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Research Article

An updated phylogeny of *Deprea* (Solanaceae) with a new species from Colombia: interspecific relationships, conservation assessment, and a key for Colombian species

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Deprea is a neotropical genus that comprises 51 species. Recent work based on molecular data has explored its monophyly and interspecific relationships, but the relationships amongst *Deprea* species were not entirely elucidated. The inclusion of more accessions and molecular markers in phylogenetic analysis is likely to produce more supported hypotheses. Therefore, the main objective of this study was to perform a combined phylogenetic analysis of *Deprea* including seven new samples representing six species and one more DNA plastid marker than in previous studies. In that process, a new species of *Deprea* from Colombia was discovered and is described and illustrated here. *Deprea teresitae* Deanna & A. Orejuela, sp. nov. is morphologically similar to *D. dilloniana* and phylogenetically closely related to *D. hawkesii* and *D. harlingiana*. This new species is distinguished by the combination of short calyx lobes, non-mucronate anthers, long staminal filaments and corolla lobes, and elongated appressed fruiting calyx around a subglobose green berry. The new phylogenetic results are presented, including discussion on phylogenetic interspecific relationships, taxonomy, geographic distribution, and conservation status from *D. teresitae*. The synonymy of *Deprea sylvarum* subsp. *novogranatensis* under *D. glabra* is also proposed and an identification key to the 10 *Deprea* species distributed in Colombia is included.

Keywords: Colombia, *Deprea*, new species, phylogeny, Solanaceae, taxonomic key

Introduction

The genus *Deprea* Raf. comprises 51 species of erect shrubs to small trees with spreading branches and axillary inflorescences 3–15-flowered, calyces shortly lobed, corollas usually funnel-shaped, campanulate or stellate, stamens broadening in width basipetally, and accrescent fruiting calyces always covering the fleshy berry when ripe (Deanna, Leiva González, & Barboza, 2015, 2016; Leiva González & Barboza, 2017). Several species have pharmacological value and alimentary uses (Cardona et al., 2005; Leiva González, Pereyra & Barboza, 2008; Leiva González & Barboza, 2009; Misico et al., 2011; Su, 2003). The genus is endemic to the neotropics, and all species are found growing in pre-montane and montane cloud forests from Costa Rica to Bolivia, with a centre of species diversity in southern Ecuador and northern Peru (Deanna, Barboza, & Carrizo García, 2017; Hunziker, 2001).

Recent phylogenetic studies have clarified the evolutionary history of *Deprea*, among other 'physaloid' genera (Deanna et al., 2017; Zamora-Tavares, Martínez, Magallón, Guzmán-Dávalos, & Vargas-Ponce, 2016). The genus falls within the Withaninae subtribe of the tribe Physalideae, and the closest relatives to *Deprea* are the genera *Aureliana* Sendtn., *Withania* Pauquy, *Nothocestrum* A.Gray, *Discopodium* and *Cuatresia* Hunz. (Deanna et al., 2017). After a complex taxonomic history, *Deprea* circumscription has been revised according to the latest morphological and molecular

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phylogenetic studies (Carrizo García, Wahlert, Orozco, Barboza, & Bohs, 2015; Deanna et al., 2017), resulting in the synonymy of *Larnax* Miers under *Deprea* and the corresponding combinations (Deanna et al., 2015).

Despite recent advances in understanding phylogenetic relationships (Deanna et al., 2017), much remains to be discovered about the ecology, diversity, and evolutionary history of *Deprea*. There are phylogenetic affinities unresolved within the Ellipsoidal berry, Subtriflora and Red-orange berry clades (Deanna et al., 2017) that could be the result of insufficient taxon or gene sampling, or incomplete lineage sorting. As part of the ongoing review of this genus, we revised 42 herbaria collections (listed in Materials and Methods) and undertook field exploration in Colombia. These visits allow us to sample more species from this country and include them in the phylogeny to resolve their circumscription and position. During fieldwork in Colombia, three populations of *Deprea* were collected that did not belong to any of the currently recognized species of the genus. After molecular phylogenetic and morphological analyses plus the review of additional material across Colombia, these individuals have been recognized as a distinct undescribed species. In this paper, we provide a complete description of this new species, along with an updated phylogeny including one more plastid region than in Deanna et al. (2017), and a revised identification key of *Deprea* for Colombia.

Materials and methods

Taxon sampling and outgroup selection

The ingroup included 53 samples, comprising 43 previously analysed species of *Deprea* (Deanna et al. 2017) plus a recently described species (*D. micrantha* S. Leiva & Barboza; Leiva González & Barboza, 2017) and a new species presented here (Appendix 1, see online supplemental material, which is available from the article's Taylor & Francis Online page at http://dx.doi.org/10.1080/14772000.2018.1483976). Recently collected samples of species that were previously not resolved monophyletic were also added (*D. auccana*, *D. subtriflora*, *D. hawkesii*) as well as of species whose identity and circumscription remain unclear (*D. darcyana*, Deanna et al., 2017). Multiple accessions of *D. sachapapa*, *D. purpurea*, and *D. longipedunculata* were removed since the monophyly of these species has already been confirmed in previous analyses (Deanna et al., 2017). The outgroup comprised 26 species, including one *Cuatresia* Hunz., six representatives of Withaninae, 13 of Iochrominae, and three of Physalidinae subtribes, and also one *Capsicum* L., one *Lycianthes* (Dunal) Hassl., and one *Salpichroa* Miers (Appendix 1). Plant material was collected during several field trips to Colombia, Ecuador, and Peru between 2012 and 2017. Leaves were dried in silica and vouchers were prepared and housed at local herbaria of each country (Colombia: COL, JBB, PSO; Ecuador: LOJA, QCA, QCNE; Peru: HAO, HUT) in addition to duplicates deposited at CORD.

DNA extraction, PCR amplification, and sequencing

Total DNA was extracted from silica-dried leaf samples using a modified 2 × CTAB procedure (Doyle & Doyle, 1987). Two nuclear DNA markers previously used in Deanna et al. (2017) were amplified by PCR for the new samples (Appendix 1, see supplemental material online): ITS (internal transcriber spacer) and *waxy* (GBSSI, granule-bound starch synthase gene). An additional chloroplast marker (*trnL-F*) was amplified for all the 53 *Deprea* samples and 13 outgroups (Appendix 1, see supplemental material online).

ITS was amplified according to the published protocol by Baum, Small & Wendel (1998) usually as one fragment (primers leu1/ITS5 – ITS4) and occasionally as two overlapping fragments (leu1/ITS5 – ITS2, 273F – ITS4; Appendix 2). PCR reactions were carried out in 25 µL reactions using 15.875 µL of distilled water, 2.5 µL of 10 × PCR Buffer buffer (Qiagen, Valencia, California, USA), 2.5 µL of $MgCl_2$, 1 µL of bovine serum albumin (BSA, 100 µg/ml), 0.5 µL of each primer (10 µM), 1 µL of dNTPs (10 mM), 0.125 µL of Taq® polymerase (5 u/µL, Qiagen), and 1 µL of total DNA (∼100 ng). The PCR program was 95 °C for 4 min, then 35 cycles of 95 °C for 45 s, 52 °C for 1 min, 72 °C for 30 min, followed by a final extension of 72 °C for 5 min. Direct sequencing was possible for all taxa and double peaks were not detected, probably because the ITS region undergoes concerted evolution, homogenizing the numerous copies (Hamby & Zimmer, 1992).

The *waxy* gene was amplified from 3 to 9 exons in two overlapping fragments, using different combinations of primers (Appendix 2, see supplemental material online). Each 25 µL of *waxy* PCR reaction contained 15.375 µL of distilled water, 2.5 µL 10× PCR Buffer buffer (Qiagen, Valencia, California, USA), 2 µL of $MgCl_2$, 1 µL of Q solution (Qiagen), 1 µL of each primer (10 µM solutions), 1 µL of dNTPs (10 mM), 0.125 µL of Taq polymerase (5 u/µL, Qiagen, Valencia, California, USA), and 1 µL of total DNA (∼ 100 ng). This PCR mix was cycled through a program of 95 °C for 2 min, then 10 cycles of 95 °C for 30 s, 56 °C for 1 min, decreasing 1 °C per cycle, 72 °C for 1:20 min, followed

by 20 cycles of 95 °C for 30 s, 50 °C for 30 s, and 72 °C for 1:20 min, then 20 more cycles with the same last conditions but increasing 5 s the extension temperature per cycle, and followed by a final extension of 72 °C for 10 min.

The chloroplast *trnL-F* region was usually amplified in one fragment (primers C–F) or less common in two parts (C–D, E–F; Appendix 2, see supplemental material online). The PCR mix followed the same recipe as *waxy*, but the PCR program was 95 °C for 4 min, then 35 cycles of 95 °C for 45 s, 55 °C for 1 min, 72 °C for 1:30 min, followed by a final extension of 72 °C for 5 min. Samples were sequenced on an ABI Prism 3730xl DNA analyser (GENEWIZ, Boston, MA, USA). Pseudogenic regions found in the *trnL-F* sequences were trimmed out to not compromise the homology requirement that could lead to false hypotheses of phylogeny (Poczai & Hyvönen, 2013).

Sequence alignment and phylogenetic analyses

Sequence quality was inspected using GENEIOUS v4.6 (Drummond et al., 2009). Previously published sequences from Deanna et al. (2017) were incorporated (Appendix 1, see supplemental material online), and sequence alignments were performed in MEGA 6 (Tamura, Stecher, Peterson, Filipski, & Kumar, 2013) using the MUSCLE algorithm (Edgar, 2004) followed by manual adjustments. Each DNA region was analysed individually with Maximum likelihood (ML) in RAxML v.8 (Stamatakis, 2014), using GTR + GAMMA approximation rate substitution model, whereas *waxy* was also analysed considering exon/intron partitions. Aligned sequences were concatenated in SequenceMatrix 1.8 (Vaidya, Lohman, & Meier, 2011) in order to obtain a combined dataset for the partitioned ML analysis. To assess nodal support of the ML trees, the rapid Bootstrap (BS) algorithm with 1000 replicates was applied.

Bayesian inference (BI) analyses were conducted for the combined dataset with four partitions, one per marker, in BEAST 2 (Bouckaert et al., 2014). Best-fit nucleotide substitution models were chosen for each partition based on the Akaike Information Criterion (AIC) using jModelTest 2.1.3 (Darriba, Taboada, Doallo, & Posada, 2012; Posada & Crandall, 1998). Three independent BEAST analyses were run for 10 million generations each with tree sampling every 1000 generations, using an uncorrelated lognormal relaxed clock model to describe the branch-specific substitution rates (Drummond, Ho, Phillips, & Rambaut, 2006) and a Birth-Death prior. Convergence and stationarity of the parameters were inspected using Tracer v1.7 (Rambaut, Drummond, Xie, Baele, & Suchard, 2018) targeting minimum effective sample sizes (ESS) of at least 200. The initial 25% of trees were discarded as burn-in, and the results were combined using LogCombiner as implemented in the BEAST package. The phylogenetic relationships were summarized in a maximum clade credibility (MCC) tree, and their posterior probabilities (PP) for all nodes were estimated using TreeAnotator v2.4.7. The trees were visualized in FigTree v.1.4.3 (Rambaut, 2016). Both ML and BI analyses were run on CIPRES platform to reduce the execution time (Miller, Pfeiffer, & Schwartz, 2010).

New species description and conservation assessment

Fresh material was preserved in FAA solution (formaldehyde – acetic acid – ethanol) to perform measurements of reproductive organs using a Zeiss Stemi 2000-C stereomicroscope at 6.5–50× magnification. Illustrations were made by composite line drawings from the preserved material. Images were diagrammed using Adobe Photoshop®. Collections from worldwide herbaria (AAU, ANDES, BAF, BM, CAUP, COAH, COL, COLO, CONC, CORD, CTES, FMB, GH, HAO, HOXA, HUA, HUAZ, HUEFS, HUT, JAUM, JBB, K, LOJA, LP, LPB, MEDEL, MO, MY, NY, PORT, PSO, Q, QCA, QCNE, QPLS, QUSF, TEX, UDBC, US, USM, VEN, W) were analysed, from digital images or in person, in order to search for specimens of the newly described species.

Species distributions were plotted using QGIS 2.8 (QGIS Development Team, 2018) and were based on georeferenced data of all the herbarium collections plus non-georeferenced localities identified by A. Orejuela and E. Calderón. Conservation status was assessed using IUCN criteria B, geographic range in the form of B1 (extent of occurrence) and B2 (area of occupancy; IUCN, 2017). The extent of occurrence and area of occupancy were calculated using the Geospatial Conservation Assessment Tool, GeoCAT (Bachman, Moat, Hill, de Torre, & Scott, 2011).

Results

Molecular phylogeny

Deprea is resolved as a monophyletic genus in every gene tree obtained (BS =87 for ITS, 100 for *trnL-F*, 99 for *waxy* without partitions, 100 for *waxy* with exon/intron partitions), except in *psbA-trnH* due to lack of resolution (Appendix 3, see supplemental material online), with similarly strongly support in the combined

dataset (BS =100; Fig. 1). All the seven clades proposed by Deanna et al. (2017) are recovered with similar supports (Fig. 1), therefore, only strongly supported incongruences with previous results and affinities of the newly included samples are presented and discussed below.

The Ecuadorian *D. micrantha* is resolved as sister to *D. longipedunculata* (PP = 1, BS = 88) within the

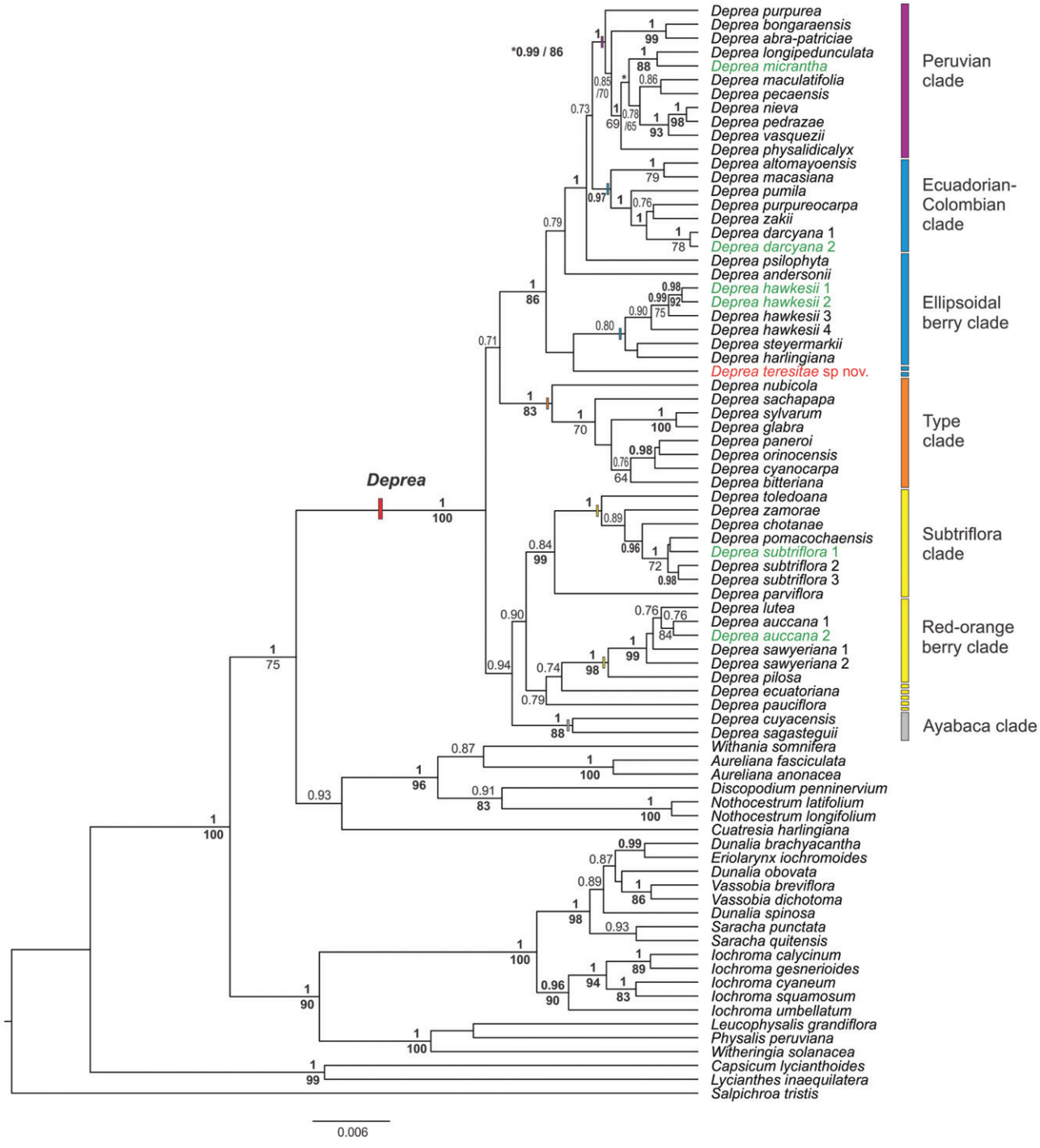

Fig. 1. Maximum clade credibility tree of *Deprea* and related genera obtained from a Bayesian inference with the combined dataset of four markers (ITS, *psbA-trnH*, *trnL-F*, and *waxy*). Posterior probabilities >0.7 are given above each branch and bootstrap support from Maximum likelihood analysis >60 are given below the branches; bold numbers indicate posterior probabilities >0.95 or bootstrap supports >80. Green-coloured tip names correspond to the new samples included here and the new species described in this study is coloured in red. The species grouping proposed is shown with coloured-bars.

strongly supported Peruvian clade (PP = 1). Sister to this clade, six species are grouped (*D. altomayoensis*, *D. macasiana*, *D. darcyana*, *D. purpureocarpa*, *D. zakii*, and *D. pumila*) in the Ecuadorian-Colombian clade. *Deprea darcyana* 1 was collected in the same locality as the type collection and falls in a strongly supported clade with *D. darcyana* 2, from Munchique National Park (Cauca, Colombia).

Within the Ellipsoidal berry clade, two new samples of *D. hawkesii* are included, one of them with purple colouration in the green corolla (Orejuela et al. 2663). All the four accessions are resolved together in the BI inference (PP = 0.9), confirming the monophyly of *D. hawkesii*. The Colombian *D. teresitae* is resolved as sister to this clade but poorly supported. However, this species is included within a larger clade formed by the Peruvian + Ecuadorian-Colombian + Ellipsoidal berry clades, with high support (PP = 1, BS = 86).

The Subtriflora clade (PP = 0.84, BS = 99) includes six taxa, *D. chotanae*, *D. parviflora*, *D. toledoana*, *D. subtriflora*, *D. pomacochaensis*, and *D. zamorae.* An additional sample of *D. subtriflora* 1 from Central Peru is included and resolved as sister of *D. pomacochaensis*, within a strongly supported clade with the two remaining samples of *D. subtriflora* (PP = 1, BS = 72).

Within the Red-orange berry clade, an extra sample of *D. auccana* 2 is incorporated, and resolved as sister of *D. auccana* 1, although poorly supported (PP = 0.76, BS = 84). This species is grouped in a strongly supported clade (PP = 1, BS = 99) with *D. lutea* and *D. sawyeriana*, whereas *D. pilosa* is resolved as sister to this clade. *Deprea ecuatoriana* and *D. pauciflora* are closely related to the Red-orange berry clade but poorly supported (PP = 0.74 and 0.79, respectively). *Deprea cuyacensis* and *D. sagasteguii* are grouped within the strongly supported Ayabaca clade (PP = 1, BS = 88).

Fig. 2. *Deprea teresitae*. **1.** Flower in lateral view. **2.** Fruit. **3.** Vegetative branch. **4.** Open flower. Drawing by L. Ribulgo (Museo Botanico CORD).

Taxonomic treatment

Deprea teresitae Deanna & A. Orejuela sp. nov.
Figs 2, 3

Type. COLOMBIA. Valle del Cauca Department: Dapa, vía Cali-Dagua, Reserva 'El Refugio', bosque secundario cercano a la casa, subiendo cerro no perturbado, zona con pendiente muy leve, 1913 m, 03°32′02,4″N 76°36′56,8″W, 1 February 2016 (fl), *Deanna & Calderón 169* (holotype PSO 047274!, isotypes COL!, CORD 00006933!, QCA!); 4 November 2011 (fl, fr), *Orejuela & Calderón 167* (paratype COL 000430986!).

Diagnosis. *Deprea teresitae* differs from *D. dilloniana* in its dimorphic leaves (the larger 8.8–17 cm long, 3.5–7.1 cm wide, the smaller 2.2–2.5 cm long, 1.4–1.6 cm wide vs 9–16.3 cm long, 4–8 cm wide in *D. dilloniana*), its 2–4 flowered inflorescence (vs. 3–6-flowered), its tiny calyx lobes of 0.1–0.4 mm long (vs. 0.6–1.1 mm long), its longer corolla lobes of 5.5–8 mm long (vs. 2.5–4.1 mm long), longer staminal filaments (1.5–2 mm long vs. 0.8–1.2 mm long in *D. dilloniana*), its cream and non-mucronate anthers (vs. purple and mucronate), and in its fruiting calyx tightly enveloping the berry and elongated at the apex (11–12.7 mm long, 6–8 mm diameter vs. calyx loose not elongated at the apex, 13–17 mm long, 12–15 mm diameter in *D. dilloniana*).

Shrubs, widely branched, plagiotropic, 1.2–1.5 m tall. Stems terete, green or greenish purple, hollow; old stems glabrescent (long simple 3–5-celled transparent non-glandular trichomes); young stems green pubescent, with long simple multicellular non-glandular trichomes; nodes usually green. Leaves alternate; petiole semiterete, 14–43 mm long, green or partially purple, pubescent, with the same trichomes of young stems; leaf blade entire, dimorphic; the larger leaves 8.8–17 cm long, 3.5–7.1 cm wide, widely elliptic, apex acute, base cuneate, slightly oblique to asymmetric; the smaller leaves 2.2–2.5 cm long, 1.4–1.6 cm wide, ovate to elliptic, apex cuspidate, base cuneate and oblique; both membranous, dark green above, dull green below, glabrescent on both surfaces with short ochraceous glandular trichomes, also with some long simple non-glandular trichomes mainly along veins abaxially. Fascicles axillary, (1–) 2–4-flowered; pedicels 5–8 mm long, light-green, filiform, pendent, pubescent, with short antrorse

Fig. 3. *Deprea teresitae.* **1.** Habit. **2.** Flower in anthesis. **3.** Mature fruit. **4-6.** Flowers in lateral view. **4, 5.** Flowers in anthesis. **6.** Immature flower. Note calyx lobes in **4, 6**, and exserted non-mucronate anthers in **5. 1, 2, 4–6** from Deanna & Calderón 169 (photo **2** by E. Calderón, the rest by R. Deanna), **3** from Orejuela & Calderón 167 (photo by A. Orejuela).

multicellular non-glandular trichomes. Flowering calyx 3–4.5 mm diameter in anthesis, dull green with dark green veins externally, light-green internally, cup-shaped, fleshy, pubescent, slightly sericeous externally, with abundant long simple non-glandular trichomes, and some short glandular trichomes (stalk unicellular, ochraceous head 6-celled), glabrous internally; tube 1.9–2.5 mm long, 2.5–4.5 mm diameter; lobes unequal, 0.1–0.5 mm long, 0.5–1.5 mm wide, triangular, acute, erect, with papillae and 2–3 celled transparent non-glandular trichomes at the apex. Corolla slightly campanulate before anthesis, clearly stellate in anthesis, (6–) 7–15 mm diameter in anthesis, fleshy; tube yellowish green on both sides, 2–3.3 mm long, glabrescent externally, with some short glandular trichomes, glabrous internally, without an inner annular ring of trichomes; lobes 5.5–8 mm long, 2–3.5 mm wide, triangular, slightly reflexed, opaque and cream externally, lustrous and deep-purple with yellowish green apex, margins and veins internally, occasionally entirely dull purple internally, margin reflexed, apex ciliate, glabrescent on both surfaces, with short non-glandular and glandular trichomes. Stamens exserted, heterodynamous; filaments glabrous, cream, two longer (1.8–2 mm long), three shorter (1.5–1.7 mm long), adnate to the corolla for 0.5–0.8 mm long, broadening abruptly in width basipetally, filament base expansion auriculate and yellowish green, auricles subtriangular, inconspicuous; anthers unequal, occurring in two or three size classes, the shorter 1.6–1.8 mm long, 1.6–1.8 mm wide, the longer 1.9–2.1 mm long, 1.5–1.7 mm wide, always cream, ellipsoidal, non-mucronate, connective cream rectangular. Ovary glabrous, globose to pyriform, 1.6–1.7 mm long, 1.5–1.7 mm wide, nectary annular, inconspicuous, greenish yellow, occupying a quarter of the ovary length; style 4.6–4.8 mm long, glabrous, cream, extending ~1 mm beyond the anthers; stigma clavate, light green to tan, 0.3–0.5 mm long. Fruit a berry, subglobose to ovoid, 7.5–8.3 mm long, 6–8 mm diameter, whitish green, fleshy, glabrous. Fruiting calyx accrescent, tightly enveloping the berry, elongated and open at the apex, 11–12.7 mm long, 6–8 mm diameter, markedly 10-costate, lustrous, green with protruding dark green ribs, pubescent externally, with abundant long, non-glandular trichomes mainly along veins, and some short and long glandular trichomes, glabrous internally; lobes conspicuous, unequal. Fruiting pedicels 13–15.5 mm long, green, pendent, pubescent. Seeds not seen.

Etymology. This new species is dedicated to Teresita Sáenz de Calderón, the owner of the private nature

reserve 'El Refugio' (type locality and where most of the collections have been made). 'Doña Teresita' has allowed the reserve to be managed as a protected area. At 90 years of age, she is still working in her garden. Her son, the Colombian botanist, Eduardo Calderón-Sáenz, has helped our research in Solanaceae over the past few years and has been a tireless partner in our field trips to Valle del Cauca Department.

Distribution and habitat. *Deprea teresitae* is known from the western cordillera of Colombia in the Department of Valle del Cauca and occurs in tropical montane cloud forest between 1900–2100 m of elevation, over an area of 2.7 km^2 (Fig. 4).

Species conservation assessment. According to IUCN criteria (IUCN, 2017), *D. teresitae* is proposed as an Endangered (EN) species. The extent of occurrence is calculated to be 2.7 km^2 (Criterion B1 < 5000 km^2, Endangered), the area of occupancy, 16 km^2 (Criterion B2 < 500 km^2, Endangered) and the species is known from only four localities (Criterion B1a ≤ 5, Endangered). Fragmentation and decline in the quality of the habitat have been observed since the populations are restricted to private lands separated by roads (Criterion B1biii), not included in the Colombian National System of Protected Areas (Sistema Nacional de Áreas Protegidas de Colombia). More collecting and population assessments will help to know if there is a decline in geographic range to confirm this assessment.

Phylogenetic position and morphologically similar species. *Deprea teresitae* is phylogenetically related to *D. harlingiana*, *D. hawkesii*, and *D. steyermarkii*, which belong to the Ellipsoidal berry clade (Fig. 1). *Deprea hawkesii* is the only species in this clade sympatric to *D. teresitae*, but this species is clearly different to *D. teresitae* by its ellipsoidal-fusiform or elongated berry and small green flowers. The Peruvian *D. dilloniana* and the Ecuadorian *D. pumila* superficially resembling to *D. teresitae* due to the subglobose berry, heterodynamous stamens, and colourful corolla, but are easily separated from *D. teresitae* by their mucronate anthers, shorter staminal filaments, and inflated fruiting calyx. Detailed differences among *D. teresitae* and the sympatric and morphologically similar species are shown in Appendix 4 (see supplemental material online).

Specimens examined. COLOMBIA. Valle del Cauca Department: Dapa, Vía Cali-Buenaventura, km 18, Finca Zingara, en bosques arriba de la casa, 2074 m, 03°32′41.6″N, 76°36′35.1″W, 12 Feb 2014 (fl, fr), *Orejuela & Ng 720* (COL 000430985!, JBB 06631!); vía Cali-Dagua, kilómetro 23, Reserva Privada 'El Refugio', creciendo en borde de quebrada, 4 Nov 2011 (fl, fr), *Orejuela & Calderón 167* (COL 000430986!, JBB 11957!); Bosque de San Antonio, W of Cali, near television tower, lower montane forest, 1950–2050 m, 15 July 1984 (fl), *Al Gentry et al. 48167* (MO 3197178!); Finca San Pablo, km 15 of Cali-Buenaventura road, 1900 m, 14 Mar 1990 (fl), *Murcia 61* (MO 04913800!); Dapa, vía Cali-Dagua, Reserva 'El Refugio', bosque secundario cercano a la casa, subiendo cerro no perturbado, zona con pendiente muy leve, 1913 m, 03°32′02.4″N, 76°36′56.8″W, 1 Feb 2016 (fl), *Deanna & Calderón 169* (PSO 047274!, CORD 00006933!).

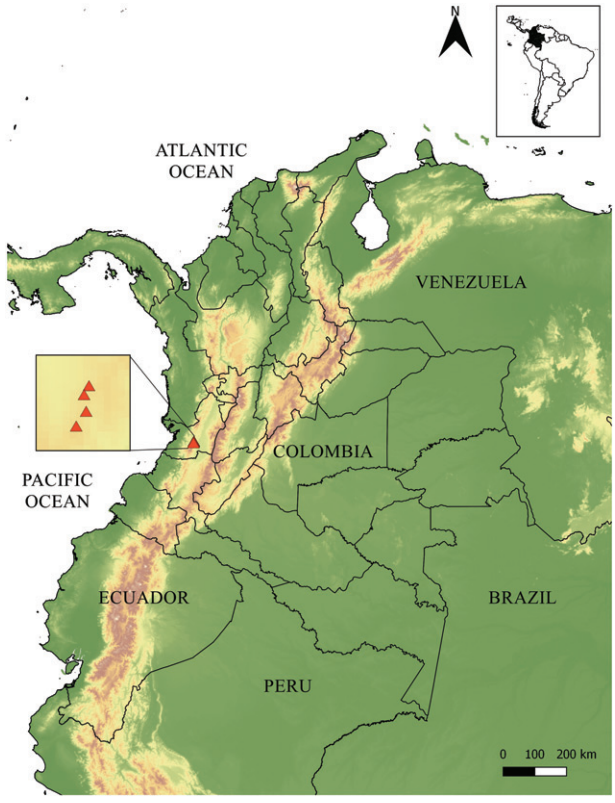

Fig. 4. Geographic distribution of *D. teresitae*.

Taxonomic notes of *Deprea* from Colombia: a new synonym

Sawyer (2001) described *Larnax sylvarum* subsp. *novogranatensis* N. W. Sawyer as a Colombian disjunct taxon from the subspecies *sylvarum* restricted to Central America. Morphometric analyses performed by Sawyer (2001) showed that these subspecies are different by the size of several structures (leaves, flowering pedicels,

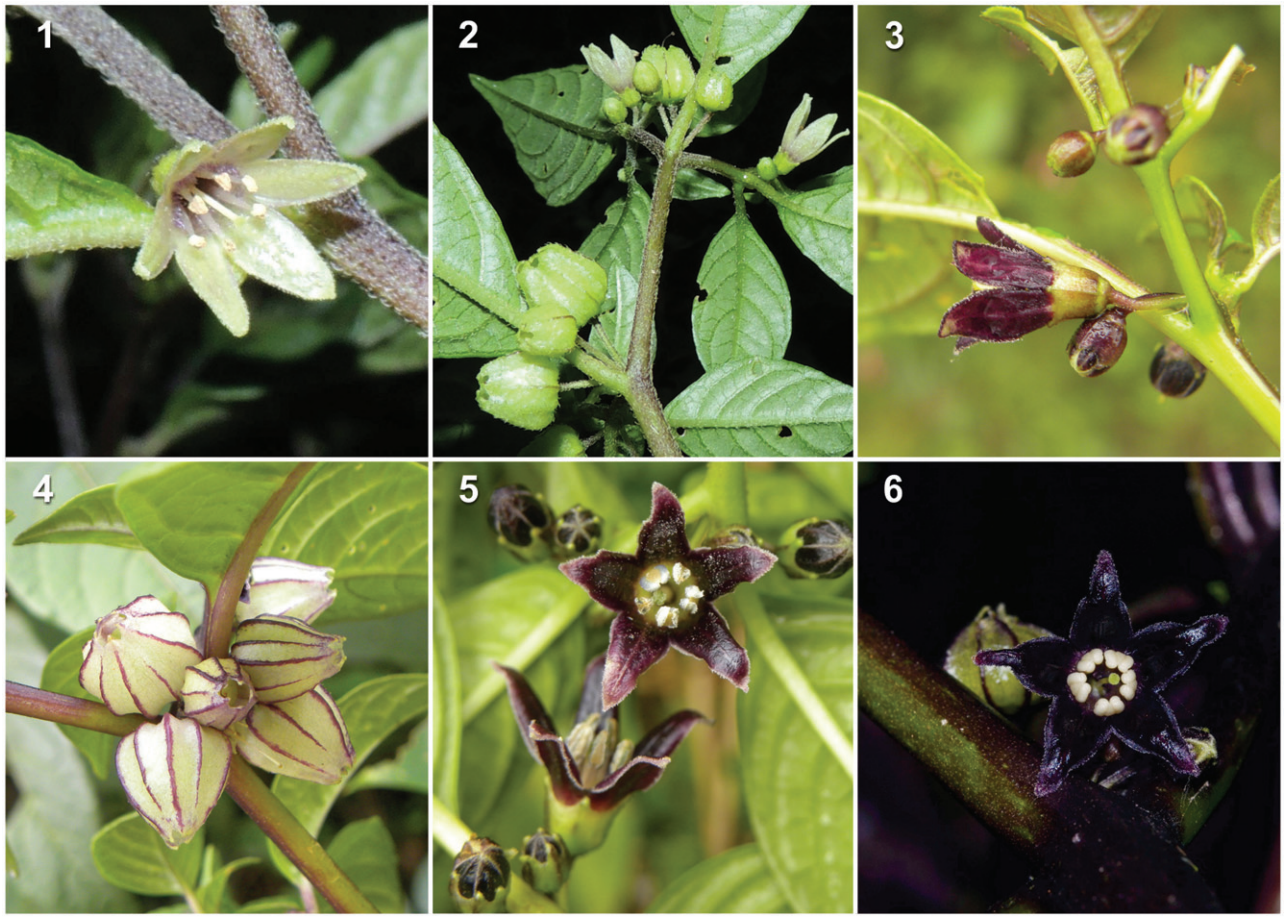

Fig. 5. Flowers and fruits of *D. sylvarum* and *D. glabra.* **1–2.** *Deprea sylvarum* from Cerro de la Muerte, Costa Rica (Kriebel 5796, photo by R. Kriebel). **3–4.** *Deprea glabra* from Munchique National Park, Cauca (Orozco *et al.* 3812, photo by G. E. Barboza). **5.** *Deprea glabra* from Laguna La Cocha, Nariño, previously considered as *D. sylvarum* subsp. *novogranatensis* (Deanna & Urbano 174, photo by R. Deanna). **6.** *Deprea glabra* from Tatamá NP, Risaralda, also considered as *D. sylvarum* subsp. *novogranatensis* (Bohórquez 1673, photo by J. M. Posada).

corolla, staminal filaments, fruiting calyx, and fruit). After a detailed analysis of the isotypes of subspecies *novogranatensis* housed at COL, HUA, and MO (previously uncited), in addition to an examination of a photograph of the holotype housed at TEX (JSTOR database, https://plants.jstor.org), the corolla lobes-tube length ratio (0.9–1.5), its glabrescent to pubescent indumentum with abundant short glandular trichomes, the bigger corolla with entirely deep purple lobes (8.5–14.1 mm vs 4.5–9.9 mm long in *D. sylvarum* subsp. *sylvarum*), larger berry (7.5–10 mm vs 4.5–7.2 mm diameter) enveloped by a greenish fruiting calyx with deep purple ribs, and its shorter flowering calyx lobes (0.4–0.7 vs 0.5–1 mm long) unequivocally match with *D. glabra*. To ensure the identity of *L. novogranatensis*, all paratypes cited by Sawyer (2001) were analysed, and new collections were performed in similar localities to the paratypes cited (Fig. 5; Laguna La Cocha, Nariño; PNN Tatamá, Risaralda).

Deprea glabra (Standl.) Hunz., Kurtziana 10: 25. 1977. Basionym: *Athenaea glabra* Standl., Tropical Woods 42: 32. 1935.

Type. ECUADOR. [Azuay]: W. cordillera above Balsapampa, 2600 m, 14 December 1934 (fl, fr), *A. Rimbach 239* (holotype F 753597!, isotypes B 100248779!, G 00343107!, GH 00046619!, MAD, MO 5472857!, NY, Y).

≡ *Larnax glabra* (Standl.) N.W.Sawyer, Novon 11 (4): 460. 2001.

= *Larnax sylvarum* subsp. *novogranatensis* N.W. Sawyer, Novon 11 (4): 461. 2001. **syn. nov**.

Type. COLOMBIA. Antioquia: Mpio. Jardín, km 20 road Jardin-Riosucio, ~15 km SSE of Jardín, Alto de Ventanas, disturbed montane forest, 2700–2790 m [05°31′16″N 75°48′50″W], October 1988 (fl, fr), *J. L. Zarucchi, G. McPherson & F. J. Roldan 6926* (holotype

TEX 00374484!, isotypes COL 000004225!, HUA 0000742!, MO 5604713!).

A key to *Deprea* species from Colombia

We present a revised analytical key restricted to the 10 species of *Deprea* that are found in Colombia, based on the key of Deanna et al. (2016), including the new species described here and excluding *D. sylvarum*, now restricted to Central America. We also provide updated information on geographic distribution on each species.

1. Corolla funnel-shaped, lobes-tube length ratio 0.15–0.6 … … … … … … … … … … … … … … … 2
2. Plants glabrescent; corolla tube without an inner ring of trichomes inside. Northern Colombia (Magdalena) … … … … … … … … … … … … *D. nubicola*

2′. Plants pubescent; corolla tube with an inner ring of trichomes inside … … … … … … … … … … … ...3

3. Leaves always with branched trichomes intermixed with simple trichomes; corolla 10.2–19.5 mm long, entirely yellow, purple, or yellow with variable quantities of purple colouration. Colombia (Antioquia, Boyacá, Caldas, Cauca, Chocó, Cundinamarca, Meta, Nariño, Norte de Santander, Quindío, Risaralda, Santander, Tolima), Ecuador (Tungurahua), Venezuela (Mérida, Táchira) … … .*D. orinocensis*

3′. Leaves with only simple, non-branched trichomes; corolla 7.5–15 mm long, always entirely purple 4

4. Calyx lobes 0.5–1.3 mm long; fruiting pedicels oblique to pendent; fruiting calyx greenish-cream with purple apex, always enveloping the berry tightly; leaves monomorphic, 3–14.2 cm long, 1.5–8.5 cm wide. Colombia (Antioquia, Boyacá, Caldas, Chocó, Cundinamarca, Meta, Quindío, Risaralda, Tolima), Ecuador (Azuay, Cañar, Tungurahua) .....*D. bitteriana*

4′. Calyx lobes (0.8–)1.5–2.5 mm long; fruiting pedicels erect to oblique; fruiting calyx deep purple with whitish-purple apex and ribs, enveloping the berry tightly or loosely; leaves dimorphic, the major 5–17 cm long, 2–7.5 cm wide, the minor 3–7 cm long, 1.5–4 cm wide. Colombia (Antioquia, Quindío, Tolima).....*D. cyanocarpa*

1′. Corolla campanulate to stellate, lobes-tube length ratio 0.9–3.7.....5

5. Corolla greenish yellow or whitish yellow, lobe-tube length ratio 2.9–3.7(–5); calyx lobes (0.6–) 1–2.5 mm long. Colombia (Antioquia, Cauca, César, Chocó, Nariño, Putumayo, Quindío, Risaralda, Valle del Cauca), Ecuador (Azuay, Bolivar, Carchi, Cotopaxi, **Esmeraldas**, **Imbabura**, **Napo**, Pichincha).....*D. sachapapa*

5′. Corolla purple, green, or green with variable amounts of purple, lobe-tube length ratio 0.9–2.5; calyx **lobes 0.1–1.2 mm long**.....6

6. Corolla entirely dark purple to blackish purple, lobe-tube length ratio 0.9–1.5; staminal filaments broadening gradually in width basipetally. Colombia (Antioquía, Caquetá, Cauca, Huila, Nariño, Putumayo, Risaralda, Valle del Cauca), Ecuador (Azuay, Bolívar, Cañar, Carchi, Chimborazo, El Oro, Imbabura, Napo, Pichincha) .....*D. glabra*

6′. Corolla entirely green, or greenish-yellow externally, deep purple internally, with margins, apex and veins of lobes greenish-yellow; lobe-tube length ratio 1.5–2.5; staminal filaments broadening abruptly in width basipetally 7

7. **Corolla entirely green; anthers mucronate**.....8

8. Berry orange when mature, globose; fruiting calyx tightly enveloping the berry, sometimes loosely enveloping the berry. Colombia (Caldas, Cauca, Huila, Risaralda)..... *D. darcyana*

8′. Berry green when mature, ellipsoidal-fusiform; fruiting calyx always tightly enveloping the berry. Colombia (Caquetá, Cauca, Huila, Putumayo, Tolima), Ecuador (Carchi, Napo, Pichincha, Sucumbios, Tungurahua).....*D. hawkesii*

7′. Corolla deep purple internally, with margins, apex and veins of lobes greenish-yellow; anthers non-mucronate 9

9. Flowers usually arranged in axillary inflorescences 2–4-flowered; corolla lobes-tube length ratio 2–2.2; calyx lobes 0.1–0.5 mm long; fruiting calyx tightly enveloping the berry and elongated at the apex. Colombia (Valle del Cauca).....*D. teresitae*

9′. Flowers usually solitary, sometimes paired; corolla lobes-tube length ratio 1.5–2; calyx lobes 0.8–0.9 mm long; fruiting calyx loosely enveloping the berry, not elongated at the apex. Southern Colombia (Caquetá), Eastern Ecuador (Morona Santiago, Napo, Pastaza) ..... *D. macasiana*

Discussion

Deprea is a monophyletic genus and is placed within the Withaninae subtribe of the Physalideae tribe according to the inferred phylogeny including an additional chloroplast region (*trnL-F*) as previously established by Deanna et al. (2017). The addition of newly collected samples allowed us to resolve some interspecific relationships, although there are still unclear affinities. We discuss each clade (highlighted in bold) where new samples and/or molecular markers improve resolution and support of phylogenetic relationships.

Deprea micrantha was recently described as an Ecuadorian endemic species (Leiva González &

Barboza, 2017). This species is phylogenetically most closely related to *D. longipedunculata* in the **Peruvian clade** that comprises only endemic Peruvian species. *Deprea micrantha* differs from *D. longipedunculata* in its larger corolla (7.7–8 vs 4.8–5 mm long) with deep purple lobes and green veins (vs entirely green corolla), non-mucronate anthers (vs. mucronate), staminal filaments homodynamous (vs. heterodynamous), and filament base expansion conspicuously auriculate (vs. auricles inconspicuous in *D. longipedunculata*). *Deprea micrantha* is morphologically close to *D. peruviana* (Zahlbr.) S. Leiva & Barboza, species not included in the phylogenetic analyses due to the absence of recent collections. After revising numerous specimens, we found that the only difference between these two species is the corolla (white in *D. peruviana* and greenish with purple colouration on lobes in *D. micrantha*), so *D. micrantha* could be considered as a synonym of *D. peruviana.* The inclusion of samples from the type locality (Tambillo, Cutervo, Peru) of this species will help to resolve this taxonomic problem.

The **Type clade** is resolved as in Deanna et al. (2017), but some differences are found in the Subtriflora and Red-orange berry clades. The **Subtriflora clade** includes *D. chotanae*, *D. parviflora*, *D. toledoana*, *D. subtriflora*, *D. pomacochaensis*, and *D. zamorae.* Our phylogenetic results, after the inclusion of an additional sample of *D. subtriflora* from Carpish (Central Peru), suggest this species as non-monophyletic (cf. Fig. 1). *Deprea pomacochaensis* should be considered as a synonym of *D. subtriflora*, based on not only the phylogenetic evidence, but also on the similarities in their karyology (Deanna, Barboza, & Scaldaferro, 2014) and morphology, especially in the yellow stellate corolla with filaments broadening gradually in width basipetally, non-mucronate anthers, and in their orange berry tightly enclosed by a partially purple fruiting calyx. *Deprea subtriflora* is the only *Deprea* species that inhabits Bolivia and one of the most widely distributed (Leiva González, Deanna, Barboza, & Cueva Manchego, 2013). This large occurrence extension plus isolation between southern populations from Bolivia and Peru and northern populations from Peru could have increased the morphological variability, but the phylogenetic results discourage the description of new taxa, a similar situation to that in *D. sachapapa* (Deanna et al., 2017).

The **Red-orange berry clade** encompasses four species (*D. auccana*, *D. lutea*, *D. pilosa*, *D. sawyeriana*) restricted to an Andean depression in the border between Ecuador and Peru, called the Amotape-Huancabamba (A–H) zone (Weigend, 2004). They share several morphological traits, such as the red or orange berry with an appressed or broken fruiting calyx, and the yellow to cream corolla with an inner ring of trichomes (Deanna et al., 2017). After including one more sample, *D. auccana* is resolved as a monophyletic species, but the affinities between the populations of *D. sawyeriana* are still unresolved.

According to Deanna et al. (2017), *D. ecuatoriana* was a member of the **Subtriflora clade** but in the updated phylogeny is resolved as sister to the **Red-orange berry clade** with low support. This species and *D. oxapampensis* M. Cueva & Treviño are the only ones with urceolate and orange corollas within *Deprea*, but the former is restricted to paramos from northern Peru (Cajamarca and Piura), and southern Ecuador (Loja and Zamora-Chinchipe) whereas *D. oxapampensis* is only found in Central Peru (Cueva & Treviño, 2012). The inclusion of samples of this last species would help to resolve the relationships between these species and their position within the genus. *Deprea pauciflora* is also closer to the **Red-orange berry clade** than in previous results (Deanna et al., 2017), but is morphologically close to *D. sachapapa* (Deanna et al., 2016) and most similar karyologically to *D. glabra* (Deanna et al., 2014). Analysis of more DNA regions would be necessary to resolve its position.

Deprea darcyana is part of the well supported **Ecuadorian-Colombian clade**, and the monophyly of this species is strongly supported after the inclusion of a sample collected in the type locality, also confirming its occurrence in Munchique National Park of Cauca Department, in addition to Huila and Risaralda (Sawyer, 2001). On the other hand, the monophyly of *D. hawkesii* was an unresolved situation in our previous phylogenetic results (Deanna et al., 2017). To address this taxonomic problem, we included two more populations from Colombia, *D. hawkesii* 2 from a close locality to where the type was collected (Hunziker, 1977) and *D. hawkesii* 1 with morphological variation in the corolla colour (green with a purple-tinge instead of green as in all the other collections). The monophyly of this species in addition to the lack of a genetically closer relationship between the most morphologically similar populations (*D. hawkesii* 2 and 4) could suggest morphological variations associated to environmental conditions, discouraging description of intraspecific taxa.

Deprea teresitae is closely related to the **Ellipsoidal berry clade**, which includes the sympatric *D. hawkesii*, and the allopatric *D. steyermarkii* and *D. harlingiana*. These three species are distinguished by their ellipsoidal-fusiform or elongated berry and small inconspicuous, usually green flowers, in contrast to *D. teresitae* with a subglobose berry with elongated fruiting calyx

and a bigger purple corolla. Morphologically similar species to *D. teresitae* are *D. dilloniana* from Peru and *D. pumila* from Ecuador, from which can easily be distinguished by the combination of short calyx lobes, non-mucronate anthers, long staminal filaments and corolla lobes, and elongated appressed fruiting calyx around a subglobose green berry (Appendix 4, see supplemental material online.).

The updated phylogeny for *Deprea* does not change previous inferences about ancestral geographic distributions (Deanna et al., 2017), but molecular dating could provide insights into the evolutionary history of this physaloid group. Ongoing analyses on the recently published new fossil evidence assigned to the physaloid group (Wilf, Carvalho, Gandolfo, & Cúneo, 2017) in relation to the previously used fossils in molecular dating analyses of the Solanaceae family (Särkinen, Bohs, Olmstead, & Knapp, 2013; Särkinen, Kottner, Stuppy, Ahmed, & Knapp, 2018) will allow us to explore potential links between the timing of lineage diversification in *Deprea* and geological events within the Andes, such as the uplift of the Eastern Cordilleras of the Central and Northern Andes (Hoorn et al., 2010).

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Supplemental data

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