



Molecular phylogenetics suggest *Osmiopsis* (Asteraceae) could be a rare inter-subtribal hybrid genus on Hispaniola

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Abstract

Osmiopsis (Asteraceae, Eupatorieae) is endemic to Hispaniola and one of the seven genera of subtribe Praxelinae. When *Osmiopsis* was established in 1975, the authors hypothesized it was a hybrid and proposed *Chromolaena* (subtribe Praxelinae) and *Koanophyllon* (subtribe Critoniinae) as putative parent genera. To clarify its origin, a phylogenetic investigation of subtribe Praxelinae, reconstructed within a matrix of 80 genera/202 species of tribe Eupatorieae (43% of genera/8% of species sampled, based on an estimated 187 genera/2500 species) was performed. An ILD test showed significant incongruity between the nuclear and chloroplast trees ($p = 0.001$). Based on Bayesian analysis of ITS, *O. plumieri* emerged in a strongly supported clade (PP = 0.98) of 23 species of Critoniinae, closely allied to six *Koanophyllon* species. Based on Bayesian analysis of *ndhF*, *O. plumieri* emerged in a strongly supported clade (PP = 1) of 20 species of Praxelinae with *Chromolaena*, *Praxelis* and three other genera. These results suggest *Osmiopsis* may be a hybrid between *Chromolaena* and *Koanophyllon*. *Osmiopsis* shares with *Koanophyllon*: infundibuliform corolla with a cylindrical base, triangular corolla lobes and anther appendages wider than longer. *Osmiopsis plumieri* shares with *Chromolaena* and *Praxelis*: semi-scandent habit and deciduous involucre bracts. As far as we are aware, this is the first case of a possible inter-subtribal nothogenus in the Asteraceae. *Koanophyllon* has more Caribbean island endemics than any other genus in the Asteraceae. This raises the question if hybridization has played a significant role in the diversification of the Caribbean flora, as has been shown in species-rich genera from volcanic archipelagos. Taxonomically, it raises the question if sister subtribes Praxelinae and Critoniinae should be united or re-circumscribed.

Keywords Caribbean · Compositae · Critoniinae · Praxelinae

Introduction

Osmiopsis R.M.King & H.Rob. (Asteraceae) was described as a monotypic genus endemic to the Caribbean Island of Hispaniola in 1975 (King & Robinson 1975). It is one of the seven genera that comprise subtribe Praxelinae R.M.King & H.Rob. and the only genus of the subtribe that does not occur in South America. Subtribe Praxelinae was considered monophyletic (Rivera et al. 2016) and is one of the 17 subtribes of tribe Eupatorieae. Tribe Eupatorieae, with an estimated c. 2500 species (Grossi et al. 2020) is one of the largest and most recent tribe of Asteraceae: it diverged from its nearest ancestor ca. 12.9 mya ago and has diversified explosively since the Miocene (Rivera 2015; Mandel et al. 2019).

Osmiopsis plumerii (Urb. & Ekman) R.M.King & H.Rob. the single species of the genus, was described by Urban and Ekman in the genus *Eupatorium* (Urban

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1931) based on several Haitian collections made in the early twentieth century. A new combination, *Chromolaena plumerii* (Urb. & Ekman) R.M.King & H.Rob. was published in 1970 (King and Robinson 1970). However, five years later, King and Robinson revised the taxonomic position of this species and proposed the genus *Osmiopsis* to accommodate it (King and Robinson 1975). The epithet that appears in the original publication was spelled *plumerii*. We herein propose that it should be corrected to *plumieri*, following Article 60.1 of the International Code of Nomenclature for algae, fungi and plants, as it is almost certainly a reference to the French monk and botanist Charles Plumier (1646–1704), one of the first Europeans to collect plants in Haiti; this epithet will be used henceforward.

Publication of *Osmiopsis* was unusual in that the authors stated that the genus was probably an intergeneric hybrid (King and Robinson 1975). They argued that a scandent habit and 4–5-seriate, imbricate, deciduous, involucre bracts were characteristic of *Chromolaena* DC. (subtribe Praxelinae), while wide, glandulose corolla lobes, short anther appendages and enlarged tips to staminal branches were typical of *Koanophyllon* Arruda (subtribe Critoniinae). Moreover, they stated that the hybrid origin was: ‘based on circumstantial evidence of character distribution’ and that ‘evidence would indicate further that such hybrids were totally viable and capable of further evolution’ (King and Robinson 1975: 250). These statements were not supported by any further discussion, nor by any numerical analysis or molecular data. The putative *Koanophyllon* parent proposed by King and Robinson was either *K. selleanum* or *K. phanioides* (King and Robinson 1970).

Osmiopsis plumieri is known from at least 12 collections made between 1924 and 1929 in Haiti; it has not been recorded from the Dominican Republic. King and Robinson (1975) observed that *Osmiopsis plumieri* is frequently misidentified in herbaria either as *K. selleanum* (Urb.) R.M.King & H.Rob. or as *K. phanioides* (Krug & Urb.) R.M.King & H.Rob. They hypothesized that one of these species was the most probable parent species in *Koanophyllon*; both are endemic to Hispaniola (POWO 2024). King and Robinson (1970) did not propose a putative parent in *Chromolaena*.

In the most recent phylogeny of Tribe Eupatorieae, Rivera et al. (2016) confirmed the monophyly of Subtribe Praxelinae, but some genera were not sampled, such as *Osmiopsis*; therefore, relationships between its genera were not fully clarified. In this study, we expanded phylogenetic studies of subtribe Praxelinae to include all accepted genera (Ribeiro 2023), including the enigmatic *Osmiopsis*. Since our analysis included markers from both the nuclear and chloroplast genomes, the latter being maternally inherited, it provided an opportunity to test King and Robinson’s hypothesis of its hybrid origin.

Material and methods

Sampling and phylogenetic analyses

Molecular analysis was done in the Plant Molecular Biology Laboratory, University of Brasília, Brazil. DNA was extracted from herbarium specimens or silica-dried leaf material collected along with the herbarium vouchers. The type species of three previously unsampled genera of subtribe Praxelinae were sampled and sequenced: *Osmiopsis plumieri* (Ekman 6490, LL, paratype; Fig. 1), *Eupatoriopsis hoffmanniana* Hieron (Braga 800, UB) and *Praxelopsis mattogrossensis* G.M.Barroso (Faria 3493, UB). Thirteen additional species belonging to genera previously sampled by Rivera et al. (2016) (but not necessarily their type species) were also included: ten *Chromolaena*, two *Praxelis* and one *Eitenia*. This sampling ensured that the type species of all seven genera of subtribe Praxelinae were included in the analysis, achieving complete sampling at generic level and raising the density of sampling at species level from 15 species (8%) to 31 (16%).

The extraction of total genomic DNA was performed using the Riahi et al. (2010) protocol, which proved more efficient than the traditional CTAB protocol (Doyle and Doyle 1987). The ITS marker of the 18S-26S ribosomal RNA genes, including the 5.8S gene (nuclear marker), and the chloroplast *ndhF* were amplified using standard PCR protocols and primers: ITS-4 (TCCTCCGCTTAT TGATATGC) and ITS-5 (GGAAGTAAAAGTCGTAAC AAGG), *ndhF* 52 (AGGTAAGATCCGGTGAATCGG AAA) and *ndhF* 1212 (GGTGAATACCACAAAGA), respectively. PCRs were carried out in a final volume of 20 µL (see Online Resource 1 A for protocol). Amplicons were sequenced using the DNA sequencing services of BPI Biotecnologia in Botucatu, Brazil. Sequences were imported into the program Geneious v.11, were aligned with MUSCLE (Edgar 2004) followed by visual inspection and manual alignment, when appropriate. Details of marker type, length in base pairs, sequences per marker, identical sites and pairwise identity are available in Online Resource 1 B.

The ITS and *ndhF* sequences of *Osmiopsis* and the two other genera were added to a matrix of ITS and *ndhF* sequences of 202 species of tribe Eupatorieae and realigned as described above. Each genetic marker was run on jModeltest 2.1.10 (Guindon and Gascuel 2003; Darriba et al. 2012); the model GTR (with gamma-distributed rate variation across sites) was selected as the best evolutionary model under the Akaike Information Criteria (AIC). Each genetic marker was also analyzed as a single partition with the above chosen model of evolution. A third matrix with additional markers was also constructed



Fig. 1 Paratype of *Osmiopsis plumieri* (Urb. & Ekman) R.M.King & H.Rob. collected by Erik L. Ekman (Ekman herbarium n. 6490), originally from the Lundell Herbarium (LL) now incorporated into TEX

to improve resolution and test the position of *Osmiopsis* (Ribeiro 2023). This matrix contained the following molecular data from nuclear and chloroplast markers: ITS and ETS (nuclear) and *ndhF*, *ndhI* and the *ndhI-ndhG* intergenic spacer (chloroplast) obtained from NCBI GenBank (Clark et al. 2016). All sequences are available (see Online Resource 2) in GenBank except for five donated by authors of unpublished doctoral theses. Sequences of *Acri-topappus* were donated by Hortensia Pousada Bautista: *A. connatifolius* (Soares Nunes) R.M. King & H.Rob., *A. diamantinicus* H.Bautista, *A. pereirae* H.Bautista and *A. teixeirae* R.M.King & H.Rob. (see Bautista 2000). The sequence of *Parapiqueria cavalcantei* R.M.King & H.Rob. was donated by Ana Cláudia Fernandes (see Fernandes 2014).

Bayesian inference (BI) analysis was undertaken on these three matrices using MrBayes 3.2.7a (Ronquist and Huelsenbeck 2003) on the CIPRES science gateway (Miller et al. 2010). The BI analyses consisted of two independent and simultaneous runs, each with four Markov Monte Carlo (MCMC) chains (three warm chains and one cold chain), for 10 million generations, sampling the trees every 10,000 generations. The stationarity of the chains was verified using Tracer v1.7.2 (Rambaut et al. 2014). Support values for the clades were obtained by posterior probabilities for Bayesian analysis. The phylogenetic tree was visualized and edited in FigTree v 1.4.4 (Rambaut 2010).

We evaluated the incongruence between the nuclear tree (ITS) and the chloroplast tree (*ndhF*) using the incongruence length difference test (ILD test; Farris et al. 1994). Both markers were highly informative in reconstructing the phylogeny of the Eupatorieae (Rivera et al. 2016). The ILD test has been criticized because of a high false positive rate (Cunningham 1997; Darlu and Lécointre 2002; Hipp et al. 2004), therefore, to reduce false positives, we followed the

recommendations of Cunningham (1997) and Pelsner et al. (2010) and only considered ILD *p-values* below 0.01 as evidence of significant incongruence. We implemented the ILD test in PAUP (Swofford 2002) on the CIPRES platform (Miller et al. 2010) as a partition-homogeneity test with a heuristic search of 1000 replicates and random addition of sequences.

Geographic distribution

Geographic distribution was obtained from the literature (Acevedo-Rodríguez and Strong 2012), Plants of the World Online (POWO 2024) and online herbaria in GBIF (18 collections of *Osmiopsis plumieri* with detailed localities). Localities were georeferenced using Google Earth Pro v.7.1.8.3036 (date of images 31st December 2020 accessed 28th August 2025). All records had images and were checked for correct identification. The map was produced with QGIS 3.10.14 software (<https://www.qgis.org>).

Morphology

We did a comparative morphological analysis of *Osmiopsis*, *Chromolaena*, *Praxelis* and *Koanophyllon* from the literature (Table 1), choosing characters that are diagnostic at generic level for the Eupatorieae (King & Robinson 1987; Nakajima et al. 2017; Ribeiro et al. 2022). The morphology of *Osmiopsis plumieri* was analyzed from the literature (Urban 1931; King & Robinson 1975) and from images of herbarium specimens available online from the NL, US and TEX herbaria (Table 2). We compared its habit, leaf shape and floral characters to possible parental species that occur on Hispaniola (Acevedo-Rodríguez and Strong 2012); the identifications of all herbarium specimens were confirmed. The iNaturalist site (www.inaturalist.org)

Table 1 Comparison of reproductive morphological traits between *Chromolaena*, *Koanophyllon*, *Osmiopsis* and *Praxelis* according to King and Robinson (1987). Involucre and anther traits were also based on Grossi et al. (2020), except for *Osmiopsis*

Character	<i>Chromolaena</i> and <i>Praxelis</i>	<i>Koanophyllon</i>	<i>Osmiopsis</i>
Involucral bract persistence	Totally deciduous, outer bracts falling first (sometimes outer bracts persistent in <i>C. sinuata</i>)	All persistent or inner bracts sometimes deciduous	All deciduous
Involucre shape	Imbricate to densely imbricate or sub-imbricate	Eximbricate to strongly subimbricate	Imbricate
Corolla shape	Funnelform or cylindrical with slightly narrowed base	Funnelform with broadly cylindrical base	Funnelform with short broadly cylindrical base
Corolla lobes	Oblong or ovate (1.5 to 3 times as long as wide)	Triangular (as long as wide to 1.5 times as long as wide)	Triangular (as long as wide to 1.5 times as long as wide)
Anther appendages	Oblong or ovate and entire, crenulate or toothed at tip, slightly to distinctly longer than wide	Null or ovate, wider than long	Semicircular, wider than long

Possible parental species of *Osmiopsis* are compared in Table 2

Table 2 Comparison of *Osmiopsis* with possible parental taxa occurring on Hispaniola. Chromosome counts obtained from the CCDB (Rice & Mayrose 2023). Characters present in *Osmiopsis* or shared with *Osmiopsis* are indicated in **bold underlined**. The source of the

information is indicated in superscript after the character states: numbers (literature); letters (images of herbarium specimens deposited in the Swedish Museum of Natural History)

Species/chromosome counts	Habit	Leaf shape	Leaf base and margin	Involucral bracts (series)	Involucre length (mm)	Involucre width (mm)
<i>Osmiopsis plumieri</i> n=?	Scandent shrubs ¹	Ovate to lanceolate ¹	Base often lobed, margin distally entire ¹	4–5 ¹	3–5 ¹	2–3 ¹
<i>C. corymbosa</i> (M?) n=20	Shrubs ²	Deltoid to cordate ²	Base round, margin often crenate	6–7 ²	7 to 9 ²	3.3 to 4 ²
<i>C. ivifolia</i> (M?) n=25	Shrubs ³	Lanceolate ³	Base often acute, margin entire or serrate ³	6–7 ³	5.5–7.8 ³	2.7 to 4 ³
<i>C. odorata</i> (M?) n=20,29,30,31,40,51,60	Scandent shrubs ³	Ovate to lanceolate ³	Base often round, margin serrate ³	5–7 ³	8.2–9.6 ³	2.6 to 3.5 ³
<i>C. sinuata</i> (M?) (n=?)	Shrubs ²	Ovate ²	Base truncate to cuneate, margin sinuate-lobed ²	3–5 ²	3–4 ²	2 ²
<i>K. selleanum</i> (P?) (n=?)	Scandent shrubs ^{a,4}	Ovate to elliptical ^{a,4}	Base subcordate, margin entire ⁴	3 ^a	3–5 ^a	2–3 ^a
<i>K. phanioides</i> (P?) (n=?)	Scandent shrubs ^b	Ovate to lanceolate ^b	Base often lobed, distal margins entire ^b	3 ^{b,1}	2–4 ^b	0.7–3 ^b

C. Chromolaena, *K. Koanophyllon*, *P?* paternal, *M?* maternal, *n* haploid chromosome count

¹ King & Robinson (1975); ²WFO (2025); ³*Chromolaena*, Flora e Funga do Brasil (2025); ⁴Urban (1921); ^a*E.L. Ekman* H 3955 (S-R-8990);

^b*E.L. Ekman* H 1667 (S15-63908)

[ralist.org](https://www.ralist.org)) was searched for images of plants identified as *Chromolaena*, *Praxelis* or *Koanophyllon* from Hispaniola, with two main objectives: 1) to detect if *Osmiopsis* still occurs on the island; and 2) to detect if any other genera of Praxelinae other than *Chromolaena* occur on the island.

Results

Phylogenetic trees

The reconstructed phylogeny of tribe Eupatorieae based on the nuclear matrix of ITS + ETS and the chloroplast matrix of *ndhF* + *ndhI* + *ndhI*-G IGS showed good resolution (Online Resource 3). *Osmiopsis plumieri* appeared nested in a highly supported clade (PP=0.97) among all sampled species of *Koanophyllon*, allied to *Idiothamnus lilloi* (B.L.Rob.) R.M.King & H.Rob. and *Chromolaena collina* (DC.) R.M.King & H.Rob.

Evidence of hybrid origin

The ILD test results showed significant incongruence between the ITS and the *ndhF* data matrices (*p*-value of 0.001). The ITS phylogenetic tree recovered a clade of 25 species of Praxelinae; however, *Osmiopsis* did not group with this clade (Ribeiro 2023). Instead, *Osmiopsis* emerged in a highly supported clade (subclade A; PP=0.99) that included most sampled taxa of the Critoniinae (but not *Critonia* P.Browne), as well as genera from two other subtribes, namely *Ageratum* L. (subtribe Ageratinae) and *Fleischmannia* Sch.Bip. (subtribe Fleischmanniinae) (Fig. 2). Within this clade, *Osmiopsis* emerged in a subclade (PP=0.83) that included five species of *Koanophyllon* (Critoniinae), *Idiothamnus lilloi* (Critoniinae) and *Chromolaena collina* (Praxelinae).

The *ndhF* phylogenetic tree (Fig. 3) recovered a Praxelinae clade with suboptimal support (PP=0.83); if *Chromolaena sagittata* (A.Gray) R.M.King, the sister to the rest of the Praxelinae, is excluded the remaining clade has

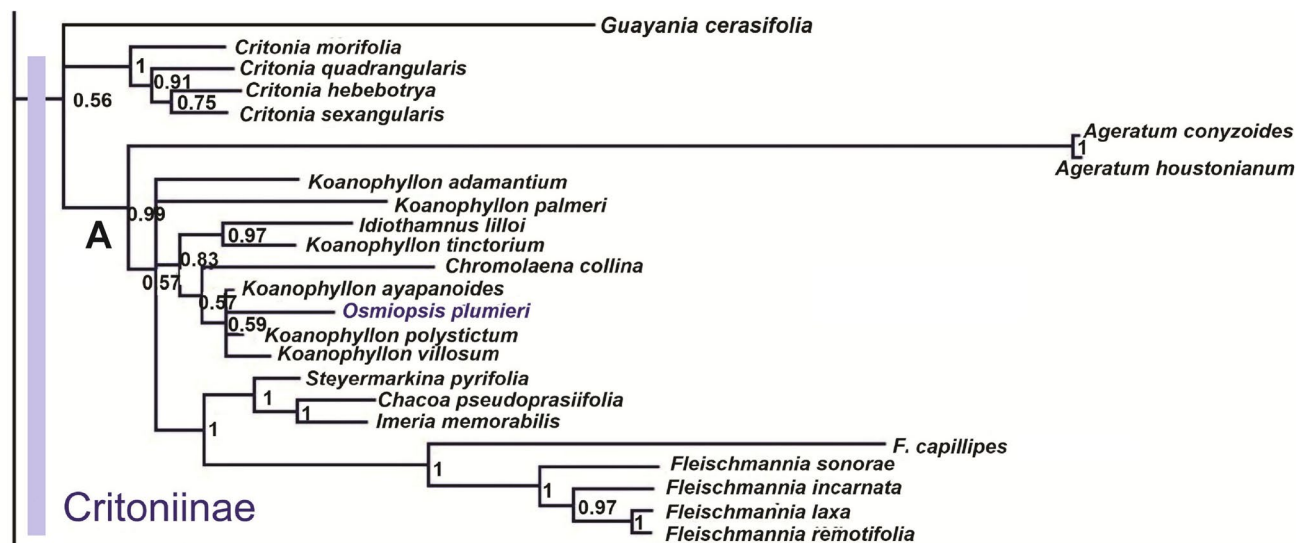
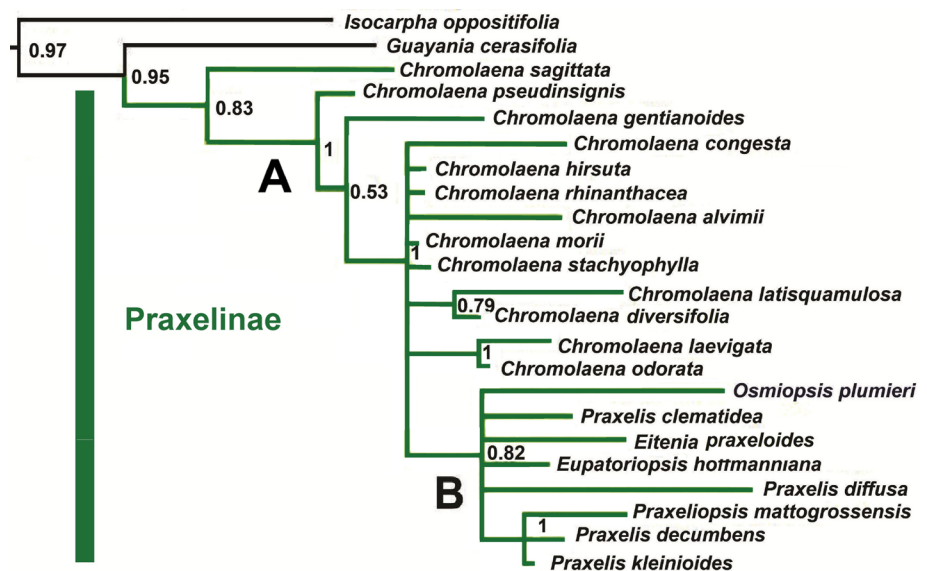


Fig. 2 Bayesian 50% majority rule consensus ITS 1 and 2 (nuclear region) phylogenetic highlighting subtribe Critoniinae (purple bar). Posterior probabilities are indicated at the nodes. *Osmiopsis plumieri*

is highlighted in purple; *F. Fleischmannia*. For full nuclear marker tree of tribe Eupatorieae see Online Resource 4

Fig. 3 Bayesian 50% majority rule consensus *ndhF* (chloroplast region) phylogenetic tree highlighting subtribe Praxelinae (green bar and branches). Posterior probabilities are indicated at the nodes. For full chloroplast marker tree of tribe Eupatorieae see Online Resource 5



maximum support (subclade A; Fig. 3; PP = 1). *Osmiopsis plumieri* emerged within this clade, and was nested within the “*Praxelis*” subclade B. This “*Praxelis*” subclade B included eight species: four species of *Praxelis* Cass., *Eitenia praxeloides* R.M.King & H.Rob, *Eupatoriopsis hoffmanniana* Hieron., *Praxeliopsis matogrossensis* G.M.Barroso and *Osmiopsis plumieri*. The *ndhF* sequence of *C. laevigata* (Lam.) R.M.King & H.Rob., is identical to that of the *Praxelis* clade B but the sequences of all other *Chromolaena* species differed by at least one base).

Geographic distribution

Osmiopsis plumieri has been recorded from both northern and southern Haiti and in Montfleury (GBIF 2023) near Port au Prince (Fig. 4). The 1968 collection made by Alain Liogier in the Dominican Republic (Liogier 12,804; P), identified by an unknown person as *Osmiopsis plumieri*, is in fact a specimen of *Koanophyllon selleanum*. We did not find any herbarium image or any field image in iNaturalist that might prove the recent presence of either *Osmiopsis*

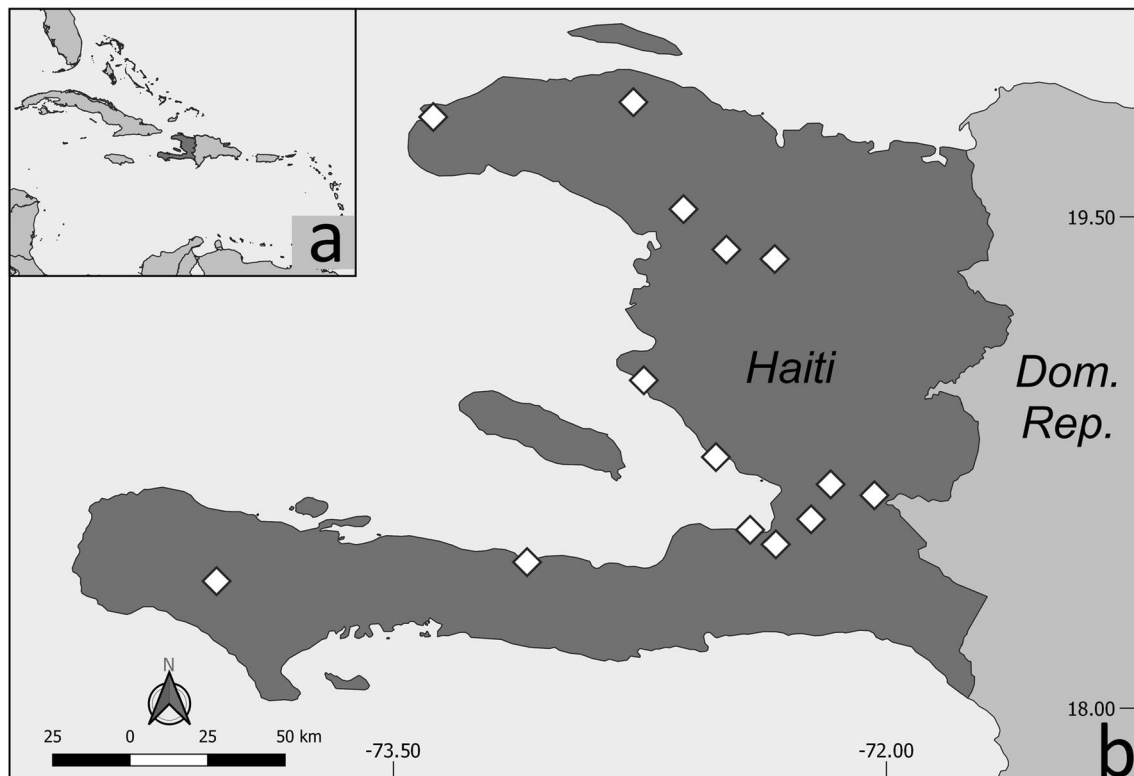


Fig. 4 Distribution map of *Osmiopsis plumieri* (Urb. & Ekman) R.M.King & H.Rob. in Haiti (represented by white diamonds). **a** Caribbean Region with Haiti shown in dark gray. **b** Hispaniola with Haiti

shown in dark gray, Dom. Rep. Dominican Republic. Plotted with QGIS 3.10.14 software; records from GBIF; coordinates inferred from Google Earth

or any other genus of subtribe Praxelinae on Hispaniola except *Chromolaena*.

Morphology

Osmiopsis plumieri shows characters that are often present in *Chromolaena*/*Praxelis*, such as the imbricate involucre and the deciduous involucre bracts (Table 1).

Discussion

Phylogenetic trees

Our phylogenetic tree shows improved sampling within the Praxelinae (compared to the most recent tree; Rivera et al. 2016) with all genera represented by their type species. However, sampling within the large genus *Chromolaena* (160 species; POWO 2024) is still poor. Only 15 species (<10%) had sequences in GenBank (search query "Chromolaena"[Organism]), to which the present study has added another 10 species (see new sequences in Online Resource 2).

The *ndhF* phylogenetic tree grouped *Osmiopsis* in a clade with *Praxelis*, *Eitenia*, *Eupatoriopsis* and *Praxeliopsis* (Fig. 3). Since chloroplasts are maternally inherited in most angiosperms (Greiner et al. 2015), it is likely that the maternal parent of *Osmiopsis* would be found in this clade. However, no species of *Praxelis*, *Eitenia*, *Eupatoriopsis* or *Praxeliopsis* have ever been recorded on Hispaniola (Acevedo-Rodriguez and Strong 2012; this study). This suggests two possibilities: 1) the maternal plant could be *Praxelis clematidea* (Hieron. ex Kuntze) R.M.King & H.Rob., a widespread invasive, now established in Australia, China, Southeast Asia and Florida (Salgado et al. 2022), that may occur in Hispaniola (or may have occurred); or 2) the maternal parent could be a *Chromolaena* species closely related to the *Praxelis* clade, as the latter is nested within *Chromolaena*.

The *ndhF* marker is a highly conserved coding gene. The *ndhF* sequence of *C. laevigata* is identical to that of the *Praxelis* clade but *C. laevigata* is not known to occur on Hispaniola (Acevedo-Rodriguez and Strong 2012). Five *Chromolaena* species are known from Hispaniola: *C. corymbosa* (widely distributed in the Caribbean), *C. heterosquamia* (Urb. & Ekman) R.M.King & H.Rob. (endemic to Hispaniola); *C. sinuata* (Lam.) R.M.King & H.Rob. (endemic

to Hispaniola), *C. ivifolia* (L.) R.M.King & H.Rob. (widely distributed in the Caribbean, North and South America) and *C. odorata* (L.) R.M.King & H.Rob., an aggressive, widely distributed alien (Acevedo-Rodriguez and Strong 2012; POWO 2024). *C. heterosquamea* can be discarded as maternal plant as it appears to belong to another genus: it has 2–3 series of involucre bracts that are subimbricate and the corolla broadens toward the apex, with triangular lobes. *C. odorata* can probably be excluded as its *ndhF* marker differs from *Osmiopsis* by two bases. The *ndhF* sequences of *C. corymbosa*, *C. ivifolia* and *C. sinuata* are unknown.

Other cases of hybrid status detected by incongruence between the chloroplast and nuclear phylogenetic trees are known in the Asteraceae, but these are either within a single genus (*Hieracium*; Fehrer et al. 2007) or different genera of the same subtribe (Liatrinae: Schilling 2011; Lactucinae: Wang et al. 2013; Fehrer et al. 2007; Kilian et al. 2017; Anthemidinae: Stace 2015). Schilling (2011) proposed a hybrid origin for two monotypic genera within subtribe Liatrinae: *Hartwrightia* A.Gray (*H. floridana* A.Gray ex S.Watson) and *Litrissa* Small (*L. carnosa* Small), based on incongruence between the nuclear and chloroplast phylogenetic trees. The Liatrinae phylogenetic tree showed two major clades. Schilling (2011) found that ITS and ETS placed *Hartwrightia* and *Litrissa* in the ‘*Trilisa* clade’ (PP=1; BS=88), while the chloroplast markers placed them in its sister clade (PP=0.74; BS<50) with *Carphephorus* Cass. and *Liatris* Gaertn. ex Schreb. *Litrissa* is morphologically intermediate between the putative parent genera but *Hartwrightia* is morphologically transgressive, showing a loss of several features that present in either one or both of the parental genera (Schilling 2011).

Robinson et al. (1989) stated that much more hybridization probably occurs in the Asteraceae than believed by botanists, and was likely to be an important contributing factor to the family’s evolutionary success. This view has been supported by later studies (Arnold 1997; Stace et al. 2015). Intergeneric hybrids, however, are uncommon in nature; in the British flora, where hybrids have been well studied, only four intergeneric hybrids (nothogenera) have been recorded, out of 57 hybrid Asteraceae (Stace et al. 2015). These nothogenera are usually morphologically intermediate between the parent taxa and sterile, with one of the parents native and the other an introduced alien (Online Resource 6). We do not have information on the fertility of *Osmiopsis plumieri*.

Hybridization facilitated ecological transitions to extreme habitats in the genus *Helianthus* L., Asteraceae (Rieseberg et al. 2003). In *Argyranthemum*, the most species-rich genus of Asteraceae among the Macaronesian-endemic genera, hybridization appears to have played an important part in its diversification (Francisco-Ortega et al. 2008): Different chloroplast lineages occupied different habitats (Francisco-Ortega et al. 1996; Barber et al. 2007) in the islands. Such

geographic structuring of chloroplasts is not restricted to islands (Rieseberg and Soltis 1991; Schuster et al. 2018) and suggests that locally optimal chloroplast genotypes can spread through hybridization. *Koanophyllon*, the richest Asteraceae genus in Caribbean endemics, with species in Cuba, Jamaica, Hispaniola and Puerto Rico (Francisco-Ortega et al. 2008), is a promising taxon to investigate hybridization in the Caribbean flora.

Within tribe Eupatorieae, Robinson et al. (2009) hypothesized that species belonging to subtribes with a chromosome base count $x=10$ would be more likely to cross than those belonging to subtribes with other counts and might result in intergeneric or inter-subtribal hybrids. We have not been able to perform a chromosome count on *Osmiopsis* due to lack of material. However, we investigated existing chromosome counts of potential parental taxa in CCDB (Rice et al. 2015). *Chromolaena* and *Praxelis* (potential maternal parent taxa) are both apomictic with base numbers $x=10$ (King and Robinson 1987; Robinson 2009).

Within the Praxelinae, there are records of $n=10$, 20 and 30 in the invasive species *Praxelis clematidea* R.M.King & H.Rob. and of a polyploid series in *Chromolaena odorata* (Table 2). Within *Koanophyllon* (potential paternal parent taxon), $n=10$ is the most common count, recorded in nine species; other counts recorded are $n=15$ (*K. longifolia* (B.L.Rob.) R.M.King & H.Rob.; Watanabe et al. 1995), $n=20$ (*K. sciagraphes* (B.L.Rob.) R.M.King & H.Rob. and *K. tatei* (B.L.Rob.) R.M.King & H.Rob.; Torres and Liogier 1970) and $n=30$ (*K. pittieri* (Klatt) R.M. King & H.Rob.; Robinson et al. 1989). Chromosome counts for either of the most likely parent plants based on morphology (*K. phanioides* or *K. selleanus*) were not found. Two species of *Koanophyllon* that occur on Hispaniola have chromosome counts: *K. sciagraphes* ($n=20$; Torres and Liogier 1970) and *K. villosum* (Sw.) R.M.King & H.Rob. ($n=10$; Keil et al. 1988). The count of *K. sciagraphes* is based on material from Hispaniola (Dominican Republic), and the count of *K. villosum* is based on material from Jamaica (Torres and Liogier 1970; Keil et al. 1988).

Geographic distribution

Recent Asteraceae collections from the Dominican Republic and Haiti are not available online (<https://sweetgum.nybg.org/science/ih/>) and presumably are only available for *in loco* examination at EHH, ELE, JBSD, HUNPHU, UCMM and USD herbarium. We have not been able to visit Hispaniola thus we do not know if *Osmiopsis plumieri* persists in the Hispaniola flora. However, the known records show a widespread distribution in Haiti (Fig. 4). This suggests that it was either an established, successful fertile hybrid (or species of hybrid origin) or that the parental taxa were common enough for independent hybridizations to be regular events.

Evidence that *Praxelis* (the most likely maternal parent genus) does not occur on Hispaniola [obtained from GBIF, iNaturalist and its absence from Acevedo-Rodríguez and Strong (2012) in their Catalogue of Seed Plants of the West Indies] is suboptimal, so botanists collecting on Hispaniola are urged to look for species of this genus.

Morphology

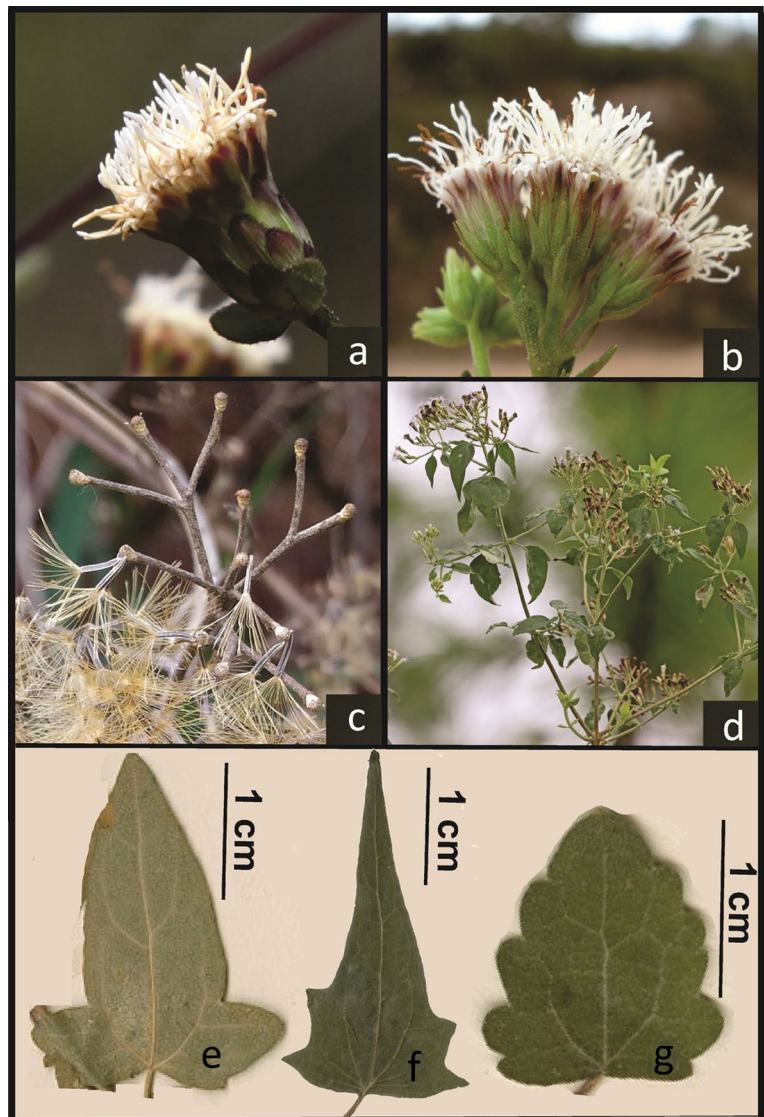
Morphologically, *Osmiopsis plumieri* is most similar to *Chromolaena sinuata* (see Table 2). We suggest that any further investigation in artificial hybridization start with this species as most likely maternal taxon, based on the *ndhF* marker in the chloroplast genome. Identifying the most likely paternal taxon, based on the nuclear ITS tree (Fig. 2) that positioned *Osmiopsis* within *Koanophyllon* is more challenging, as *Koanophyllon* is a very species-rich genus

on Hispaniola (c. 35 species; Acevedo-Rodríguez and Strong 2012). Among these 35 species, *K. phanioides*, one of the putative parents suggested by King and Robinson (1975), appears to be morphologically most similar to *O. plumieri* (Table 2). In addition to the reproductive characteristics cited by King and Robinson, we would add the leaf shape, that is lobed at the base and entire in the upper half, and the long petioles (Fig. 5).

Conclusion

Our work adds further evidence to the theory that hybridization is common in the Asteraceae (Harris & Ingram 1992; Fehrer et al. 2007; Mandel et al. 2019). Testing for incongruence between nuclear and chloroplast phylogenetic trees is essential in this family if trees that combine nuclear

Fig. 5 Illustration of morphological terms used in the text and in Table 2. **a** Imbricate involucre bracts. **b** Eximbricate involucre bracts. **c** Involucre bracts not persisting in fruiting capitula (receptacle exposed). **d** Semi-scandent habit. **e–g** Leaves. Vouchers: **a** *Chromolaena arrayana* (Gardner) R.M.King & H.Rob., *Bringel* and *Moreira* 930 (UB); **b** *Koanophyllon myrtilloides* (DC.) R.M.King & Rob., *Sobral* 16036 (HUFJSJ); **c** & **d** *C. odorata* (L.) R.M.King & H.Rob., not vouchered; **e** *Koanophyllon phanioides* (Urb. & Ekman) R.M.King & H.Rob., *Ekman* 3955 (S); **f** *Osmiopsis plumieri* (Urb. & Ekman) R.M.King & H.Rob., *Ekman* 6490 (LL); **g** *Chromolaena sinuata* (Lam.) R.M.King & H.Rob., *Ekman* 1914 (S). Photo credits & image rights: **a** Henrique J.C. Moreira; **b** Marcos E.G. Sobral; **c** Vijayan Rajapuram; **d** Steve Collins; **e–g** copyright belongs to the cited herbaria



and plastid data are to be correctly interpreted (see Online Resource 3).

This raises the interesting question if the sister subtribes Praxelinae and Critoniinae (Rivera et al. 2016) should be combined or re-circumscribed. In this context, results from target enrichment sequence capture (universal Angiosperms353 probe) that densely samples the nuclear genome are interesting (Zuntini et al. 2024, Suppl. Figures 8, 18–22), see also the continuously updated *Tree of Life* (Baker et al. 2022; <https://treeoflife.kew.org/tree-of-life>). Both trees show a highly supported clade (PP=0.94 in *Tree of Life*, incongruent bipartitions ~80% in Zuntini et al. 2024) of four genera, two Critoniinae and two Praxelinae. For the Critoniinae, *Koanophyllum* and *Aristeguietia* R.M. King & H. Rob. were sampled, and for the Praxelinae, *Chromolaena* and *Praxelis*. These are very large genera but were represented by one species each. The genera did not segregate as would have been expected in the currently accepted sister subtribes circumscription: it showed a ladder-like structure in which *Aristeguietia* was closer to *Chromolaena* and *Praxelis* (PP = 1 in *Tree of Life*, incongruent bipartitions ~60–70% in Zuntini et al. 2024) than to *Koanophyllum*.

As far as we are aware, our study is the first to suggest an inter-subtribal generic hybrid supported by molecular data in the Asteraceae. However, hybrid status of *Osmiopsis* should be confirmed by further studies, such as chromosome counts, complete sequencing of its chloroplast genome and that of possible parental taxa and experimental hybridization of the hypothetical parent taxa. Also, the possibility that the subtribal circumscription is erroneous cannot be disregarded. Our study is based on a moderately robust sample of subtribe Praxelinae (100% of the genera and 16% of the species), but subtribe Critoniinae remains vastly under-represented with only 26% of its genera and 6% of the species sampled (Herz 2004, updated by POWO 2024; Rivera et al. 2016). Denser sampling in the Critoniinae is clearly much needed: only with additional sampling we will be able to state with confidence that *Osmiopsis* is a hybrid between genera of two different subtribes, or between two genera of the same subtribe.

Information on Electronic Supplementary Material

Online Resource 1. a Protocol for the PCR reactions. b Details of molecular markers.

Online Resource 2. Vouchers for molecular markers with GenBank accessions.

Online Resource 3. Bayesian 50% majority rule consensus phylogenetic trees of Tribe Eupatorieae based on all markers (ITS, ETS, *ndhF*, *ndhI* and *ndhI-G* IGS).

Online Resource 4. Bayesian 50% majority rule consensus phylogenetic trees of Tribe Eupatorieae based on the nuclear markers (ITS1, ITS2 and ETS).

Online Resource 5. Bayesian 50% majority rule consensus phylogenetic trees of Tribe Eupatorieae based on the chloroplast markers (*ndhF*, *ndhI* and *ndhI-G* IGS).

Online Resource 6. Intergeneric Asteraceae hybrids in the British Isles.

Alignments and figures available at: <https://doi.org/10.5281/zenodo.17831643>.

Competing interests The authors declare no competing interests.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00606-026-01990-5>.

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Author contributions R.N.R. and V.L.R. conceived the idea and experimental design for the study. R.N.R. and A.L.C. collected material in the field and examined herbarium material to gather morphological and molecular data. R.N.R., C.C.V. and A.L.C. did laboratory work (DNA extraction and amplification and/or measurements of plant structures). A.L.C. produced the map. R.N.R. and V.L.R. curated and analyzed the data. R.N.R. wrote the first draft of the manuscript and produced the tables, illustrations and figures. C.E.B.P. supervised and provided significant contributions to the manuscript. All authors provided comments that improved the final version of the manuscript.

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Data availability DNA Sequences have been uploaded to GenBank without embargo. Alignments and trees have been uploaded to Zenodo.

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