology, as *Judd 8116* is very similar to *Timyan 18* and *29*, *Majure 4276* and *Ionta 2036;* and *Majure 4362* is extremely similar to *Ionta 2034*).

Our morphological consideration of numerous herbarium specimens indicates that the populations of *Miconia subcompressa* growing in the Sierra de Bahoruco east of the Hoyo de Pelempito, i.e., the "Monteada Nueva" region, are morphologically more or less diagnosable from those occurring farther west, i.e., in the Sierra de Bahoruco west of the Pelempito depression, in the adjacent Massif de la Selle, and in the Massif de la Hotte (Fig. 3). These "Monteada Nueva" populations have broad leaves (i.e., length/width quotient of blade 1.5–2.15) with the leaf apex obtuse, obtuse-mucronate, or broadly and shortly acuminate, forming an angle of 44–76° to midvein, and the base rounded to slightly cordate (Fig. 5). They also tend to have slightly shorter calyx lobes, i.e., 1–1.7 mm long (see Figs. 5 and 2F, H). The contrasting character conditions of the plants of the Massif de la Selle/Sierra de Bahoruco west of the Hoyo de

Pelempito and the Massif de la Hotte are indicated in the key and the descriptions. However, these distinctions are nearly continuous—as seen in the range of values of both the length/width quotient and the leaf angle. In addition, all other morphological characters are either the same or show broadly overlapping ranges (see descriptions). In our DNA-based phylogenetic analyses the "Monteada Nueva" entity of *M. subcompressa* is represented by several accessions (i.e., *Judd 8085, 8098* and *8110*) placed with representatives of *M. subcompressa* from the Massif de la Hotte in the unresolved, basal part of a clade that also includes *M. xenotricha* (Fig. 1, 6). Few DNA-based molecular markers, however, support this clade, so phylogenetic relationships are unclear.

FIGURE 1. Most likely topology from our ML analysis (topology identical to our 50 % majority rule phylogeny using MP) of numerous accessions of *Miconia subcompressa* and various other species of *Miconia* sect. *Chaenopleura* based on our combined ETS/ITS data set. Bootstrap values for ML and MP are given above branches (i.e., ML/MP).

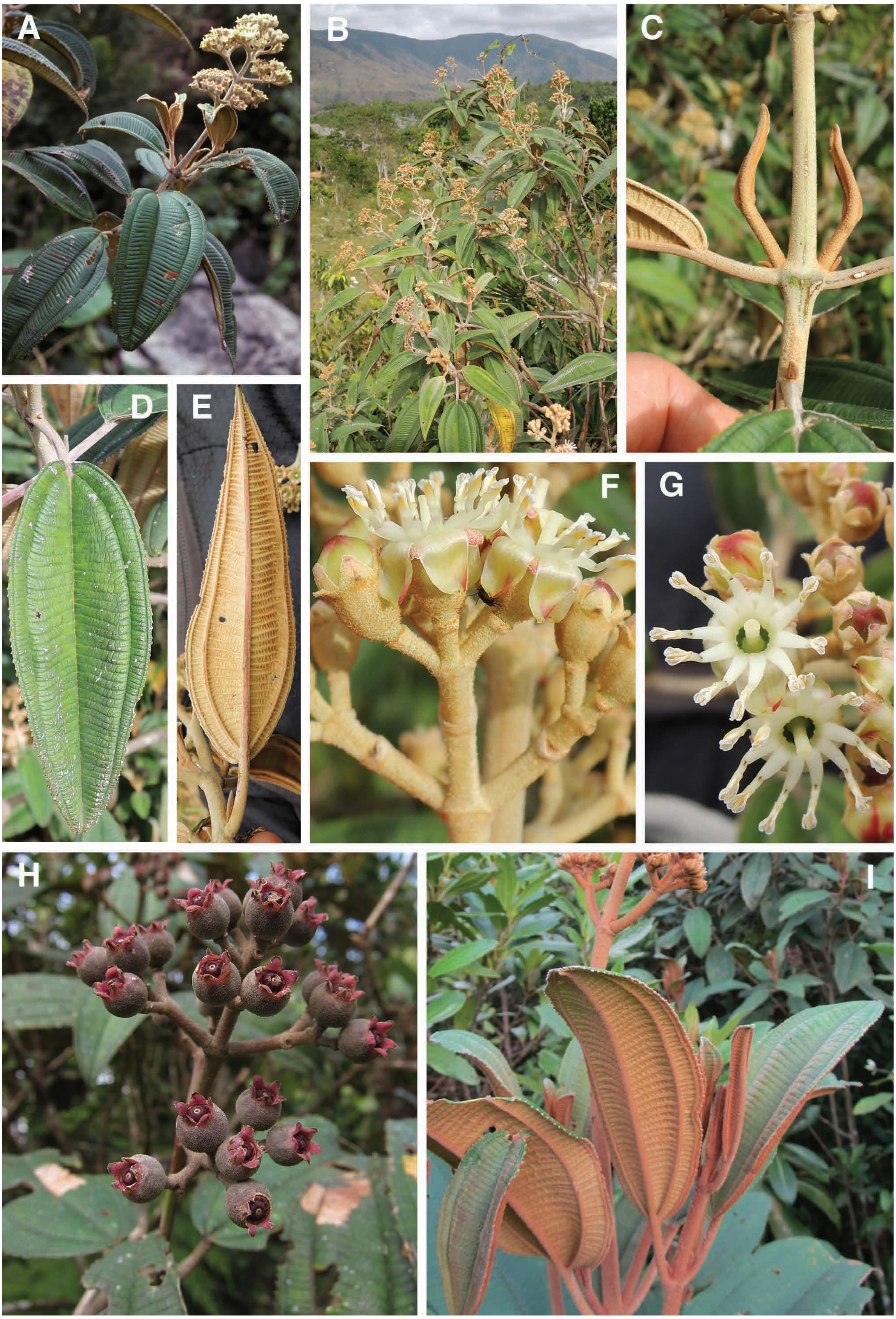

FIGURE 2. *Miconia subcompressa* subsp. *subcompressa*. A. Branch with flowers and young fruits; note lack of longitudinal "ridge" on adaxial leaf surface (*Judd 3933*, from Massif de la Hotte, 1200 m). B. Habit (*Majure 4276*; Massif de la Hotte, 989 m). C. Stem; note appressed hairs (*Majure 4276*). D. Leaf, adaxial surface (*Majure 4276*). E. Leaf, abaxial surface; note acute apex, pale ferrugineous indumentum (*Majure 4276*). F. Flowers, side view; note well developed calyx lobes (*Majure 4276*). G. Flowers, top view; note actinomorphic androecium of white stamens with obovate anthers opening by longitudinal slits (*Majure 4276*). H. Berries, nearly mature; note rather large calyx lobes (*Timyan 35*; Massif de la Hotte, 1156 m). I. Branch with young inflorescence; note moderately ferrugineous abaxial leaf indumentum (*Timyan 11*; Massif de la Selle, 1443 m). Photo A taken by W.S. Judd, B–G taken by G.M. Ionta, and H–I taken by J. Timyan.

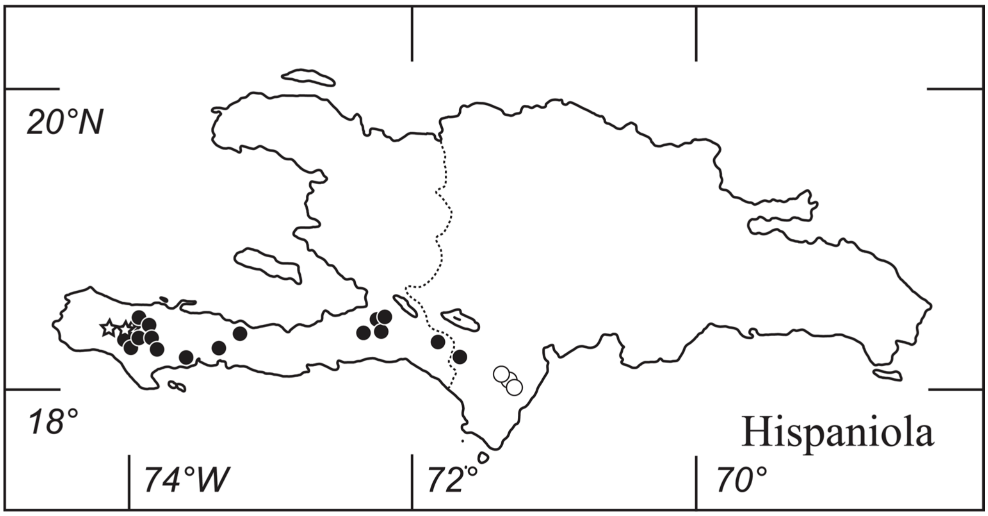

FIGURE 3. Distribution of *Miconia subcompressa*. *Miconia subcompressa* subsp. *beverlyana* (open circles), *M. subcompressa* subsp. *subcompressa* (close circles), *M. subcompressa* subsp. *plumieri* (open stars).

The populations of *Miconia subcompressa* in the Massif de la Hotte are highly variable, with the variation correlated with both forest type and elevation. Plants of cloud forest and moist forest of *Pinus occidentalis* Swartz (1788: 103, Pinaceae), occurring mainly at elevations of 1450–2300 m (recognized as *Miconia plumerii,* sic, by Urban and Ekman 1929) have stems with more or less erect dendritic to globular-stellate hairs (Fig. 4C), while populations in moist forests over limestone (i.e., *rak bwa*), usually at elevations of 700–1550 m, have stems with more or less appressed, globular-stellate hairs (and represent the nominate element of *M. subcompressa*) (Fig. 2C). The cloud forest/pine forest entity also usually has leaves with more strongly bullate areoles, and an evident "ridge" of especially bullate areoles running longitudinally between the midvein and innermost secondary vein (Fig. 4B, D; vs. leaves lacking this "ridge" or with only a slightly developed bullate "ridge," Fig. 2A, D). This feature, unfortunately, is often obscured in dried material. The cloud forest/pine forest populations tend to have more darkly ferrugineous hairs on the abaxial leaf surface (compare Fig. 4B, E with Fig. 2E), however, there is complete intergradation of abaxial coloration (see key, and Fig. 2I). Finally, the leaves of the cloud forest/pine forest populations are more frequently elliptic or oblong-elliptic, and also tend to have less well-developed marginal serrations (Fig. 4B), but extensive overlap in the range of variation occurs (see descriptions). The DNA-based phylogenetic analyses are insufficiently resolved to support the differentiation of the cloud forest/pine forest populations from those of the lower elevation *rak bwa* in the La Hotte Mountains (Fig. 1). Our two accessions representing these cloud forest/pine forest populations (i.e., *Ionta 2034* and *Majure 4290*) are not placed as sisters, instead both are positioned in a highly unresolved portion of the cladogram, including other accessions of *M. subcompressa*, as well as other species of *Miconia* sect. *Chaenopleura.*

The La Hotte plants characteristic of *rak bwa* (i.e., nominate element of *M. subcompressa*) are not morphologically distinguishable from those populations of *M. subcompressa* growing farther east in the Massif de la Selle and the adjacent regions of the Sierra de Bahoruco (west of the Hoyo de Pelempito). There is a slight tendency for the La Selle plants to have more intensely ferrugineous abaxial leaf surfaces (Fig. 2I), but again, complete intergradation occurs, and some La Hotte *rak bwa* specimens are indistinguishable from those from the Massif de la Selle or the Sierra de Bahoruco. In addition, some collections from the Massif de la Selle, e.g., *Judd 4251*, *Skean 2040*, have scattered more or less erect, dendritic hairs on their stems. Our molecular phylogeny (Fig. 1) places the accession of *M. subcompressa* from the Sierra de Bahoruco (west of the Hoyo de Pelempito) within a large polytomy that also includes a population from the Massif de la Hotte (*Majure 4290*, from south slope of Morne Formon), while most of the *rak bwa* populations comprise a clade (along with *M. xenotricha*). This is puzzling since the *rak bwa* La Hotte populations of *M. subcompressa* are not morphologically diagnosable from those of the Massif de la Selle or the Sierra de Bahoruco (west of the Hoyo de Pelempito), however, statistical support for this divergent placement of *Judd 8116* is nonexistent.

FIGURE 4. *Miconia subcompressa* subsp. *plumieri*. A. Branch with young fruits (*Judd 3669*). B. Leaves, adaxial and abaxial surfaces; note oblong-elliptic to ovate shape, adaxial longitudinal “ridge” formed by bullate areoles between midvein and innermost secondary veins, abaxial dark ferrugineous indumentum, adaxial and tertiary veins connected by percurrent quaternary veins (*Judd 3669*). C. Stem; note erect-scurfy hairs (*Majure 4290*). D. Leaf, adaxial surface; note prominent “ridge” formed by bullate areoles between midvein and innermost secondary veins (*Majure 4290*). E. Leaf, abaxial surface; note dark ferrugineous indumentum (*Majure 4290*). F. Flowers (*Majure 4290*). Photos A–B taken by W. S. Judd, C–F taken by G. M. Ionta.

FIGURE 5. *Miconia subcompressa* subsp. *beverlyana*. A. Branches with flowers and fruits; note blunt leaf apices (*Judd 5177*). Photo taken by W.S. Judd..

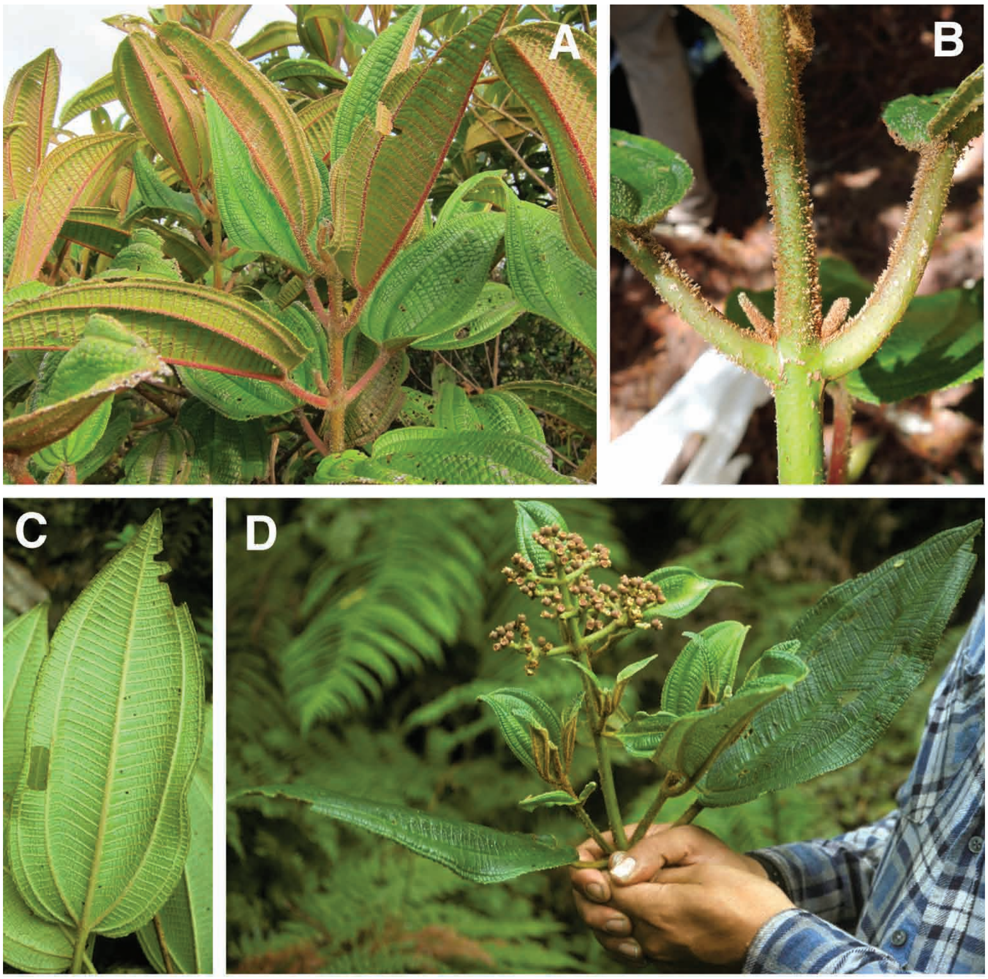

FIGURE 6. *Miconia xenotricha*. A. Habit; note slightly cordate base and bullate adaxial surface (*Timyan s.n.*), B. Stem; note erect dendritic hairs and nodal lenticels (*Majure 4293*), C. Abaxial leaf surface; note evident epidermis (*Judd 6971*), D. Inflorescence; note rounded form (*Judd 6971*). Photo A taken by J. Timyan, B taken by G.M. Ionta, and C–D taken by W.S. Judd.

The results of the principal components analyses (Figs. 7, 8) support our conclusions based on more subjective observations of herbarium material, and also provide useful visualization of the pattern of variation along with reinforcement of the characters useful in diagnosing the eco-geographical entities encountered within *Miconia subcompressa*. The OTUs representing populations from the mountains east of the Hoyo de Pelempito, i.e., "Monteada Nueva" region, are phenetically distinctive, being separated mainly on PC I (Fig. 7), which is significantly correlated with the angle of the leaf apex and leaf width (PCA character loadings of 0.990 and 0.111 respectively, and representing the two highest character loadings). The populations west of the Hoyo de Pelempito form the second cluster, within which no clear gaps are seen. In order to more clearly investigate phenetic relationships within this cluster, the OTUs representing the specimens collected east of the Hoyo de Pelempito were removed and the analysis run a second time. This analysis (Fig. 8) indicates that populations of cloud forest/moist pine forest habitats in the Massif de la Hotte are slightly differentiated from those of lower elevation, *rak bwa* habitats, and these two phenetic groups are separated along PC II, for which the highest character loadings (in order of importance) are: leaf width (0.712), distance between the tertiary veins (0.368), petiole length (0.301), stem indumentum (0.246), leaf base (0.208), leaf teeth size (0.153), and number of secondary veins (0.114). Additionally, the characters of abaxial leaf color (-0.233)and development of bullate lamina ridge (-0.224) are both significantly negatively loaded onto PC II. However, no clear phenetic gap in the pattern of variation is evident—the cloud forest/pine forest and *rak bwa* entities intergrade (Fig. 8).

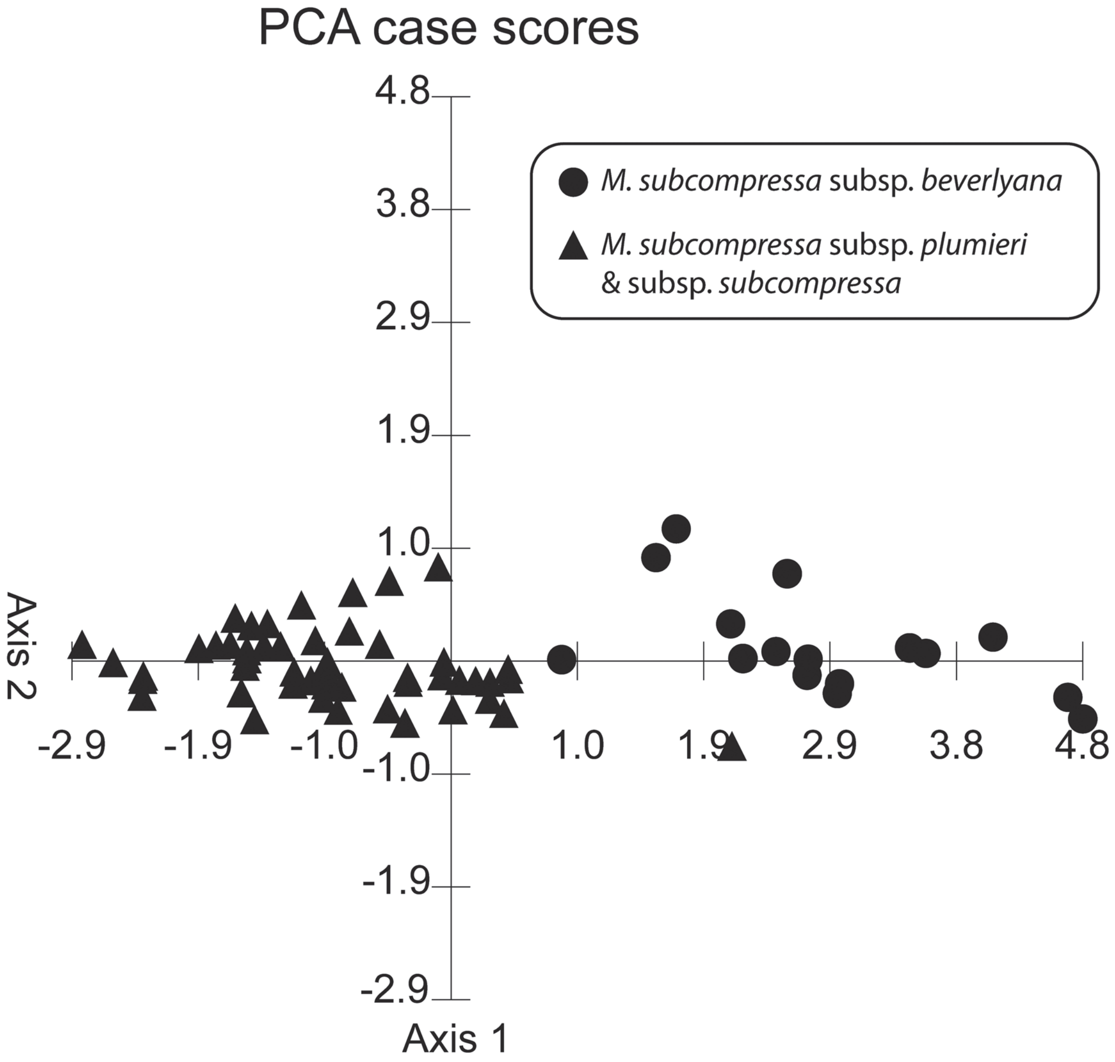

FIGURE 7. Graph of the first two principal components resulting from phenetic analysis of *Miconia subcompressa* complex. PC I describes 95.079% of the variation; PC II describes 3.274% of the variation. Triangles represent OTUs of populations of *M. subcompressa* west of the Hoyo de Pelempito, while circles represent OTUs of populations of *M. subcompressa* east of this depression, i.e., subsp. *beverlyana,* of the "Monteada Nueva" region.

Discussion

Given the pattern of morphological variation (summarized above, but see also key and descriptions) and the topology of our phylogenetic analysis (Fig. 1), what is the best taxonomic treatment of *Miconia subcompressa* (as circumscribed by Judd 2007)? Certainly the populations of this species occurring in the Massif de la Hotte and Massif de la Selle/Sierra de Bahoruco, of southern Hispaniola, are phenetically easily diagnosable from *M. septentrionalis* and *M. jimenezii*, both of which occur only in northern Hispaniola (Judd & Beaman 1988, Judd 2007). Our phylogenetic results also suggest that these southern Hispaniolan populations are closely related, as little sequence divergence is seen, and they fall within a large polytomy except for *Judd 8116* and *Majure 4362* (Fig. 1). However, as noted above, it is likely (on morphological grounds) that these two accessions also belong within the large clade containing the remaining accessions of *M. subcompressa*. *Miconia subcompressa* is certainly morphologically cohesive (Figs. 7, 8), and it is separated from the other species of *Miconia* sect. *Chaenopleura* by a discrete gap in the pattern of variation (i.e., it is a morphological-phenetic species; Judd 2007). Yet the phenetically distinct and easily differentiated *M. xenotricha*

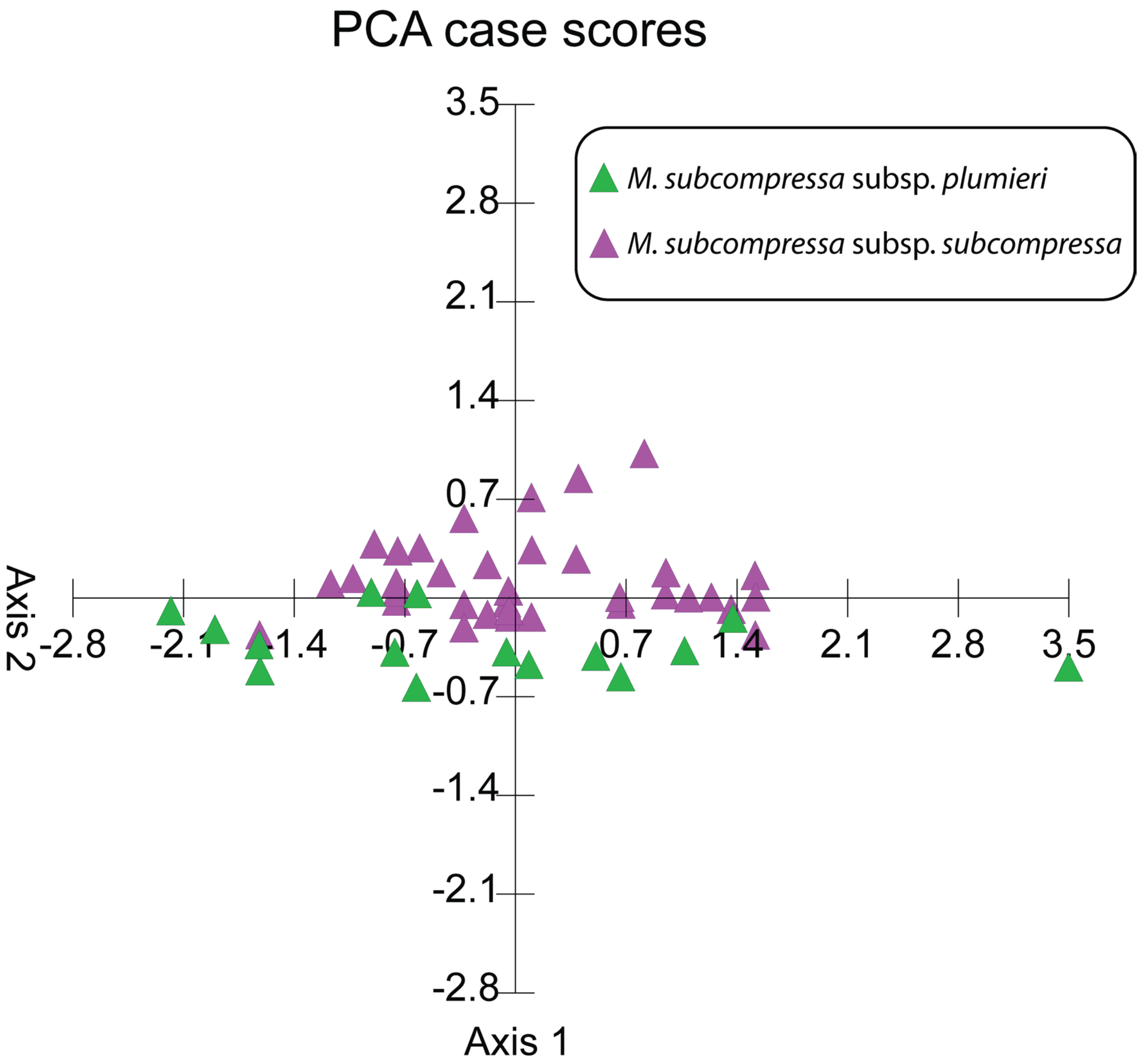

FIGURE 8. Graph of the first two principal components resulting from a phenetic analysis of the *Miconia subcompressa* complex, excluding the OTUs representing populations east of the Hoyo de Pelempito. PC I describes 85.165% of the variation; PC II describes 8.622% of the variation. Pink triangles represent OTUs of subsp. *subcompressa* (plants of usually lower elevation*, rak bwa* habitats), while green triangles represent OTUs of subsp. *plumieri* (plants of usually higher elevation, cloud forest or pine forest habitats).

(Fig. 6), which was supported as not closely related to *M. subcompressa* in a morphology-based phylogenetic analysis (see Judd 2007), is suggested as derived from within *M. subcompressa,* especially the *rak bwa* populations of the Morne Formon region, Massif de la Hotte, i.e., *Ionta 2036*, *Majure 4276*, *Timyan 29* (Fig. 1). Perhaps the pattern of molecular divergence is not well correlated with morphological diversification, and one could envisage a mosaic pattern of geographically correlated divergence, with related allopatric or ecologically isolated populations undergoing unequal rates of morphological and molecular divergence. Thus *M. xenotricha* may have diverged markedly in its morphological characters, as evidenced by this species differing from *M. subcompressa* in its nodes with prominently thickened lenticels (Fig. 6B), frequently cordate-based leaves (Fig. 6A, C, D), more strongly bullate leaf areoles (Fig. 6A), having dendritic hairs on the abaxial leaf surface that do not obscure the epidermis (Fig. 6A, C), and inflorescences with rounded cymes (Fig. 6D; and Judd *et al.* (2012, fig. 3); see also Judd (2007), in which this species is suggested to be more closely related to *M. favosa*, *M. sintenisii* Cogniaux (1886b: 281), and *M. howardiana,* than to *M. subcompressa*).

In contrast, the populations of *M. subcompressa* are morphologically either only minimally divergent (in the case of the populations from the "Monteada Nueva" region, and those of the high elevation, cloud forest/pine forest habitats of the Massif de la Hotte; Figs. 7, 8) or non-divergent (in the case of the populations from the Massif de la Selle and the lower elevation, *rak bwa* habitats of the Massif de la Hotte), and thus were considered together, as *M. subcompressa,* by Judd (2007). Among these *M. subcompressa* populations, most also show very little molecular divergence, with the exception of the *rak bwa* populations of the Morne Formon region of the Massif de la Hotte, which are more strongly divergent in DNA sequence characters, some of which are shared with *M. xenotricha* (Fig. 6). This lack of resolution among the populations of *M. subcompressa* limits our ability to use molecular data to infer phylogenetic relationships within this species. Until molecular markers with more resolving power at this level are identified (e.g., microsatellites)—activities beyond the scope of this paper—morphology, which seems to be evolving more rapidly than DNA sequences, is considered to be more useful for elucidating relationships within the *M. subcompressa* complex.

Given our still quite preliminary molecular phylogenetic results and the phenetic similarity (and lack of easy diagnosability) among the geographically isolated populations of *Miconia subcompressa* in southern Hispaniola, we suggest that the "Monteada Nueva" entity (= populations of the Sierra de Bahoruco, in the region east of the Hoyo de Pelempito; Fig. 5) and the *M. plumieri* entity (= populations of the Massif de la Hotte, in cloud forest/moist pine forest; Fig. 4) each be recognized at the subspecific level, within a broadly circumscribed *M. subcompressa*. The populations from the low elevation *rak bwa* of the Massif de la Hotte and the populations occurring in cloud forests, moist montane forests, and pine forests of the Massif de la Selle/Sierra de Bahoruco (west of the Hoyo de Pelempito) together comprise the third (and nominate; Fig. 2) subspecies. This approach is appropriate given the difficulty in diagnosing these three entities and the lack of resolution in the DNA-based phylogeny, even though the species is supported (see Fig. 1) as paraphyletic. Thus, the morphologically divergent and clearly specifically distinct *M. xenotricha* (Fig. 6) may be its closest relative (Fig. 1). *Miconia xenotricha* likely is a cladospecies, as evidenced by its distinctive morphology, especially the unusual indumentum of the stems (Fig. 6B) and abaxial leaf surfaces (Fig. 6C)and greenish white petals (see Judd 2007). Parapatric/peripheral isolate speciation mechanisms should inevitably lead to such patterns, i.e., non-monophyletic and phylogenetically unresolved species should be common (see general discussion in Donoghue 1985, Olmstead 1995, Reiseberg & Brouillet 1994, Reiseberg & Brouillet 1994, Willman & Meier 2000, de Queiroz 2007, Vanderpoorten & Shaw 2010, and the specific examples in Crisp & Chandler 1996, Thulin *et al.* 2012, Porter-Utley 2014). Thus, as stated by Vanderpoorten and Shaw (2010, p. 234), "evidence for paraphyly does not necessarily provide strong evidence for combining paraphyletic and nested species"—and we emphasize that it is not at all problematic that *M. subcompressa*, as here circumscribed, is non-monophyletic. Vanderpoorten and Shaw (2010) further note that nucleotide sequence data from one or a few loci are often insufficient at the species level. We agree, along with many others (e.g., Despres *et al.* 2003, Hughes *et al.* 2006, Fazekas *et al.* 2009). We note, additionally, that nucleotide sequence data may be impacted by hybridization and/or lineage sorting (see discussion in Edwards *et al.* 2006, 2008a, 2008b, 2009). Therefore, at this time, we consider the pattern of morphological variation, as illustrated in Figures 7 and 8 and reflected in our careful study of herbarium material (see key and descriptions), to be more reflective of evolutionary pattern within *M. subcompressa* than our poorly resolved DNA-based phylogeny (Fig. 1). More empirical study is needed, of course, to determine the extent of non-monophyly among plant species (Rieseberg & Brouillet 1994), but we believe it is important to build up evidence regarding the extent of non-monophyly at the species level. Our tentative phylogenetic result, i.e., that the morphologically divergent *M. xenotricha* (Fig. 6) is likely derived out of a non-monophyletic *M. subcompressa* (Figs. 2, 4, 5), is thus significant, and it should be added to the growing list of such examples (see Crisp & Chandler 1996, Vanderpoorten & Shaw 2010, Thulin *et al.* 2012, Porter-Utley 2014). The "Monteada Nueva" entity is spatially (thus likely reproductively) isolated from populations of *Miconia subcompressa* to the west of the Hoyo de Pelempito, a geological depression. Habitat specialization in the La Hotte region, i.e., *rak bwa* vs. moist pine forest/cloud forest, likewise may limit gene exchange between the *M. plumerii* entity and the nominate entity of *M. subcompressa*. However, the somewhat mosaic pattern of morphological variation in the plants of the Massif de la Hotte, coupled with evidence that the two entities can occur in close proximity (see *Ionta 2036*, *Judd 4034*) suggest that some interbreeding may occur. The presumed lack of interbreeding between populations of the "Monteada Nueva" region and those occurring farther west may be one reason why these populations are phenetically more clearly differentiated than are the ecological entities within the Massif de la Hotte (compare Figs. 7, 8).

Therefore, we describe one new subspecies (for the "Monteada Nueva" populations) and propose recognition of *Miconia plumieri* at subspecific rank, under *M. subcompressa*.

Taxonomy

1. ***Miconia subcompressa*** Urban, Ark. Bot. 17(7): 45, 1921.

Type:—HAITI. Dept. du Sud, Massif de la Hotte, near aux Cayes, ca. 800 m, fl, 11 Jun 1917, *E. L. Ekman H206* (holotype S!).

Evergreen shrub or small tree to ca. 5 m tall. Indumentum of multicellular, ferrugineous, globular-stellate hairs. Young twigs not ridged, ± elliptic in cross-section, 4–9.5 (–11) mm wide, sometimes ± sulcate, becoming terete with age, the indumentum usually dense, globular-stellate to elongate-stellate or dendritic hairs, often ± glabrescent with age; internodes 1–7.5 (–9) mm long. Leaves with petiole 1–5 cm long, the indumentum dense; blade 6.3–31.5 cm long, 2.3–12 (–15.8) cm wide, with length/width quotient 1.5–3.85 (–4.9), ovate to elliptic or elliptic-oblong, sometimes broadly so, ± flat, coriaceous, the apex acute to slightly and/or shortly acuminate, or obtuse to obtuse- or rounded-mucronate, the base acute or obtuse to slightly cordate, the margin plane, obscurely to clearly and irregularly serrate, the largest teeth 0.2–4 mm long, becoming entire near base, 3–33% of margin entire; venation acrodromous, slightly suprabasal, with midvein and 4 or 6 secondary veins, with 2 conspicuous (i.e., the innermost) secondary veins placed 3–27 mm from margin and 4 or 2 inconspicuous secondary veins closer to margin, and numerous percurrent tertiary veins oriented subperpendicular to midvein, the tertiary veins jointed by percurrent-orthogonal quaternary veins; adaxial surface green to dark green, shiny to dull, the indumentum dense when young, but quickly glabrescent, the midvein and major secondary veins impressed, minor secondary, tertiary veins, quaternary veins, and some and higher order veins slightly impressed, and the areoles thus slightly to moderately bullate and sometimes with a "ridge" of prominently bullate areoles running longitudinally between midvein and innermost secondary vein (but both extent of areole bullation and development of "ridge" obscured when blade pressed and dried), the surface minutely papillose when dry due to numerous druse crystals; abaxial surface ± ferrugineous, nearly white to dark reddish brown, sometimes with darker hairs on the veins than the lamina, densely covered with multicellular, globular-stellate hairs to ca. 0.8 mm across (but epidermis only moderately covered in very juvenile material), the midvein and major secondary veins prominently raised, minor secondary and tertiary, and quaternary veins raised, the higher order veins slightly to not at all raised. Inflorescences many-flowered, open, paniculate cymes of usually 3–5 major branch-pairs, 3.5–15 cm long, 3.5–12 cm in diameter; proximal segment of lowermost inflorescence branches 1–4.7 cm long, distal internodes increasingly shorter, the ultimate branches (1.5–) 2–6 mm long, all with dense pale to deeply ferrugineous globular-stellate indumentum; peduncle 3–10.5 cm long; each inflorescence branch associated with an early caducous, broadly elliptic to narrowly ovate bract, 5.5–15 mm long, 1.5–2.5 mm wide, the apices acute; flowers in dichasia, each flower associated with a pair of caducous, narrowly elliptic to ovate or linear bracteoles, ca. 2–6 mm long, 0.5–1 mm wide, the indumentum dense, their apices acute to obtuse. Flowers with pedicel 0.4–1.3 mm long. Hypanthium ± cylindrical, 2.5–4 mm long, free portion ca. 1.7–2.2 mm long, the outer surface with moderate to dense, ferrugineous, globular-stellate hairs, the inner surface glabrous and 10-ridged, the apices of the ridges forming minute projections ca. 0.1 mm long. Calyx teeth (= external calyx lobes) 5, 0.4–3 mm long, 0.9–1.5 mm wide, broadly to narrowly triangular with acute to acuminate apex, dense ferrugineous, globular-stellate indumentum; calyx lobes 5, 1–3.5 mm long, 2.3–3 mm wide, moderately to broadly ovate-triangular, pale green, green with red tinge, or red, with sparse to dense ferrugineous indumentum on both surfaces, the apex rounded (obtuse to acute), the margin minutely erose; calyx tube 0.3–0.8 mm long. Petals 5, 3.8–6.3 mm long, 2.8–4.8 mm wide, broadly ovate to elliptic or obovate, glabrous, white, sometimes pink tinged; margin entire. Stamens 10, geniculate; proximal segment 1.3–2.9 mm long; distal segment 2.6–4.2 mm long, with minute dorsal projection, the anther 1.8–3.2 mm long, with fertile portion of anthers sacs 1.6–2.8 mm long, the connective/distal part of filament extending 1.6–2.8 mm beyond the base of the anther sacs. Ovary 5-loculate, ± half-inferior, 2.2–3.4 mm long, 2.9–4.5 mm in diameter, short-ovoid, glabrous and 10-ridged, lacking a crown, but with a collar with minute apical projections, to ca. 0.4 mm long, encircling base of style; style 3.3–4.8 mm long, glabrous; stigma truncate. Mature berries ca. 8–11 mm in diameter, globose, pale blue (red when immature), moderately to sparsely covered with globular-stellate hairs. Seeds 0.5–0.8 mm long, angular-obovoid; testa smooth, with differentiated and flattened raphe.

Distribution and Habitat:—Hispaniola (Haiti and the Dominican Republic), Massif de la Hotte and Massif de la Selle/Sierra de Bahoruco (both east and west of the Hoyo de Pelempito), and thus limited to the southern portion of the island; cloud forest, moist forest of *Pinus occidentalis*, and moist forest on limestone (= *rak bwa*); 700–2300 m.

Phenology:—Flowering throughout the year.

Key to the subspecies of *Miconia subcompressa*

1. Stems of current growth flush with hairs ± scurfy-erect, globular-stellate to dendritic; leaves with only 2 pairs of secondary veins, abaxially with moderately ferrugineous to dark reddish brown, globular-stellate hairs, adaxially with areoles bullate and forming a conspicuous longitudinal "ridge" between midvein and the major secondary veins; plants of cloud forests to moist pine forests,

(1100–) 1450–2300 m, in the Massif de la Hotte .... 1b. subsp. *plumieri*

1. Stems of current growth flush with hairs ± impressed, globular-stellate; leaves with only 2 pairs of secondary veins, 2 or 3 pairs of secondary veins, or consistently 3 pairs of secondary veins, abaxially with nearly white to pale or moderately ferrugineous, globular-stellate hairs, adaxially with areoles ± bullate and either not forming an evident longitudinal "ridge" between midvein and the major secondary veins, or such "ridge" only slightly developed; plants growing in the Massif de la Selle/Sierra de Bahoruco, or if in the Massif de la Hotte then usually in moist broadleaved forests over limestone (*rak bwa*) from 700–1550 m 2

2. Leaf apex obtuse, obtuse-mucronate, or broadly and shortly acuminate, forming an angle of 44–76° to midvein; length/width quotient of leaf blade 1.5–2.15; leaf base rounded to slightly cordate; plants of the Sierra de Bahoruco, in the "Monteada Nueva" region, i.e., the peaks east of the Hoyo de Pelempito (cloud forest, 1300–1425 m).. 1c. subsp. *beverlyana*

2. Leaf apex acute to slightly and/or shortly acuminate, forming an angle of 18–41° to midvein; length/width quotient of leaf blade (2.05–) 2.15–3.3 (-4.9); leaf base acute to rounded; plants of the Massif de la Hotte (usually *rak bwa*, 700–1550 (–1700) m), Massif de la Selle/Sierra de Bahoruco, in areas west of the Hoyo de Pelempito (cloud forest, moist pine forest, 1100–1800 m) .... 1a. subsp. *subcompressa*

1a. ***Miconia subcompressa*** Urban subsp. ***subcompressa*** (Fig. 2; see also Judd, 2007, fig. 63b–e, g–h)

Young stems with ± appressed, globular-stellate hairs. Leaf blade 3–11.8 cm wide (ave. 6.01), the length/width quotient (2.05–) 2.15–3.3 (–4.9) (ave. 2.55), ovate to occasionally ± elliptic, the "length/length from blade base to point along midvein where leaf is the widest" quotient 1.9–3.3 (ave. 2.55), the apex acute to slightly and/or shortly acuminate, forming an angle of 18–41° (ave. 30.9°) to midvein, the base acute to obtuse or rounded, the largest teeth 0.3–3 (–4) mm (ave. 1.03); the venation with 4 or 6 secondary veins, the innermost secondary vein placed 5–17 mm from margin (at point where leaf is widest; ave. 8.97); adaxial surface with areoles bullate and either not forming an evident longitudinal "ridge" between midvein and the major secondary veins, or such "ridge" only slightly developed; abaxial surface with dense indumentum of nearly white to pale ferrugineous or occasionally moderately ferrugineous globular-stellate hairs. Flowers with calyx lobes 1.3–3.5 mm long; calyx teeth 0.6–2 mm long.

Distribution and Habitat:—Hispaniola (Haiti and the Dominican Republic); Massif de la Hotte, Massif de la Selle, and the Sierra de Bahoruco (in areas west of the Hoyo de Pelempito); moist forest on limestone (*rak bwa*; in the Massif de la Hotte, see Judd 1987, Judd *et al.* 1990, 1998, Majure *et al.* 2013b) and moist montane forest, cloud forest, or moist forest of *Pinus occidentalis* (in the Massif de la Selle and adjacent areas of the Sierra de Bahoruco, see Judd 1987) from 700–1800 m, but usually not over 1550 in the Massif de la Hotte (Fig. 3). Associated melastomes include *Calycogonium ekmanii* Urban (1929: 52), *C. torbecianum* Urban & Ekman (1929: 51), *Conostegia icosandra* (Swartz ex Wikström 1828: 64) Urban (1921a: 404), *Mecranium birimosum* (Naudin 1851: 335) Triana (1871: 140), *M. crassinerve* (Urban 1921b: 48) Skean (1993: 50), *M. haitiense* Urban (1921b: 46), *M. microdictyum* Urban & Ekman (1929: 55), *M. multiflorum* (Desrousseaux 1797: 35) Triana (1871: 139), *M. revolutum* Skean & Judd (1986: 230), *Meriania brevipedunculata* Judd & Skean (1987b: 374), *Miconia crotonifolia* (Desrousseaux 1797: 43) Judd & Ionta (2013: 83), *M.* (*Sagraea*) *curvipila* (Urban & Ekman 1929: 61) Ionta, Judd & Skean (2012: 66), *M. dodecandra* (Desrousseaux 1797: 46) Cogniaux (1886a: 21), *M. favosa* (Desrousseaux 1797: 47) Naudin (1851: 190), *M. ferruginea*, *M.* (*Sagraea*) *hottensis* Ionta, Judd & Skean (2012: 67), *M. laevigata* (Linnaeus 1753: 390) de Candolle (1828: 188), *M. mirabilis* (Aublet 1775: 441) L.O. Williams (1963: 574), *M.* (*Sagraea*) *navifolia* Ionta, Judd & Skean (2012: 69), *M. ossaeifolia* Urban & Ekman (1929: 36), *M.* (*Sagraea*) *polychaete* (Urban & Ekman 1929: 60) Ionta, Judd & Skean (2012: 66), *M. punctata* (Desrousseaux 1797: 50) D. Don (1823: 316), *M. pyramidalis* (Desrousseaux 1797: 53) de Candolle (1828: 188), *M.*(*Sagraea*) *rubrisetulosa* Ionta, Judd & Skean (2012: 66), *M. tetrastoma* Naudin (1851: 236), *M. umbellata* Miller (1768: n. 10) Judd & Ionta (2013: 73), *M. xenotricha*, and *Tibouchina longifolia* (Vahl 1797: 39) Baillon ex Cogniaux (1885: 402).

Additional specimens examined: Dominican Republic. PEDERNALES (all in the Sierra de Bahoruco). Formon, Bois Cavalier, al SE de Kay Michel, 1100 m, 18° 19' 47.3" N, 74° 01' 38.5" W, *Clase et al. 4130* (FLAS); along the International Highway, several km N of Pedernales, ca. 3 km S of Los Arroyos, 1100 m, 18° 9' 2"N, 71° 53' 58.2"W, *Judd 8116** (FLAS, JBSD); near Los Arroyos, along International Highway, from Pedernales to Duvergé, 1600 m, *Liogier 13963* (NY, US); ibid., 1500–1600 m, *Liogier16789* (NY, UCMM, US); ibid., 1500 m, *Liogier 23208* (GH, JBSD, NY). Haiti. GRAND ANSE. 8.7 mi N of Camp Perrin on rd to Jérémie (Rt 214), at "Morne Rhamp" to Tete Cavaillon, along hike from rd E about 2 hrs, 750–820 m, *Judd 6843** (A, DUKE, FLAS, JBSD, MSC, NY, S); 11.8 mi N of Camp Perrin on rd to Jérémie, at "Ti Roche," 800 m, *Judd 6864** (FLAS, GH, JBSD); rd between Camp Perrin and Jérémie, just N of crest, on W side of rd, 700 m, *Skean 2064** (FLAS, JBSD, NY, S, US); 8.7 km N of Camp Perrin on rd to Jérémie (Rt 214), Morne "Rhamp" to Téte Cavaillon, 750–820 m, *Skean 3358** (FLAS, MSC); "Geffrard," 18 km N of Camp Perrin on rd to Beaumont and Jérémie, 18° 22'N, 73° 53'W, 850 m, *Zanoni 25668** (FLAS, JBSD). NIPPES. M. Rochelois, Miragoane, limestone crag near Quatre-Chemins, 980 m, *Ekman H7931* (NY, S). OUEST (all in the

Massif de la Selle). Pétionville, Furcy, ridge between Morne Tranchant and Morne Brouet, slope of Rivière Thébaud, 1400 m, *Ekman H1228* (GH, IJ, S, US); Furcy, 1550 m, *Ekman H3202* (IJ, S, US); Morne des Commissaires, 1500 m, *Holdridge 1243* (BRIT, F, GH, NY, US); Morne Gordé, N-facing slopes below Morne Tranchant, 1550 m, _Skean 2040_* (A, DUKE, EHH, F, FLAS, JBSD, MICH, MO, MSC, NY, S, US). Sud-est (all in the Massif de la Selle). Parc National Morne La Visite, ravine of Rivière Blanche, near where crossed by rd from Seguin to Furcy, S of Morne la Visite, 1800 m, _Judd 4251_* (FLAS); near Morne d'Enfer, ca. 3 km SE of peak, 1437 m, 18.32969°N, 72.37263°W, *Timyan 5* (FLAS); ibid., 1443 m, *Timyan 6* (FLAS), ibid., 1437 m, 18.33006°N, 72.37217°W, *Timyan 11* (FLAS). Sud (all in the Massif de la Hotte). Camp Perrin, N slope of Morne Vandervelde, in "Jardins Coutard," *Ekman H5245* (S, US); Parc National Pic Macaya, S slope of Morne Formon, 1701 m, 18.34201°N, 74.02194°W, *Ionta 2036* (AUC, FLAS, NY); ibid., Bois Formon, just S of Ville Formon, 950–1040 m, _Judd 3460_* (A, EHH, FLAS); ibid., limestone hills N of Ville Formon, just S of Morne Formon, 1200 m, _Judd 3933_* (FLAS, S); ibid. Morne Cavalier, *Judd 4034* (FLAS p.p.); ibid., 1530–1560 m, _Judd 4044_* (FLAS); Parc National Pic Macaya, Bwa Formon, karst hills S of Morne Formon, near Ville Formon, near "Experiment Station" on Deron Plain, 1150 m, _Judd 5732_* (FLAS); ibid., karst hills just S of Ville Formon (=Bwa Formon), 1000 m, *Judd 6893* (EHH, FLAS, JBSD, NY); ibid., karst hills separating Deron and Formon plains, near Ville Formon, 1050 m, _Judd 6896_* (EHH, FLAS); ibid., karst ridge above Experiment Station House (="Cay Florence") and Biosphere Reserve House, near Deron plain, Bwa Deron, 1150–1190 m, _Judd 6906_* (FLAS, JBSD, US, S); ibid., *Judd 6907* (FLAS, US); ibid., foothills S of Morne Formon, just N of "Cay Florence," 1300–1400 m, _Judd 6946_* (FLAS, FTG); in route to Pic Macaya National Park, ca. 0.2 km N of Sou Bwa, 989 m, 18.311490°N, 74.009880°W, *Majure 4276* (AUC, FLAS, JBSD, NY, S); Parc National Pic Macaya, Bois Formon, ca. 1 km S of "Base Camp," 1000 m, _Skean 1145b_* (A, EHH, FLAS, MO, S, US); ibid., Formon, slopes S and below Morne Cavalier, 1200 m, *Skean 1652* (EHH, FLAS); ibid., Bois Formon, near Sous Bois, 950–970 m, _Skean 2084_* (EHH, F, FLAS, MO); ibid., Ravine du Sud, between Morne Macaya and Morne Formon, 1350–1500 m, _Skean 2118_* (B, FLAS); ibid., Bwa Deron-Bwa Formon, S of Morne Formon, 1000–1100 m, _Skean 2481_* (FLAS, MSC); trail between Les Platons and Sou Bwa, 900 m, _Skean 3392_* (FLAS, MSC, S); 0.9 km NW of Pic Tete Boeuf and 9.5 km NNE of St. Louis du Sud, 1168 m, 18.33726°N, 73.51084°W, *Timyan 18* (FLAS); ibid., *Timyan 19* (FLAS); near Morne Bois Pagnol, 12.7 km NE of Duchity, 1157 m, 18.41939°N, 73.77319°W, *Timyan 29* (FLAS); ibid., 1156 m, 18.41922°N, 73.77341°W, *Timyan 35* (FLAS); near Se Vre, Morne Grand Bois, 1084 m, 18.37377°N, 74.29432°W *Timyan 38* (FLAS).

Although *Miconia subcompressa* subsp. *subcompressa* is almost exclusively found in *rak bwa*, a few collections (i.e., *Ionta 2036*, *Judd 3034*, *Judd 4044*), were made in cloud forest/moist pine forest habitats. Conversely, plants of subsp. *plumieri* do rarely occur in *rak bwa* (i.e., *Skean 2538*). Thus, although subsp. *subcompressa* almost always occurs from 700–1550 m in the Massif de la Hotte, occasionally it reaches 1700 m. *Miconia subcompressa* subsp. *plumieri* usually occurs from 1450–2300 m, but rarely occurs as low as 1100 m. The extent of gene flow between these taxa needs investigation.

Populations from the Massif de la Selle have leaves that are more frequently moderately ferrugineous abaxially; however, some individuals from the Massif de la Hotte are also moderately ferrugineous. Also, their stems sometimes possess erect, dendritic hairs mixed in with the more appressed, globular-stellate hairs. Thus the La Selle populations can more easily be confused with subsp. *plumieri* than La Hotte populations. It is of interest that the La Selle populations, like those of subsp. *plumieri*, occur in cloud forests and moist forests of *Pinus occidentalis* (not *rak bwa*, as in the La Hotte populations).

Miconia subcompressa subsp. *subcompressa* is endemic to the Massif de la Hotte and Massif de la Selle/Sierra de Bahoruco. Within the Melastomataceae, only *Henriettea barkeri* (Urban & Ekman 1927: 48) Alain ([=Liogier] 1965: 299), *Mecranium birimosum* and *M. multiflorum* show a similar distributional pattern (Skean 1993, Liogier 2000).

1b. ***Miconia subcompressa*** Urban subsp. ***plumieri*** (Urban & Ekman) Judd, Majure & Ionta *comb. et stat. nov*. (Fig. 4; see also Judd, 2007, fig. 63f)

Miconia plumieri Urban & Ekman, Ark. Bot. 22(17): 38. 1929. (Published as *M. plumerii*, sic.)
Type:—HAITI. Dept. du Sud, Massif de la Hotte, near Torbec, pine forest on S slope of Morne Formon, ca. 1900 m, fl, 31 Dec 1926, *E. L. Ekman H7466* (holotype S!).

Young stems with ± scurfy-erect, globular-stellate to dendritic hairs. Leaf blade 2.3–7 cm wide (ave. 4.48), the length/width quotient (1.84–) 2.45–3.85 (ave. 2.93), ovate to elliptic or oblong-elliptic, the "length/length from blade base to point along midvein where leaf is the widest" quotient 1.7–2.75 (–3.88) (ave. 2.26), the apex acute to slightly acuminate, forming an angle of 15–40° (–55°) (ave. 29°) to midvein, the base acute to obtuse or rounded, the largest teeth 0.2–1 mm (ave. 0.65); the venation with 4 secondary veins, the innermost secondary vein placed 3–9 mm from margin (at point where leaf is widest; ave. 6.25); adaxial surface with areoles bullate and forming a conspicuous longitudinal "ridge" between midvein and the major secondary veins; abaxial surface with dense indumentum of moderately ferrugineous to dark reddish brown globular-stellate hairs. Flowers with calyx lobes 1–2.3 mm long; calyx teeth 0.5–1.7 mm long.

Distribution and habitat:—Haiti; Massif de la Hotte; cloud forest and moist forest of *Pinus occidentalis*; (1100–) 1450–2300 m (Judd 1987, Judd *et al.* 1990, 1998, Majure *et al.* 2013b) (Fig. 3). Associated melastomes include *Henriettea barkeri*, *Mecranium alpestre* Urban & Ekman (1929: 53), *M. tricostatum* Urban & Ekman (1929: 53), *Meriania ekmanii* Urban (1927: 37), *M. squamulosa* Urban & Ekman (1929: 28), *Miconia alloeotricha, M. apiculata* Urban & Ekman (1929: 48)*, M. barkeri* Urban & Ekman (1927: 41), *M. hypiodes*, *M. tetrastoma*, *M.* (*Sagraea*) *woodsii* (Judd & Skean 1987a: 141) Ionta, Judd & Skean (2012: 67), and *M. xenotricha.*

Additional specimens examined. Haiti. Sud (all in the Massif de la Hotte). Formon, Bois Cavalier, 1120 m, 18° 19' 25.2" N, 74° 01' 47" W, *Clase et al. 4167* (FLAS); Formon, Pic Le Ciel, 1800–1900 m, 18° 21' 18/2" N, 74° 01' 9.7" W, *Clase et al. 4184* (FLAS); Formon, Plain Boeuf, 1950 m, 18° 20' 41.8" N, 73° 59' 40.4" W, *Clase et al. 4193* (FLAS); Torbec, ridge above La-Mare-Proux, 1550 m, *Ekman H5297* (A, IJ, NY, S); ibid., 1600–1700 m, *Ekman H5302* (NY, S); Torbec, Morne Formon, top of mountain, 2225 m, *Ekman H7474* (S); Parc National Pic Macaya, Pic Macaya, just below peak, ca. 2300 m, 18.382106°N, 74.024660°W, *Ionta 2034* (AUC, FLAS, JBSD, NY); ibid., ridge and S slope of Morne Formon, 1670–1770 m, *Judd 3669** (EHH, FLAS); ibid., Morne Cavalier, 1530–1560 m, *Judd 4034** (FLAS p.p., JBSD); ibid., S slopes of Morne Formon, just E of Pic La Ciel, 1850–1950 m, *Judd 5737** (FLAS); ibid., Morne Formon, from Experiment Station House to ridge of mountain, 1630–1880 m, *Judd 6944** (EHH, FLAS, USF); ibid., Morne Formon, along trail from mountain ridge down into Ravine du Sud, 1600–2000 m, *Judd 6967** (EHH, FLAS, JBSD, MO, NY, S, US); ibid., S slopes of Morne Formon, Pic le Ciel, 1466 m, 18.34584°N, 74.02220°W, *Majure 4290* (AUC, FLAS, NY, US); ibid., first major ridge above Ville Formon, 1100–1200 m, *Skean 2538** (FLAS, MICH, MSC); Grand Colline, 1799 m, 18.38234°N, 74.09681°W, *Timyan 52* (FLAS).

Miconia subcompressa subsp. *plumieri* typically occurs in cloud forests or moist forests of *Pinus occidentalis* from 1450–2300 m, however, occasionally these plants occur as low as 1100 m in *rak bwa* (see discussion under subsp. *subcompressa*). For a detailed discussion of the distribution of these forest types in the Massif de la Hotte, along with an indication of their dominant species see Judd (1987), Judd *et al.* (1990, 1998).

This subspecies is endemic to the high elevation forests of the Massif de la Hotte. Other melastomes also restricted to these diverse cloud forest/moist pine forest habitats are *Mecranium alpestre*, *M. microdictyum*, *M. tricostatum*, *Meriania ekmanii, M. squamulosa*, *Miconia apiculata, M. alloeotricha, M. apiculata*, *M. barkeri*, *M. hypiodes*, *M. macayana* Judd & Skean (1987a: 145), *M. woodsii*, and *M. xenotricha* (Judd & Skean 1987a, Skean 1993, Liogier 2000, Judd *et al.* 2004, Judd 2007).

As noted in Judd (2007), the specific epithet "*plumerii*" is likely a typographic error. Urban and Ekman (1929) probably intended the spelling "*plumieri*" in honor of Charles Plumier (1646–1704). We are not aware of anyone named Plumer associated with West Indian botany, and Urban and Ekman are unlikely to have made the mistake of adding the second "i" to the epithet. In addition, when the derivation of a new name was not obvious, Urban noted for whom the species was named. In this case he did not do so, probably because Plumier doesn't require an explanation.

1c. ***Miconia subcompressa*** Urban subsp. ***beverlyana*** Judd *subsp. nov*. (Fig. 5; see also Judd, 2007, fig. 63a, drawn from holotype)

Diagnosis: *Subspecies haec ab Miconia subcompressa subsp. subcompressa differt foliis latioribus, i.e., quoto pro longitudine/latitudine 1.5–2.15 (non (2.05–) 2.15–3.3 (–4.9)), apice foliorum obtuso, obtuso-mucronato, rotundo-mucronato, vel breviter acuminato (non acuto vel breviter acuminato), et base foliorum obtuse vel leviter cordata (non acuta, obtuse, vel rotunda).*

Type:—DOMINICAN REPUBLIC. Prov. Barahona, Sierra de Bahoruco, Monteada Nueva, near Polo, ca. 1400 m, fr, 28 May 1986, *W. S. Judd 5177** *with J. D. Skean, Jr. & R. S. Beaman* (holotype FLAS!; isotypes A!, F!, FLAS, 2 sheets!, JBSD!, MICH!, S!, US!).

Young stems with ± appressed, globular-stellate hairs. Leaf blade (4.7–) 6–15.8 cm wide (ave. 10.1), the length/width quotient 1.5–2.15 (ave. 1.81), broadly ovate to occasionally ± broadly elliptic, the "length/length from blade base to point along midvein where leaf is the widest" quotient 1.8–3.54 (ave. 2.47), the apex obtuse, obtuse- or rounded-mucronate, to broadly and/or shortly acuminate, forming an angle of 44–76° (ave. 59.9°) to midvein, the base rounded to slightly cordate, the largest teeth 0.3–1.6 mm (ave. 0.81); the venation with usually 6 secondary veins, but sometimes these only 4, the innermost secondary vein placed 7.5–27 mm from margin (at point where leaf is widest; ave. 17.4);

adaxial surface with areoles bullate and either not forming an evident longitudinal “ridge” between midvein and the major secondary veins, or such “ridge” only slightly developed; abaxial surface with dense indumentum of ± pale ferrugineous globular-stellate hairs. Flowers with calyx lobes 1–1.7 mm long; calyx teeth 0.5–1.2 mm long.

Etymology:—This taxon is named after my wife, Beverly J. Judd, who assisted during fieldwork in the Dominican Republic in 1981, and kept the household running smoothly during 15 other trips to various countries in the Caribbean region during which research on Melastomataceae tribe Miconieae was conducted.

Distribution and Habitat:—Dominican Republic; Sierra de Bahoruco, east of the Hoyo de Pelempito, in the “Monteada Nueva” region (= Loma Trocha de Pey, and vicinity); cloud forest; 1300–1425 m (Guerrero 1993) (Fig. 3). Associated melastomes include _Henriettea barkeri_, _Mecranium ovatum_ Cogniaux (1913: 528), _Meriania involucrata_, _Miconia alainii_ Judd & Skean (1994: 112), _M. dodecandra_, _M. howardiana_, _M._ (_Lima_) _lima_ (Desrousseaux 1797: 47) M. Gómez (1984: 69), _M._ (_Lima_) _limoides_ (Urban 1927: 50) Majure & Judd (2013: 269), _M. tetrastoma_, _M. umbellata_, and _Sagraea gracilis_ (Alain [=Liogier] 1971: 167) Alain (1999: 1048) (actually a species of _Miconia_ sect. _Sagraea;_ see Ionta _et al._ 2012).

Additional specimens examined: Dominican Republic. BARAHONA (all in the Sierra de Bahoruco). Monteada Nueva, 6.3 km from Cruc de El Puerto—Monteada Nueva, 3.4 km E of Cortico, 1390 m, 18° 10’N, 71° 15’W, _Gentry 50697_ (US); Monteada Nueva, near Polo, 1300 m, _Judd 1089_ (A); Monteada Nueva, above (E of) Polo, 1325–1400 m, _Judd 6561_* (DUKE, FLAS, JBSD, MO, NY, S); Monteada Nueva region, S on Cabral-Polo rd, then 5.9 km SE on “riverbed rd” and 0.15 km more on turn-off toward Monteada Nueva (peak is Loma Trocha de Pey), 1330 m, 18° 6’ 51”N, 71° 14’ 5”W, _Judd 8085_* (FLAS, JBSD); Monteada Nueva region (peak is Loma Trocha de Pey), S on Cabral-Polo rd, then 7.1 km SE on “riverbed rd” and dirt rd to “Cortico” and silica mine, ca. 0.7 km NNW of silica mine, on crest of rd, 1340–1350 m, 18° 6’ 36.6”N, 71° 13’ 36.9”W, _Judd 8098_ (FLAS, JBSD); Monteada Nueva region (peak is Loma Trocha de Pey), 1.2 km down rd from old silica mine, 1330–1350 m, 18° 6’ 51.4–53.9”N, 71° 14’ 6.2”–13’ 53.6”W, _Judd 8110_* (FLAS, JBSD); Monteada Nueva, Caña Brava, S of Cabral, 1300 m, _Liogier 11652_ (NY, US); ibid., _Liogier 14363_ (NY, US); ibid., _Liogier 25152_ (JBSD); Monteada Nueva, along rd to silica mine, beginning at water tower between Cabral and Polo, 1400–1425 m, _Skean 1817_* (FLAS, JBSD, MSC); 4 km above village of “Entrada de Cortico” on rd to “El Gajo” (site traditionally referred to as “Monteada Nueva” by botanists), 4100–4200 ft, 18° 07.5’N, 71° 13.5’W, _Zanoni 18892_* (FLAS, JBSD, NY); “El Gajo,” ca. 7 km from the rd between Cabral and Polo on rd to “Entrada de Cortico,” 1400 m, 18° 07.5’N, 71° 13.5’W, _Zanoni 35614_* (FLAS, JBSD); entrada de El Cortico, on summit of Loma Trocha de Pey (= Monteada Nueva, as used by botanists), 1400 m, 18° 07.5’N, 71° 13.5’W, _Zanoni 40674_* (FLAS, JBSD, NY); 4 km above village of “Entrada de Cortico” on rd to “El Gajo,” 1320–1340 m, 18° 07’N, 71° 13’W, _Zanoni 44254_* (FLAS, JBSD).

Miconia subcompressa subsp. _beverlyana_ is geographically the most restricted of the three subspecies and is morphologically quite uniform. It is most similar to subsp. _subcompressa_, especially some plants from the Sierra de Bahoruco occurring west of the Hoyo de Pelempito. It may seem surprising to find a distinct subspecies isolated in the “Monteada Nueva” region (= Loma Trocha de Pey), however several species of Melastomataceae are similarly restricted to this small geographical area, i.e., _Henriettea uniflora_ Judd _et al._ (2008: 219), _Mecranium ovatum_ (except for a single collection in the mountains south of Puerto Escondido, see Skean 1993), _Miconia alainii_, _M. howardiana_, and _Sagraea gracilis_ (Liogier 1971, 2000, Judd & Skean 1994, Judd _et al._ 1995, 2008, Judd 2007). A striking tree of these forests, which is also endemic, is _Magnolia hamori_ Howard (1948: 351, Magnoliaceae; see also Guerrero 1993). For a detailed description of the forests of Loma Trocha de Pey, and the adjacent peaks Loma Remigio and Loma Pie de Palo, see Guerrero (1993). These forests, unfortunately, are not protected from agricultural development, so _Miconia subcompressa_ subsp. _beverlyana_ (along with the other endemics listed above) should be considered endangered. The diverse and highly endemic flora of the Sierra de Bahoruco is also treated in Hager & Zanoni (1993) and García _et al._ (2001).

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Appendix 1. GenBank accession numbers for sequences of the two loci (ETS, ITS) used in this study. Missing sequences are represented by an em dash (—).

Miconia barkeri* Urban & Ekman,** *Ionta 2028* (FLAS) KJ149255, KJ149271. ***Miconia dielsiana* Urban,** *Judd 8217* (FLAS) KF821014, EU055766. ***Miconia ferruginea* (Desrousseaux) de Candolle,** *Majure 4362* (FLAS) KJ149266, KJ149282; *Skean 4313* (FLAS) KF821039, KF821611. ***Miconia foveolata* Cogniaux,** *Struwe 1136* (NY) KF821041, AY460511. ***Miconia howardiana* Judd, Salzman & Skean,** *Judd 8099* (FLAS) KF821060, AY460512. ***Miconia hypiodes* Urban& Ekman,** *Ionta 2030* (FLAS) KJ149256, KJ149272. ***Miconia rufa* C. Wright**, *Bécquer 81649* (HAJB) KF821197, EU055829. ***Miconia samanensis* Urban,** *Judd 8216* (FLAS) KF821202, EU055832. ***Miconia selleana* Urban & Ekman,** *Skean 4135* (FLAS) KF821209, EF418904. ***Miconia septentrionalis Judd & R.S. Beaman, *Skean 4115* (FLAS) KF821211, EU055837. ***Miconia sintenisii* Cogniaux,** *Struwe 1138* (NY) KF821215, AY460529. ***Miconia subcompressa* Urban *subsp. beverlyana* Judd*,*** *Judd 8085* (FLAS) KJ149268, KJ149283; *Judd 8090* (FLAS) KJ149269, KJ149284; *Judd 8110* (FLAS) KJ149270, KJ149285. ***Miconia subcompressa* Urb. *subsp. plumieri* (Urban & Ekman) Judd, Majure & Ionta*,*** *Ionta 2034* (FLAS) KJ149257, KJ149273; *Majure 4290* (FLAS) KJ149263, KJ149279. ***Miconia subcompressa* Urban *subsp. subcompressa,*** *Judd 8116* (FLAS) KF821233, EU055845; *Ionta 2036* (FLAS) KJ149258, KJ149274; *Majure 4276* (FLAS) KJ149262, KJ149278; *Timyan 18* (FLAS) KJ149260, KJ149276; *Timyan 29* (FLAS) KJ149261, KJ149277. ***Miconia xenotricha* Urban & Ekman,** *Majure 4291* (FLAS) KJ149264, KJ149280; *Majure 4293* (FLAS) KJ149265, KJ149281; *Timyan 116* (FLAS) KJ149259, KJ149275.