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Phylogenetic relationships in *Mormodes* (Orchidaceae, Cymbidieae, Catasetinae) inferred from nuclear and plastid DNA sequences and morphology

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Abstract

Interspecific phylogenetic relationships in the Neotropical orchid genus *Mormodes* were assessed by means of maximum parsimony (MP) and Bayesian inference (BI) analyses of non-coding nuclear ribosomal (nrITS) and plastid (*trnL–trnF*) DNA sequences and 24 morphological characters for 36 species of *Mormodes* and seven additional outgroup species of Catasetinae. The bootstrap (>50%) consensus trees of the MP analyses of each separate dataset differed in the degree of resolution and overall clade support, but there were no contradicting groups with strong bootstrap support. MP and BI combined analyses recovered similar relationships, with the notable exception of the BI analysis not resolving section *Mormodes* as monophyletic. However, sections *Coryodes* and *Mormodes* were strongly and weakly supported as monophyletic by the MP analysis, respectively, and each has diagnostic morphological characters and different geographical distribution. The geographic structure reflected by the recovered phylogenetic patterns suggests that it is possible to undertake taxonomic revision of regional clades, which eventually will lead to a thorough revision of the genus.

Key words: nrITS, morphology, Neotropics, phylogenetics, protandry, sexual polymorphism, *trnL–trnF*

'*Mormodes* presents some peculiarities of so strange a nature that, if they were not found constant in several distinct species, we should be tempted to regard them as monstrosities. In particular the column, instead of being straight and standing erect in the centre of the flower, is bent over to one side, just as if it had been subjected to violence.'
John Lindley, *Edward's Botanical Register* 29 (1843).

Introduction

Mormodes Lindley (1836: 446) encompasses about 80 species of epiphytic orchids that prefer living on dead trees (saprolignophilous) and are distributed throughout mainland Tropical America, from Mexico to Bolivia and Brazil. *Mormodes* belongs in a clade within subtribe Catasetinae (sensu Chase *et al.* 2015) that also includes *Catasetum* Rich. ex Kunth (1822: 330–331), *Clowesia* Lindley (1843: Misc. 25–26), *Cycnoches* Lindley (1832: 154) and *Dressleria* Dodson (1975: 131). Such a clade, henceforth referred to as "core" Catasetinae, is characterized by the possession of dichogamous flowers pollinated by fragrance-collecting male euglossine bees (Dodson 1975, Romero-González 1990, Chase & Hills 1992, Salazar *et al.* 2009). *Mormodes* is easily distinguished from other Catasetinae, and all other orchids, by its flowers, which are asymmetric as a result of the torsion of column, labellum and sometimes other perianth parts (Fig. 1A–D) and the elongate stigmatic cavity that occupies most of the ventral surface of the column. Most species of *Mormodes* are protandrous; at anthesis, the column is arcuate and twisted 90–180°. Its apex is in contact with the upper surface of the labellum, and the stigmatic cavity is directed toward one side (Fig. 1E, left-hand flower). In this "pollen-donor" phase, mechanical stimulation of the apical filament of the column (Fig. 1F) occurs when the pollinator contacts it as it brushes the labellum surface to collect the floral fragrances present as droplets of aromatic compounds. This stimulus triggers the violent ejection of the pollinarium, which adheres to the dorsal surface of the thorax (more rarely the head or abdomen) by means of the massive viscidium (Dressler 1968, Salazar *et al.*

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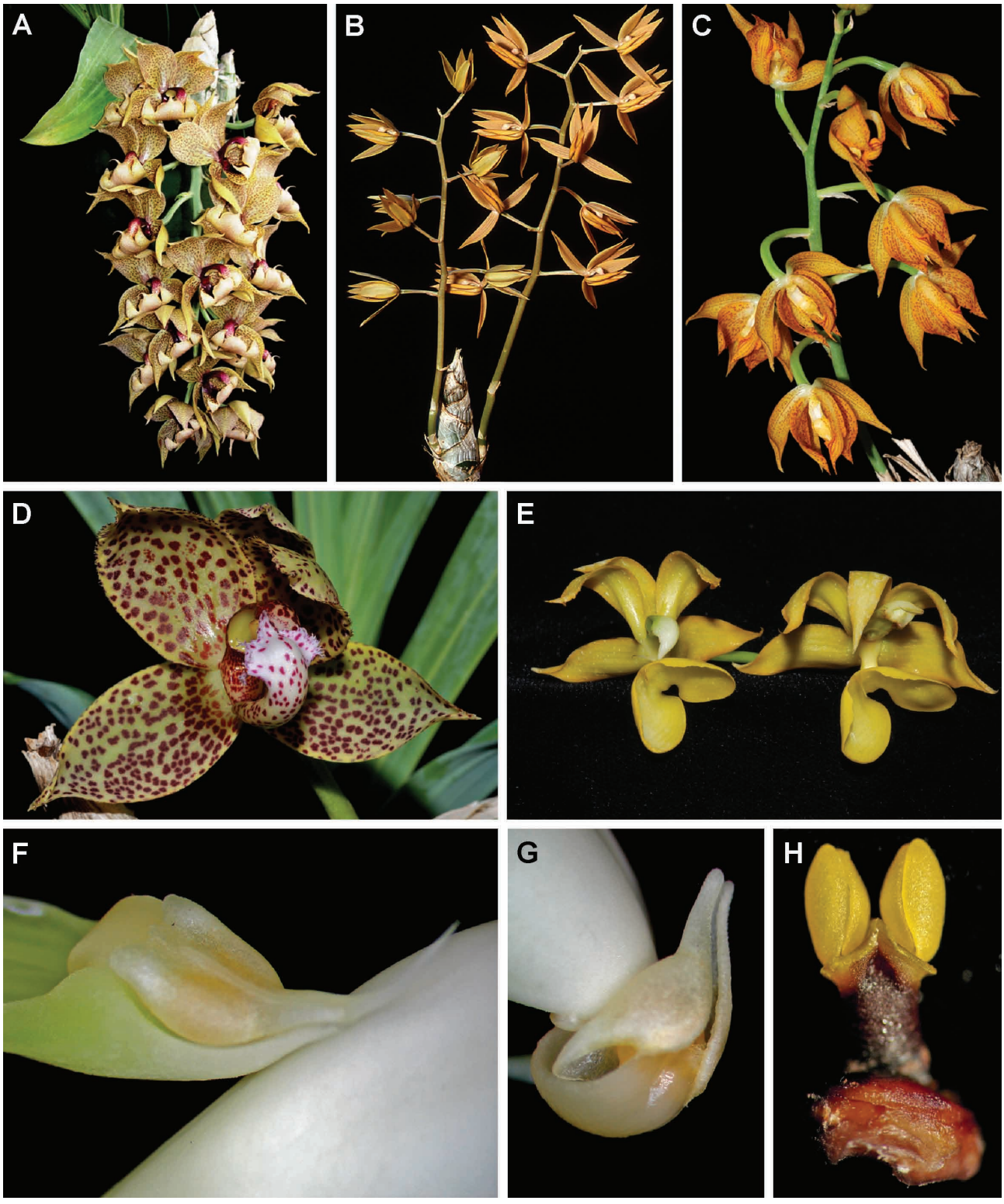

FIGURE 1. Morphology of *Mormodes*. A. *Mormodes pardalinata* (Mexico, *Soto et al. 9860*). B. *Mormodes powellii* Schltr. (Panama, *Munich-Nymphenburg Botanical Garten s.n.*). C. *Mormodes aromatica* var. *oleoaurantiaca* Rchb.f. (Mexico, *Figueroa s.n.*). D. *Mormodes uncia* (Mexico, *Salazar et al. 7577*). E. *Mormodes badia* illustrating protandry: left-hand flower in male phase with arcuate column in contact at apex with the labellum; right-hand flower in female phase with the column extended and separated from the labellum, exhibiting the stigmatic cavity (Mexico, *Hágsater 13905*). F. Column apex of protandrous *M. tezontle* in the male phase, with its back in contact with the labellum prior to ejection of the pollinarium (Mexico, *Francke s.n.*). G. Newly ejected pollinarium of *M. tezontle* with anther covering the pollinia and curled stipe (Mexico, *Francke s.n.*). H. Pollinarium of *M. pardalinata* (Mexico, *Soto et al. 9860*). Photographers: Gerardo A. Salazar (A, C–H) and Günter Gerlach (B).

2009; Fig. 1G, H). Several hours after discharge of the pollinarium the column becomes more or less straight and separate from the labellum, exhibiting in this "pollen-receptor" phase a broader stigmatic cavity facing the labellum (Fig. 1E, right-hand flower; see also Dodson 1962, Romero-González 1990, Chase & Hills 1992, Pridgeon & Chase 1998, Salazar *et al.* 2009). Traditionally, it was assumed that *Mormodes* only produces monomorphic, protandrous flowers—in contrast with the usually dimorphic, unisexual flowers of *Catasetum* and *Cycnoches* (Dodson 1975, Gregg 1975, 1978, Romero-González 1990, Romero-González & Nelson 1986, Senghas 1992). However, now it is clear that at least some species of *Mormodes* produce sexually dimorphic or polymorphic flowers, although this is not as dramatic as in *Catasetum* and *Cycnoches* (Correll 1941, Allen 1959, Dressler 1968, Monnier 1992, Salazar 1994a, Salazar *et al.* 2009, Hágsater *et al.* 2015; Pérez-Escobar *et al.* 2016).

The monophyly of *Mormodes*, as well as its derived position in core Catasetinae as the sister of *Cycnoches*, have both been supported by previous morphological and molecular phylogenetic studies (Romero-González 1990, Chase & Hills 1992, Pridgeon & Chase 1998, Romero-González & Pridgeon 2009, Salazar *et al.* 2009). On the other hand, the species-level taxonomy of *Mormodes* is problematic because of the noticeable variation in floral size and color, as well as in shape and pubescence, or lack thereof, of the labellum (Dodson 1962, Pabst 1978, Salazar 1994a). Some of this variation is related to sexual polymorphism, although the exceedingly broad species concepts used in some floras (e.g., Allen 1949, Williams 1951, Ames & Correll 1952) and the paucity of specimens with precise locality data available for study in herbaria and botanical gardens also have contributed to the confusion surrounding many species of *Mormodes* (Pabst 1968, Horich 1976, Salazar 1994a, b, Salazar & Hágsater 1990). *Mormodes* has never been thoroughly revised. Pabst (1978, 1982) published illustrated keys to the species known to him, but these are now out of date.

Pfitzer (1889) proposed the earliest infrageneric classification of *Mormodes*, which relied entirely on floral features. In this, two species showing distinctive autapomorphic labellum features, namely *M. luxata* Lindley (1842: Misc. 60) and *M. uncia* Reichenbach (1869: 892, as its synonym, *M. greenii* Hooker 1869: t. 5802), were assigned to the monospecific sections *Coryodes* Pfitzer (1889: 159) and *Coelodes* Pfitzer (1889: 159), respectively. All remaining species were placed in section "*Eumormodes*" (i.e., autonymic section *Mormodes* according to current nomenclatural standards). Subsequently, Fowlie (1965: 26) proposed a further section, *Klotzschia*, containing *M. flavida* Klotzsch (1852: 113, as its synonym, *M. stenoglossa* Schlechter 1923: 225) and *M. horichii* Fowlie (1964: 6). However, all these infrageneric taxa were disregarded by Pabst (1968, 1978, 1982), who considered them as poorly defined. More recently, Fowlie (1970, 1972) noted that the species of *Mormodes* could be divided into two groups based on the position of the inflorescence, i.e. basal versus lateral. This attribute is correlated with the timing of development of the inflorescence: in species with a basal inflorescence, development starts soon after the new shoot starts to grow, and anthesis occurs before the pseudobulb matures and while leaves are still present. In contrast, in species with lateral inflorescences (i.e. arising several nodes above the node that bears the renewal bud) the inflorescence starts developing after the pseudobulb has thickened, and anthesis occurs while the leaves are wilting or after their shedding (Salazar 1994a, 1999, Salazar *et al.* 2009). Salazar *et al.* (2009) presented a phylogenetic tree based on a preliminary phylogenetic analysis of nuclear ribosomal (nr)ITS DNA sequences and 21 morphological characters (by error indicated as "51" in the legend of their Fig. 440.3). Such analysis supported monophyly of *Mormodes* and recovered two major clades within the genus, which were treated by them as sections *Mormodes s.l.* (including *Klotzschia*) and *Coryodes s.l.* (including *Coelodes*). Those sections correspond with the late-flowering and early-flowering groups noted above, respectively.

We reassess here phylogenetic relationships in *Mormodes* using a more inclusive sample of taxa and characters. In addition to nrITS analyzed by Salazar *et al.* (2009), we sequenced the noncoding plastid *trnL–trnF* region, which consists of the group I intron of the *trnL* gene, the short 3' exon of *trnL* and the intergenic spacer (IGS) between *trnL* and *trnF* (Taberlet *et al.* 1991). These relatively rapidly evolving regions were chosen because they have been shown to have enough variation to elucidate intergeneric and interspecific relationships in various taxa across the orchid family (reviewed in Cameron 2007), including subtribe Catasetinae (Pridgeon & Chase 1998). We also coded 24 vegetative and floral characters. Our aim was to generate a robust hypothesis of the phylogenetic relationships among the species of *Mormodes* as a basis for evaluating previous infrageneric classifications and providing a phylogenetic framework for subsequent taxonomic revision of the genus.

Materials and methods

Taxonomic sampling:—Accessions of 36 species of *Mormodes* were included in the analyses. These represent about 40% of the species currently recognized and much of generic morphological diversity and geography. Seven additional species belonging to six genera of Catasetinae *s.l.* (Pridgeon *et al*. 2009, Chase *et al.* 2015) were used as outgroups.

DNA extraction, amplification and sequencing:—Total DNA was usually extracted from fresh or silica gel-dried leaf or perianth tissue, but in some instances from pollinia recovered from herbarium specimens, using a 2× CTAB protocol based on Doyle & Doyle (1987) modified by adding 2% (w/v) polyvinyl pirrolidone (PVP) to the extraction buffer. DNA extracts were purified in Qiaquick silica columns (Qiagen, Crawley, West Sussex, UK) or by precipitation with chilled isopropanol with a subsequent wash in 70% ethanol.

Amplification was carried out in 25 µL PCR reactions using a commercial PCR mix (Taq Core PCR Kit, Qiagen), adding 1 µL of 0.4% aqueous solution of bovine serum albumin (BSA) to neutralize potential inhibitors (Kreader 1996) and 0.5 µL of dimethyl sulfoxide (DMSO) to reduce problems related to secondary structure in template DNA. The nrITS region was usually amplified as a single fragment with primers 17SE/26SE of Sun *et al.* (1994) and the following PCR profile: 2-min premelt at 94°C, 28–30 cycles of 1-min denaturation at 94°C, 1-min annealing at 50° and 2-min extension at 72°C, with a final extension of 7 min at 72°C. However, degraded DNA extracted from herbarium specimens was amplified in two steps, which included a first amplification as above followed by a "semi-nested" PCR, in which 0.3–0.5 µL of unpurified PCR product from the first amplification were used as template for a second reaction with 16-28 additional cycles. Re-amplifications were carried out with primer combinations 17SE/nrITS2 and nrITS3/26SE (primers nrITS2 and nrITS3 from White *et al.* 1990). This approach increased DNA yield while reducing sequence noise caused by an excess of primer dimers that often formed when performing more than 30 cycles in a single PCR reaction.

The *trnL–trnF* region was usually amplified as a single fragment using the c/f primer pair of Taberlet *et al.* (1991) and the same PCR mix and thermal cycler program as for nrITS, except for a lower annealing temperature of 48°C. As in the case of the nrITS region, weak *trnL–trnF* PCR products from degraded DNA were re-amplified in semi-nested PCR reactions, using primer combinations c/d and e/f (Taberlet *et al.* 1991). In some instances, PCR of the *trnL–trnF* region produced two bands, as reported previously for the same region in a molecular phylogenetic study of Cymbidieae by Whitten *et al.* (2000). Using a higher annealing temperature (52−53°C) sometimes resulted in a single band, but its sequence was distinctly longer than the one we routinely amplified using 48°C. This was the case with two outgroup species, namely *Clowesia thylaciochila* (Lemaire 1856: Misc. 90) Dodson (1975: 136) and *Galeandra batemanii* Rolfe (1892: 431), which had a sequence length similar to those of various members of Cymbidieae from the study of Whitten *et al.* (2000). For instance, our sequence of *C. thylaciochila* was 544 base pairs (bp) longer than the average *Mormodes* sequence length of 547 bp. In the following, we will refer to the most common, shorter sequences we obtained for *Mormodes* and *Cycnoches* as the "short copy" and to the longer sequences of our *C. thylaciochila* and *G. batemanii*, as well as the sequences of Whitten *et al.* (2000), as the long copy (see further details under Discussion). We were unable to obtain reliable *trnL-trnF* sequences for *Catasetum* aff. *laminatum* Lindley (1840a: 384) and three species of the ingroup, namely *Mormodes buccinator* Lindley (1840b: Misc. 9), *M. luxata* and *M. lineata* Lindley (1842: t. 43).

PCR products were purified with Qiaquick silica columns (Qiagen) according to the manufacturer's protocol and used in cycle-sequencing reactions with the ABI Prism Big Dye™ Terminator Cycle Sequencing Ready Reaction kit with AmpliTaq® DNA polymerase, versions 3 or 3.1 (Applied Biosystems Inc., Warrington, Cheshire, UK). The cycle sequencing reactions included 2 µL terminator mix, 0.25 µL primer at PCR concentration (100 ng/µL) and 3 µL of PCR product. The products of cycle-sequencing were cleaned by precipitation with ethanol or in CentriSep columns with Sephadex (Princeton Separations, Inc., Adelphia, New Jersey, USA). Both DNA strands were sequenced in a PE 377 automated sequencer (Applied Biosystems Inc.) or a 3100 Genetic Analyzer (Applied Biosystems Inc.). The electropherograms were edited and assembled with Sequencher (Gene Codes Corp., Ann Arbor, Michigan, USA) and aligned manually. A list of the taxa analyzed, including voucher information and GenBank/European Nucleotide Archive accessions for the DNA sequences, is given in Table 1. The aligned matrices in NEXUS format are available from TreeBase (study accession URL: http://purl.org/phylo/treebase/phylows/study/TB2:S15963).

Morphological data:—Twenty-four morphological characters were usually coded based on direct observation of live, herbarium and ethanol-preserved specimens and flowers or under a stereomicroscope, except for two micro-morphological characters, namely presence/absence in the leaf mesophyll of mucilaginous idioblasts containing spirals of cellulosic material (Stern & Judd 2001) and the patterns of epicuticular wax on the leaf surface (Barthlott & Frölich 1983, Salazar 1999; Table 2–3). All characters were explained and discussed previously in Salazar (1999). For this study we examined collections of *Mormodes* and related groups from the following herbaria: AMES, AMO, BIGU, BM, BR, CAS, COL; CR, ENCB, F, GH, HB, HEPH, IAN, IBUG, IEB, INB, K, LA, M, MEXU, MG, MICH, MO, NY, P, QCA, QCNE, R, RB, SEL, SP, UB, UC, US, USJ, UVAL, VEN, W and XAL.

Presence/absence of mucilaginous idioblasts with cellulosic spirals in the leaf mesophyll was determined by light microscopy of cleared leaf fragments. Fresh leaf material was fixed in FAA (50% absolute ethanol, 5% glacial acetic

acid, 10 % formalin, 35% water) for at least 48 h and stored in 70% ethanol; 10 × 10 mm leaf fragments were placed in a 10% aqueous solution of KOH or NaOH for 30 min and subsequently in 10% NaClO for 20 min; fragments were stained with 1% "O" safranin, dehydrated in an alcohol series, cleared in eugenol 2 h and rinsed 2−3 times in xylol for 15 min. Slides mounted with Canada balsam or synthetic resin were observed under bright field illumination with blue and green filters in an Axioskope photomicroscope (Carl Zeiss, Göttingen, Germany; Salazar, 1999).

Patterns of epicuticular wax of leaves were studied by scanning electron microscopy; 7 × 7 mm fragments of leaf tissue from herbarium specimens or air-dried fresh leaves were mounted in aluminium stubs, covered with gold and observed in high vacuum with a Hitachi S-2460 N (Tokyo, Japan) scanning electron microscope (SEM) operating at 15 kv. Although both leaf surfaces bear epicuticular wax, wax patterns were better conserved and more clearly observed on the leaf underside; therefore, scoring of epicuticular wax attributes refer only to this surface (Salazar 1999).

TABLE 1. Taxa analyzed, voucher information and GenBank/European Nucleotide Archive accession numbers for the DNA sequences.

Species	Voucher	nrITS	*trnL-trnF*
Catasetum aff. *laminatum* Lindl.	Mexico, *Salazar 6565* (MEXU)	LK054139	--
Clowesia thylaciochila (Lem.) Dodson	Mexico, *Jiménez 2580* (AMO)	LK054140	--
Cycnoches egertonianum Bateman	Mexico, *Francke s.n.* (MEXU)	LK054141	LK054179
Cycnoches ventricosum Bateman	Mexico, *Francke s.n.* (MEXU)	LK054142	LK054180
Dressleria dilecta (Rchb.f.) Dodson	Tropical America, Whitten *et al.* 2000	AF239411	--
Galeandra batemanii Rolfe	Mexico, *Salazar 7631* (MEXU)	LK054138	--
Grobya galeata Lindl.	Brazil, van den Berg *et al*. 2002	AF470487	--
Mormodes andreettae Dodson	Ecuador, *Bröde s.n.* (M)	LK054149	LK054186
Mormodes aromatica Lindl. var. *oleoaurantiaca* Rchb.f.	Mexico, *Salazar 6087* (AMO)	LK054173	LK054209
Mormodes badia Rolfe ex Watson	Mexico, *Salazar 6088* (MEXU)	LK054143	LK054181
Mormodes buccinator Lindl.	Colombia, *Giraldo 31* (COL)	LK054148	--
Mormodes castroi Salazar	Brazil, *Salazar 4960* (AMO)	LK054150	LK054187
Mormodes colossa Rchb.f.	Costa Rica, Munich Bot. Gard. 93/2826 (M)	LK054157	LK054194
Mormodes dasilvae Salazar	Brazil, *Salazar 4961* (AMO)	LK054151	LK054188
Mormodes elegans Miranda	Brazil, *Shaw s.n.*, MEXU (photograph)	LK054152	LK054189
Mormodes escobarii Pabst	Colombia, *Salazar s.n.* (MEXU, spirit)	LK054159	LK054196
Mormodes fractiflexa Rchb.f.	Costa Rica, Munich Bot. Gard. s.n. (M)	LK054160	LK054197
Mormodes hookeri Lem.	Panama, Munich Bot. Gard. 02/3024 (M)	LK054161	LK054198
Mormodes horichii Fowlie	Costa Rica, *Salazar 5348* (USJ)	LK054162	LK054199
Mormodes ignea Lindl. & Paxton	Panama, *Salazar 6372* (MEXU, spirit)	LK054163	LK054200
Mormodes lawrenceana Rolfe	Ecuador, *Salazar s.n.* (MEXU, spirit)	LK054146	LK054184
Mormodes lineata Lindl.	Mexico, Salazar *et al. 5838* (MEXU)	LK054164	--
Mormodes lobulata Schltr.	Costa Rica, *Pupulin 3008* (USJ)	LK054165	LK054201
Mormodes luxata Lindl.	Mexico, *Salazar et al. 3602* (AMO)	LK054174	--
Mormodes maculata (Klotzsch) L.O.Williams	Mexico, *Salazar et al. 4215* (AMO)	LK054170	--
	Mexico, *Salazar 5002* (AMO)	--	LK054206
Mormodes nagelii L.O.Williams	Mexico, *Salazar 6046* (MEXU, photograph)	LK054172	LK054208
Mormodes oestlundiana Salazar & Hágsater	Mexico, *Salazar 4195* (AMO)	LK054144	LK054182
Mormodes paraënsis Salazar & da Silva	Brazil, *Salazar s.n.* (MEXU, spirit)	LK054153	LK054190
Mormodes pardalinata Rosillo	Mexico, *Soto & Huerta 8662* (AMO)	LK054175	LK054210
Mormodes rolfeana Linden	Peru, *Rolando s.n.* (MEXU, photograph)	LK054156	LK054193
Mormodes salazarii M.A.Blanco, J.E.Jiménez & P.Juárez	Costa Rica, *Horich 4/81* (MEXU, photograph)	LK054166	LK054202
Mormodes sanguineoclaustra Fowlie	Mexico, *Soto & Salazar 1123* (AMO)	LK054176	LK054211
Mormodes skinneri Rchb.f.	Costa Rica, Munich Bot. Gard. 02/3026 (M)	LK054167	LK054203
Mormodes sotoana Salazar	Guatemala*, Salazar & Soto 4450* (AMO)	LK054168	LK054204
Mormodes aff. *sotoana* Salazar	Costa Rica, *Horich 3/77-3* (MEXU, photograph)	LK054158	LK054195
Mormodes tapoayensis Miranda & Lacerda	Brazil, *Salazar s.n.* (MEXU, spirit)	LK054154	LK054191
Mormodes tezontle Rosillo	Mexico, *Salazar 2659* (AMO)	LK054145	LK054183
Mormodes theiochlora (Rchb.f.) Salazar	Ecuador, *Salazar s.n.* (MEXU, spirit)	LK054147	LK054185
Mormodes tuxtlensis Salazar	Mexico, *Salazar et al. 5801* (MEXU)	LK054171	LK054207
Mormodes uncia Rchb.f.	Mexico, *Soto 7434A* (AMO)	LK054177	LK054212
Mormodes variabilis Rchb.f.	Ecuador, *Salazar 6098* (MEXU, spirit)	LK054169	LK054205
Mormodes warszewiczii Klotzsch	Peru, *Salazar 6375* (MEXU, spirit)	LK054155	LK054192
Mormodes williamsii Hort. ex Williams	Mexico, *Salazar et al. 3686* (AMO)	LK054178	LK054213

TABLE 2. Morphological characters coded and their states (after Salazar 2009).

No.	Character	States
1	Clinandrium filament	0 = absent/1 = present
2	Elastic stipe	0 = absent/1 = present
3	Stipe after discharge	0 = straight/1 = curled
4	Leaves	0 = deciduous/1 = persistent
5	Stigma size	0 = small/1 = large
6	Column change of position	0 = absent/1 = present
7	Flower asymmetry	0 = absent/1 = present
8	Position of inflorescence	0 = basal/1 = lateral/2 = subapical/3 = apical
9	Timing of flowering	0 = early/1 = late
10	Epicuticular wax on leaves	0 = indistinct/1 = horizontal platelets/2 = erect platelets
11	Mucilaginous idioblasts in mesophyll	0 = absent/1 = scarce/2 = abundant
12	Flower resupination	0 = absent/1 = present/2 = intermediate
13	Lip fovea	0 = absent/1 = present
14	Lip flexion	0 = funnel-shaped/1 = concave/2 = hypochile trigonous, epichile concave/3 = tubular/4 = upturned lateral lobes/5 = saddle-shaped
15	Clinandrium margins	0 = reduced/1 = prominent
16	Column apex	0 = entire/1 = emarginate or bifid
17	Shape of filament	0 = subulate/1 = oblong/2 = filament absent
18	Purple stripe on labellum base	0 = absent/1 = present
19	Lip pubescence	0 = absent/1 = present
20	Lip lobulation	0 = entire/1 = shallowly lobed/2 = deeply lobed/3 = bilobed longitudinally
21	Lip callus	0 = absent/1 = thickened apex of column foot/2 = transverse thickening on labellum/3 = tabular keel/4 = non-tabular keels on labellum /5 = central prominence on labellum
22	Shape of lip apex or midlobe	0 = truncate or rounded/1 = acute/2 = acuminate/3 = apiculate
23	Shape of lateral lobes	0 = no lobes/1 = linear/2 = semiovate/3 = semiorbicular
24	Degree of torsion of column	0 = none/1 = 45–90°/2 = 135–180°

Phylogenetic analyses:—We conducted maximum parsimony (MP) analyses of four datasets, namely nrITS sequences, *trnL–trnF* sequences, morphological characters and all data combined. Additionally, since the separate parsimony analyses did not reveal conflicting groupings among datasets receiving bootstrap support >50%, we conducted a Bayesian inference (BI) analysis of the combined dataset, including morphological characters, which enabled us to compare the results of MP with a method that uses explicit models of character evolution. The MP analyses were carried out using the program PAUP* version 4.0b10 (Swofford 2003), and each consisted of a heuristic search with 1000 replicates of random sequence addition with tree bisection-reconnection (TBR) branch-swapping and the MULTREES option on, saving up to 20 most-parsimonious trees (MPTs) per replicate to reduce the time spent in swapping large islands of trees (Maddison 1991). All characters were unordered and equally weighted. Individual gap positions were treated as missing data. Internal support for clades was evaluated by 1000 bootstrap replicates (Felsenstein 1985), each consisting of 20 replicates of random addition, TBR branch-swapping and saving up to 20 trees per heuristic replicate.

The BI analysis was conducted with MrBayes version 3.2.2 (Ronquist *et al.* 2012). Two simultaneous analyses were run for four million generations, sampling trees every one-thousand generations. Suitable substitution models were selected for the nrITS and *trnL-trnF* datasets using the Akaike information criterion (Akaike, 1974) with the program jModelTest version 2.1.4 (Darriba *et al.* 2012). The "standard discrete model" implemented in MrBayes (based on Lewis 2001) was set for the morphological data. The models selected were TIM3+G and TPM1uf+I for the nrITS and *trnL-trnF* datasets, respectively, which were set up using the options available in Modeltest. Convergence of the Markov chains was determined using the AWTY software (Nylander *et al*. 2008).

In all analyses involving of the *trnL-trnF* region, either separately or in combination with nrITS and the morphological characters, we included only the sequences of the species of *Cycnoches* and *Mormodes* (see Results and Discussion), all of which represent the short copy of this region, avoiding mixing them with the likely non-orthologous sequences of the long copy. The corresponding positions of the other outgroups were scored as missing data.

TABLE 3. Codification of morphological characters (see Table 2 for a list of characters/character states).

Species/characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Catasetum aff. *laminatum*	0	1	0	0	0	0	0	0	1	0	0	0/1	0	1	1	0	2	0	0	0	3	0	0	0
Clowesia thylaciochila	1	1	0	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	0	0	4	0	0	0
Cycnoches egertonianum	1	1	1	0	0	0	0	2	1	0	2	0	0	4/5	1	1	0	0	0	0	1	0	0	0
Cycnoches ventricosum	1	1	1	0	0	0	0	2	1	0	2	0	0	5	1	1	0	0	0	0	1	0	0	0
Dressleria dilecta	1	1	1	1	0	0	0	0	0	?	?	0	0	1	1	0	0	0	0	0	0	0	0	0
Galeandra batemanii	0	0	0	0	0	0	0	3	1	0	?	1	0	0	0	0	2	0	1	0	0	0	0	0
Grobya galeata	0	0	0	1	0	0	0	0	1	0	?	1	0	4	0	0	2	0	0	2	5	0	1	0
Mormodes andreettae	1	1	1	0	1	1	1	1	1	0	0	1	1	5	1	1	1	0	1	1	0	3	3	1
Mormodes aromatica	1	1	1	0	1	1	1	0	0	0	1	2	0	2	0	0	0	0	0	3	2	3	3	1
Mormodes badia	1	1	1	0	1	1	1	1	1	0	0	1	1	5	1	0	0	0	0	0	0	3	0	1
Mormodes buccinator	1	1	1	0	1	1	1	1	1	0	?	1	1	5	1	?	?	0	0	1	0	3	3	1
Mormodes castroi	1	1	1	0	1	1	1	1	1	0	0	1	1	5	1	1	1	0	0	2	0	3	1	1
Mormodes colossa	1	1	1	0	1	1	1	1	1	0	0	1	1	5	1	1	1	0	0	0	0	2	0	1
Mormodes dasilvae	1	1	1	0	1	1	1	1	1	0	0	1	1	5	1	1	1	0	0	1	0	3	3	1
Mormodes elegans	1	1	1	0	1	1	1	1	1	0	0	1	1	5	1	1	0	0	0	0	0	2	0	1
Mormodes escobarii	1	1	1	0	1	1	1	1	1	0	0	1	1	5	1	1	1	0	0/1	1	0	3	3	1
Mormodes fractiflexa	1	1	1	0	1	1	1	1	1	0	0	0	1	5	1	1	1	0	0	0	0	3	0	1
Mormodes hookeri	1	1	1	0	1	1	1	1	1	0	0	0	1	5	1	1	1	0	0/1	0	0	3	0	1
Mormodes horichii	1	1	1	0	1	1	1	1	1	0	0	1	1	1	1	1	1	0	0	0	0	3	0	1
Mormodes ignea	1	1	1	0	1	1	1	1	1	0	0	0	1	5	1	1	1	0	0	0	0	3	0	2
Mormodes lawrenceana	1	1	1	0	1	1	1	1	1	0	?	0	1	5	1	?	?	0	1	0	0	3	0	1
Mormodes lineata	1	1	1	0	1	1	1	1	1	0	0	1	1	5	1	1	1	0	0/1	2	0	3	1	1
Mormodes lobulata	1	1	1	0	1	1	1	1	1	0	0	1	1	5	1	1	1	0	0	1	0	3	3	1
Mormodes luxata	1	1	1	0	1	1	1	0	0	2	1	2	0	1	1	0	0	1	1	2	2	3	2	1
Mormodes maculata	1	1	1	0	1	1	1	0	0	1	1	1	0	1	1	0	0	0	0	2	0	2	2	1
Mormodes nagelii	1	1	1	0	1	1	1	0	0	1	1	1	0	5	1	0	0	0	0	1	0	3	3	2
Mormodes oestlundiana	1	1	1	0	1	1	1	1	1	0	0	0	1	5	1	0	0	0	0	1	0	3	3	1
Mormodes paraënsis	1	1	1	0	1	1	1	1	1	0	0	1	1	5	1	1	1	0	0	1	0	3	3	1
Mormodes pardalinata	1	1	1	0	1	1	1	0	0	2	1	1	0	1	1	0	0	1	1	2	2	3	2	1
Mormodes rolfeana	1	1	1	0	1	1	1	1	1	0	0	0	1	5	1	1	1	0	0	0	0	3	0	1
Mormodes salazarii	1	1	1	0	1	1	1	1	1	0	0	0	1	5	1	1	1	0	0	0	0	3	0	1
Mormodes sanguineoclaustra	1	1	1	0	1	1	1	0	0	2	?	1	0	5	1	0	0	1	1	2	0	3	2	1
Mormodes skinneri	1	1	1	0	1	1	1	1	1	0	0	0	1	5	1	1	1	0	0/1	1	0	3	3	1
Mormodes sotoana	1	1	1	0	1	1	1	1	1	0	0	1	1	5	1	1	1	0	0/1	1	0	3	3	1
Mormodes aff. *sotoana*	1	1	1	0	1	1	1	1	1	0	0	1	1	5	1	1	1	0	0	1	0	3	3	
Mormodes tapoayensis	1	1	1	0	1	1	1	1	1	0	0	0	1	5	1	1	1	0	0	0	0	3	0	1
Mormodes tezontle	1	1	1	0	1	1	1	1	1	0	0	1	1	5	1	0	0	0	0	0	0	3	0	2
Mormodes theiochlora	1	1	1	0	1	1	1	1	1	0	?	1	1	5	1	?	?	0	1	1	0	3	3	1
Mormodes tuxtlensis	1	1	1	0	1	1	1	0	0	1	1	1	0	1	1	0	0	0	1	2	0	2	2	1
Mormodes uncia	1	1	1	0	1	1	1	0	0	2	1	1	0	3	1	0	0	0	1	0	2	3	0	1
Mormodes variabilis	1	1	1	0	1	1	1	1	1	0	0	1	1	5	1	1	1	0	0/1	0	0	3	0	1
Mormodes warzsewiczii	1	1	1	0	1	1	1	1	1	0	0	1	1	5	1	1	1	0	0/1	2	0	3	1/2	1
Mormodes williamsii	1	1	1	0	1	1	1	0	0	2	1	2	0	1	1	0	0	1	1	2	2	3	2	1

Results

The nrITS dataset comprised 734 characters, of which 120 were potentially parsimony-informative. The heuristic search found 61 trees with a length of 328 steps, consistency index (CI, excluding uninformative characters) of 0.71 and retention index (RI) of 0.88. The *trnL-trnF* dataset included 753 characters, of which 23 were potentially parsimony-informative. The analysis found eight trees with a length of 23 steps, CI of 0.88 and RI of 0.88. Analysis of the morphological matrix, consisting of 24 characters (all of them informative), resulted in 2765 MTPs with a length of 73 steps, CI of 0.60 and RI of 0.86. The bootstrap consensus trees (nodes >50%) from each separate MP analysis are depicted in Fig. 2A–C.

nrITS and morphological MP analyses strongly support the monophyly of *Mormodes* (bootstrap percentage, BP, 100 and 93, respectively). In the *trnL-trnF* analysis, most outgroups were excluded because the short copy of this region could not be reliably sequenced, and therefore generic monophyly was not assessed stringently. Both resolution and overall clade support were greater for nrITS, followed by *trnL-trnF* and lastly the morphological dataset. Although there are some differences between groups recovered by each dataset, none of the clades differing among the separate analyses obtained strong support in more than one dataset, which suggests 'soft' incongruence likely caused by insufficient variation (cf. Wiens 1998). Moreover, some groups were recovered by more than one dataset; for instance, both the nrITS and *trnL-trnF* analyses recovered a clade including *M. uncia*, *M. sanguineoclaustra* Fowlie (1970: 217), *M. pardalinata* Rosillo (1979: 169) and *M. williamsii* Hort. ex Nicholson (1885: 385; plus *M. luxata* in the nrITS analysis, not included in the *trnL-trnF* analysis; Fig. 2A, B). All these species also fall in a single clade in the morphological analysis, although their relationships to one another and to other species such as *M. aromatica* Lindley (1841: 76) and *M. nagelii* Williams (1940: 153) were unresolved in the latter (Fig. 2C). Likewise, both the nrITS and *trnL-trnF* trees include a clade with *M. nagelii* sister to [*M. maculata* (Klotzsch 1838: 306) Williams (1950: 188)-*M. tuxtlensis* Salazar (1988: 52)], among other shared groupings.

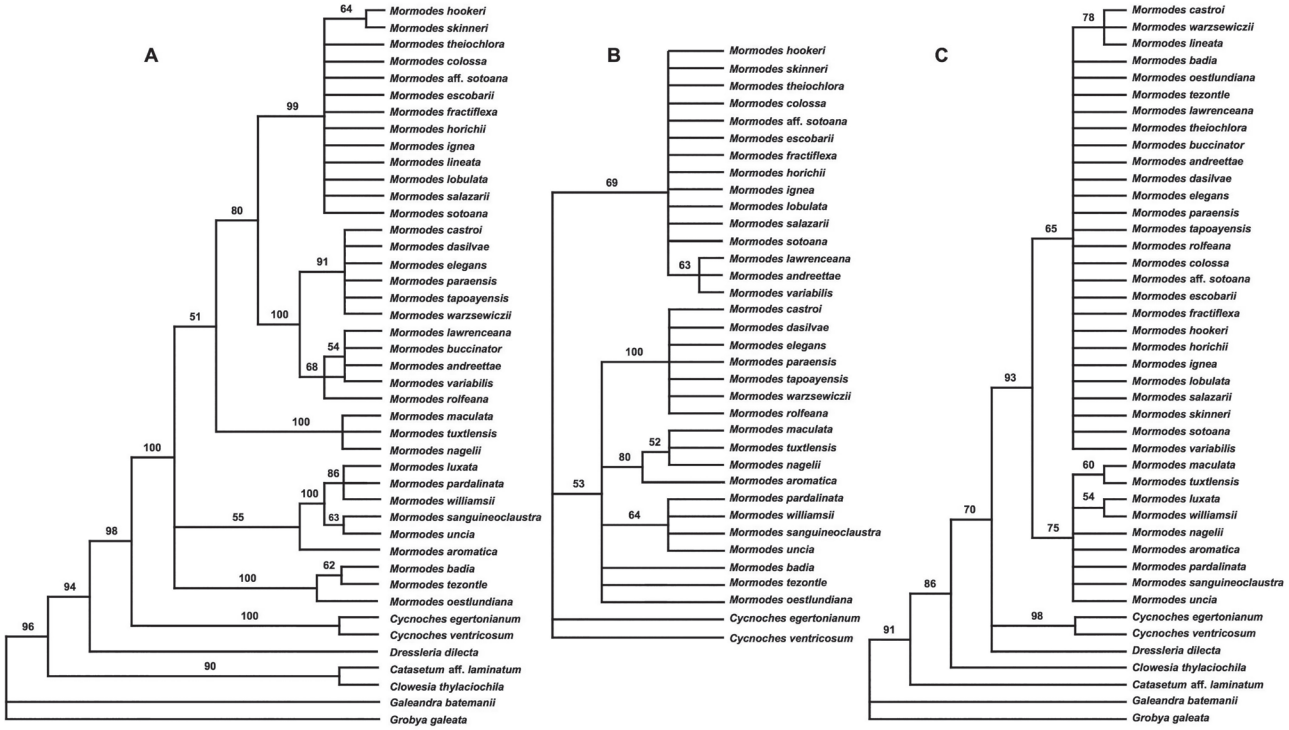

FIGURE 2. Bootstrap consensus trees (>50%) from the MP analyses. A. Nuclear ribosomal ITS region. B. Plastid *trnL–trnF* region. C. Morphological characters. Numbers above branches are bootstrap percentages.

The combined dataset, including the nrITS and *trnL-trnF* sequences plus the morphological characters, consisted of 1,511 characters, 167 of which were potentially parsimony-informative. The analysis found 174 MPTs with a length of 456 steps, CI of 0.65 and RI of 0.86. The consensus tree was more resolved and included more clades receiving strong support (BP>90; Fig. 3A) than any of the separate analyses (Fig. 2A–C). Monophyly of *Mormodes* was strongly supported (BP 100), whereas sections *Coryodes* sensu Salazar *et al.* (2009; including clades 1–2) and section *Mormodes* (clades 3–6) received strong (BP 90) and weak support (BP 70), respectively. Each of these clades includes two or more major subclades that received moderate to strong bootstrap support (Fig. 3A).

The BI analysis of the combined dataset recovered relationships similar to the combined MP analysis, differing most notably in that in the BI analysis section *Mormodes* is not monophyletic (Fig. 3B). Instead, section *Coryodes* (clades 1–2) formed a trichotomy with clade 3 and a more inclusive, strongly supported group (posterior probability, PP, 1.00) encompassing other groups assigned to section *Mormodes* by Salazar *et al.* (2009).

Discussion

Homology of *trnL–trnF* sequences:—As noted earlier, the *trnL–trnF* sequences of *Mormodes* and *Cycnoches* generated for this study were consistently shorter than those of some of the outgroups, and also from an assortment of species representing most of the subtribes of Cymbidieae sensu Chase *et al*. (2015) analyzed by Whitten *et al.* (2000). The difference in length is substantial, and it results in two short (12 and 19 bp) deletions and one long (650 bp) one in the aligned *trnL* intron of *Mormodes* and *Cycnoches* relative to other Cymbidieae. Parsimony analysis of an alignment including both our short *Mormodes* and *Cycnoches* sequences, our long sequence of outgroup species *Clowesia thylaciochila*, plus ten additional long sequences of various Cymbidieae from Whitten *et al.* (2000), resulted in paraphyly of core Catasetinae. Short-copied *Cycnoches* and *Mormodes* formed a clade, whereas the long-copy of *Dressleria dilecta* (Reichenbach 1866: 73) Dodson (1975: 132) and *Clowesia thylaciochila* grouped with *Cyrtopodium punctatum* (Linnaeus 1759: 1246) Lindley (1833: 188; Cyrtopodiinae) in a separate clade (data not shown; alignment and tree available from http://purl.org/phylo/treebase/phylows/study/TB2:S15963). Such length difference, as well as occurrence of two bands of PCR product in some amplifications noted here and in Whitten *et al*. (2000), and non-monophyly of core Catasetinae when the short and long sequences are aligned and analyzed together, all point to the

existence of more than one version of *trnL* in Cymbidieae. Previous phylogenetic studies using the *trnL-trnF* region have revealed instances of two copies of this region in other flowering plant groups, such as Zeugites Browne (1756: 341), Poaceae (Soriano *et al.* 2007) and *Unonopsis* Fries (1900: 26), Annonaceae (Pririe *et al.* 2007). Exclusion from our analyses of the long version of the *trnL-trnF* region obtained for several outgroup taxa avoids mixing likely paralogous versions of *trnL*, which would lead to spurious phylogenetic results. The issue of more than one version of *trnL-trnF* in these orchids deserves further research, which is beyond the scope of this study.

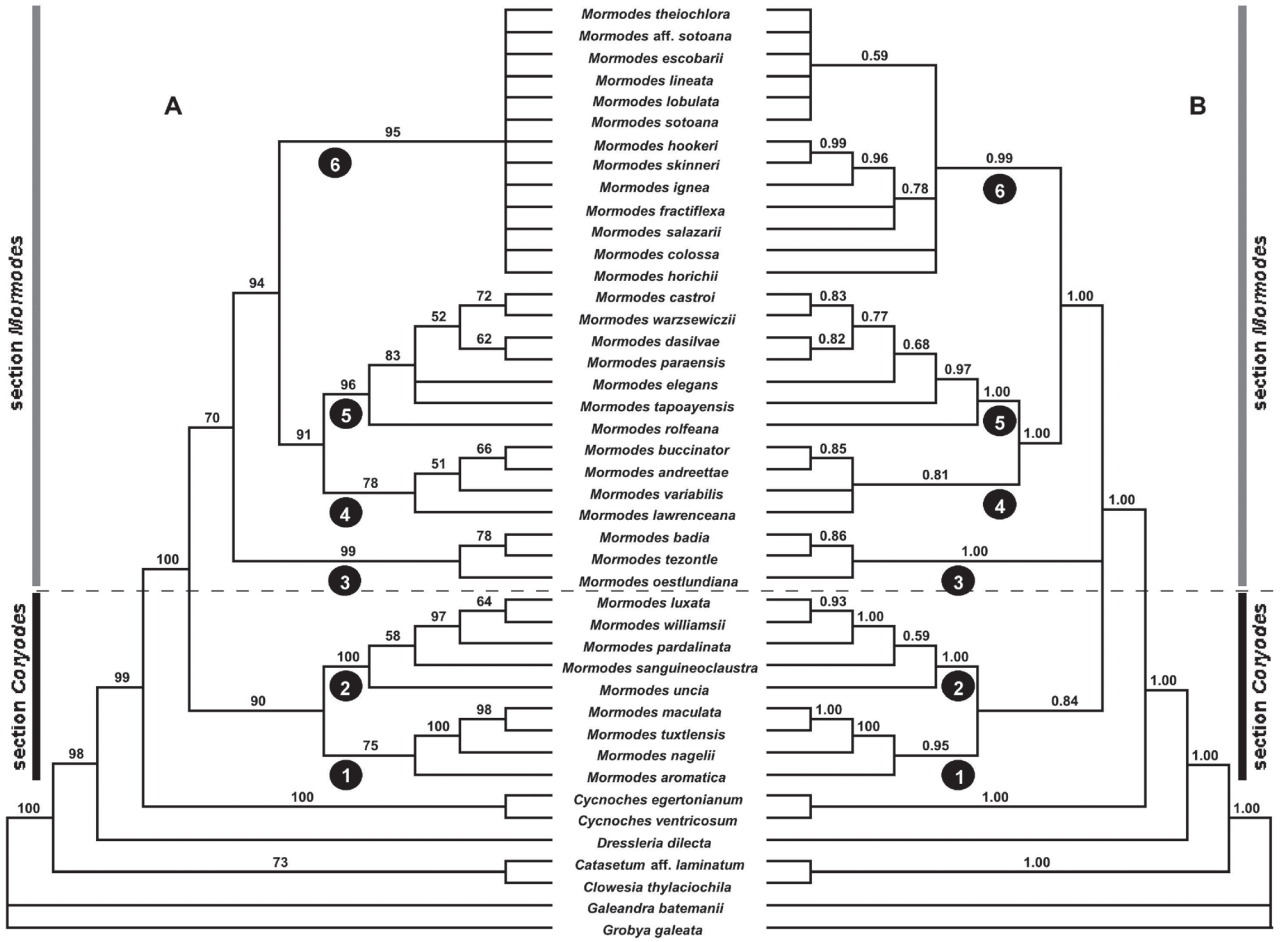

FIGURE 3. Phylogenetic relationships in *Mormodes* from the MP and BI analyses of combined nrITS DNA sequences, plastid *trnL–trnF* DNA sequences and 24 morphological characters. A. Bootstrap consensus tree (>50%) from the MP analysis; numbers above branches are bootstrap percentages. B. Summary consensus tree (>50%) from the BI analysis; numbers above branches are posterior probabilities. Numbers 1–6 in filled circles refer to clades discussed in the text: 1–2, section *Coryodes*; 3–6, section *Mormodes*.

Phylogenetic analyses:—Both the MP and BI analyses of all datasets recovered *Mormodes* as monophyletic, in agreement with previous morphological (Romero-González 1990, Chase & Hills 1992) and molecular studies (Pridgeon & Chase 1998, Salazar *et al.* 2009, Pérez-Escobar *et al.* 2015). Both analyses also support monophyly of section *Coryodes* (BP 90, PP 0.84, respectively), but section *Mormodes* received low support from the MP analysis (BP 70) and was not recovered as monophyletic in the BI analysis (Fig. 3B). Nevertheless, both sections are distinguishable by several morphological attributes and show substantial geographical structure (as noted previously by Salazar *et al.* 2009). In section *Coryodes* the leaf mesophyll contains mucilaginous idioblasts, inflorescences are basal and produced from the developing shoot, and anthesis occurs before maturation of the pseudobulb and the shedding of the leaves. Section *Coryodes* (Fig. 3, clades 1–2) is restricted to mountain ranges of Mexico and adjacent Central America south to Honduras. *Mormodes maculata*, *M. tuxtlensis* and *M. nagelii* occur in wet cloud forests and their ecotones with lowland tropical forests along the mountain ranges of the Gulf of Mexico slope, whereas all the species of their sister group (clade 2; Fig. 3) are restricted to moist or wet pine-oak barranca forests on the sierras facing the Pacific Ocean west of the Isthmus of Tehuantepec. *Mormodes aromatica* is widespread along the Sierra Madre del Sur and the mountains of Chiapas through Guatemala, El Salvador and Honduras, with a vicariant species in western Mexico (*M. ramirezii* Rosillo 1983: 61, not sampled for this study).

Section *Mormodes* lacks mucilaginous idioblasts with cellulosic spirals in the leaf mesophyll and inflorescences develop laterally from the mature pseudobulb, usually after the leaves were shed. The earliest-diverging clade of section *Mormodes* (clade 3 in Fig. 3), which includes *M. badia* Rolfe ex Watson (1897: 54), *M. tezontle* Rosillo (1980: 306), *M. oestlundiana* Salazar & Hágsater (1990: 66) and likely *M. cozticxochitl* Salazar (1990: 75, not sampled), is also restricted to the foothills of the mountain ranges of the Pacific coast of Mexico west of the Isthmus of Tehuantepec. The relationships among the remaining species of section *Mormodes* also show geographic structure, with clade 5 being exclusively South American, whereas clade 6 is predominantly Central American but also includes species from adjacent northwestern South America, i.e. *M. escobari* (Pabst 1969: 113) and *M. theiochlora* (Reichenbach 1881: 428) Salazar (1994b: 27).

The phylogenetic framework provides a basis to assess different taxonomic views, even those regarding species limits. As noted earlier, some floras have used exceedingly broad specific concepts for *Mormodes*, which results in the impression that some species have extensive distributions; conversely, different sexual "morphs" of the same species have been treated as different species. For instance, considerable confusion has surrounded the identity of *Mormodes lineata*, *M. histrio* Linden & Reichenbach (1859: 54) and *M. warszewiczii* Klotzsch (1854: 65). Lindley (1841) described *M. lineata* without providing an illustration, but the following year published another account of the species accompanied by a color drawing (Lindley 1842), stating that the color of the flowers had changed since the first flowering. Indeed, a comparison of a drawing by Lindley of a flower from the original flowering (K-L!) with the color plate shows differences not only in color but also in the overall shape and proportions of the lobes of the labellum. Correll (1941) noted the floral similarity of the 1842 color illustration to a record of Reichenbach's drawing of a flower from the type of *M. histrio*, concluding that two different species were involved: genuine *M. lineata* (in Lindley 1841) and *M. histrio*, with the color illustration in Lindley (1842) representing the latter. These conclusions were supported by Garay (1976), who considered that Lindley's (1841) original species, the "lost" type of which he found at P, represented a different species from that pictured in the 1842 color plate, but assigned the later to *M. warszewiczii* with *M. histrio* as its synonym. Nevertheless, field and greenhouse observations have demonstrated that *M. lineata* is a polymorphic species (Teuscher 1952, Allen 1959, Oesterreich 1970, Hágsater *et al.* 2015, Pérez-Escobar *et al*. 2016, G.A. Salazar, pers. obs.) and that its range of variation encompasses the morphotypes represented by both *M. lineata* and *M. histrio*. Moreover, study of South American collections has demonstrated that *M. warszewiczii* occurs in Peru, as stated in its protologue (Klotzsch 1954), not in Mexico and Central America as *M. lineata*. Our phylogenetic analysis indicates that, despite overall floral similarity, *M. lineata* (including *M. histrio*) and *M. warszewiczii* are not closely related (Fig. 3). Detailed study of other "widespread and variable species," such as *M. buccinator* in the sense of various floras, has uncovered other instances of mixtures of different species with consistent morphological differences and mutually exclusive distributions (e.g. Salazar 1994c). The fact that there are clades within the genus distributed in distinct geographic areas enables taxonomists to undertake regional revisions. Such work is currently being conducted for Mexican and Central American taxa (G.A. Salazar, unpubl.) and will eventually permit comprehensive revision of the genus.

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