Systematic Revision of the *Epipetrum* Group of *Dioscorea* (Dioscoreaceae) Endemic to Chile

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Systematic Revision of the *Epipetrum* Group of *Dioscorea* (Dioscoreaceae) Endemic to Chile

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**Abstract**—A systematic revision of the *Epipetrum* group of *Dioscorea* (Dioscoreaceae), which traditionally included three taxa endemic to Chile, is presented. We evaluated the taxonomic value of macro- and micromorphological traits to delimit generic boundaries with respect to other yams and to identify and separate its taxa. The comprehensive survey included 10 qualitative and 45 quantitative traits related to all plant organs and new micromorphological features of leaf, fruits, seeds, and pollen. Discriminant analyses were conducted with three accumulative morphological data sets to test seven taxonomic hypotheses of differentiation among taxa. Our results indicate that these taxa are characterized by the combination of prominent pistillodes in male flowers and a base chromosome number of *x* = 7, which separate it from all other Dioscoreaceae, plus different sets of morpho-anatomical traits that differentiate it from other putatively closely related yams with unwinged seeds in *Dioscorea* (the *Borderea* group, the *Nanarepenta* group, the *Tamus* group, etc.). *Dioscorea humilis* is the most distinctive species. Our analyses revealed significant morphological differences between northern and southern populations of this species resulting in the recognition of two subspecies, the northern *D. biloba* subsp. *biloba*, and the new southern *D. biloba* subsp. *coquimbana*. *Dioscorea humilis* and *D. polyanthes* are morphologically similar and only differ in qualitative leaf traits. This minor variation is better treated by reducing *D. polyanthes* to subspecific rank in *D. humilis*, and the combination *D. humilis* subsp. *polyanthes* is made herein.

**Keywords**—Discriminant analysis, morphology, pollen, SEM, South America, taxonomy.

*Epipetrum* Phil. has long been considered one of the five narrow genera of Dioscoreaceae, comprising only three species endemic to Chile (Knuth 1924; Burkill 1960). Specimens of the most common species of this genus, collected by Bertero (1829) from Central Chile, were first described as *Luzuriaga cordata* Bertero, although the plant does not show any morphological affinities with the members of this unrelated genus of Philesiaceae. This misinterpretation was noticed by Colla (1836) who redescribed the species as *Dioscorea humilis* Colla, creating a nomenclatural conflict that has been recently clarified (Viruel et al. 2009). *Dioscorea humilis* was later transferred to a new genus, *Epipetrum* [*E. humilis* (Colla) Phil.] by Philippi (1862) after the rupiculous habitat of the plant. According to Philippi (1862, 1864), the separation of this new genus from *Dioscorea* L. was justified by the absence of winged seeds. This remarkable trait is also shared with three other small genera of the yam family: the Mediterranean-Macaronesian *Tamus* L., which possesses a baccate fruit rather than a capsule (as in almost all other *Dioscorea* s. l. species), the Pyrenean *Borderea* Miégeville, and the Mexican *Nanarepenta* Matuda (Matuda 1961; Téllez-Valdés and Dávila-Aranda 1998), African *Dioscorea gilletii* Milne-Redh. (Milne-Redhead 1963), Caribbean *Rajania* L., and some other *Dioscorea* species with samaroid fruits. The combination of unwinged seeds produced in three-angled capsules, and a dwarf trailing habit shared with *Borderea*, led Pax (1887) to place *E. humile* within *Borderea* [B. *humilis* (Bertero ex Colla) Pax], a classification later criticised based on morphological and biogeographical studies of Dioscoreaceae (Reiche 1908; Burkill 1960). None of the preceding nomenclatural combinations took into account the original and validly published specific epithet of this plant as *L. cordata*, and thus this epithet became substituted in the literature by the currently accepted one (*humile*), forcing the rejection of *cordata* to promote nomenclatural stability (Viruel et al. 2009).

Despite the low taxonomic diversity within *Epipetrum*, the boundaries among some of its taxa are not completely clear. Three decades after the description of *L. cordata* (*E. humile*), Philippi (1892) described an additional species that he collected from northern Chile (Antofagasta, Region II) and named *E. bilobum* Phil. after its strongly bilobed leaves. Almost simultaneously, Reiche collected some individuals of *Epipetrum* from south-central Chile (near Constitución, Maule, Region VI), which resembled *E. humile* in overall gross morphology. Nonetheless, a careful inspection of the specimens by Philippi (1896) resulted in the description of a third species, *E. polyanthes* F. Phil., which differed from typical *E. humile* by its flashter leaves lacking marked secondary venation. Nevertheless, the fruits and seeds of the two new species remained undescribed.

A later revision of *Epipetrum* with comparison to *Borderea* revealed the morphological differences between the genera (Reiche 1908). Despite the thorough revision of Reiche (1908), the differences between *E. humile* and *E. polyanthes* were not adequately translated into the identification key and did not agree with observations made by Philippi (1896).

As mentioned above, the taxonomic identity of this poorly known genus has been controversial, as different authors have either synonymized it under other genera of Dioscoreaceae (Colla 1836; Pax 1887; Caddick et al. 2002a, b) or have treated it as an independent genus (Philippi 1862, 1864; Reiche 1908; Knuth 1924). Recent phylogenetic studies, with a broader perspective of Dioscoreaceae and based on morphological and molecular data, placed the wingless-seeded genera (*Borderea, Epipetrum, Nanarepenta*, and *Tamus*) as nested within a large paraphyletic *Dioscorea* clade (Caddick et al. 2002a, b) and subsequently subsumed them within *Dioscorea* (Caddick et al. 2002b). The pan-Mediterranean *Tamus* and the Pyrenean *Borderea* were placed as sister taxa within a weakly supported African *Dioscorea* clade in trees based on plastid *rbcl* (Caddick et al. 2002a) and combined *rbcl*–*matK* plastid data (Wilkin et al. 2005). However, the apparent close relationships of *Epipetrum* to *Borderea* and *Tamus* were inferred solely based...
on morphological characters, since no molecular data were obtained for *Epipetrum* (Caddick et al. 2002a, b). The phylogenetic relationships of *Epipetrum* to other taxa of the family Dioscoreaceae requires confirmation from molecular data. However, a preliminary analysis indicates that *Epipetrum* emerges as a monophyletic group embedded within a South American clade of *Dioscorea* (Viruel et al. unpublished data), supporting the findings of Caddick et al. (2002a, b) and the reassessment of *Epipetrum* within *Dioscorea* (Caddick et al. 2002b). Therefore, we hereafter treat *Epipetrum* as a species group in *Dioscorea*.

Additional samples of these *Epipetrum* taxa collected in the early to middle 1900s provided more data on their geographical distribution (Fig. 1). The most common species, *Dioscorea humilis*, is presently known from five areas in central Chile (from central Valparaíso to southern Bío-Bío). The known range of *D. polyanthes* has remained unchanged and is restricted to the area around the type locality at Constitución (Maule region), whereas for *D. biloba*, in addition to the northern locality in Antofagasta, a disjunct southern population was found in the Limarí province (Coquimbo region) in 1948. The southern population of *D. biloba* has not been found recently and consequently the species was assessed as insufficiently known and presumed extinct (Marticorena et al. 2001). Surprisingly, none of these three species were included in the catalogue of threatened plant species from central-southern Chile (Hechenleitner et al. 2005) but were included in the Millennium Seed Bank Project led by the Chilean Instituto de Investigaciones Agropecuarias (INIA) and the Royal Botanic Gardens, Kew.

Historical collections of the *Epipetrum* group have been scarce, precluding any detailed study of their morphological variation. Given that most of the available data for these three species comes from their original descriptions, with few updates, we have undertaken a systematic revision of the genus based on newly collected specimens and an exhaustive morphological study. Statistical methods widely used in plant systematics (Baum 1989; Torrecilla et al. 2003; Pimentel and Sahuquillo 2007) have also been incorporated in the analysis as a suitable approach for detecting significant differences among taxa. Specifically, our study is aimed at (i) conducting a thorough survey of macro- and micromorphological traits that would reveal the extent of morphological differences among the three taxa, with special emphasis on the most similar, *D. humilis* and *D. polyanthes*; (ii) analyzing the extent of morphological differentiation between disjunct areas of *D. biloba*; (iii) assigning populations and individuals to predefined groups based on discriminant analyses; (iv) comparing the morphological similarities and differences with other natural groups in *Dioscorea*, with special reference to the wingless-seeded species; (v) providing updated geographical distributions and habitat descriptions for each taxon; and (vi) supplying detailed illustrations showing the distinctive characters of each species.

**Materials and Methods**

**Sampled Materials**—Due to the scarcity of herbarium specimens from the *Epipetrum* group in both Chile (SGO, CONC) and internationally (B, G, K, MO, NY, SI, TO), two expeditions were organized to Chile from which abundant materials were collected for the three taxa. Samples were collected from a total of 25 populations, including 14 populations of *D. humilis* covering the entire distributional range of the species, nine populations of *D. biloba*, six corresponding to the southern range and three to the northern range for this species, and two populations of the rarest species, *D. polyanthes* (Fig. 1). High resolution scans of the type specimens of the three species were obtained from G, SGO, and TO.

**Analysis of Macromorphological Traits**—Measurements of macromorphological traits were taken from the new collections deposited at JACA. A total of 53 morphological characters (43 quantitative and 10 qualitative characters; Table 1) were measured from 188 plants, including 79 individuals of *D. biloba*, 99 of *D. humilis*, and 10 of *D. polyanthes* (from 32, 32, and three herbarium vouchers, respectively; see representative material examined) using an SM7800 stereomicroscope and a micrometer to the nearest 0.05 mm. Eight plants were excluded because they were incomplete.

![Fig. 1. Geographical distributions of the Epipetrum group of Dioscorea taxa in Chile. Dioscorea biloba (circles), D. humilis (squares), D. polyanthes (triangles). Filled symbols represent new collections from this study, white symbols represent additional historical records taken from both old herbarium specimens and the literature where different from our sampled sites. Dashed lines encircle the type locality of each taxon. Roman numbers denote Chilean administrative regions: II-Antofagasta, III-Atacama, IV-Coquimbo, V-Valparaíso, VI-Metropolitan region of Santiago, VII-O’Higgins, VIII-Maule and IX-Bío-Bío.](image-url)
for the characters studied. Vegetative characters were studied in all 181 individuals whereas floral and/or fruit characters were scored from a subset of 120 mature individuals. For each individual, ten measurements per character were taken and the averages were calculated for the multivariate analysis.

Scanning Electron Microscopy Analysis—Maternal leaves and capsules were dehydrated in increasing ethanol series and critical-point dried using carbon dioxide in an AUTOSAMDR 840 (Tousimis) and mounted afterwords on stubs for gold/palladium coating. Mature pollen and seeds were mounted on stubs using double-sided adhesive tape and coated with gold/palladium in a BIORAD SC-500 ion sputtering coater. Morphological observations were carried out in a Hitachi S-4100 field emission scanning electron microscopy (SEM). Nomenclature for pollen characters follows Caddick et al. (1998) and Schols et al. (2001, 2003, 2005).

Statistical Analyses—Statistical analyses were aimed at revealing whether morphological variation was consistent with currently recognized species within the Epipetrum group and identifying the most informative morphological characters for the differentiation of the taxa. A Shapiro-Wilk test (Shapiro and Wilk 1965) was used to check for departures of quantitative characters from a normal distribution before excluding them from further analyses. Four out of 43 quantitative characters (tl, tw, snl, nfm, and lpf, Table 1) were not continuous within individual taxa and were excluded from the analysis. We conducted a classification discriminant analysis (DA) using SPSS for Windows v. 15 (SPSS Inc., Chicago, Illinois). This method calculates the probabilities of membership of each OTU to the taxonomically predefined groups (D. humilis, D. biloba, and D. polyanthes, and different combinations of them), allowing the identification of the more discriminant variables by means of Fisher’s coefficient (Fisher 1936; Anderson 1996) at the significant threshold value of 0.05. In subsequent analyses, both invariant and nonsignificant (Fisher’s test p value > 0.05) variables for the corresponding analyzed groups of samples were excluded. The number of informative morphological characters varied from six to 16, depending on the group of samples analysed each time. Seven different hypothetical classifications were tested to identify the different taxonomic units: (1) D. humilis versus D. polyanthes; (2) D. biloba versus D. humilis; (3) northern D. biloba versus southern D. biloba; (4) D. biloba versus D. humilis versus D. polyanthes; (5) D. biloba versus D. humilis with D. polyanthes assignment not predefined; (6) D. biloba versus D. humilis + D. polyanthes; (7) northern D. biloba versus southern D. biloba versus D. humilis versus D. polyanthes. The posterior probability of classification of each sample and the Wilks’ Lambda value of each discriminant function and sampled group considered were calculated (Wilks 1932). The Wilks’ Lambda value expresses the proportion of total variability between predefined groups allowing the contrast of the null hypothesis of equality of multivariate average of groups or centroids (Visanta-Vinacua 1998). As the value of Wilks’ Lambda approaches zero, the discrimination between the predefined groups is better. Analyses were conducted using three different subsets of morphological characters, including quantitative stem and leaf traits, quantitative and qualitative stem and leaf traits, and combined datasets of quantitative and qualitative traits of stem, leaves, and fruits.

Results

Morphological Characters and their Taxonomic Importance in the Systematics of the Epipetrum group of Dioscorea—All plant organs were investigated in the search for potentially taxonomically valuable characters. These included both macroscopic (Table 1) and microscopic (SEM) features (Figs. 2–6). Species of the Epipetrum group showed a high overall similarity in gross morphological traits, especially the species pair D. humilis-D. polyanthes. Little variation was found within these two species, but unexpectedly higher differentiation was found between northern and southern populations of D. biloba. Morphological variation was mostly related to vegetative characters, especially leaf features, but differences were also observed for some fruit traits. A summary of the range and mean values of the analyzed quantitative traits and the character states of qualitative traits studied in these species is presented in Table 2.

Tubers—All three Dioscorea species exhibited similar values for both quantitative and qualitative morphological traits derived from tubers. In these taxa, dark brown tubers are totally covered by roots and show an irregular, sometimes branched, to globose shape. Because of the lack of infragenus variability, the traits derived from tubers (tl, tw, color) were of little value for species differentiation (Tables 1, 2).

Stem—Each year the plants produce a single, slender (up to 4 mm in diam.), tetragonal aerial stem that divides into as many as 9 branches at the first branching point. The distance from the base to the branching point seems to depend on the depth at which the tuber is buried and therefore this character has no taxonomic value (Table 2).

Leaves—Most of the morphological differences found among this group of Dioscorea taxa occur in leaf characters (Figs. 2 and 3). Leaves are petiolar in the three species, but they are whorled (three-14 per node) in D. biloba, alternate in D. polyanthes, and alternate, opposite or more rarely whorled (up to six per node, in the population of Catapilco, Region V) in D. humilis. Leaves of D. biloba are wider than they are long and strongly bilobed, in contrast to those of D. humilis and D. polyanthes which are obovate with a weakly emarginate apex. The leaf texture is membranous in D. biloba and D. humilis, but somewhat fleshy in D. polyanthes. All taxa have mucronate leaves, with entire to slightly papillose-crenulate margins in older leaves. Primary venation is inconspicuous in D. biloba (Figs. 2A, B, D, E), but strongly conspicuous (with three to seven primary veins) in D. humilis and D. polyanthes (Figs. 2G, H, J, K). Secondary venation is prominent in D. humilis giving the leaves a grooved texture, a character unique to this taxon (Figs. 2G, H), while it is almost undetectable in D. biloba (Figs. 2A, B, D, E) and D. polyanthes (Figs. 2J, K), giving the
Table 2. Summary of morphological characters studied in the *Epipetrum* group of *Dioscorea*. Values of morphological traits are reported separately for northern and southern populations of *D. biloba*.

<table>
<thead>
<tr>
<th>Character</th>
<th>Northern <em>D. biloba</em></th>
<th>Southern <em>D. biloba</em></th>
<th><em>D. humilis</em></th>
<th><em>D. polyanthes</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Tubers Shape</td>
<td>irregular</td>
<td>globose</td>
<td>globose</td>
<td>globose</td>
</tr>
<tr>
<td>Size (cm)</td>
<td>8 × 3</td>
<td>2.8 × 3</td>
<td>3 × 2.5</td>
<td>2.5 × 2.5</td>
</tr>
<tr>
<td>Color</td>
<td>brown</td>
<td>brown</td>
<td>brown</td>
<td>brown</td>
</tr>
<tr>
<td>Stem Length (cm)</td>
<td>(49.5–115.23)</td>
<td>(7–18.34–33.5)</td>
<td>(2.5–16–34)</td>
<td>(6.5–14.5–28)</td>
</tr>
<tr>
<td>Width (mm)</td>
<td>(0.1–0.17)</td>
<td>(0.1–0.28)</td>
<td>(0.2–0.42)</td>
<td>(0.3–0.4)</td>
</tr>
<tr>
<td>Papillae</td>
<td>present</td>
<td>present</td>
<td>present</td>
<td>present</td>
</tr>
<tr>
<td>Leaf petiole Length (mm)</td>
<td>(1.2–5.77)–26</td>
<td>(3–17.56–82)</td>
<td>(2.3–20.3–128)</td>
<td>(10–29.28–96)</td>
</tr>
<tr>
<td>Papillae</td>
<td>acute with striate ornamentation</td>
<td>rounded, bulging with striate ornamentation</td>
<td>acute with striate ornamentation</td>
<td>acute with striate ornamentation</td>
</tr>
<tr>
<td>Leaves Phyllostaxis</td>
<td>whorled</td>
<td>whorled</td>
<td>alternate or opposed, rarely whorled</td>
<td>alternate</td>
</tr>
<tr>
<td>Shape</td>
<td>bilobed</td>
<td>bilobed</td>
<td>obovate</td>
<td>obovate</td>
</tr>
<tr>
<td>Size (mm)</td>
<td>(1.1–2.6 (8) × (1.7–4.3–11.8)</td>
<td>(1.1–4.15–(15.8) × (1.5–6.7–17.5)</td>
<td>(2–10.8–(29) × (2.5–12.3–33)</td>
<td>(5–13.98–(24) × (6.8–16.15–28)</td>
</tr>
<tr>
<td>Margin</td>
<td>papillose-crenulate</td>
<td>papillose-crenulate</td>
<td>papillose-crenulate</td>
<td>papillose-crenulate</td>
</tr>
<tr>
<td>Consistency</td>
<td>membranous flat</td>
<td>membranous flat</td>
<td>membranous grooved</td>
<td>membranous grooved</td>
</tr>
<tr>
<td>Secondary veins</td>
<td>not prominent</td>
<td>not prominent</td>
<td>prominent</td>
<td>not prominent</td>
</tr>
<tr>
<td>Papillae ornamentation</td>
<td>stellate-reticulate</td>
<td>stellate-reticulate</td>
<td>stellate-reticulate</td>
<td>stellate-reticulate</td>
</tr>
<tr>
<td>Adaxial side</td>
<td>stellate-reticulate</td>
<td>stellate-reticulate</td>
<td>stellate</td>
<td>stellate</td>
</tr>
<tr>
<td>Abaxial side</td>
<td>reddish</td>
<td>reddish</td>
<td>colorless</td>
<td>Colorless to reddish</td>
</tr>
<tr>
<td>Papillae color on abaxial side</td>
<td>colorless</td>
<td>colorless</td>
<td>Colorless to reddish</td>
<td>Colorless to reddish</td>
</tr>
<tr>
<td>Bacts Length (mm)</td>
<td>(0.5–0.82)–(1)</td>
<td>(0.4–0.97)–(1.4)</td>
<td>(0.5–0.97)–(1.3)</td>
<td>1.7</td>
</tr>
<tr>
<td>Male inflorescences Number of flowers</td>
<td>(2–3)–(6)</td>
<td>(1–) 5–(8)</td>
<td>(1–) 3–(5)</td>
<td>2–(3)</td>
</tr>
<tr>
<td>Pedicel (mm)</td>
<td>(0.75–2.67)–(4.1)</td>
<td>(4–8.09–16)</td>
<td>(4–10.17–18)</td>
<td>11</td>
</tr>
<tr>
<td>Tepals (mm)</td>
<td>(0.7–1.03)–(1.2) (x (0.4–0.51–0.6)</td>
<td>(0.9–1.19–(1.8) × (0.4–0.61–1)</td>
<td>(0.8–1.2–(1.6) × (0.4–0.6–0.75)</td>
<td>1.7 × 0.8</td>
</tr>
<tr>
<td>Stamens (mm)</td>
<td>(0.2–0.28–0.3)</td>
<td>(0.3–0.33–0.45)</td>
<td>(0.2–0.29–0.4)</td>
<td>0.4</td>
</tr>
<tr>
<td>Pistillodes (mm)</td>
<td>(0.4–0.82)–(1)</td>
<td>(0.4–0.9)–(1.3)</td>
<td>(0.6–1.24)–(4.4)</td>
<td>1.5</td>
</tr>
<tr>
<td>Female inflorescences Number of flowers</td>
<td>(1–3)</td>
<td>(1–) 1–(3)</td>
<td>(1–) 1–(3)</td>
<td>1</td>
</tr>
<tr>
<td>Tepals (mm)</td>
<td>(0.8–0.98)–(1.1) × (0.4–0.48–0.6)</td>
<td>(1–1.11–(1.2) × (0.4–0.67–1.4)</td>
<td>(0.5–0.89–1.2) × (0.3–0.42–0.6)</td>
<td>(0.5–1.1–(1.3) × (0.3–0.5)–0.6)</td>
</tr>
<tr>
<td>Ovary</td>
<td>(1.5–2.06)–(3)</td>
<td>(1.5–2.06–(3)</td>
<td>(0.8–1.55–2.5)</td>
<td>(0.9–2–2.5)</td>
</tr>
<tr>
<td>Peduncle of Capsule Shape</td>
<td>filiform, straight or flexuose</td>
<td>filiform, straight or flexuose</td>
<td>spirally curled</td>
<td>spirally curled</td>
</tr>
<tr>
<td>Length (mm)</td>
<td>(10–16)–(20)</td>
<td>(4–12.24–(26)</td>
<td>(0.3–11.29–32)</td>
<td>(7–9.4–18)</td>
</tr>
<tr>
<td>Papillae</td>
<td>present, rounded</td>
<td>present, rounded</td>
<td>present, acute</td>
<td>present, acute</td>
</tr>
<tr>
<td>Capsule Shape</td>
<td>ovoid</td>
<td>ovoid</td>
<td>globose</td>
<td>globose</td>
</tr>
<tr>
<td>Papillae</td>
<td>stellate-reticulate</td>
<td>stellate-reticulate</td>
<td>stellate-reticulate</td>
<td>stellate-reticulate</td>
</tr>
<tr>
<td>Seeds Color</td>
<td>reddish</td>
<td>reddish</td>
<td>brownish</td>
<td>brownish</td>
</tr>
<tr>
<td>Shape</td>
<td>globose</td>
<td>globose</td>
<td>globose</td>
<td>globose</td>
</tr>
<tr>
<td>Size (mm)</td>
<td>2 × 1</td>
<td>(1.5–1.9–(2.3) × (1.2–1.61–2)</td>
<td>(1–1.97)–(2.8) × (0.8–1.4)–(2)</td>
<td>(1.4–2–(2.2) × (1.2–1.8)–(2)</td>
</tr>
<tr>
<td>Caruncle (mm)</td>
<td>0.3</td>
<td>0.3–0.31 (–0.7)</td>
<td>0.1–0.24 (–0.4)</td>
<td>0.15–0.3 (–0.4)</td>
</tr>
</tbody>
</table>
leaves a flat appearance. The pattern is reticulate in all three taxa. All parts of the leaves, including petioles, are covered by small glandular hairs and papillae in each of the three taxa (Figs. 2A-C, F, I, L, 3). The glandular hairs of these taxa are composed of a one-celled stalk and a gland of up to six cells. Due to their size (5 μm), these glands were previously only visible in histological preparations (Reiche 1908); here we present SEM observations at much greater resolution (Figs. 2I, L, 3N). The papillae in the Epipetrum group (Figs. 2A-C, F, I, L, 3) consist of enlarged and bulging epidermal cells. They are colorless on the adaxial side of leaves of all taxa. On the abaxial side, they are colorless in southern populations of D. biloba, reddish in northern populations of D. biloba, and colorless to reddish in D. humilis and D. polyanthes. The sculpturing of the pericinal wall of the leaf papillae is stellate-reticulate in both sides of the leaf in northern D. biloba (Figs. 3A-C) and D. humilis (Figs. 3G-I). In southern D. biloba, it is stellate on both sides of the leaf (Figs. 3D, F), and in D. polyanthes, it is stellate-reticulate on the adaxial side (Figs. 3J, L) but striate or smooth on the abaxial side (Fig. 3K). Papillae on the leaf petioles are rounded and strongly bulging in southern D. biloba (Figs. 2F, 3M), in contrast to the conical and sharply pointed ones of northern D. biloba, D. humilis, and D. polyanthes (Fig. 3Q). In all three taxa, the pericinal walls of the papillae show a striate sculpturing.

Inflorescences—Inflorescences are axillary. Male plants have shortly racemose to cymose inflorescences (occasionally because of suppression of internodes between flowers) that produce up to eight flowers. Those of D. humilis and D. polyanthes are very fragile and ephemeral, falling soon after anthesis, whereas those of D. biloba remain attached to the male plant for a longer period. Female inflorescences generally produce a single flower or more rarely two to three flowers, born on a long flexuose pedicel. In most populations of the Epipetrum group, male and female inflorescences are found on separate individuals, and are thus strictly dioecious. Occasionally, however, some monocious individuals, producing both male and female inflorescences, are found in otherwise dioecious populations of D. humilis.

Flowers—The flowers are trimerous, pedicellate, and unisexual by reduction. Perianths of male and female flowers are two-whorled and isomeros; they are composed of six greenish tepals. The male flowers are produced on erect and fragil pedicels in D. humilis and D. polyanthes, but in erect and robust ones in D. biloba. Male flowers are hypogynous; the androecium is composed of six subsessile stamens and the gynoecium is reduced to prominent, dark purple, sterile pistillodes, without an ovary. All taxa in the Epipetrum group exhibit bisulcate pollen with a perforate to finely reticulate exine (Fig. 4). Female flowers are epigynous and are generally solitary at the end of long, flexuose pedicels. The androecium of female flowers is reduced to six staminodes. The gynoecium is tricarpellate, with a syncarpic ovary and trifid stigma.

Fruits—The fruit is a 3-locular capsule, crowned by the persistent perianth (Fig. 5), and dehisces by valves from the apex towards the base. Capsules are supported by long filiform and papillos peduncles, which are straight with rounded papillae in D. biloba (Fig. 5) but spirally curled with acute papillae in D. humilis and D. polyanthes (Figs. 5K, L). Capsule shape is obovoid (i.e. wider towards apex) in D. biloba and globose (i.e. wider towards middle) in D. humilis and D. polyanthes. Capsules of all three taxa are triquetrous, with three-angled locules that enclose two seeds each, and have undulate margins (Figs. 5A, D, G). The epidermis of young capsules is papillose and glandulose (Fig. 5B). The glandular hairs are identical to those present in leaves and petioles (Fig. 3N, 5B). The papillae show stellate-reticulate to striate-reticulate pericinal walls (Figs. 5C, E, F, H, I) in the three species.

Seeds—The seeds of the Epipetrum group are globose to ellipsoid and wingless (Fig. 6). They are reddish-brown in all three taxa. The seeds are relatively small, (1–2.8 × 0.8–2 mm), and have a caruncle up to 0.7 mm long (Figs. 6B, E). The seed coat is smooth with irregularly shaped cells. The cells of the testa show a flat pericinal wall that becomes convex and bulging towards the caruncle (Figs. 6C, F). There is no difference among taxa in the seed characters studied.

Classification Discriminant Analyses—Different subsets of the morphological variables that showed significant values of Fisher’s coefficient (p < 0.05) were used to conduct the corresponding classification discriminant analyses (DA). These subsets included nine variables of the stem and the leaves with quantitative variation: stw, nsln, pl, nln, lpn, ll, lw, lb/lb, lm; four variables of the leaves with qualitative variation: pt, lo, lner, lc; three variables of the fruits with quantitative variation: cl, cv, lpd; and two variables of the fruits with qualitative variation: sp, fs (Table 1). Analyses were performed in three independent and additive series of variables, including quantitative traits of stem and leaves, quantitative and qualitative traits of stems and leaves and quantitative and qualitative traits of stems, leaves, and fruits, respectively. This complete set of variables was considered for DAs of the three taxa and infraspecific subgroups (northern and southern D. biloba populations) of the Epipetrum group. However, for particular species combinations (D. humilis versus D. polyanthes, D. biloba versus D. humilis) some of the analyses were not attempted because the variables were either constant or showed non-significant (p > 0.05) values of Fisher’s coefficient (results not shown). The seven following species groups (i.e. taxonomic hypotheses) were tested.

1. DIOSCOREA HUMILIS VERSUS D. POLYANTHES—The standard classification method for samples resulted in the correct classification of 84.9% and 93.6% of D. humilis and D. polyanthes samples to their predefined groups considering quantitativa traits of stems and leaves alone. However, all of them showed posterior probabilities lower than 1.0 in the cross-validation test (results not shown). The inclusion of qualitative variables of leaves slightly improved the classification with 97.8% and 100% of the samples of D. humilis and D. polyanthes correctly classified, respectively, but 87% samples showed posterior probabilities lower than 1.0. The inclusion of fruit characters resulted in 100% correct classification of samples of D. humilis and D. polyanthes, respectively; however, two samples showed posterior probabilities lower than 1.0. Wilks’ Lambda values of the discriminant function for the three data sets were 0.731, 0.344, and 0.001, respectively. The addition of fruit characters did not increase significantly the separation of D. humilis and D. polyanthes, indicating the better performance of qualitative characters of leaves and the poor taxonomic value of the fruit characters in the differentiation of these two taxa.

2. DIOSCOREA BILoba VERSUS D. HUMILIS—The standard classification method of samples resulted in the correct classification of 60% of the D. biloba and 98.9% of the D. humilis samples to their predefined groups considering quantitative traits of
stem and leaves alone. Forty-eight of 170 samples showed posterior probabilities lower than 1.0 in the cross validation test (results not shown). The inclusion of qualitative variables of leaves resulted in 100% correct classification of samples of both species, 22 of them with posterior probabilities lower than 1.0. The inclusion of fruit characters resulted in the correct classification of all samples with the maximum posterior probability. Wilks’ Lambda values of the discriminant function for the three datasets were 0.162, 0.136, and 0.006, respectively, indicating the better performance of the last combined matrix.

3. Northern D. biloba versus southern D. biloba—The standard classification method of samples resulted in the correct classification of 96.3% and 98% of the northern and southern D. biloba samples, with respect to their predefined groups considering quantitative traits of stems and leaves alone. Forty-three out of 77 samples showed posterior probabilities lower than 1.0 in the cross validation test (results not shown). The inclusion of qualitative variables of leaves did not change the previous percentages of correct classification. The inclusion of fruit characters resulted in the correct classification of all samples with the maximum posterior probability. Wilks’ Lambda values of the discriminant function for the three datasets were 0.162, 0.136, and 0.006, respectively, indicating the better performance of the last combined matrix.

4. Dioscorea biloba versus D. humilis versus D. polyanthes—The standard classification method of samples resulted in the correct classification of 100%, 83.9%, and 80% of the D. biloba, D. humilis, and D. polyanthes samples to their predefined groups, respectively considering quantitative traits of stems and leaves alone. However, 120 out of 180 samples showed posterior probabilities lower than 1.0 in the cross validation test (results not shown). In the two-dimensional scatterplot, the D. biloba samples clustered in the right side of the first discriminant function, which accumulated 95.8% of the total variation, whereas samples of D. humilis and D. polyanthes clustered oppositely and were intermingled (Fig. 7A). The inclusion of qualitative variables of leaves resulted in the correct classification of all D. biloba and D. polyanthes samples, whereas 2.2% of the D. humilis samples were classified as D. polyanthes. Thirty-seven samples had a posterior probability value lower than 1.0. The 2-D scatterplot revealed an almost complete separation of the samples of D. biloba from the remaining samples along the first axis that accumulated 83.5% of the variation, whereas D. polyanthes and D. humilis separated along the second axis that accumulated 16.5% of the variation (Fig. 7B). However, one sample of D. humilis clustered close to D. polyanthes. The inclusion of fruit characters resulted in 100% correct classification of D. biloba and D. polyanthes samples and 96.6% of the D. humilis ones with all samples showing posterior probabilities of 1.0. The 2-D scatterplot
Fig. 7. Two-dimensional scatterplots of classification Discriminant Analysis (DA) of the Epipetrum group of Dioscorea samples for taxonomic hypotheses 4 (A, B and C) and 7 (D, E and F) (see results). A, D. Quantitative dataset of stem and leaf characters. B, E. Combined quantitative and qualitative dataset of stem and leaf characters. C, F. Combined quantitative and qualitative dataset of leaf and fruit characters (see Table 2). The first Canonical discriminant function explained A, 95.8%, B, 83.5%, C, 99.5%, D, 82.8%, E, 95.7% and F, 98.2% of interspecies variation in each case. *D. biloba* s.l. (white circles in plots A, B and C), northern *D. biloba* (black diamonds in plots D, E and F), southern *D. biloba* (white circles in plots D, E and F), *D. humilis* (white squares) and *D. polyanthes* (black triangles); asterisks indicate group centroids.
(Fig. 7C) revealed similar patterns to those obtained with the previous datasets (Figs. 7B, C) but a higher percentage of variance was accumulated along the first axis (99.5%). The DAs confirmed that the separation of the morphologically similar *D. humilis* and *D. polyanthes* is supported solely by qualitative characters of leaves. Wilks’ Lambda values of the first and second discriminant functions for the three datasets were 0.128–0.810, 0.056–0.429, and 0.003–0.590, respectively. The lower Wilks’ Lambda values obtained for the first discriminant function that separates *D. biloba* from the other two taxa of the *Epipetrum* group, indicates the greater morphological differentiation of this species, supporting its recognition at specific rank. By contrast, the higher Wilks’ Lambda values obtained for the second discriminant function that separates *D. humilis* from *D. polyanthes* in all three datasets considered indicates the subtle morphological differentiation between these two taxa.

5. **Dioscorea biloba versus *D. humilis* (and *D. polyanthes* not assigned to a predefined group)**—The standard classification method of samples resulted in the correct classification of 100% and 98.9% of samples of *D. biloba* and *D. humilis* to their predefined groups considering quantitative traits of stems and leaves alone. Only 10 of 170 samples showed posterior probabilities lower than 1.0 in the cross validation test (results not shown). The inclusion of qualitative variables of leaves and quantitative and qualitative variables of fruits resulted in the correct classification of 100% of the samples; however, the posterior probabilities of classification of samples were 1.0 only in the latter case. Wilks’ Lambda values of the discriminant function for the three datasets were low (0.162, 0.136, and 0.006) in all cases. All samples of *D. polyanthes* grouped with *D. humilis*, regardless of the subset of morphological characters considered, and all classifications showed posterior probabilities of 1.0 in the three cases (results not shown), supporting the close morphological similarity of these two taxa.

6. **Dioscorea biloba versus *D. humilis* (including *D. polyanthes*)**—This analysis showed similar percentages of classification values to analysis 5 (above). The standard classification method of samples resulted in the correct classification of 100% and 91.8% of samples of *D. biloba* and *D. humilis* to their respective predefined groups considering quantitative traits of stem and leaves alone. Forty-five out of 170 samples showed posterior probabilities lower than 1.0 in the cross validation test (results not shown). The inclusion of qualitative variables of leaves and quantitative and qualitative variables of fruits resulted in the correct classification of 100% of the samples, but the posterior probabilities of classification of samples were 1.0 only in the latter case. Wilks’ Lambda values of the discriminant function for the three datasets were, however, slightly lower (0.158, 0.132, and 0.006, respectively), indicating a less homogeneous structure of *D. humilis* if *D. polyanthes* is included within it.

7. **Northern Dioscorea biloba versus southern *D. biloba* versus *D. humilis* versus *D. polyanthes*—**The standard classification method of samples resulted in the correct classification of 96.3%, 96%, 81.7%, and 80% of the northern *D. biloba*, southern *D. biloba*, *D. humilis*, and *D. polyanthes* samples to their predefined groups considering quantitative traits of stems and leaves alone. However, 139 of 180 samples showed posterior probabilities lower than 1.0 in the cross validation test (results not shown). In the two-dimensional scatterplot, the *D. biloba* samples clustered in the right side of the first discriminant function that accumulated 82.8% of the total variation, whereas samples of *D. humilis* and *D. polyanthes* clustered oppositely and were intermingled (Fig. 7D). Northern and southern samples of *D. biloba* partially separated along the second discriminant function that accumulated 14.3% of the total variance. The inclusion of qualitative variables of leaves did not change the percentages of correct classification relative to northern and southern *D. biloba* samples, but improved the correct classification of all *D. polyanthes* samples, and 95.7% of the *D. humilis* ones. Seventy-eight samples had a posterior probability value lower than 1.0. The 2-D scatterplot revealed a complete separation of the samples of *D. biloba* from the remaining samples along the first axis that accumulated 75.6% of the variation, whereas *D. polyanthes* and *D. humilis* partially separated along the second axis that accumulated 13.1% of the variation (Fig. 7E). One sample of *D. humilis* clustered close to *D. polyanthes* and northern and southern samples of *D. biloba* separated along the third discriminant function (not shown). The inclusion of fruit characters resulted in 100% correct classification of northern and southern *D. biloba* and *D. polyanthes* samples and 96.6% of the *D. humilis* ones with all samples showing posterior probabilities of 1.0. The 2-D scatterplot (Fig. 7F) revealed a neat separation of *D. biloba* from *D. humilis* and *D. polyanthes* along the first axis that accumulated 98.2% of the variance. Northern and southern samples of *D. biloba* clearly separated along the second axis that accumulated 1.4% of the variance, whereas samples of *D. humilis* and *D. polyanthes* were intermingled. Wilks’ Lambda values of the three discriminant functions for the three datasets were 0.052–0.386–0.816, 0.024–0.205–0.471, and 0.001–0.226–0.593, respectively. The lower Wilks’ Lambda values obtained for the first discriminant function that separates *D. biloba* s. l. from *D. humilis*-*D. polyanthes* indicates the greater differentiation between the two morphological groups of readily recognized taxa of the *Epipetrum* group, suggesting the recognition of two species *D. biloba* and *D. humilis*. By contrast, the higher Wilks’ Lambda values obtained for the second and third discriminant functions indicate the high similarity found within the two sample groups: *D. humilis*-*D. polyanthes*, which differ only in qualitative traits of the leaf (Fig. 4E), and northern and southern *D. biloba* populations, which separate in quantitative and qualitative traits of leaves and fruits (Fig. 4D, F). These results suggest the recognition of two subspecies within each *D. biloba* and *D. humilis*.

**Discussion**

The macromorphological analysis has enabled us to characterize and differentiate the *Epipetrum* group taxa at the specific and subspecific levels and to compare them to other wingless-seeded taxa of Dioscoreaceae. The *Epipetrum* group shows an exclusive combination of morphological traits that differentiate it from all other wingless-seeded members of the family (Figs. 8–11). It differs from the *Tamus* group of *Dioscorea* in the absence of a climbing habit, the shorter stems and smaller leaves, and the presence of capsules (instead of fleshy berries); from the *Borderea* group in the globose tuber totally covered by roots, in contrast to the elongate xylopodium (Segarra and Catalán 2005); and from the *Nanarepenta* group in leaf morphology and male and female inflorescence types (shorly racemose to cymose male inflorescences producing pedicellate six-staminate flowers in the *Epipetrum* group versus racemose male inflorescences with sessile three-staminate flowers.)
Fig. 8. *Dioscorea biloba* subsp. *biloba*. A. Habit of male plant. B. Habit of female plant. C. Adaxial side of leaf. D. Detail of leafy stem node. E. Detail of a male flowering node. F. Detail of a female flowering node. G. Male flower. H. Female flower. I. Fruit. J. Seed. Scale bars: A, B, 1 cm; D, E, F, 5 mm; C, 2 mm; G, I, J, 1 mm. (A, C-E, G, from R284623, JACA; B, F, H, from R284624, JACA; I, J, from Werdermann 866, K).
in the *Nanarepenta* group, and long female inflorescences usually producing a single flower in the *Epipetrum* group versus shorter inflorescences producing up to five flowers in the *Nanarepenta* group; Téllez-Valdés and Dávila-Arandá 1998). The *Epipetrum* group also differs from all these groups in having prominent pistillodes in male flowers (Figs. 8–11) and a base chromosome number of \( x = 7 \), with mostly diploid individuals (\( 2n = 14 \)) (Viruel et al. 2008), in contrast to the base chromosome numbers of \( x = 6 \) with tetraploids (\( 2n = 24 \)) in the *Borderea* group (Heslot 1953; Catalán et al. 2006) and octoploids (\( 2n = 48 \)) in the *Tamus* group (Meurman 1925), and of \( x = 9, 10, \) or 20 with diploid to 14-ploids in *Dioscorea* s. s. (Smith 1937; Scarcelli et al. 2005; Bousalem et al. 2006; Viruel et al. 2008). The character of prominent pistillodes is restricted in *Dioscorea* s. s., reported only for *Dioscorea* Sect. *Macrogynodium* Ulíne (Knuth, 1924), which includes *D. stegelemanniana* Knuth, with pistillodes that are three times shorter than in the *Epipetrum* group, the edible yam *D. trifida* L. with \( x = 20 \) (Bousalem et al. 2006), and *D. renolutiflora* Knuth,, with rugulate pollen ornamentation (Schols et al. 2003).

The pollen of the *Epipetrum* group is shown here to be bisulcate in all taxa (Fig. 4), contrasting with a previous report of monosulcate pollen in *D. biloba* (Caddick et al. 1998). This difference might have resulted from difficulties in establishing the number of pollen apertures in SEM analysis or from the infraspecific variability of the number of pollen aperture number, as reported for other *Dioscorea* taxa (Caddick et al. 1998; Schols et al. 2003, 2005). Our pollen analysis has also shown the presence of a perforate-reticulate exine (Fig. 4), which has been recognized as separate species. Our analyses also revealed remarkable differences both in macro- and micromorphological traits between the two latter taxa differ slightly in the ornamentation of the papillae of the abaxial sides of the leaf, which are stellate-reticulate in *D. humilis* (Fig. 3H) and striate in *D. polyanthus* (Fig. 3K). Fruit (Fig. 5) and seed (Fig. 6) micromorphological traits do not provide a clear differentiation of any of the four taxa.

The statistical analyses have provided the means to select the quantitative and qualitative traits that best discriminate the four taxa of the *Epipetrum* group (Fig. 7; Tables 1–2). The classification DA approach has been widely employed in systematic studies of a variety of angiosperm genera (Robart 2005) and to discern among closely related taxa and potential hybrids, including complex aggregates with few morphological differences (Christensen 1984; Oja and Paal 2006; Koutecky 2007; McCauley and Ballard 2007). Our analyses demonstrate that the distinctness of *D. biloba* from the remaining taxa of the *Epipetrum* group is clear and supported by many quantitative and qualitative traits (Figs. 8–9) of different vegetative and reproductive plant organs, confirming its recognition at specific rank. Our analyses also revealed remarkable differences both in macro- and micromorphological traits between northern and southern populations of *D. biloba*. Northern *D. biloba* are distinguishable by the overall smaller size of vegetative organs, the densely papillose leaves (Fig. 8), and the reddish abaxial sides of the leaf (a character that is maintained when plants are cultivated in common garden conditions), compared to the larger size of vegetative organs, the slightly papillose leaves (Fig. 9), and the green abaxial sides of the leaf observed in southern *D. biloba*. Analysis of micromorphological characters of papillae also revealed the stellate-reticulate ornamentation in northern *D. biloba* (Fig. 3A-C), which differs from the stellate ornamentation in southern *D. biloba* (Fig. 3D-F). Therefore, a new subspecies is described below for the southern populations of *D. biloba*.

By contrast, the recognition of *D. humilis* and *D. polyanthus* as separate species is less clear. Discriminant analyses confirm the paucity of differences observed between these two taxa based on both macro- and micromorphological characters, suggesting that a reliable identification of individuals is only possible with qualitative traits of leaves (Figs. 2, 10C, 11C-D). These small morphological differences between *D. humilis* and *D. polyanthus* do not justify recognition at the rank of species, and these taxa are recognized as two subspecies of the same species in the treatment below.

**Taxonomic Treatment**

**General Characters of the Epipetrum group of Dioscorea—**

Geophytes with herbaceous annual aerial shoots. Tubers to
3 × 3 cm, irregularly shaped to globose, covered by roots. Shoots single, trailing, branching at 0.4–15 cm from the tuber, herbaceous. Leaves petiolate; petioles up to 13 cm long, papillose and glandulose (glands visible only under microscope). Leaves alternate, opposite or whorled, obovate or bilobate, papillose, and sparsely covered with glandular hairs on both sides; leaf apex emarginate, mucronate; leaf margin entire or slightly papillose-crenulate. Dioecious or rarely monoecious. Flowers unisexual by reduction. Flowers bracteolate, with two bracteoles up to 1.7 mm long; trimerous; perianth 2-whorled, isomerous, greenish, composed of six tepals up to 1.8 × 1 mm, patent, horizontal, or squarrose. Male inflorescences many-flowered and in axillary cymes, persistent or deciduous. Male flowers pedicellate, hypogynous; androecium with six stamens up to 0.4 mm long; gynoecium reduced to a dark-purple prominent pistillode comprising 3 styloides up to 4.4 mm long. Pollen bisulcate with perforate-finely reticulate exine. Male flowers hermaphroditic. It was Philippi who pointed out the existence of prominent pistillodes in the male flowers, the most notable diagnostic feature of the genus together with its unique base chromosome number of $x = 7$ (Viruel et al. 2008). Although there is no explicit reference to this trait in the original description of *D. humilis*, this species was described as having separate-sex inflorescences but not being strictly dioecious (Colla 1836). The *Epipetrum* group is mostly dioecious, although monoecious individuals having both male and female unisexual flowers are present in some northern populations of *D. humilis* and in some southern populations of *D. biloba*, mixed with typically dioecious ones. Although those individuals are not rare in the northern populations of *D. humilis*, they indicate that the mechanism of sex determination in this group of *Dioscorea* still needs to be investigated.

1. Leaves wider than longer, distinctly bilobed. Fruiting peduncles linear, filiform. Capsule obovoid (1.1–3.7 × 0.6–1.44 mm, reddish, wingless, with a small caruncle 0.1–0.31 mm long. **Notes**—Despite the application of the neuter epithet “bilobum” to the feminine generic name *Dioscorea* by Caddick et al. (2002b), Article 32.7 of the International Code of Botanical Nomenclature (Vienna Code) provides for an orthographic correction of such an error (without amendment of the authority or publication date) and thus the name appeared correctly (as *Dioscorea biloba*) in Govaerts et al. (2007).

1. **Dioscorea biloba** (Phil.) Caddick & Wilkin, *Taxon* 51: 112. 2002. *Epipetrum bilobum* Phil., *Anales del Museo Nacional de Santiago de Chile*, p. 11, Table 3. Figure 1. 1892.—**TYPE:** CHILE. “Habitat in desierto Atacama loco dicto Breas, Nov 1888, Alamiro Larraínaga”, 47242 (holotype: SGO! sub Thaumasta biloba Phil. nomen in schedis).

Tubers irregularly shaped to globose, 8 × 3 cm, covered by roots. Annual aerial shoots herbaceous, single, trailing and branching at 1–15 cm from the tuber, to 33.5 cm long. Leaves whorled (up to 14 per node), petiolate and bilobed; petioles (1.2–) 14.05 (–82) mm long, papillose, the papillae spirally curled. Capsule globose (2.0–) 3.7 (–15.8) × (1.2–) 5.54 (–17.5) mm, wider than longer, reddish-brown. Figure 8. Seeds ovoid and globose, 2 × 1 mm, reddish-brown. Figure 8.
Phenology—Flowering from August to October.

Habitat and Distribution—Dry limestone rocks and crevices in open habitats near Taltal in Antofagasta (II) region (Figs. 1, 12A, C).

Notes—This taxon is currently known from three geographically close populations located in a single mountain (Cerro Perales) covering an area of no more than 1 km². As far as we know, there are a total of about 300 individuals, of which only 10% are reproductive. The distribution has not increased since the time of the original description more than a century ago in 1892. It is restricted to an arid habitat with frequent fogs, where individual recruitment is extremely difficult and there is abundant mining activity in the surrounding areas. Given all this, this taxon should be considered Critically Endangered CR B1a, b[iii,iv], B2a, B(iv, v), C2a (IUCN 2008), and habitat protection is strongly encouraged.


Tubers irregularly shaped to globose, 2.5–3 × 2.5 cm, covered by roots. Annual aerial shoots herbaceous, single, trailing and branching at 0.4–8.5 cm from the tuber, up to 34 cm long. Leaves alternate, opposite or rarely whorled, petiolate; petioles (2.3–) 21.2 (–128.0) mm long, papillose. Papillose acute with stellate pericilinal walls. Pedicels of male flowers (4–) 8.9 (16) mm long. Female flowers solitary, rarely geminate; pedicel of female flowers (1.2–) 14.25 (–35) mm long. Capsule obovoid, (3–) 5.55 (–9) × (3–) 5.36 (–9) mm. Seeds ovoid and globose, (1–) 1.75 (–2.3) × (0.6–) 1.46 (–2) mm, reddish. Figure 9.

Etymology—The subspecific epithet refers to the Chilean region of Coquimbo, where this taxon is distributed.

Phenology—Flowering from July to August.

Habitat and Distribution—Dry limestone rocks and crevices in open habitats in Coquimbo (IV) region (Figs. 1, 12B, D).

Notes—The status of this taxon was provisionally recorded as insufficiently known and presumably extinct from the Limarí province and the Ovalle Common at Coquimbo region (Marticorena et al. 2001) based on the lack of records of D. biloba in the region since 1948. During our expeditions in 2006 and 2008, six new populations of D. biloba subsp. coquimbana were discovered in this area (Figs. 1, 11A-C). These populations occupy dry stony habitats in calcareous outcrops and were generally in a healthy condition, but the number of individuals within each population barely reaches a few hundred and they are close to cultivated fields or found among pastures. The species should be considered as Vulnerable VU B2a, b[iii,iv], c (IUCN 2008), and ecologically similar sites should be explored to search for additional populations.
Fig. 12. Natural habitats and appearance of the Epipetrum group of Dioscorea taxa. A. Habitat of D. biloba subsp. biloba (Antofagasta, Taltal). B. Habitat of D. biloba subsp. coquimbana (Coquimbo, La Aguada). C. Male plant of D. biloba subsp. biloba. D. Individuals of D. biloba subsp. coquimbana growing on limestone rocks among cacti. E. Individuals of D. humilis subsp. polyanthes growing among limestone rocks (Maule, Constitución). F. Detail of D. humilis subsp. polyanthes showing the leaves without marked secondary veins.
and glandulose; papillae with reticulate periclinal walls. Seeds ovoid and globose (1.0–2.0) (2.8) × (0.8–) 1.5 (–2) mm, brownish, wingless, with a small caruncle (0.1–) 0.26 (–0.4) mm long. Two subspecies are recognized within this taxon.

2.1. Dioscorea humilis Colla subsp. humilis.

Tubers 3 × 2.5 cm. Leaves alternate, opposite or rarely whorled, petiolate; petioles (2.3–) 20.3 (–128) mm long. Lamina (2–) 10.8 (–29) × (2.5–) 12.3 (–33) mm, membranous, not fleshy; papillae with stellate-densely reticulate periclinal walls. Secondary venation marked giving the abaxial side of the leaf a grooved to reticulate appearance. Pedicels of male flowers (4–) 10.17 (–18) mm long. Pedicel of female flowers (3–) 11.5 (–32) mm long. Capsule (3.3–) 4.4 (–7) × (3–) 3.7 (–5.6) mm. Seeds (1–) 1.97 (–2.8) × (0.8–) 1.4 (–2) mm, with a small caruncle (0.1–) 0.24 (–0.4) mm long. Figure 10.

Phenology—Flowering from June to August.

Habitat and Distribution—Wet limestone rocks and crevices in shady habitats, more rarely on sandy soil, from Valparaíso (V) to Bio-Bío (VIII) regions (Figs. 1 and 13). Individuals are generally abundant within populations, sometimes numbering in the thousands. This taxon does not require specific conservation policies, neither should it be considered as threatened.

Representative Specimens Examined—CHILE. Región de Valparaíso (Region V): Catapilco, rincón de La Mestiza, 32°32.556’S, 71°17.629’W, require specific conservation policies, neither should it be sometimes numbering in the thousands. This taxon does not crevices in shady habitats, more rarely on sandy soil, from Valparaíso (V) to Bío-Bío (VIII) regions (Figs. 1 and 13).

Phenology—Flowering from June to August.

Habitat and Distribution—Wet limestone rocks and crevices in shady places in pine forests in the Maule (VII) region, near Constitución (Figs. 1, 12F, E).

Notes—The epithet polyanthes refers to the apparently more prolific male inflorescences of this taxon compared to those of D. humilis subsp. humilis. This trait has been probably misinterpreted because both subspecies produce a similar number of male inflorescences. The confusion may be due to the different times of collection of the respective type specimens. Male inflorescences in both subspecies remain for only short periods on the plant as male flowers senesce rapidly when the pedicels break, and the inflorescences soon disappear. The type of Dioscorea humilis subsp. polyanthes was collected earlier in the growing season, when male inflorescences were just developing (SGO 038160), whereas D. humilis subsp. humilis may have been collected later in its growing season, when male inflorescences were disappearing. This could explain the higher number of male flowers recorded in D. humilis subsp. polyanthes than in D. humilis subsp. humilis. Further support for this hypothesis is that capsules were never described for subsp. polyanthes, which would be consistent with collection of the material at an earlier stage of development. In recent work produced for the Flora of Chile (www.chlorischile.cl/Monocotyledones/epipetrumgen.htm), the differentiation between subsp. polyanthes and humilis is mainly based on the supposed presence of reddish papillae in the leaves of the latter and the absence of papillae in the former. Such differences were not reported in the original description of D. polyanthes, which was described as papilloose. As shown here, both taxa have similar papillae (Fig. 3) that could have passed undetected on old herbarium specimens.

Dioscorea humilis subsp. polyanthes is the rarest taxon of the Epipteryx group and is poorly represented in herbaria. It is currently known from only two critically small populations near Constitución (Maule Region) that barely sum up 150 reproductive individuals. They inhabit pine forests that are intensively exploited for timber, constituting a further threat to the populations due to habitat destruction. Given


Phenology—Flowering from June to July.

Habitat and distribution—Wet limestone rocks and crevices and shady places in pine forests in the Maule (VII) region, near Constitución (Figs. 1, 12F, E).

Notes—The epithet polyanthes refers to the apparently more prolific male inflorescences of this taxon compared to those of D. humilis subsp. humilis. This trait has been probably misinterpreted because both subspecies produce a similar number of male inflorescences. The confusion may be due to the different times of collection of the respective type specimens. Male inflorescences in both subspecies remain for only short periods on the plant as male flowers senesce rapidly when the pedicels break, and the inflorescences soon disappear. The type of Dioscorea humilis subsp. polyanthes was collected earlier in the growing season, when male inflorescences were just developing (SGO 038160), whereas D. humilis subsp. humilis may have been collected later in its growing season, when male inflorescences were disappearing. This could explain the higher number of male flowers recorded in D. humilis subsp. polyanthes than in D. humilis subsp. humilis. Further support for this hypothesis is that capsules were never described for subsp. polyanthes, which would be consistent with collection of the material at an earlier stage of development. In recent work produced for the Flora of Chile (www.chlorischile.cl/Monocotyledones/epipetrumgen.htm), the differentiation between subsp. polyanthes and humilis is mainly based on the supposed presence of reddish papillae in the leaves of the latter and the absence of papillae in the former. Such differences were not reported in the original description of D. polyanthes, which was described as papilloose. As shown here, both taxa have similar papillae (Fig. 3) that could have passed undetected on old herbarium specimens.
Fig. 13. Natural habitats and appearance of Dioscorea humilis subsp. humilis. A. Habitat of the species in sclerophyllous open wood (Metropolitan region, Til-Til). B. Group of individuals growing on wet limestone rocks (Metropolitan region, Cerros de Acúleo). C. Detail of a female individual showing the tuber covered with roots and developing fruits (arrows). D-E. Individuals growing among shaded limestone rocks and mosses showing the leaves with marked secondary veins (reticulate appearance).
its highly restricted distribution and the significant threats to its survival, D. humilis subsp. polyanthes should be considered a critically endangered taxon CR B1a (i) II; B2 (i) B1a, B2a, B1 (ii); C2a, C2b, (IUCN 2008), and habitat protection is an immediate necessity.}

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