



## Floral similarity and vegetative divergence in a new species of *Bletia* (Orchidaceae) from Mexico

GERARDO A. SALAZAR<sup>1</sup>, CÉSAR CHÁVEZ-RENDÓN<sup>2</sup>, ALEJANDRO DE ÁVILA B.<sup>2</sup> & ROLANDO JIMÉNEZ-MACHORRO<sup>3</sup>

<sup>1</sup>Departamento de Botánica, Instituto de Biología, Universidad Nacional Autónoma de México, Apartado Postal 70-367, 04510 Mexico City, Mexico; e-mail: [gasc@ib.unam.mx](mailto:gasc@ib.unam.mx)

<sup>2</sup>Jardín Etnobotánico de Oaxaca, Reforma s.n. esq. Constitución, Centro, 68000 Oaxaca City, Oaxaca, Mexico.

<sup>3</sup>Herbario AMO, Montañas Calizas 490, Lomas de Chapultepec, 11000 Mexico City, Mexico

### Abstract

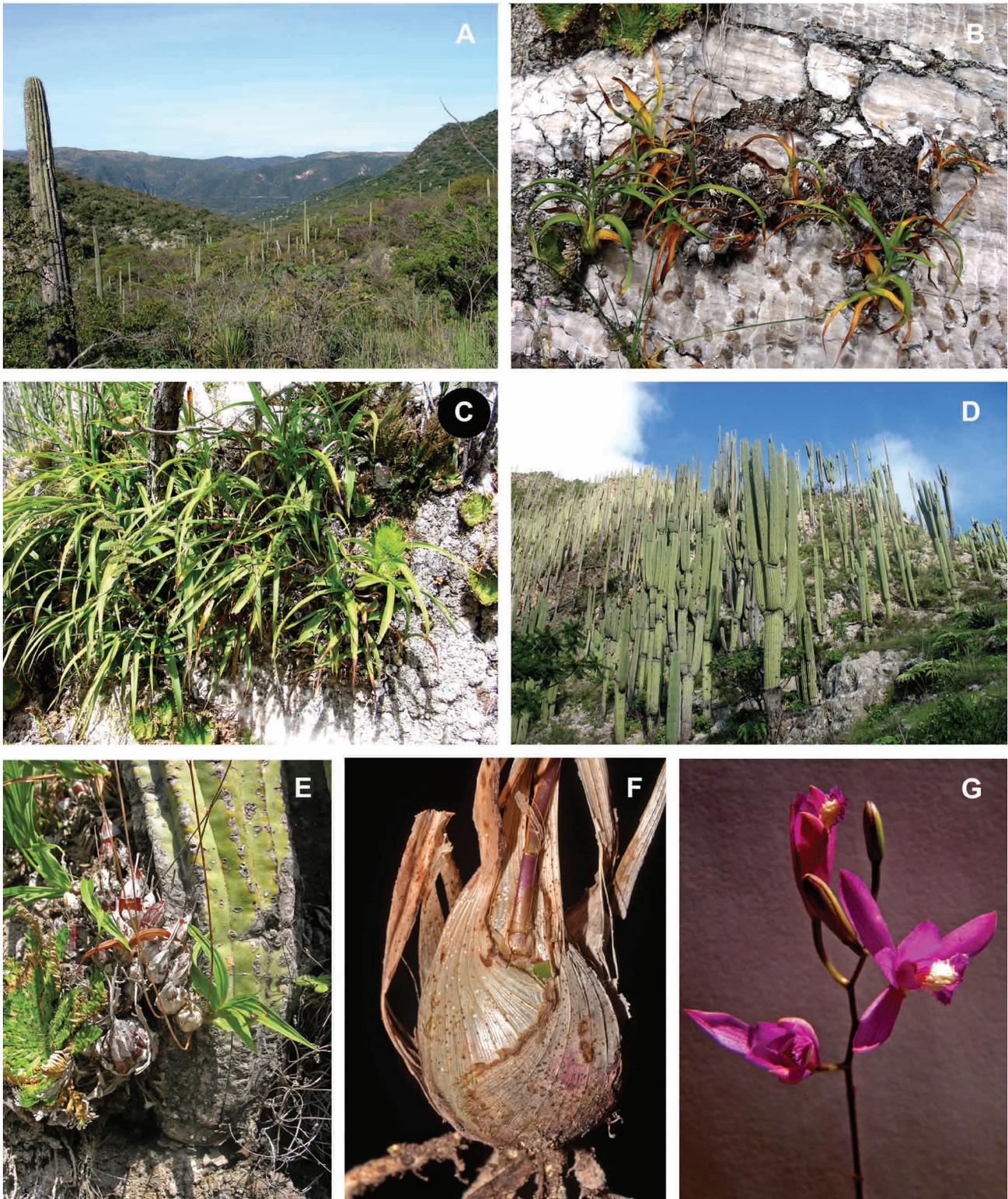
*Bletia mixtecana*, a new species from Oaxaca, Mexico is described and illustrated. This species is florally similar to *B. parkinsonii* but differs in its aerial thickened stems ('pseudobulbs') and several floral attributes. A phylogenetic analysis of nuclear ribosomal ITS DNA sequences indicates that *B. mixtecana* and *B. parkinsonii* are not closely related, suggesting that floral similarity represents either parallelism or shared ancestral (symplesiomorphic) traits. The new species is a strict gypsophile known only from two populations and it qualifies as endangered based on the small number of known populations and individuals, high habitat specificity and the observed loss of plants at one of the two known locations.

**Key words:** *Bletia mixtecana*, endemism, ITS, gypsophily, Mixtec region, Oaxaca, phylogenetics

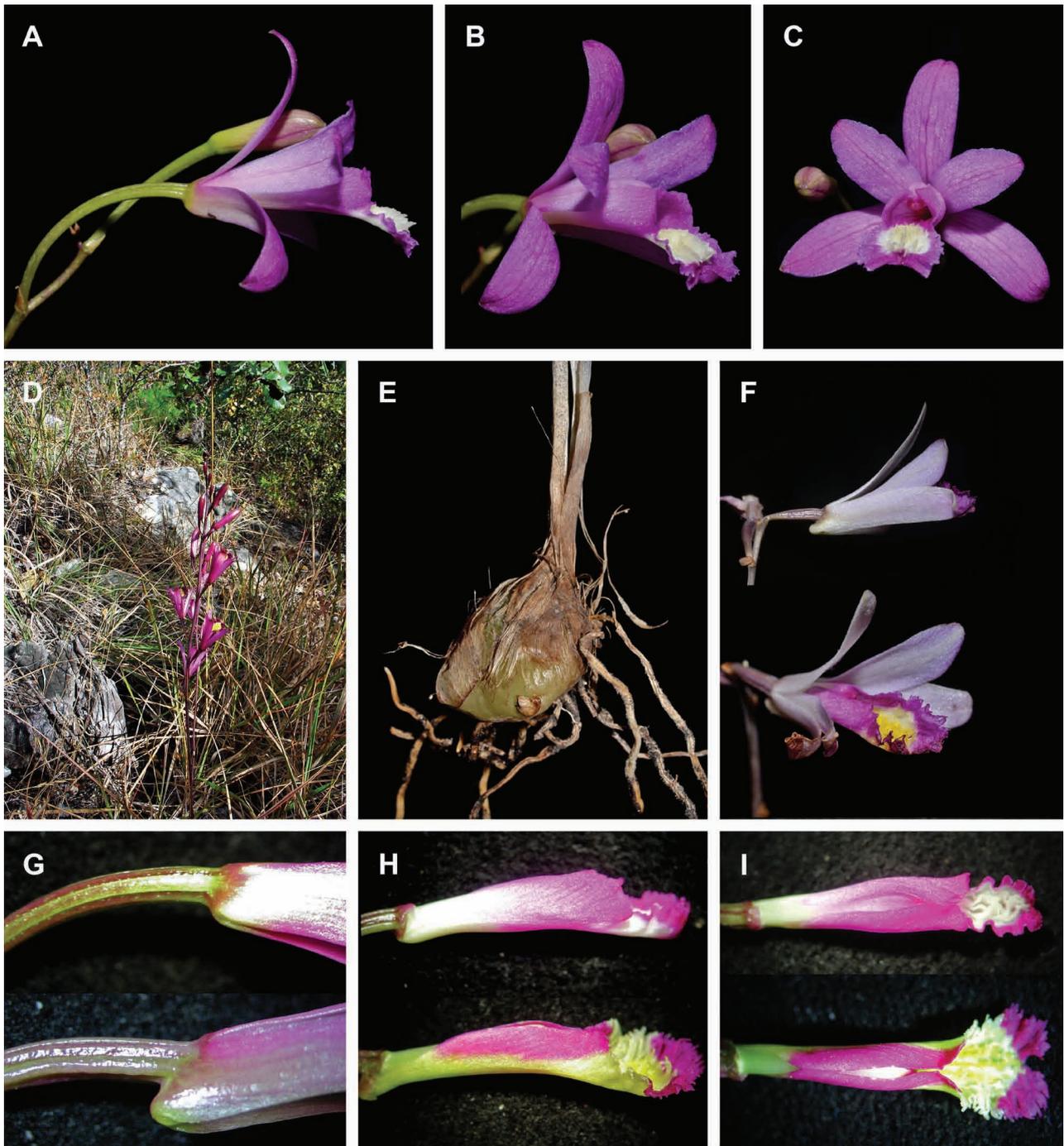
### Introduction

The Neotropical genus *Bletia* Ruiz & Pavón (1794: 119) consists of about 30 species of terrestrial orchids and attains its greatest diversity in Mexico, where around 25 species have been recorded (Soto *et al.* 2007). *Bletia* belongs to subtribe Bletiinae Benth (1881: 287, tribe Epidendreae, subfamily Epidendroideae), which, as currently delimited based on molecular phylogenetic studies, also includes the genera *Basiphyllaea* Schlechter (1921: 77), *Chysis* Lindley (1837: t. 1937) and *Hexalectris* Rafinesque (1825: 4, Sosa *et al.* 2005, van den Berg *et al.* 2005, Chase *et al.* 2015). Monophyly of *Bletia* is supported by molecular and morphological data (Sosa 2007), and the genus is characterized by usually underground, thickened stems ('corms') made up of several unequal internodes, plicate, deciduous leaves and relatively showy flowers with an usually three-lobed labellum provided with prominent longitudinal keels, arching column and eight pollinia (Sosa *et al.* 2005, Sosa 2007).

In the course of botanical exploration conducted recently in the Mixtec region, state of Oaxaca, Mexico, an undescribed species of *Bletia* was discovered which, while having a floral morphology typical for the genus, is vegetatively unusual in possessing aerial, thickened stems ('pseudobulbs'; Fig. 1). The peculiar vegetative structure of the new species poses interesting evolutionary questions, such as whether its aerial thickened stems represent a derived specialization or an ancestral trait in the genus. This sort of questions can only be meaningfully explored against a phylogenetic framework; hence, besides describing and illustrating the new species, in this work we assess its phylogenetic relationships analysing nucleotide sequences of the internal transcribed region of nuclear ribosomal DNA (nrITS, Baldwin *et al.* 1995). This marker has been used previously to assess relationships both within *Bletia* and among the genera of Bletiinae (Sosa 2007), as well as in many other orchid lineages (reviewed in Cameron 2007). We also provide a detailed comparison of the floral morphology of the new species with that of *Bletia parkinsonii* Hooker (1839: t. 3736), to which the new species is florally most similar (Figs. 2–3).



**FIGURE 1.** A. Tropical deciduous forest around La Cuchara gypsum mine, type locality of *Bletia mixtecana*. B. Plant of *B. mixtecana* growing on a gypsum wall. C. Massive plant on an unstable bank of a ravine, growing alongside *Selaginella* sp. D. Columnar cactus (*Neobuxbaumia* sp.) scrub on a gypsum outcrop at Cerro Jacaba, the second known locale for *B. mixtecana*. E. Plants of *B. mixtecana* and *Selaginella* sp. growing at the base of *Neobuxbaumia* sp. F. Pseudobulb of a plant of *B. mixtecana* at flowering time during the dry season, after shedding the leaves, showing the base of the inflorescence emerging from a lateral node. G. Inflorescence of the type plant (Chávez-Rendón *et al.* 5598R). Photographers: César Chávez-Rendón (A–E, G); Gerardo A. Salazar (F).



**FIGURE 2.** A–C. Three views of a flower of *B. mixtecana*. D. Flowering plant of *B. parkinsonii* in situ. E. Corm of *B. parkinsonii* at flowering time during the dry season. F. Two views of flowers of *B. parkinsonii*. G. Comparison of ovary and perianth base of *B. mixtecana* (above) and *B. parkinsonii* (below). H. Side views of the labellum of *B. mixtecana* (above) and *B. parkinsonii* (below). I. Top views of the labellum of *B. mixtecana* (above) and *B. parkinsonii* (below). Photographers: Gerardo A. Salazar (A–C, E–I); Jerónimo Reyes (D).

## Materials and methods

**Morphological observations:**—We studied live, pickled and pressed material from the two known populations of the new species (six plants in total). Fresh flowers from one plant each of the new species and of *B. parkinsonii* were dissected and photographed *in vivo* under a stereomicroscope (Stemi SV 6, Carl Zeiss Mikroskopie, Jena, Germany) to compare their morphological features. Measurements of vegetative and floral parts of the new species were made on fresh and pickled material, complemented with herbarium specimens; flowers from herbarium material were softened in hot, soapy water prior to measuring.

**Taxa included in the phylogenetic analysis:**—We analysed sequences from 20 accessions of 18 species of *Bletia*, including two accessions each of the new species (hereafter referred to as *Bletia mixtecana* Salazar & Chávez-Rendón; see Taxonomy, later) and of *B. parkinsonii*. Additionally, we included one species each of *Basiphyllaea*, *Chysis* and *Hexalectris*, all belonging in Bletiinae *sensu* Chase *et al.* (2015), plus representatives of other subtribes of Epidendreae, namely *Arpophyllum giganteum* Hartweg ex Lindley (1840a: 384) and *Nidema boothii* (Lindley 1838: misc. 52–53) Schlechter (1922: 43), both Laeliinae; *Dilomilis montana* (Swartz 1788: 121) Summerhayes (1961: 253) and *Dracula chimaera* (Reichenbach 1872: 463) Luer (1978: 194), both Pleurothallidinae; *Helleriella guerrensis* Dressler & Hágsater (1975: 36) and *Isochilus alatus* Schlechter (1912: 360), both Ponerinae. *Coelia triptera* (Smith 1793: t. 14) Don ex von Steudel (1840: 394), a member of Calypsoinae *sensu* Chase *et al.* (2015), was used as functional outgroup. Five of the sequences were generated newly for this study and the remaining 25 were downloaded from GenBank. A list of the species analysed, including voucher information for the new sequences and GenBank accessions, is given in Table 1. The aligned matrix was deposited in TreeBase (study accession URL: <http://purl.org/phylo/treebase/phylostudy/TB2:S19302>).

**TABLE 1.** Taxa analysed, voucher information or reference and GenBank accessions.

Taxon	Voucher or reference	ITS
Subtribe Bletiinae		
<i>Basiphyllaea hamiltoniana</i> Ackerman & Whitten	van den Berg <i>et al.</i> (2005)	AF521050
<i>Bletia adenocarpa</i> Rchb.f.	Sosa (2007)	DQ445817
<i>Bletia campanulata</i> Lex.	Sosa (2007)	DQ445818
<i>Bletia catenulata</i> Ruiz & Pav.	van den Berg <i>et al.</i> (2009)	AY008461
<i>Bletia coccinea</i> Lex.	Sosa (2007)	DQ445819
<i>Bletia gracilis</i> Lodd.	Mexico, Salazar <i>et al.</i> 7225 (MEXU)	KX241468
<i>Bletia jucunda</i> Linden & Rchb.f.	Sosa (2007)	DQ445821
<i>Bletia lilacina</i> A.Rich. & Galeotti	Sosa (2007)	DQ445822
<i>Bletia macristhmochila</i> Greenm.	Sosa (2007)	DQ445823
<i>Bletia mixtecana</i> Salazar & Chávez-Rendón 1	Mexico, Chávez-Rendón <i>et al.</i> 5598R (MEXU)	KX241469
<i>Bletia mixtecana</i> Salazar & Chávez-Rendón 2	Mexico, Chávez-Rendón <i>et al.</i> 7241C (MEXU)	KX241470
<i>Bletia neglecta</i> Sosa	Sosa (2007)	DQ445824
<i>Bletia parkinsonii</i> Hook. 1	Sosa (2007)	DQ445825
<i>Bletia parkinsonii</i> Hook. 2	Mexico, Soto Arenas <i>et al.</i> 10700 (AMO)	KX241471
<i>Bletia punctata</i> Lex.	Sosa (2007)	DQ445826
<i>Bletia purpurata</i> A.Rich. & Galeotti	Mexico, Salazar <i>et al.</i> 6397 (MEXU)	KX241467
<i>Bletia purpurea</i> (Lam.) DC	Sosa (2007)	DQ445828
<i>Bletia reflexa</i> Lindl.	Sosa (2007)	DQ445829
<i>Bletia roezlii</i> Rchb.f.	Kennedy & Watson (2010)	FJ427907
<i>Bletia stenophylla</i> Schltr.	Sosa (2007)	DQ445830
<i>Bletia urbana</i> Dressler	Sosa (2007)	DQ445831
<i>Chysis bractescens</i> Lindl.	van den Berg <i>et al.</i> (2005)	AF260150
<i>Hexalectris revoluta</i> Correll	van den Berg <i>et al.</i> (2000)	AY008479
Subtribe Calypsoinae		
<i>Coelia triptera</i> (Sm.) G.Don ex Steud.	van den Berg <i>et al.</i> (2005)	AF260151
Subtribe Laeliinae		

...Continued on next page

TABLE 1. (Continued)

Taxon	Voucher or reference	ITS
<i>Arpophyllum giganteum</i> Hartw. ex Lindl.	van den Berg <i>et al.</i> (2005)	AF266742
<i>Nidema boothii</i> (Lindl.) Schltr.	van den Berg <i>et al.</i> (2000)	AY008522
Subtribe Pleurothallidinae		
<i>Dilomilis montana</i> (Sw.) Summerh.	Pridgeon <i>et al.</i> (2001)	AF262915
<i>Dracula chimaera</i> (Rchb.f.) Luer	Pridgeon <i>et al.</i> (2001)	AF262766
Subtribe Ponerinae		
<i>Helleriella guerrerensis</i> Dressler & Hágsater	van den Berg <i>et al.</i> (2009)	AF260142
<i>Isochilus alatus</i> Schltr.	van den Berg <i>et al.</i> (2000)	AY008482

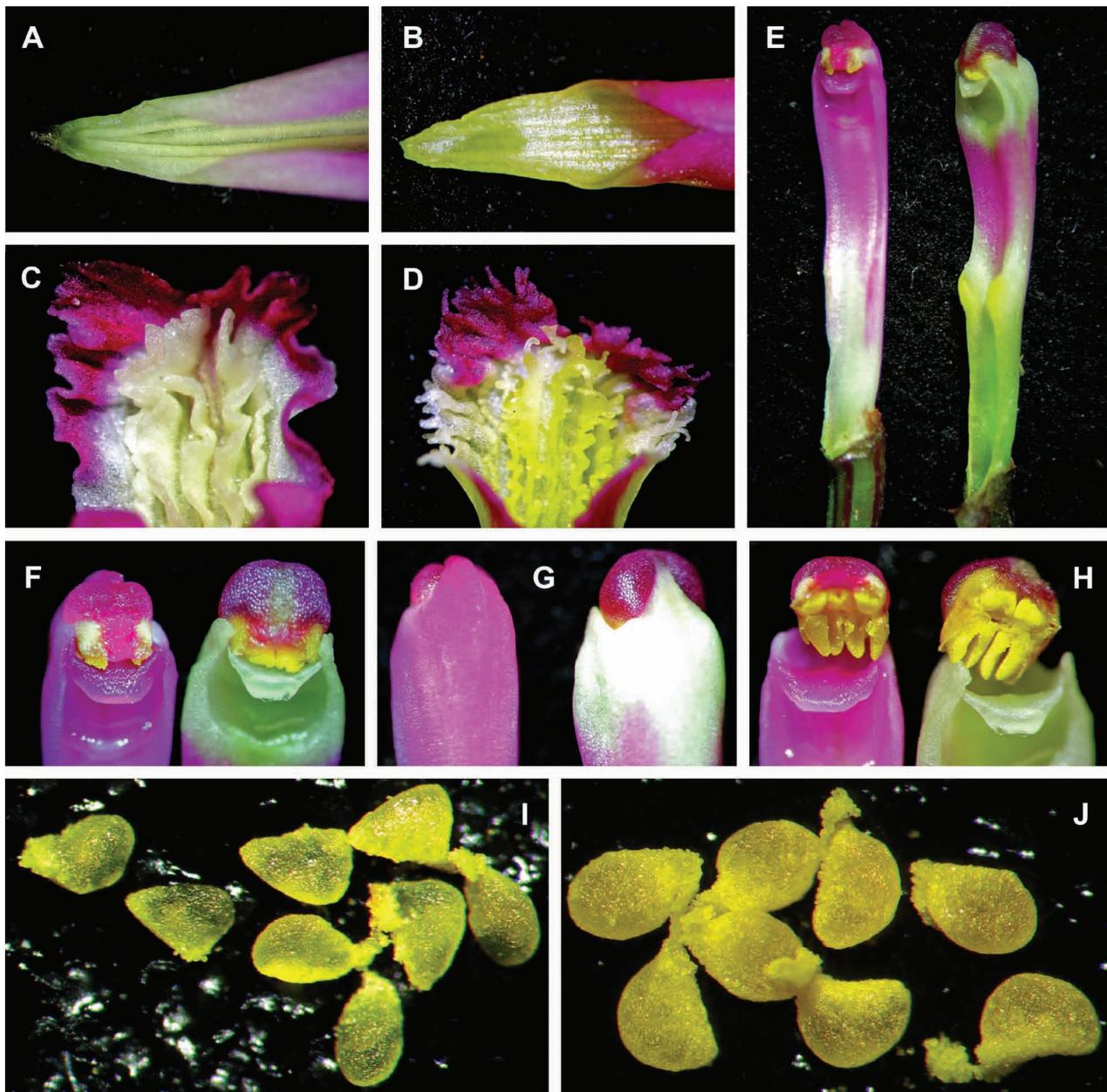


FIGURE 3. Comparison of some floral attributes of *Bletia mixteca* and *B. parkinsonii* (in all instances, placed on the left and right, respectively). A–B. Base of labellum; note in A the central channel formed by the thickened veins that turn into keels further up towards the apex. C–D. Midlobe of labellum. E. Column; note the prominent, yellow auricles on the ventral margins of *B. parkinsonii* (right). F. Ventral view of column apex. G. Dorsal view of column apex. H. Ventral view of column apex after dislodging the anther to show the pollinia. I–J. Pollinaria. Photographer: Gerardo A. Salazar.

**Molecular data:**—DNA extraction, amplification (PCR) and sequencing were carried out using standard methods and primers described in Sosa (2007). Bidirectional sequence reads were assembled and edited with Sequencher (GeneCodes Corp., Ann Arbor, Michigan, USA). Alignment was carried out using the L-INS-I method (Kato *et al.* 2005) of the online version of the program MAFFT v. 7 (Kato & Standley 2013), with minor manual adjustment in Mesquite v. 3.03 (Maddison & Maddison 2011). The individual gap positions were treated as missing data.

**Phylogenetic analysis:**—We analysed the ITS sequences using two different methods, namely maximum parsimony (MP) and maximum likelihood (ML), which allowed us to compare the results from MP with a method that uses explicit models of nucleotide substitution (ML). The MP analysis was conducted with the programme PAUP\* v. 4.0a144 for 32-bit Microsoft Windows (Swofford 2015) and consisted of a heuristic search with 1,000 replicates with random order addition of taxa for the starting trees and TBR branch-swapping, saving in memory all the most-parsimonious trees (MPTs) found. Branch support was assessed by 1,000 bootstrap replicates (Felsenstein 2015), each with 20 heuristic searches with random order of taxa and TBR branch-swapping, saving up to 20 MPTs per search. The ML analysis was carried out using RaxML v. 8 (Stamatakis 2014), implemented at the Cyberinfrastructure for Phylogenetic Research (CIPRES) Science Gateway v. 3.3 (Miller *et al.* 2010). One thousand rapid bootstrap replicates (Stamatakis *et al.* 2008) were followed by a search for the tree that maximizes the likelihood function with the default value of 25 rate categories and using in both instances the GTRGAMMA model for nucleotides.

## Results

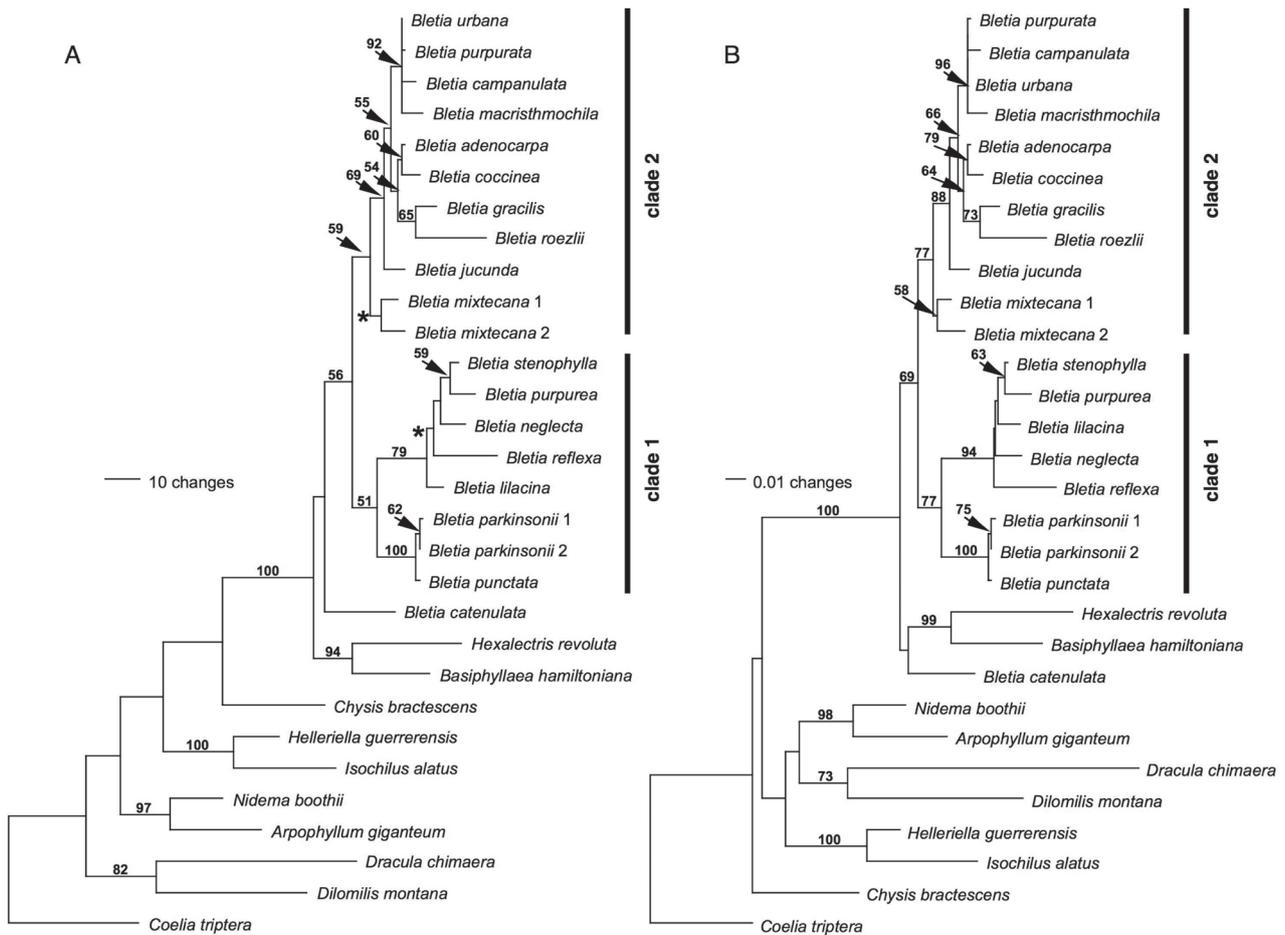
**Phylogenetic analysis:**—The aligned ITS matrix consisted of 713 characters, of which 311 were variable and 179 were potentially parsimony-informative. The MP analysis found six trees with a length of 652 steps, consistency index (CI, excluding uninformative characters) of 0.52 and retention index (RI) of 0.67. One of the six trees, on which the bootstrap percentages from the bootstrap analysis are indicated, is shown in Fig. 4A. The MP analysis recovered a strongly supported clade (bootstrap percentage, BP, 100) that includes all members of Blettiinae sensu Chase *et al.* (2015) except *Chysis bractescens* Lindley (1840b: misc. 61). The latter is sister to the remaining Blettiinae, although this relationship did not obtain bootstrap support greater than 50%. In the strict consensus (not shown), ‘core’ Blettiinae (except *Chysis*) consist of a polytomy formed by *Bletia catenulata* Ruiz & Pavón (1798: 229), the strongly supported pair *Basiphyllaea hamiltoniana* Ackerman & Whitten in Ackerman *et al.* (2001: 13)-*Hexalectris revoluta* Correll (1941: 19, BP 94) and a weakly supported group comprising all the other species of *Bletia* (BP 56). The latter in turn includes two main groups, marked as clades 1 and 2 in Fig. 4. Clade 1 is marginally supported (BP 51) and encompasses, on the one hand, a strongly supported subgroup with *B. punctata* Lexarza (1925: 15) sister to *B. parkinsonii* (BP 100), and on the other hand a subclade encompassing *B. reflexa* Lindley (1835: t. 1760) through *B. stenophylla* Schlechter (1919: 42, BP 79). Clade 2 is also weakly supported (BP 59) and, within it, the two accessions of *B. mixtecana* form a polytomy with a group that includes the remaining species (BP 69; Fig. 4A).

The ML tree, with the respective bootstrap percentages, is shown in Fig. 4B. Unlike MP, the ML analysis failed to group *Chysis* with the core Blettiinae. The latter are strongly supported (BP 100) but *Bletia* is paraphyletic, although the association of *Basiphyllaea hamiltoniana*-*Hexalectris revoluta* to *Bletia catenulata* is only weakly supported (BP 55). The same two major clades (1 and 2) of remaining *Bletia* recovered in the MP analysis were found by ML. In clade 1, *B. punctata* is the strongly supported sister of *B. parkinsonii* (BP 100), whereas in clade 2 the two accessions of *B. mixtecana* are collective sisters to the rest (BP 77). In contrast with the MP analysis, in which the two accessions of *B. mixtecana* did not receive support as sisters to one another (BP <50; relationship collapsed in the strict consensus), in the ML analysis the new species was recovered as monophyletic, although with low support (BP 58).

## Discussion

The overall relationships among species of *Bletia* and other genera of Blettiinae have been explored by Sosa (2007) based on separate and combined MP analyses of DNA sequences of the ITS region and plastid *trnL-trnF* intergenic spacer, and morphological characters. In that study, the ITS matrix included more taxa than other datasets and had more phylogenetically informative characters. A detailed re-examination of Blettiinae relationships is beyond the focus of the present study. Our discussion is mainly focused on establishing the phylogenetic position of *B. mixtecana*, its relationship to *B. parkinsonii* as the species to which it is florally most similar (Figs. 3–4), and some implications of the inferred relationships for our understanding of the evolution of floral and vegetative morphology in the genus.

Other than the non-monophyly of *Bletia* implied by the marginally supported nesting of the *Basiphyllaea-Hexalectris* clade in that genus in our ML analysis, our results are similar to those of Sosa (2007) regarding interspecific relationships in *Bletia* (Fig. 4). Both studies recovered two main clades of *Bletia* and differ mainly in the position of *B. purpurata* Richard & Galeotti (1845: 23), for which we generated a new sequence from newly collected, fresh material. Whereas in the study of Sosa (2007) *B. purpurata* was sister to a clade formed by *B. punctata* and *B. parkinsonii*, here it belongs in the other major clade of the genus, particularly in the subgroup that also includes *B. urbana* Dressler (1968: 186), *B. campanulata* Lexarza (1825: 17) and *B. macristhmochila* Greenman (1878: 297). Sosa (2007) did not include *B. roezlii* Reichenbach (1877: 7) in her ITS analysis, but our sequence of this species groups with *B. gracilis* Loddiges (1833: t. 1977) as expected, since they share several morphological attributes (e.g. elliptic leaves tinged with purple on the underside, greenish-yellow flowers with lustrous red veining on the labellum, and prominent, somewhat reflexed anther cap).



**FIGURE 4.** Phylogenetic relationships in *Bletia* inferred by maximum parsimony (MP) and maximum likelihood (ML) analyses of ITS DNA sequences. A. One of the six shortest trees found by the MP analysis; an asterisk (\*) indicates that the clade collapses in the strict consensus. B. ML tree. On both trees branch lengths are drawn proportional to the number of character changes; numbers associated to branches are bootstrap percentages.

Both our MP and ML analyses (Fig. 4) indicate that *B. mixtecana* is not particularly closely related to *B. parkinsonii*, in spite of their resemblance in floral morphology (Figs. 2–3). Such resemblance includes the flowers that open widely only in sunny weather, otherwise opening only partially, which gives them a tubular appearance. In other species of *Bletia* flower aperture is constant, i.e. it does not change depending on sunlight intensity. In both *B. mixtecana* and *B. parkinsonii* the labellum is distinctly longer than wide and shallowly three-lobed, lacking deep sinuses that sharply separate the midlobe from the lateral lobes (Fig. 3C–D, 5J). In other species of *Bletia* the labellum is about as wide as long or wider and deeply three-lobed. The columns of *B. parkinsonii* and *B. mixtecana* are similar, but in the former there are prominent, rounded ventral auricles near the middle that are absent in the latter. The main differences between these two species are indicated in Table 2.

**TABLE 2.** Comparison of flowers of *Bletia mixtecana* and *B. parkinsonii*.

Feature	<i>B. mixtecana</i>	<i>B. parkinsonii</i>
Retrorse mentum at base of perianth	absent	present
Adnation of base of labellum to column	marginal	intramarginal (the margins themselves are free)
Channel on proximal part of labellum	present, formed by the thickened veins that further up become keels	absent
Colour of labellum keels	deep magenta on their proximal two-thirds, white above	deep yellow on their proximal two-thirds, pale yellow above
Structure of labellum keels	entire on their proximal two-thirds, irregularly dentate and undulate above; surface smooth	entire on their proximal two-thirds, irregularly dentate-laciniate above; surface warty (more prominently so in front of the stigma)
Column	ventral surface flat, margins prominent near the middle but devoid of distinct auricles	ventral surface channelled, each margin provided with a fleshy, yellow, somewhat involute round auricle near the middle

Since *B. mixtecana* and *B. parkinsonii* do not share an immediate common ancestor, their floral similarity might represent either a parallelism resulting from adaptation to the same or similar pollinators, or a plesiomorphic set of traits in *Bletia* to the exclusion of *B. catenulata*. If the last scenario holds true, the more or less tubular flower with narrow labellum was modified subsequently in the last common ancestors of the remaining species in both major subclades of *Bletia* (clades 1 and 2 in Fig. 4).

*Bletia mixtecana* and *B. parkinsonii* diverged at or near the base of their respective clades, and beside their floral similarity they share a preference for seasonally dry tropical deciduous forests. Most other species of *Bletia* dwell in more mesic habitats such as pine-oak forests or, in the case of *B. purpurea* Lamarck (1791: 515) de Candolle (1841: 97) and *B. stenophylla* Schlechter (1919: 42), savannas, steep hillsides, roadside banks and other locations with open vegetation in areas dominated by warm, moist or wet tropical forests. The ‘basal’ position of *B. mixtecana*, *B. parkinsonii* and *B. punctata* suggests that their seasonally dry tropical habitat may be plesiomorphic in the main clade of *Bletia*, with derived transitions toward mesic pine-oak forests and tropical moist forests and savannas.

Both *B. mixtecana* and *B. parkinsonii* flower during the dry season (mainly December to April), when the leaves are withered or absent altogether. *Bletia punctata*, a widespread Mexican species recovered both in this study and in that of Sosa (2007) as the sister of *B. parkinsonii*, also occurs in seasonally dry, warm areas but more commonly is found in moister pine-oak forests, blooming during the rainy season (June to September), when the leaves are present. The corms of *B. punctata* are more globose and less oblique than those of *B. parkinsonii* (Fig. 2E) and florally the former is very different from the latter, with the sepals and petals standing erect on the upper part of the flower and having a deeply three-lobed labellum. The divergent lateral lobes are separated from the obtusate midlobe by deep sinuses. Line drawings of *B. parkinsonii* and *B. punctata* useful for comparison can be found in Espejo *et al.* (2002: 33 and 35, respectively).

*Bletia mixtecana* and *B. parkinsonii* occur syntopically at the type locality of the former. However, *B. mixtecana* grows on exposed chalk along the steep banks of a ravine (Fig. 1B–C), whereas *B. parkinsonii* occurs in flat, rocky areas with open grassland and shallow soil (G. A. Salazar, pers. obs.; cf. Fig. 2D). Both species flower at the same time, as demonstrated by flowering specimens of both species collected on the same day and a few metres apart (*B. mixtecana*: L. A. Hernández & A. Torres 869, MEXU!; *B. parkinsonii*: L. A. Hernández & A. Torres 870, MEXU!). The fact that *Bletia mixtecana* and *B. parkinsonii* coexist and flower simultaneously in at least one locality raises the question on how reproductive isolation is achieved, since these two species are similar in flower size and overall morphology (Fig. 2–3), and in the repetitive, partial opening and closure of the perianth apparently regulated by sunlight intensity. Other than early reports of pollination of *B. purpurea* and *B. catenulata* by various bees, and sparse observations on autogamy, nothing is known on natural pollination of *Bletia* (Dressler 1968; Sosa *et al.* 2005 and references therein; Salazar 2009). Nectar was absent in the fresh flowers of both *B. mixtecana* and *B. parkinsonii* examined by us, in agreement with previous observations on various other species of *Bletia*, and it is likely that pollination involves some sort of deceit (Salazar 2009). To our knowledge, no individuals with intermediate attributes suggesting hybridization

between *B. mixtecana* and *B. parkinsonii* are known, although several instances of natural hybridization have been recorded elsewhere between co-occurring species of *Bletia* (e.g. Salazar 2009, Serguera & Sánchez 2011, Hågsater *et al.* 2005).

No other mainland member of *Bletia* has aerial thickened stems like those of *B. mixtecana*, which represent an autapomorphic, diagnostic attribute of the species. Aerial pseudobulbs are present in *B. patula* Graham (1836: 155), a species restricted to Florida (U.S.A.), Cuba, Haiti, the Dominican Republic and Puerto Rico, but in this case the pseudobulbs are globose to conical, not ovoid (Sosa & Díaz 2014). The pseudobulbs of *B. mixtecana* are reminiscent of those of some members of tribe Cymbidieae, such as certain species of *Acriopsis* Blume (1825: 376), *Cyrtopodium* Brown (1813: 216) and *Eulophia* Brown ex Lindley (1821: 573). At first, such resemblance suggested to us the possibility that it could represent the long-lost *Eulophia filicaulis* Lindley (1842: 184), a species supposedly collected in Mexico by Karwinskii in the first half of the nineteenth century (Lindley 1842), which was never collected again in this country. However, study of the type of *E. filicaulis* and other relevant material at K and M demonstrated that *E. filicaulis* is a genuine species of *Eulophia* and conspecific with West African *Eulophia ramifera* Summerhayes (1958: 50), most likely having been attributed to Mexico by error (Salazar & Cribb 2007).

*Bletia mixtecana* is the only recorded instance of strict edaphic endemism for *Bletia* in the mainland. Eastern Cuban *B. antillana* M.A. Díaz & Sosa in Sosa & Díaz (1997: 81) grows along the margin of streams in acid, humus-rich serpentine soil (Sosa & Díaz 1997), but there is no published information indicating edaphic specialization in other species of this genus. One of the two known populations of *B. mixtecana* occurs at Cerro Jacaba, which is the type (and only locality known so far) of *Galeoglossum cactorum* Salazar & Chávez-Rendón in Salazar *et al.* (2011: 262), another obligate gypsophilous orchid. As noted above, *B. parkinsonii* co-occurs with *B. mixtecana* at La Cuchara. However, *B. parkinsonii* is one of the most widespread Mexican species of *Bletia* and is not restricted to gypsum, but it grows in a variety of soil conditions, both on volcanic and limestone or gypsum substrates (i.e. it is a ‘gypsovag’; see Palacio *et al.* 2007; Escudero *et al.* 2015). Gypsum soils have stressful physical and chemical properties for plants, including a hard surface crust that could limit plant establishment, mechanical instability, an excess of S, and Ca/Mg imbalances, among others (Parsons 1976; Palacio *et al.* 2007; Escudero *et al.* 2015). The aerial thickened stems of *B. mixtecana* may represent an adaptation to gypsum outcrops in ravines and steep slopes by allowing the plant to grow on the surface, instead of within and across the surface crust (Fig. 1A–E). This hypothesis, as well as the apparent reproductive isolation between co-occurring *B. mixtecana* and *B. parkinsonii* in spite of their striking floral similarity, are but two of the many aspects of these peculiar plants requiring further research.

## Taxonomy

### *Bletia mixtecana* Salazar & Chávez-Rendón, *sp. nov.*

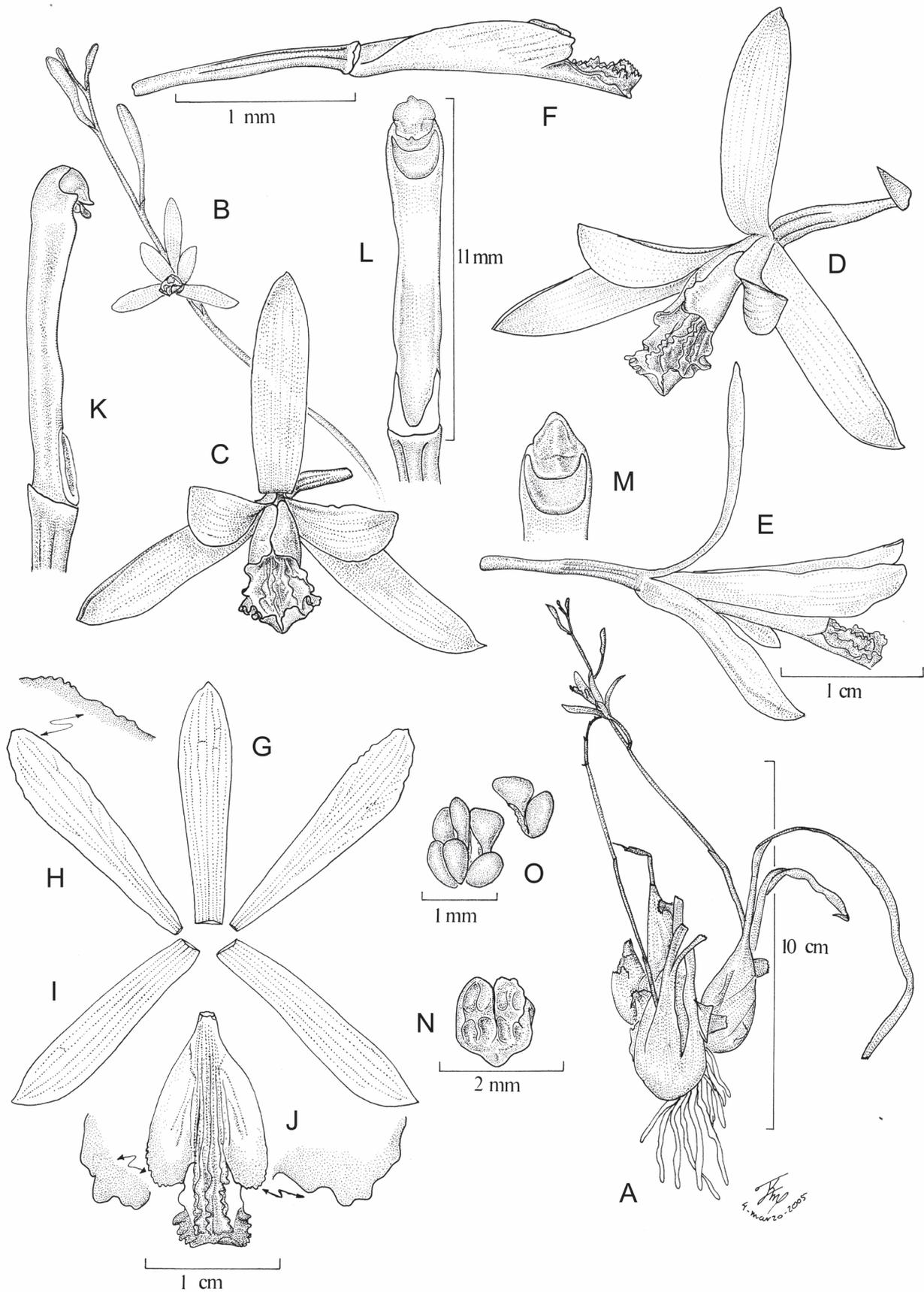
Vegetatively it differs from all other species of *Bletia* in its ovoid pseudobulbs and its restriction to gypsum outcrops along ravines and steep slopes. Florally it is similar to *B. parkinsonii*, but differs from the latter in the absence of a distinct retrorse mentum at the base of the floral tube; labellum marginally adnate to the column at base; proximal portion of the labellum provided with a central channel formed by prominent, thickened veins; labellum disc provided with 5–7 prominent, entire keels, these coloured deep magenta on their proximal two-thirds, irregularly dentate, undulate and cream-white above; column devoid of distinct ventral auricles near the middle.

**Type:**—MEXICO. Oaxaca: distrito Huajuapán, municipio Santo Domingo Tonalá, La Cuchara, 1538 m elev., collected 4 September 2002, pressed in cultivation 8 April 2006, Chávez-Rendón *et al.* 5598R (holotype MEXU, isotypes IEB!, SERO!).

Terrestrial herb, 15–32 cm in height including the inflorescence. Roots simple, terete, flexuous, dull white to pale brown, glabrous to pubescent-lanuginose, 1.5–2.0 mm in diameter. Pseudobulbs epigeous, ovoid, slightly compressed laterally, consisting of 6–7 internodes, when young completely concealed by sheaths, when old naked, green with reddish-brown nodes, smooth, longitudinally sulcate, 3.4–6 cm long, 1.0–2.3 cm in diameter. Leaves deciduous, shedding at maturity of the pseudobulb, absent at flowering time, when present 7–8, progressively larger toward the apex of the pseudobulb, the imbricating sheaths of the 4–5 distalmost leaves forming a pseudostem up to 3.5 cm long; leaf blades plicate, green, articulate to the sheaths that conceal the pseudobulb, linear to ensiform or the lowermost one sometimes lanceolate, long-acuminate at apex, truncate and channelled at base, 9-veined, 4–24 cm long, 0.8–1.4 cm wide; sheaths conspicuous, concealing completely the newly developed pseudobulb, tight, papery-fibrous, whitish,

eventually disintegrating (after about ca. 4 years), up to 4 cm long and 2 cm wide. Inflorescence racemose, 1–2 per pseudobulb, up to 23 cm long, arising from the nodes on the distal two-thirds of the mature pseudobulb, erect; peduncle slender, terete, rigid, ca. 11 cm long and 0.9 mm in diameter, with 4–5 internodes and an equal number of tight to loose, scarious bracts up to 7 mm long; raceme lax, ca. 10 cm long, rachis glabrous, 0.25–0.8 mm in diameter, slightly flexuous, producing 5–10 flowers in succession. Floral bracts thin, scarious, glabrous, covering less than one-fifth to one-fourth of the ovary, triangular-ovate or ovate, sometimes that of the lowermost flower tubular, apex acute or obtuse, apiculate, 5–12-veined, (0.6–)2.4–4.4 mm long, 1–2 mm wide. Ovary glabrous, ascending, slightly arcuate, subterete, 6-sulcate on the distal two-thirds, gently tapering and obscurely twisting towards the base, pale green to purplish-red with three green ribs, 10.0–16.5 mm long, ca. 1 mm in diameter near the apex. Flowers resupinate, widely open in warm, sunny weather but the sepals and petals barely opening in cloudy weather; floral segments inconspicuously connate at base for up to 0.5 mm, bearing sparse, minute idioblasts apparently containing crystals. Sepals completely magenta or externally white with magenta suffusion on margin and internally magenta except for the white base, bearing at base 5 main veins that branch above; lateral sepals free except as noted above, variably spreading, obliquely oblong-ob lanceolate, slightly recurved near the acute apex, obscurely keeled dorsally, 15.5–20.0 mm long, 4.0–4.5 mm wide; dorsal sepal oblanceolate, recurved, 15.0–19.3 mm long, 2.9–4.1 mm wide. Petals homogeneously magenta, free or fused basally to the labellum for 0.7–2.0 mm (degree of adnation variable even among flowers of the same inflorescence), bearing at the base 3 main veins that branch above, obliquely oblanceolate or oblanceolate-spathulate, minutely crenate-lacerate and slightly undulate on the distal one-fourth to one-third, acute to obtuse, 15–20 mm long, 2.9–5.0 mm wide. Labellum white on the proximal half with the lateral lobes and the margins of midlobe magenta, the centre of the midlobe white; base adnate to the column for 1.8–2.4 mm, otherwise free, obscurely three-lobed above the middle, in natural position with the lateral margins below the lateral lobes embracing the column, 16.8–19.5 mm total length, 9.4–9.5 mm wide across the lateral lobes when spread out; lateral lobes semiorbicular, somewhat divergent, rounded, erose and slightly undulate, protruding 1–2 mm at apex; midlobe obcordate to cuneate-obcordate, 5.0–6.5 mm long, 5.8–6.7 mm wide, deeply emarginate at apex, the resulting lobules obliquely ovate-flabellate, ruffled, margins erose and undulate, apex shortly apiculate (sometimes the apicule inconspicuous); base bearing 5 main veins that branch profusely above (the three central veins nearly reach the apex of the midlobe); disc provided with 5–7 prominent keels, these entire and deep magenta on their proximal two-thirds, irregularly dentate, undulate and cream-white above, sometimes a few more lateral veins slightly thickened but not distinctly keeled, base of the labellum channelled inside the short tube resulting from its partial adnation to the column, the channel formed by the basal portions of the keels that run at each side of the central one (the last one does not reach the base); no nectar is produced. Column elongate, slightly arching, white near the base and magenta above, ventrally flat with thin, slightly prominent margins, more noticeably so below the middle, 10.8–11.5 mm long including the short, inconspicuous column foot, 2 mm wide near the apex; anther incumbent, semi-globose, versatile, with slightly prominent apical margin, 8-celled, ca. 1.5 mm long and wide; pollinia 8, yellow, laterally compressed, with granulose caudicles; rostellum laminar, semiorbicular, reflexed, provided on its adaxial surface (facing the stigma) with a lunate viscarium. Stigma semiorbicular, concave, with margins slightly raised, covered by a shiny, transparent fluid in fresh condition. Capsules not seen.

**Distribution and ecology:**—*Bletia mixtecana* is known only from two populations distant from one another c. 76 air kilometres, both within the Mixtec region in the Sierra Madre del Sur, state of Oaxaca. The plants live on gypsum in banks along ravines and on steep slopes. At the type locality (La Cuchara; Fig. 1A–C) the dominant vegetation is tropical deciduous forest with *Acaciella angustissima* (Miller 1768: *Mimosa* no. 19) Britton & Rose (1928: 100), *Agave* aff. *angustifolia* Haworth (1812: 72), *Brahea dulcis* (Kunth 1816: 300) Martius (1838: 244), *Bursera mirandae* Toledo (1984: 441), *Euphorbia* aff. *rossiana* Pax (1910: 162), *Fouquieria ochoterena* Miranda (1942: 458), *Neobuxbaumia mezcalaensis* (Bravo 1932: 378) Backeberg (1941: 3), *Opuntia* Tournefort ex Miller (1754: *Opuntia*) sp., *Plumeria rubra* Linnaeus (1753a: 209), and the orchids *Bletia parkinsonii*, *Cyrtopodium macrobulbon* (Lexarza 1825: 42) Romero-González & Carnevali (1999: 331), *Dichromanthus cinnabarinus* (Lexarza 1825: 3) Garay (1982: 314) subsp. *galeottianus* (Schlechter 1918: 432) Soto Arenas & Salazar (in Hágsater & Soto Arenas 2003: xii) and *Ponthieva angustipetala* Greenwood (1986: 9). At the other known locality (Cerro Jacaba; Fig. 1D–E) the steep gypsum slope is covered by a tall scrub of *Neobuxbaumia* Backeberg (1938: 20) sp. with sparse individuals of *Brahea dulcis*, *Hechtia* Klotzsch (1835: 401) sp. and *Agave* Linnaeus (1753a: 323) sp., with a sparse herbaceous stratum including *Selaginella* Palisot de Beauvois (1805: 101) sp., *Begonia* Linnaeus (1753b: 1056) sp., *Sedum* Linnaeus (1753a: 430) sp., *Pinguicula* Linnaeus (1753a: 17) sp., some grasses and xeromorphic ferns and two further orchid species, *Galeoglossum cactorum* and an unidentified species of *Malaxis* Solander ex Swartz (1788: 119).



**FIGURE 5.** *Bletia mixtecana*. A. Flowering plant. B. Inflorescence. C. Flower, front view. D. Flower, oblique view. E. Flower, side view. F. Flower from side with sepals and petals excised to show the sides of the labellum embracing the column. G. Dorsal sepal. H. Petal. I. Lateral sepal. J. Labellum. K. Column, side view. L. Column, ventral view. M. Ventral view of column apex after removal of anther and pollinarium. N. Anther. O. Pollinarium. Drawn by R. Jiménez-Machorro from Chávez-Rendón *et al.* 5598R.

**Conservation status:**—From the small number of known populations (two), the small area that they occupy (less than 1 km<sup>2</sup>), the small number of individuals known (a few dozen) and its habitat specificity, this species qualifies as ‘Endangered’ according to the ‘MER-Plantas’ (the method for assessing the risk of extinction for plants established by the relevant Mexican legal norm; SEMARNAT 2010). Likewise, based on IUCN’s red list categories and criteria (IUCN 2012), *B. mixtecana* qualifies as ‘Endangered’ because of its area of occupancy estimated to be <500 km<sup>2</sup>, less than five known locations and an observed decline in the number of mature individuals, at least at La Cuchara (criteria B2, a(iii)). Nevertheless, the two known populations of *B. mixtecana* occur on a rough, botanically little-explored area with seemingly extensive spans of potential habitat. It is likely that further exploration will lead to the discovery of additional populations, and its conservation status should be then revised accordingly.

**Etymology:**—The specific epithet refers to the Mixtec region of Oaxaca, an area to which the new species seems to be restricted.

**Additional specimens examined:**—MEXICO. Oaxaca: distrito Huajuapán, municipio Santo Domingo Tonalá, paraje Cerro de la Cuchara-Barranca, 1,383 m, 13 January 2009, *Hernández & Torres 869* (MEXU!, SERO!); municipio Santo Domingo Tonalá, La Cuchara, 1,518 m, 10 February 2009, *Torres & Hernández 910* (MEXU!); distrito Tlaxiaco, municipio San Bartolomé Yucuañe, Cerro Jacaba, 1708 m elev., collected 15 August 2008, pressed in cultivation 17 March 2015, *Chávez-Rendón et al. 7421C* (MEXU!).

## Acknowledgements

The authors thank the late Miguel Ángel Soto Arenas for discussions on this species; Jerónimo Reyes for plants and photographs of *B. parkinsonii*; Lidia I. Cabrera and Laura Márquez Valdelamar for assistance with DNA sequencing; the Curators of AMES, AMO, CHAPA, ENCB, K, MEXU, M, MO, NY, SERO, US and XAL for facilitating study of the collections in their charge; and Angel Vale and Cássio van den Berg for constructive criticisms to an earlier version of the manuscript. C.C.-R. and A.de Á.B. thank the authorities of Santo Domingo Tonalá and San Bartolomé Yucuañe for permission for botanical collecting. This work was partially supported by an infrastructure grant from CONACYT (project 224743).

## Literature cited

- Ackerman, J.D., Tremblay, R.L. & Whitten, W.M. (2001) Notes on the Caribbean flora. III. New species of *Basiphyllaea* and *Lepanthes*. *Lindleyana* 16: 13–16.
- Backeberg, C. (1938) Zur systematische Übersichtsarbeit. *Blätter für Kakteenforschung* 6: n. 20.
- Backeberg, C. (1941) Die Kakteen des Zopilote-Cañons (Geierschlucht) in Guerrero (Mexico). *Beiträge zur Sukkulentenkunde und -pflege* 1941: 1–5.
- Baldwin, B.G., Sanderson, M.J., Porter, J.M., Wojciechowski, M.F., Campbell, C.S. & Donohue, M.J. (1995) The ITS region of nuclear ribosomal DNA: a valuable source of evidence on angiosperm phylogeny. *Annals of the Missouri Botanical Garden* 82: 247–277.  
<http://dx.doi.org/10.2307/2399880>
- Bentham, G. (1881) Notes on Orchideae. *The Journal of the Linnean Society* 18: 281–360.  
<http://dx.doi.org/10.1111/j.1095-8339.1881.tb01258.x>
- Blume, C.L. von (1825) *Bijdragen tot de Flora van Nederlandsch Indië, Part 8*. Published by the author, Jakarta, 80 pp.
- Bravo, H. (1932) Contribución al conocimiento de las cactáceas del estado de Guerrero. Cactáceas del cañón del Zopilote. *Anales del instituto de Biología de la Universidad Nacional de México* 3: 375–398.
- Britton, J.N. & Rose, N.L. (1928) *North American flora*, 23. Lancaster Press, Lancaster, 349 pp.
- Brown, R. (1813) *Hortus Kewensis, 2<sup>nd</sup> ed.*, 5. Taylor, London, 568 pp.
- Cameron, K.M. (2007) Molecular phylogenetics of Orchidaceae: the first decade of DNA sequencing. In: Cameron, K.M., Arditti, J. & Kull, T. (Eds.) *Orchid Biology: Reviews and Perspectives*, 9. New York Botanical Garden, New York, pp. 163–200.
- Chase, M.W., Cameron, K.M., Freudenstein, J.V., Pridgeon, A.M., Salazar, G.A., van den Berg, C. & Schuiteman, A. (2015) An updated classification of Orchidaceae. *Botanical Journal of the Linnean Society* 177: 151–174.  
<http://dx.doi.org/10.1111/boj.12234>
- Correll, D.S. (1941) Studies in *Isochilus*, *Mormodes* and *Hexalectris*. *Botanical Museum Leaflets, Harvard University* 10: 1–20.
- de Candolle, A.P. (1841) 11. *Bletia purpurea*. *Mémoires de la Société de Physique et d’Histoire Naturelle de Genève* 9: 97–101.

- Dressler, R.L. (1968) Notes on *Bletia* (Orchidaceae). *Brittonia* 20: 182–190.  
<http://dx.doi.org/10.2307/2805621>
- Dressler, R.L. & Hágsater, E. (1975). Una nueva especie del sur de México: *Helleriella guerrerensis*. *Orquídea (Mexico City)*, n.s. 5: 35–42.
- Escudero, A., Palacio, S., Maestre, F.T. & Luzuriaga, A.L. (2015) Plant life on gypsum: a review of its multiple facets. *Biological Reviews* 90: 1–18.  
<http://dx.doi.org/10.1111/brv.12092>
- Espejo, A., García-Cruz, J., López-Ferrari, A.R., Jiménez-Machorro, R. & Sánchez-Saldaña, L. (2002) Orquídeas del estado de Morelos. *Orquídea (Mexico City)*, n.s. 16: 1–332.
- Felsenstein, J. (1985) Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783–791.  
<http://dx.doi.org/10.2307/2408678>
- Garay, L.A. (1982) A generic revision of the Spiranthinae. *Botanical Museum Leaflets, Harvard University* 28: 277–425.
- Graham, R. (1836) Description of several new or rare plants which have lately flowered in the neighbourhood of Edinburg, chiefly in the Royal Botanic Gardens. *The Edinburgh New Philosophical Journal* 21: 154–158.
- Greenman, J.M. (1878) III. Descriptions of new and little known plants from Mexico. *Proceedings of the American Academy of Arts and Sciences* 32: 295–311.
- Greenwood, E.W. (1986) *Ponthieva angustipetala* Greenwood, una especie inesperada del sur de México. *Orquídea (Mexico City)*, n.s. 10: 7–26.
- Hágsater, E. & Soto Arenas, M.A. (Eds.) (2003) *Icones Orchidacearum* 5–6: pls. 501–700.
- Hágsater, E., Soto, M.A., Salazar, G.A., Jiménez, R., López, M.A. & Dressler, R.L. (2005) *Orchids of Mexico*. Instituto Chinoín, Mexico City, 302 pp.
- Haworth, A.H. (1812) *Synopsis Plantarum Succulentarum*. Taylor, London, 207 pp.
- Hooker, J.D. (1839) *Bletia parkinsonii*. Mr. Parkinson's bletia. *Botanical Magazine* 66: t. 3736.
- IUCN. (2012) *IUCN Red List Categories and Criteria Version 3.1*, 2<sup>nd</sup> ed. IUCN, Gland & Cambridge, 32 pp.
- Katoh, K., Kuma, K., Toh, H. & Miyata, T. (2005) MAFFT version 5: improvement in accuracy of multiple sequence alignment. *Nucleic Acids Research* 33: 511–518.  
<http://dx.doi.org/10.1093/nar/gki198>
- Katoh, K. & Standley, D.M. (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30: 772–780.  
<http://dx.doi.org/10.1093/molbev/mst010>
- Kennedy, A.H. & Watson, L.E. (2010) Species delimitations and phylogenetic relationships within the fully myco-heterotrophic *Hexalectris* (Orchidaceae). *Systematic Botany* 35: 64–76.  
<http://dx.doi.org/10.1600/036364410790862489>
- Klotzsch, J.F. (1835) *Hechtia*, eine neue Gattung der Bromeliaceen. *Allgemeine Gartenzeitung* 3: 401–403.
- Kunth, K.S. (1816) *Nova Genera et Species Plantarum (quarto ed.)* 1. D'Hautel, Paris, 377 pp.
- Lamarck, J.B. (1791) *Encyclopédie méthodique, Botanique* 3. Panckoucke, Paris, 753 pp.
- Lexarza, J. (1825) *Novorum vegetabilium descriptiones, orchidianum opusculum*. Martín Rivera, México City, 43 pp.
- Lindley, J. (1821) *Lissochilus speciosus*. *Botanical Register* 7: t. 573. [text as “578”]
- Lindley, J. (1835) *Bletia reflexa*. *Edwards's Botanical Register* 21: t. 1760
- Lindley, J. (1837) *Chysis aurea*. *Edwards's Botanical Register* 23: t. 1937.
- Lindley, J. (1838) 95. *Maxillaria boothii*. *Edwards's Botanical Register* 24: misc. 52–53.
- Lindley, J. (1840a) XLV. New Orchidaceae. *Annals of Natural History* 4: 381–385.
- Lindley, J. (1840b) 131. *Chysis bractescens*. *Edward's Botanical Register* 26: misc. 61.
- Lindley, J. (1842) XXIX. A century of new genera and species of orchidaceous plants. *Annals of Natural History* 10: 184–186.
- Linnaeus, C. (1753a) *Species plantarum* 1. Salvius, Stockholm, 560 pp.
- Linnaeus, C. (1753b) *Species plantarum* 2. Salvius, Stockholm, 1200 pp.
- Loddiges, C. (1833) *Bletia gracilis*. *Botanical Cabinet* 20: t. 1977.
- Luer, C.A. (1978) *Dracula*, a new genus in the Pleurothallidinae. *Selbyana* 2: 190–198.
- Maddison, W.P. & Maddison, D.R. (2011) *Mesquite: a Modular System for Evolutionary Analysis*. Version 2.75. Available from: <http://mesquiteproject.org> (accessed 1 September 2016)
- Martius, C.F.P. (1838) *Historia naturalis palmarum* 3. Weigel, Leipzig, 502 pp.
- Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshop (GCE)* 2010: 1–8.
- Miller, P. (1754) *The Gardeners Dictionary, abridged 4<sup>th</sup> ed.*, 2: *Opuntia: the Indian fig*. Printed by the author, London, without

pagination.

- Miller, P. (1768) *The Gardeners Dictionary*, 8<sup>th</sup> ed.: *Mimosa* no. 19. Printed by the author, London, without pagination.
- Miranda, F. (1942) Nuevas fanerógamas del SO del estado de Puebla. *Anales del Instituto de Biología de la Universidad Nacional de México* 13: 451–462.
- Palacio, S., Escudero, A., Montserrat-Martí, G., Maestro, M., Milla, R. & Albert, M.J. (2007) Plants living on gypsum: beyond the specialist model. *Annals of Botany* 99: 333–343.  
<http://dx.doi.org/10.1093/aob/mcl263>
- Palisot de Beauvois, A.M.F.J. (1805) *Prodrome des Cinquième et Sixième Familles de l'Aethéogamie*, Fournier, Paris, 114 pp.
- Parsons, R.F. (1976) Gypsophily in plants—a review. *The American Midland Naturalist* 96: 1–20.  
<http://dx.doi.org/10.2307/2424564>
- Pax, F.A. (1910) XLVI. Einige neue Euphorbiaceen aus Amerika. *Repertorium Specierum Novarum Regni Vegetabilis, Beihefte* 8: 161–162.
- Pridgeon, A.M., Solano, R. & Chase, M.W. (2001) Phylogenetic relationships in Pleurothallidinae (Orchidaceae): combined evidence from nuclear and plastid DNA sequences. *American Journal of Botany* 88: 2286–2308.  
<http://dx.doi.org/10.2307/3558390>
- Rafinesque, C.S. (1825) *Neogenyton*. Published by the author, Lexington, 4 pp.
- Reichenbach, H.G. (1872) New garden plants. *Masdevallia chimaera*, n. sp. *The Gardeners' Chronicle and Agricultural Gazette* 1872: 463.
- Reichenbach, H.G. (1877) Orchidaceae roezliana novae seu criticae. *Linnaea* 41: 1–16.
- Richard, A. & Galeotti, H. (1845) Orchidographie mexicaine, d'après les échantillons, notes et dessins de MM. Galeotti, Linden, Funk, Ghiesbreght. *Annales des Sciences Naturelles; Botanique, sér. 3* 3: 15–33.
- Romero-González, G.A. & Carnevali, G. (1999) Notes on the species of *Cyrtopodium* (Cyrtopodiinae, Orchidaceae) from Florida, the Greater Antilles, Mexico, Central and northern South America. *Harvard Papers in Botany* 4: 327–341.
- Ruiz, H. & Pavón, J. (1794) *Flora peruviana et chilensis prodromus*. Sacha, Madrid, 153 pp.
- Ruiz, H. & Pavón, J. (1798) *Systema Vegetabilium Florae Peruviana et Chilensis I*. Sacha, Madrid, 455 pp.
- Salazar, G.A. (2009) Orquídeas. In: Lot, A. & Cano, Z. (Eds.) *Biodiversidad del Ecosistema Reserva Ecológica del Pedregal de San Ángel*. Universidad Nacional Autónoma de México, Mexico City, pp. 153–169.
- Salazar, G.A. & Cribb, P.J. (2007) On the identity of *Eulophia filicaulis* Lindl. (Orchidaceae). *Kew Bulletin* 62: 147–149.
- Salazar, G.A., Chávez-Rendón, C., Jiménez-Machorro, R. & de Ávila, A. (2011) A new species of *Galeoglossum* (Orchidaceae, Cranichidinae) from Oaxaca, Mexico. *Systematic Botany* 36: 261–267.  
<http://dx.doi.org/10.1600/036364411x569462>
- Schlechter, R. (1912) LX. Orchidaceae novae et criticae. *Repertorium Specierum Novarum Regni Vegetabilis, Beihefte* 10: 352–363.
- Schlechter, R. (1918) Kritische Aufzählung der bisher aus Zentral-Amerika bekanntgewordenen Orchidaceen. *Beihefte zum Botanischen Centralblatt* 36: 321–520.
- Schlechter, R. (1919) Orchideenfloren der südamerikanischen Kordillerenstaaten. *Repertorium Specierum Novarum Regni Vegetabilis, Beihefte* 6: 1–100.
- Schlechter, R. (1921) *Basiphyllaea*, eine verkannte westindische Orchidaceae. *Repertorium Specierum Novarum Regni Vegetabilis, Beihefte* 17: 76–78.
- Schlechter, R. (1922) Beiträge zur Orchideenkunde von Zentralamerika. I. Orchidaceae powellianae panamenses. *Repertorium Specierum Novarum Regni Vegetabilis, Beihefte* 17: 1–95.
- SEMARNAT. (2010) Norma Oficial Mexicana NOM-059-ECOL-2010. Protección ambiental-Especies nativas de México de flora y fauna silvestres-Categorías de riesgo y especificaciones para su inclusión o cambio-Lista de especies en riesgo. *Diario Oficial de la Federación*.
- Serguera, M. & Sánchez, M. (2011) A new natural hybrid, *Bletia* × *ekmanii* (Orchidaceae), from Cuba. *Willdenowia* 41: 107–111.
- Smith, J.E. (1793) *Icones Pictae Plantarum Rariorum Descriptionibus et Observationibus Illustratae*, fasc. 3. Davis, London, t. 14.
- Sosa, V., Veitch, N. & Grayer, R.J. (2005) 281. *Bletia*. In: Pridgeon, A.M., Cribb, P.J., Chase, M.W. & Rasmussen, F.N. (Eds.) *Genera Orchidacearum 4, Epidendreae part 1*. Oxford University, Oxford, pp. 167–170.
- Sosa, V. (2007) A molecular and morphological phylogenetic analysis of subtribe Bletiinae (Epidendreae, Orchidaceae). *Systematic Botany* 32: 34–42.
- Sosa, V. & Díaz, M.A. (1997) Orchids from the Greater Antilles I: a new species of *Bletia*. *Brittonia* 49: 79–83.  
<http://dx.doi.org/10.2307/2807699>
- Sosa, V. & Díaz, M.A. (2014) 7. *Bletia*. In: Ackerman, J.D. (Coord.) *Orchid Flora of the Greater Antilles*. Memoirs of the New York Botanical Garden 109. New York Botanical Garden, New York, pp. 38–41.
- Soto, M.A., Hágsater, E., Jiménez-Machorro, R., Salazar, G.A., Solano-Gómez, R., Flores, R. & Contreras, I. (2007) *Orchids of Mexico*:

*Digital Catalogue*. Instituto Chino, Mexico City.

- Stamatakis, A. (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30: 1312–1313.  
<http://dx.doi.org/10.1093/bioinformatics/btu033>
- Stamatakis, A., Hoover, P. & Rougemont, J. (2008) A rapid bootstrap algorithm for the RAxML web-servers. *Systematic Biology* 75: 758–771.  
<http://dx.doi.org/10.1080/10635150802429642>
- von Steudel, E.G. (1840–1941) *Nomenclator Botanicus*, ed. 2. Cottae, Stuttgart, 810 pp.
- Summerhayes, V.S. (1958) *Eulophia ramifera*. *Kew Bulletin* 1958: 50.
- Summerhayes, V.S. (1961) Two Rafinesque orchid generic names. *Taxon* 10: 253.  
<http://dx.doi.org/10.2307/1216352>
- Swartz, O. (1788) *Nova Genera et Species Plantarum seu Prodrromus*. Nordstrom, Stockholm, 152 pp.
- Swofford, D.L. (2015) PAUP\*. *Phylogenetic Analysis Using Parsimony (\*and Other Methods)*, v. 4.0a144. Sunderland: Sinauer.
- Toledo, C.A. (1984) Contribuciones a la flora de Guerrero. Tres especies nuevas del género *Bursera* (Burseraceae). *Biotica* 9: 441–449.
- van den Berg, C., Higgins, W.E., Dressler, R.L., Whitten, W.M., Soto Arenas, M.A., Culham, A. & Chase, M.W. (2000) A phylogenetic analysis of Laeliinae (Orchidaceae) based on sequence data from internal transcribed spacers (ITS) of nuclear ribosomal DNA. *Lindleyana* 15: 96–114.
- van den Berg, C., Goldman, D.H., Freudenstein, J.V., Pridgeon, A.M., Cameron, K.M. & Chase, M.W. (2005) An overview of the phylogenetic relationships within Epidendroideae inferred from multiple DNA regions and recircumscription of Epidendreae and Arethuseae (Orchidaceae). *American Journal of Botany* 92: 613–624.  
<http://dx.doi.org/10.3732/ajb.92.4.613>
- van den Berg, C., Higgins, W.E., Dressler, R.L., Whitten, W.M., Soto Arenas, M.A., Culham, A. & Chase, M.W. (2009) A phylogenetic study of Laeliinae (Orchidaceae) based on combined nuclear and plastid DNA sequences. *Annals of Botany* 104: 417–430.  
<http://dx.doi.org/10.1093/aob/mcp101>