

## MOLECULAR PHYLOGENETICS OF *MAXILLARIA* AND RELATED GENERA (ORCHIDACEAE: CYMBIDIEAE) BASED ON COMBINED MOLECULAR DATA SETS<sup>1</sup>

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The orchid genus *Maxillaria* is one of the largest and most common of neotropical orchid genera, but its current generic boundaries and relationships have long been regarded as artificial. Phylogenetic relationships within subtribe Maxillariinae sensu Dressler (1993) with emphasis on *Maxillaria* s.l. were inferred using parsimony analyses of individual and combined DNA sequence data. We analyzed a combined matrix of nrITS DNA, the plastid *matK* gene and flanking *trnK* intron, and the plastid *atpB-rbcL* intergenic spacer for 619 individuals representing ca. 354 species. The plastid *rpoC1* gene (ca. 2600 bp) was sequenced for 84 selected species and combined in a more limited analysis with the other data sets to provide greater resolution. In a well-resolved, supported consensus, most clades were present in more than one individual analysis. All the currently recognized minor genera of “core” Maxillariinae (*Anthosiphon*, *Chrysocynis*, *Cryptocentrum*, *Cyrtidiorchis*, *Mormolyca*, *Pityphyllum*, and *Trigonidium*) are embedded within a polyphyletic *Maxillaria* s.l. Our results support the recognition of a more restricted *Maxillaria*, of some previously published segregate genera (*Brasiliorchis*, *Camaridium*, *Christensonella*, *Heterotaxis*, *Ornithidium*, *Sauvetea*), and of several novel clades at the generic level. These revised monophyletic generic concepts should minimize further nomenclatural changes, encourage monographic studies, and facilitate more focused analyses of character evolution within Maxillariinae.

**Key words:** *atpB-rbcL* spacer; *matK*; *Maxillaria*; Maxillariinae; molecular phylogenetics; nrITS; Orchidaceae; *rpoC1*.

Botanists have long been fascinated by large, hyperdiverse genera and the evolutionary forces that create them. Govaerts (2001) lists over 50 seed plant genera that contain more than 500 species. Orchidaceae are one of the largest plant families and include several megagenera (1000+ spp.) including

*Bulbophyllum* Thouars, *Epidendrum* L., *Pleurothallis* R. Br., and *Dendrobium* Sw. What causes explosive speciation, and how can such radiations be explained by ecological adaptations, physiological/morphological innovations, or accelerated rates of morphological/molecular change? As presently circumscribed, *Maxillaria* (ca. 580 spp.; Kew Monocot Checklist; Govaerts, 2005) ranks seventh in number of species for orchid genera (Cribb and Govaerts, 2005) and probably ranks among the 50 largest angiosperm genera (Frodin, 2004). Maxillariinae is one of the most conspicuous and diverse subtribes of neotropical Orchidaceae. The species are common, floristically important elements in humid neotropical forests and widespread from southern Florida (USA) to northern Argentina, with centers of diversity in southern Central America, along the Andes, and in southeastern Brazil. Floristic, biogeographic, and evolutionary studies of such large genera are hampered by the large number of species, the difficulty of defining manageable monophyletic units, and often by the paucity of morphological and molecular characters that distinguish species. In this study, we use combined molecular data sets to test the monophyly of the large genus *Maxillaria*. Does *Maxillaria* consist of one megagenus, or is its present circumscription artifactual, the result of orchid taxonomists’ overemphasis on homoplasious vegetative and pollination-related floral traits? Can *Maxillaria* be subdivided into more manageable clades defined by strong molecular support and putative morphological synapomorphies?

In the most recent subtribal classifications of Orchidaceae (Dressler, 1993; Chase et al., 2003), the neotropical subtribe Maxillariinae Benth. was broadened to include genera formerly

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placed in Bifrenariinae Dressler and Lycastinae Schltr. sensu Dressler (1981). Genera now included in Maxillariinae are: *Anguloa* Ruiz & Pav., *Ida A.* Ryan & Oakeley, *Lycaste* Lindl., *Neomoorea* Rolfe, *Xylobium* Lindl. (all previously Lycastinae); *Bifrenaria* Lindl. (including *Adipe* Raf., *Cydoniorchis* Senghas, and *Stenocoryne* Lindl.; Koehler and do Amaral, 2004), *Guanchezia* G.A. Romero & Carnevali, *Horvatia* Garay, *Hylaeorchis* Carnevali & G.A. Romero, *Rudolfiella* Hoehne, *Scuticaria* Lindl., *Teuscheria* Garay (all previously Bifrenariinae); *Anthosiphon* Schltr., *Brasiliorchis* R. Singer, S. Koehler & Carnevali, *Cryptocentrum* Benth., *Chrysocycnis* Linden & Rchb.f., *Cyrtidiorchis* Rauschert, *Maxillaria* Ruiz & Pavón, *Mormolyca* Fenzl, *Pityphyllum* Schltr., and *Trigonidium* Lindl. Orchid classifications of recent decades (Dressler, 1981, 1993; Senghas, 1993, 1994; Szlachetko, 1995) have all recognized these genera as a closely related, monophyletic or paraphyletic (Szlachetko, 1995) group; the classification of Dressler (1993) is most congruent with current molecular data. Maxillariinae are members of a neotropical clade that includes Coeliopsidiinae, Oncidiinae, Stanhopeinae, and Zygopetalinae; these five subtribes are each strongly monophyletic and are sister to Eriopsidiinae, but relationships among them are still poorly resolved (Whitten et al., 2000; M. Whitten, unpublished data). Wider phylogenetic analyses of epidendroid orchids (Freudenstein et al., 2004; van den Berg et al., 2005) showed that Coeliopsidiinae, Maxillariinae, Oncidiinae, Stanhopeinae, and Zygopetalinae form a clade within a grade that includes members of Cyrtopodiinae and Cymbidieae (sensu Dressler, 1993); consequently, Chase et al. (2003) lumped tribe Maxillarieae into a broader tribe Cymbidieae.

As presently circumscribed, subtribe Maxillariinae s.l. includes species with diverse vegetative morphology, but their flowers usually have a prominent column foot (a ventral extension of the base of the column to which the labellum is attached) and pollinaria with a viscidium, four pollinia in two superposed pairs, and often a prominent stipe. Generic relationships within Maxillariinae were partially clarified by Whitten et al. (2000); phylogenetic relationships within the *Lycaste* alliance sensu Dressler (1993) were analyzed by Ryan et al. (2000), and within the *Bifrenaria* alliance by Koehler et al. (2002). The remaining large clade of species (corresponding to Maxillariinae sensu Dressler [1993], hereafter referred to as core Maxillariinae) currently consists of eight genera (*Anthosiphon*, *Chrysocycnis*, *Cryptocentrum*, *Cyrtidiorchis*, *Maxillaria*, *Mormolyca*, *Pityphyllum*, and *Trigonidium*) with about 609 species, currently recognized by the World Checklist of Orchidaceae (Govaerts et al., 2005). Dressler (1981), Senghas (1994) and Szlachetko (1995) included *Scuticaria* in core Maxillariinae, but molecular data place it in the *Bifrenaria* alliance (Whitten et al., 2000; Koehler et al., 2002).

Core Maxillariinae are characterized by the presence of conduplicate leaves (sometimes modified as terete, subterete, or ensiform, but never plicate), single-flowered inflorescences (sometimes produced in fascicles), four pollinia with or without a stipe attached to an often lunate viscidium, and usually a prominent column foot that is typically persistent in the fruit.

Vegetative structure varies greatly among species groups. Stems can be monopodial (forming long canes with apparently indeterminate growth) or more frequently sympodial. In the latter case, each growth unit can either be terminated by a heteroblastic (single internode) pseudobulb or be relatively uniform in thickness. The rhizome segments between growth units can be very short (producing caespitose plants) or long

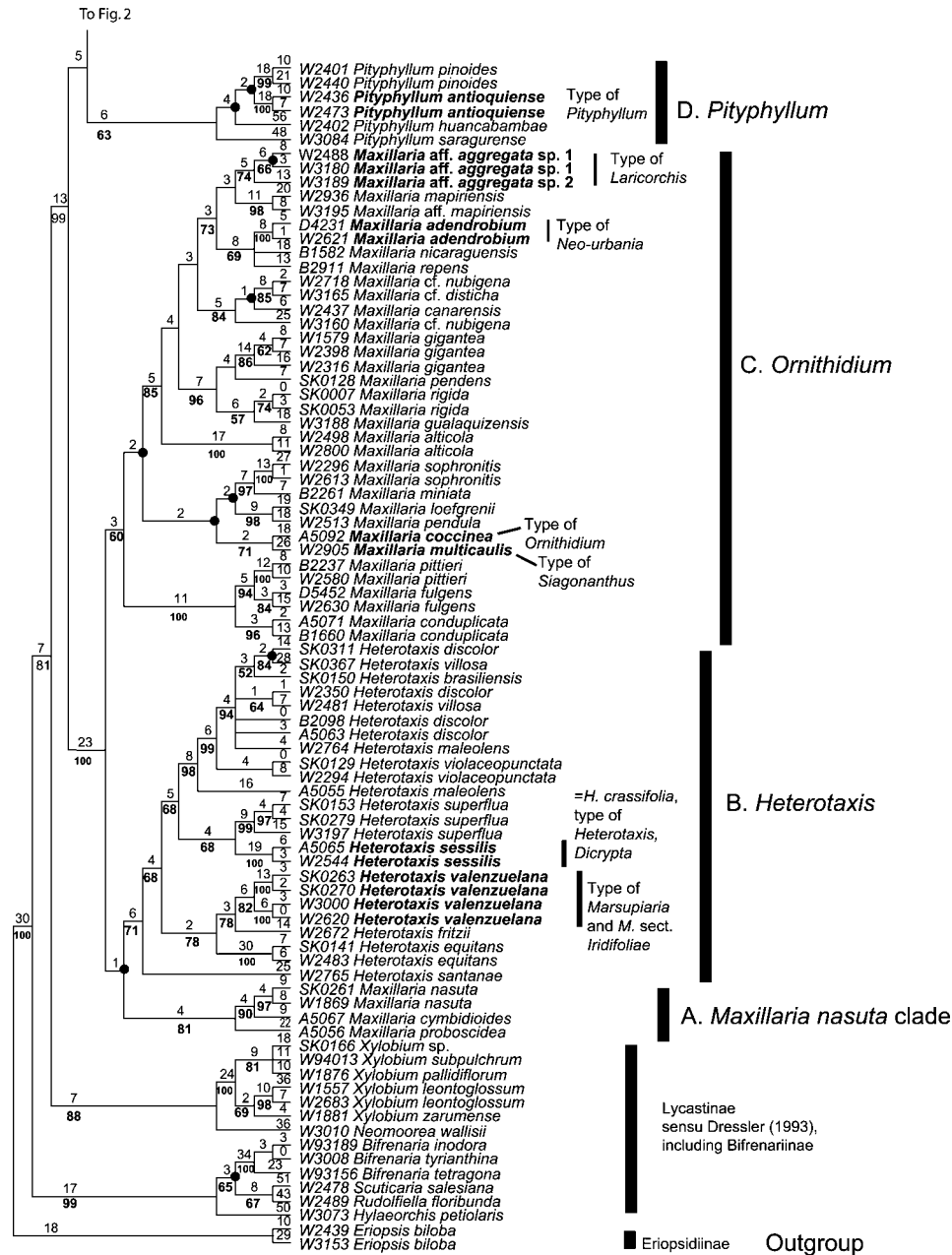
(producing rhizomatous, rambling plants). Plants of *Cyrtidiorchis* and some species in the *Camaridium* and *Ornithidium* clades (see Discussion) have dimorphic growth; the sympodial juveniles bear pseudobulbs, whereas the mature shoots that bear flowers are monopodial. Leaves can be produced throughout the stem or only from the terminal part of each sympodium. The number of apical leaves per pseudobulb ranges from one to five, and bracts subtending the pseudobulbs may be large and foliaceous or scarious.

In contrast to vegetative structure, floral morphology in core Maxillariinae is relatively uniform compared to other groups in Cymbidieae (e.g., Oncidiinae, Stanhopeinae). Conspicuous fiber bundles may be present or absent in sepals and petals (readily evident when sepals are torn; Fig. 10R). Most species do not offer any floral reward and seem to be food-deceptive. The widespread (possibly pleisiomorphic) occurrence of scutellar pollinarium attachment to pollinating bees results in a stereotypic floral morphology that has hampered attempts at generic and subgeneric classification. Apparent floral rewards in some clades include nectar, triterpenoid resins, and pseudopollen (van der Pijl and Dodson, 1966; Davies et al., 2000, 2003a, b, 2005; Singer, 2003; Flach et al., 2004; Singer and Koehler, 2004; Stpiczynska et al., 2004; Singer et al., 2006). Radiations to novel pollination syndromes (e.g., putative moth pollination in *Cryptocentrum*; pseudocopulation in *Mormolyca*, *Trigonidium*, *Chrysocycnis*, and *Cyrtidiorchis*; hummingbird pollination in some *Camaridium* and *Ornithidium*) are associated with numerous floral apomorphies that resulted in segregation of these clades at the generic level by previous workers. Pseudocopulation may have evolved at least four times within Maxillariinae, and resin rewards may have several independent origins. Floral rewards and pollination syndromes will be discussed in subsequent papers.

Fruits of Maxillariinae are always capsules that dehisce along six longitudinal seams, resulting in six separate valves: three “placentiferous” ones alternating with three “sterile” ones (Blanco et al., 2006). In some taxa, these valves separate apically and become reflexed; in most taxa, the valves remain united both distally and proximally, with seeds dispersing through lateral openings. These two types of fruit dehiscence (apical vs. lateral) and the presence/absence of perianth fiber bundles correlate with major clades (see Discussion).

Reported chromosome numbers for core Maxillariinae are  $2n = 28, 30, 32, 34, 36, 38, 40,$  and  $42$  with  $40$  being the most common number for 68 species sampled (Blumenschein, 1960; Blumenschein and Paker, 1963; Tanaka, 1966; Carnevali, 1991; Félix and Guerra, 2000). The lowest counts of  $2n = 28$  and  $30$  are from *Cryptocentrum* (Carnevali, 1991). Diploids and tetraploids of *M. mosenii* have  $2n = 38$  and  $76$ , respectively (S. Koehler, unpublished data). Blumenschein and Paker (1963) reported triploids in three species. At present, chromosome counts are too few for meaningful taxonomic correlations, and reported counts often vary within species. Most chromosome counts lack corresponding herbarium vouchers (allowing the corroboration of their identity), which further diminishes their scientific value.

Taxonomists have long recognized that generic delimitations within core Maxillariinae are unsatisfactory (Dressler, 1981; Carnevali, 1991; Senghas, 1993, 1994, 2000; Whitten et al., 2000; Christenson, 2002a, b; Szlachetko et al., 2006; Szlachetko and Šmiszek, 2007). Several segregate genera have been created during the last 150 yr, but most recent taxonomic and floristic treatments favor a broad generic concept of



Figs. 1–7. Single, randomly selected most parsimonious cladogram from a combined analysis of nrITS, *matK+trnK*, and *atpB-rbcL* spacer sequence data for Maxillariinae. Values above branches are Fitch lengths; values below branches are bootstrap percentages  $\geq 50\%$ . Black circles indicate nodes that collapse in the strict consensus of shortest trees. Lettered clades correspond to those mentioned in Results/Discussion. Names in boldface indicate the type species of genera or sections. Species names are prefaced with collector initial and collection number (Appendix 1). Collector abbreviations are: A = Atwood & Whitten; B = Blanco; D = Dressler & Atwood; GG = Gerlach; H = Hirtz; J = Jost; SK = Koehler; FP = Pupulin; W = Whitten.

*Maxillaria* while suspecting the polyphyly of the genus (e.g., Atwood and Mora de Retana, 1999; Govaerts et al., 2005). A comprehensive monograph of *Maxillaria* has never been attempted, and given the present circumscription of the genus, developing such a monograph would represent a gigantic effort (Christenson, 2002a, b; Monro, 2006).

The circumscription of *Maxillaria*, the largest genus in the subtribe, has plagued taxonomists since its origin. It was established by Ruiz and Pavón (1794) with a short description of the genus and an engraving of a flower and capsule by Félix

Prieto. In the first volume of their later *Systema Vegetabilium Florae Peruvianae et Chilensis*, Ruiz and Pavón (1798) listed 16 species in *Maxillaria* (13 of these are now relegated to other genera and subtribes; Garay, 1997b). *Maxillaria platypetala* Ruiz & Pav. is currently regarded as the valid lectotype (Brieger and Hunt, 1969; Garay, 1997a, b; McIlmurray and Oakeley, 2001). The large number of species described in the last two centuries, the conservative floral morphology, and the diverse vegetative habits among species have resulted in great confusion in the circumscription and taxonomy of *Maxillaria*

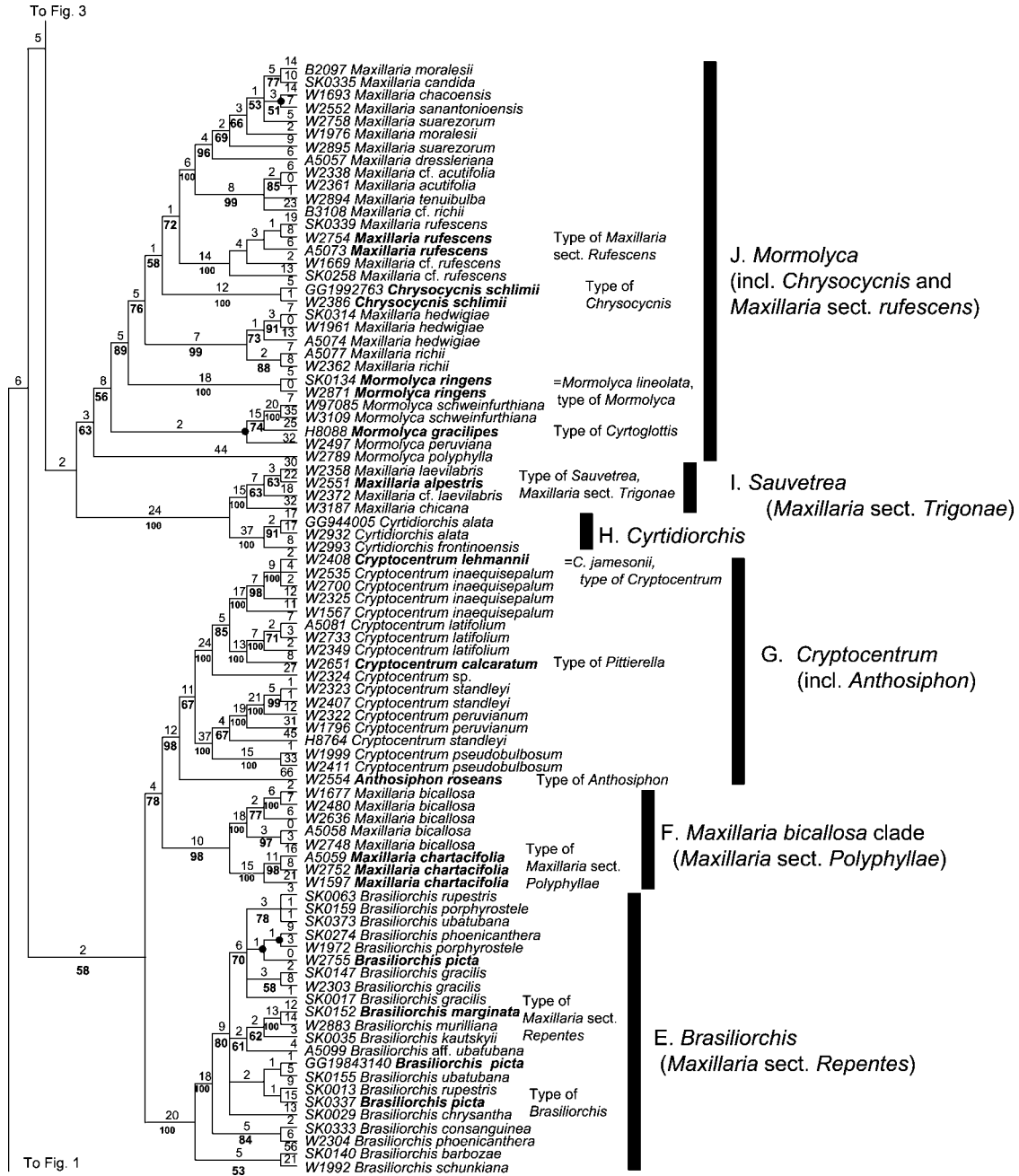


Fig. 2.

and closely related genera (Carnevali, 1991; Dressler, 1993; Christenson, 2002a, b). Generic names currently regarded as synonyms of *Maxillaria* (Govaerts et al., 2005) include *Camaridium* Lindl., *Dicrypta* Lindl., *Heterotaxis* Lindl., *Marsupiaria* Hoehne, *Menadena* Raf., *Neo-urbania* Fawc. & Rendle, *Ornithidium* Salisb., *Pentulops* Raf., *Pseudomaxillaria* Hoehne, *Psittacoglossum* La Llave & Lex., *Sepalosaccus* Schltr., and *Siagonanthus* Poepp. & Endl. Recently, *Heterotaxis* has been resurrected (Barros, 2002; Ojeda et al., 2005), and five more genera (*Adamanthus* Szlach., *Brasiliorchis* R. Singer, S. Koehler & Carnevali, *Christensonella* Szlach., Mytnik, Górnjak & Śmiszek, *Laricorchis* Szlach., and *Sauvetrea* Szlach.) have

been segregated from *Maxillaria* (Szlachetko et al., 2006; Singer et al., 2007; Szlachetko and Śmiszek, 2007).

There have been several recent attempts to produce a generic and infrageneric classification of *Maxillaria* and relatives, all without the benefit of a phylogenetic framework and with conflicting results. Using pollinarium characters and chromosome numbers, Carnevali (1991) divided *Maxillaria* into two major groups, four alliances, 47 suballiances, and more than 10 series. Senghas (2000) created a classification based on growth habit, floral characters, and leaf texture, recognizing 12 groups and giving generic status to *Marsupiaria*, *Ornithidium*, and *Sepalosaccus*. Christenson (2002a, b) provided an overview of

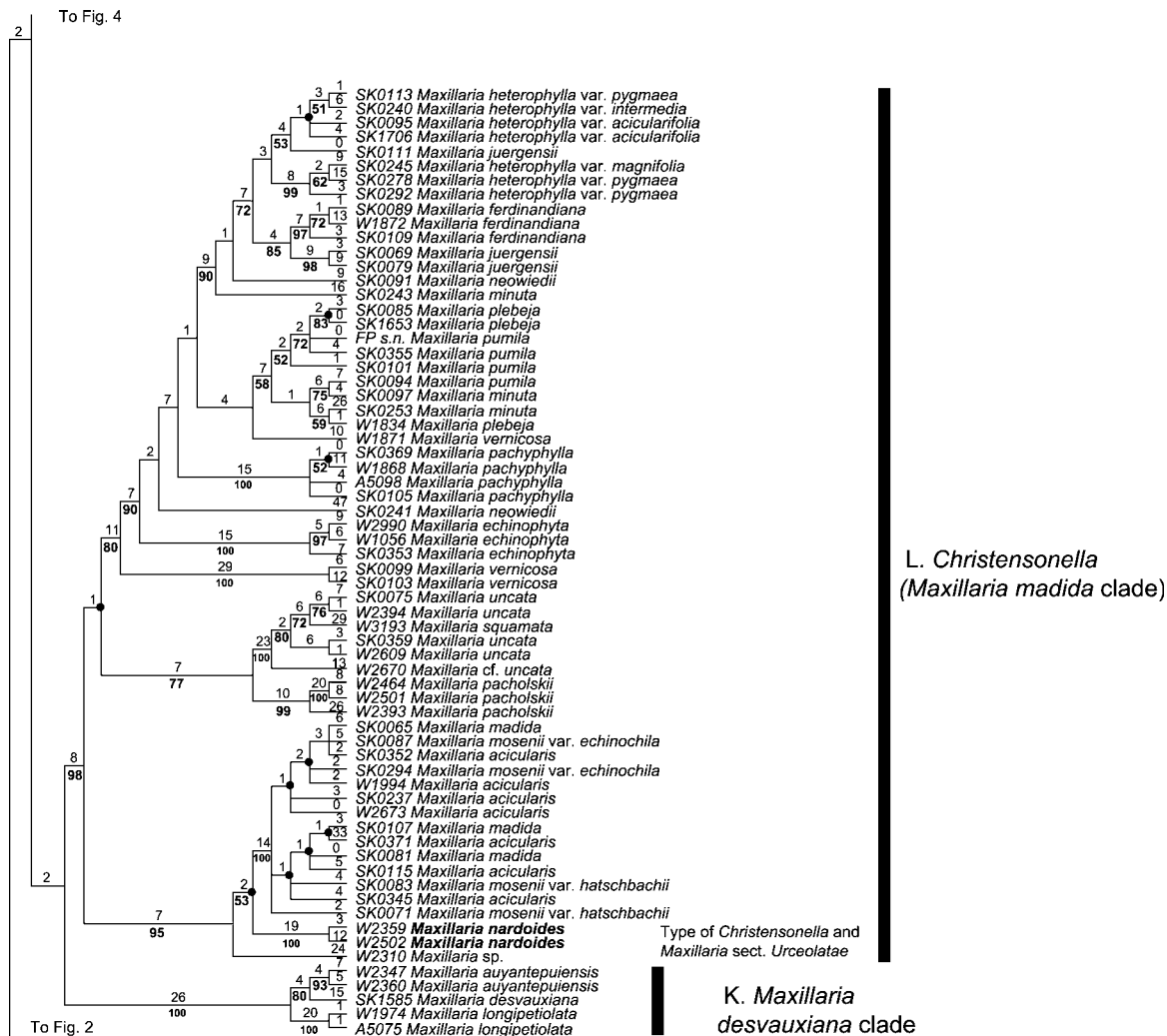


Fig. 3.

vegetative and floral variation within *Maxillaria* and presented a partial infrageneric classification with 19 sections.

Dathe and Dietrich (2006) analyzed nrITS sequences and morphology for 30 species of core Maxillariinae. They concluded that *Maxillaria* is grossly polyphyletic, that most morphological characters examined were homoplasious, and that the current classification is based on groupings that are somewhat useful for identification purposes but are not monophyletic. They also stated that greater taxon sampling was needed before core Maxillariinae could be reclassified.

The objective of this study was to use combined molecular data sets and extensive taxon sampling to reevaluate generic boundaries and to define well-supported clades within core Maxillariinae. This clade constitutes a large fraction of neotropical Orchidaceae, which in turn are a major component of neotropical floristic diversity. The monographic revision of large genera such as *Maxillaria* is hampered by the difficulty of defining manageable monophyletic subdivisions (Monro, 2006). The identification of such clades in this study should facilitate more intensive taxonomic, morphological, molecular, and biogeographic studies, and analyses of character evolution.

MATERIALS AND METHODS

Specimens were field collected or were obtained from various botanical gardens, private collections, and commercial vendors (Appendix 1). Nomenclature largely follows the World Checklist of Orchidaceae (Govaerts et al., 2005), except where we disagree on certain species circumscriptions. The sister group of Maxillariinae is still unclear. A 215-accession, combined *matK/ITS* cladistic analysis of neotropical Cymbidiaceae (M. Whitten, unpublished data) strongly supports a clade consisting of Maxillariinae (including Bifrenariinae and Lycastinae), Stanhopeinae, Coeliopsidinae, Zygopetalinae, and Oncidiinae, but relationships among subtribes are not well supported. Consequently, *Eriopsis* (Eriopsidiinae) was used as an outgroup. Sampling included 604 specimens of ingroup core Maxillariinae, representing approximately 354 species plus 13 placeholder individuals (representing 12 species) of Bifrenariinae and Lycastinae (both sensu Dressler [1981]). Representatives of all genera (including almost all type species) were sampled. A few specimens could not be unequivocally identified to species, reflecting either alpha-taxonomic problems or undescribed species. Whenever possible, these are identified with a species modifier “aff.” or “cf.” and the probable name of the species or that of its putative closest relative, respectively. Apparently undescribed species are indicated with the abbreviation “sp. nov.” after the genus. Digital photographs of most sampled plants are being placed in a database with voucher data at FLAS (<http://www.flmnh.ufl.edu/natsci/herbarium/cat/catsearch.htm>). The alpha-taxonomy of *Maxillaria* s.l. is still incomplete,

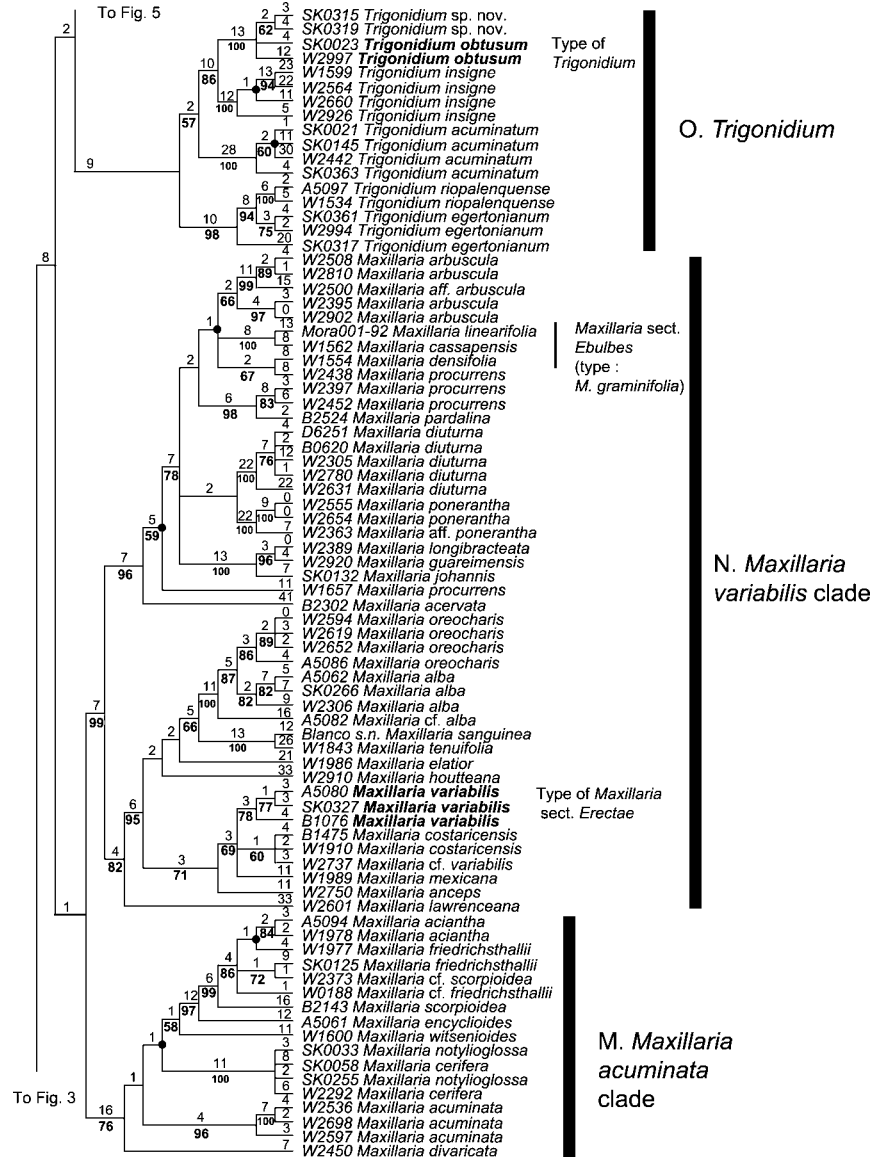


Fig. 4.

and several new species are discovered each year, especially in the Peruvian Andes (E. Christenson, BRIT, personal communication). Nevertheless, we are confident that our taxon sampling of ca. 354 species includes representatives of all major morphological groups of core Maxillariinae and that the resulting cladograms adequately reflect relationships among them.

**DNA extraction, amplification, and sequencing**—DNA was extracted mostly from fresh leaves, flowers, and silica-gel-dried leaves and flowers, using a modified version of the 2× CTAB procedure of Doyle and Doyle (1987) with exclusion of beta-mercaptoethanol and inclusion of five units of proteinase K to improve yield and quality of DNA. Nearly all material was extracted from fresh or silica-dried tissue; extractions from herbarium specimens were rarely successful. Precipitated DNA pellets were resuspended in 200 µL of Tris-EDTA (TE) buffer and then cleaned using Qiaquick columns (Qiagen, Valencia, California, USA) with 2–3 washes with Buffer PE to remove potent PCR inhibitors present in many samples.

All amplifications used Sigma Jumpstart *Taq* polymerase and reagents (Sigma-Aldrich, St. Louis, Missouri, USA) in 25-µL reactions with 2.5 mM MgCl<sub>2</sub>. Amplification and sequencing of nrITS utilized the primers 17SE and

26SE of Sun et al. (1994) and a PCR program consisting of an initial 10 min bake at 99°C, followed by individual addition of 0.5 unit of *Taq* polymerase; 30 cycles of 94°C denaturation for 45 s, 60°C annealing for 45 s, and 72°C extension for 1 min; and a final extension of 72°C for 3 min. To minimize the effects of secondary structure during nrITS amplification, 7 µL of 5 M betaine were added to the PCR mix. The *matK*+*trnK* intron region was usually amplified as a single piece, using the primers 19F (Goldman et al., 2001) and *trnK*2R (Johnson and Soltis, 1994); primers 308F (TATCAGAAGGTTTTG-SA) and 1100F (CATTTCATAATAACTCTGAC) were used as additional internal sequencing primers. Some species were amplified using the primers 56F (ACTTCTCTATCCGCTACTCCTT) and 1520R (CGGATAATGTC-CAAATACCAAATA) that yielded a shorter but nearly complete portion of *matK*. PCR conditions consisted of a hot start with 2 min of initial denaturation at 94°C; followed by 33 cycles of 94°C denaturation for 45 s, 60°C annealing for 45 s, and 72°C extension for 2 min 45 s; and a final extension at 72°C for 3 min. The plastid *trnL-F* region has been widely used in orchid phylogenetics, but in preliminary surveys within Maxillariinae, many species yielded several-banded PCR products suggestive of multiple copies and possible pseudogenes. We therefore abandoned use of this region and substituted the *atpB-rbcL* spacer region. The *atpB-rbcL* intergenic spacer was amplified with the primers

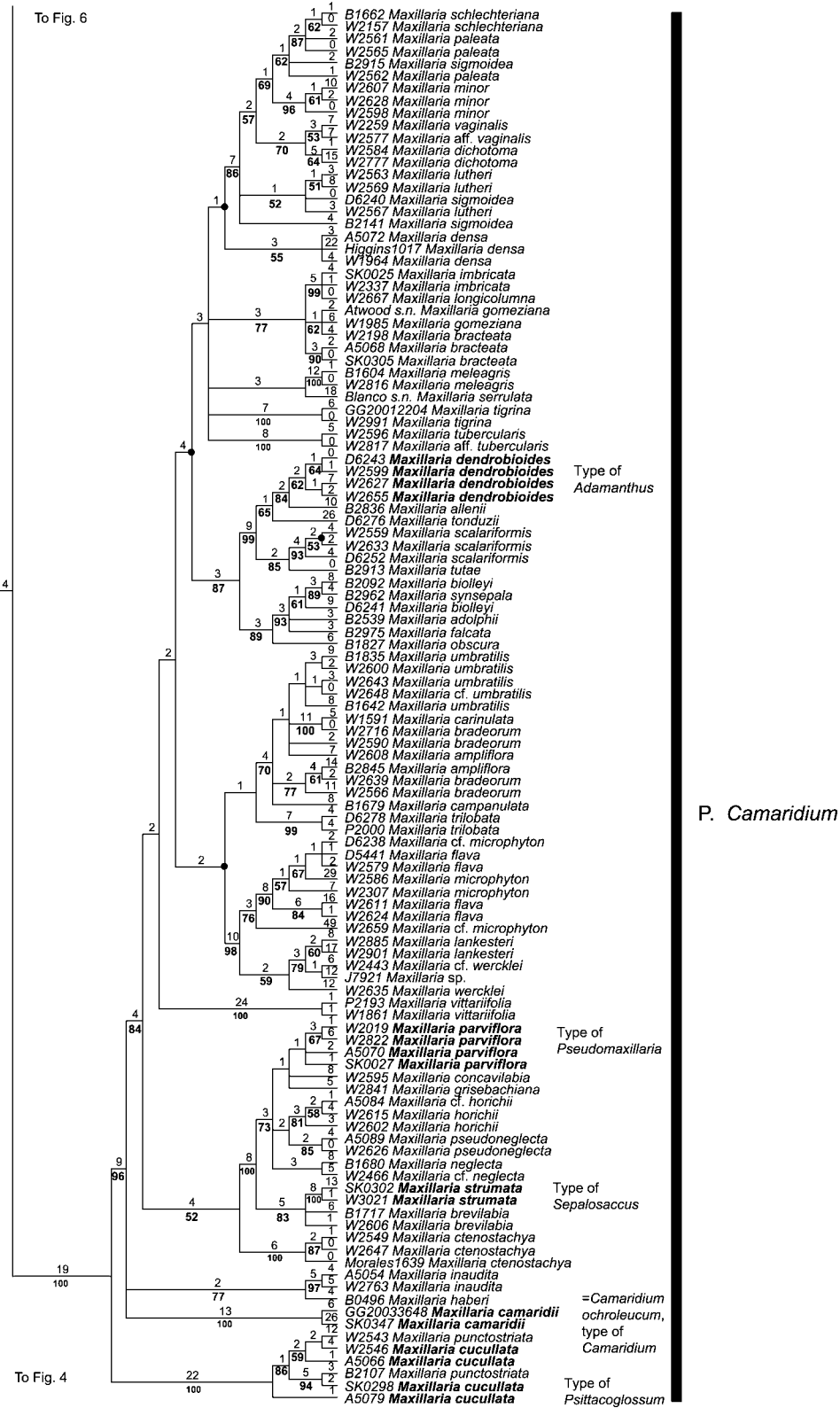


Fig. 5.

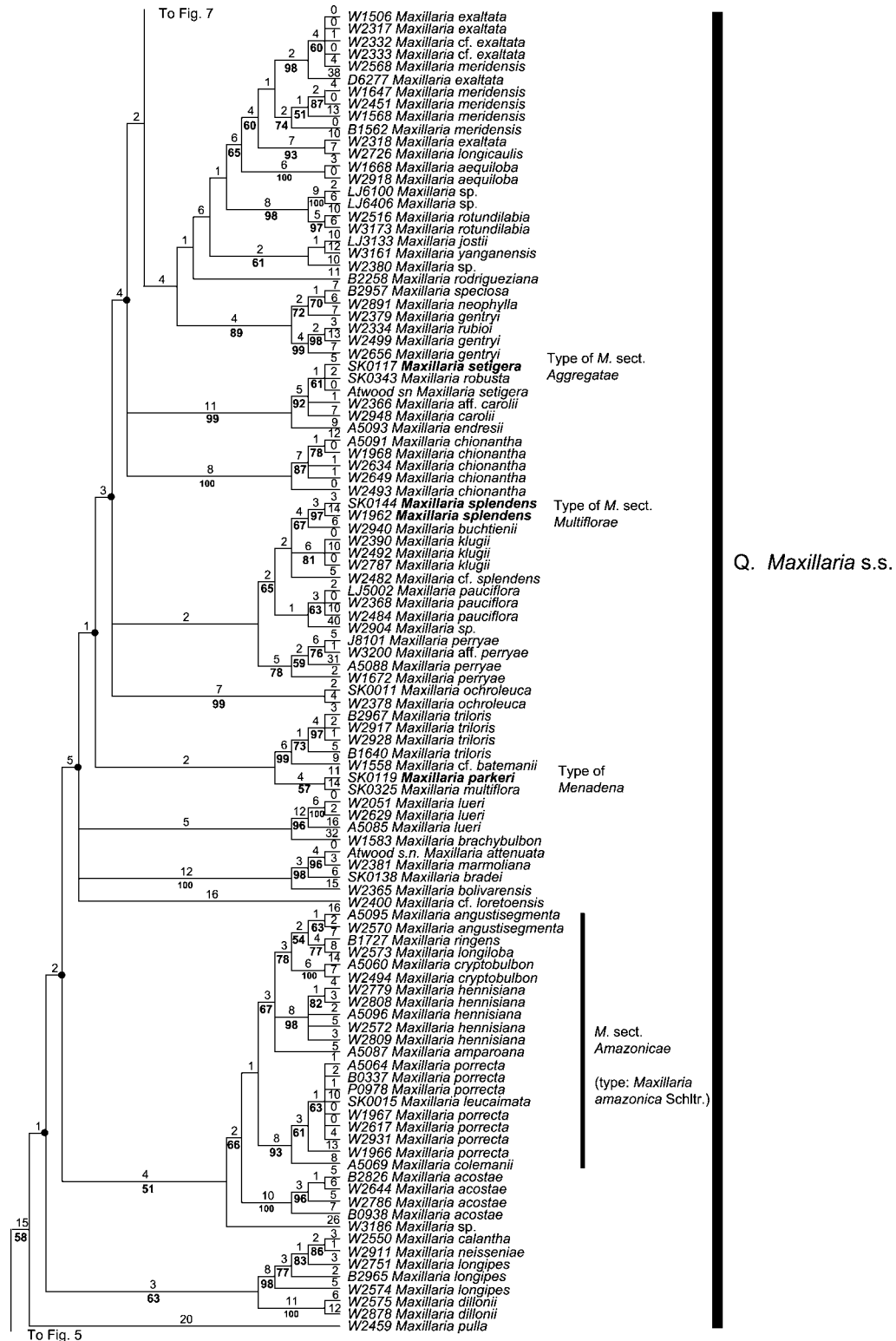


Fig. 6.

(designed by MW) Max F (CTAGGTTTTGTCTTCAAGTGTA) and Max R (GTCAATTTGTAATCTTTAACACCAGC). PCR conditions consisted of an initial 10 min bake at 99°C followed by individual addition of *Taq* polymerase hot start with 2 min of initial denaturation at 94°C; followed by 33

cycles of 94°C denaturation for 45 s, 60°C annealing for 45 s, and 72°C for 2 min; and a final extension at 72°C for 3 min. Although the RNA polymerase beta subunit 1 (*rpoC1*) intron has been used in a few phylogenetic analyses of angiosperms (e.g., Plunkett et al., 2004), we are unaware of any studies using



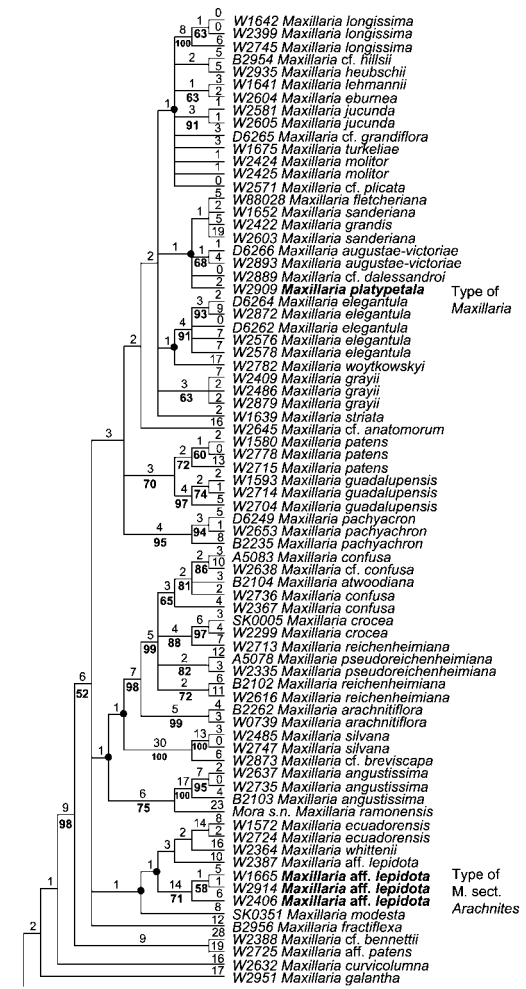


Fig. 7.

the nearly complete gene (2818 bp in *Phalaenopsis* chloroplast genome, GenBank AY916449). Based on the *Phalaenopsis* sequence and related monocots, we designed primers to amplify a ca. 2600-bp portion of *rpoC1* from Maxillarieae. Amplimers were 1F (ATGAATCAGAATTCTATCTATG) and 2604R (TCCACCGAAGCCACAAAGGACTAT). Internal sequencing primers used were 560F (AGGAGGAACATGAAGCTCAG), 700R (TGTGAAATCTTGAGTAGTCTAC), 1887F (ACTCTGCTTGG-TAAACGGGTGCAT), 1910R (ATCGACCCGTTACCAAGCAGAGT), and 1137F (TTGAGCCGATGAGAGGAAACCTT). This region was amplified and sequenced for 84 selected species. For some species, the region was amplified in two overlapping pieces using the primer combinations 1F +1910R and 1137F + 2604R. Amplification protocols were identical to those used for *matK*. Purification of PCR products was performed with Microclean (Gel Co., San Francisco, California, USA) following the manufacturer's protocols. PCR products were sequenced in both directions, using the BigDye Terminator reagents on an ABI 377 or 3130 automated sequencer following manufacturer's protocols (Applied Biosystems, Foster City, California, USA). Electropherograms were edited and assembled using the program Sequencher 4.6 (Genecodes Inc., Ann Arbor, Michigan, USA), and the resulting sequences were aligned manually using the program Se-Al (Rambaut, 1996) following the guidelines of Kelchner (2000). All sequences were deposited in GenBank (see Appendix 1), and aligned matrices were deposited in TreeBase.

**Data analysis**—Analyses were performed using PAUP\* version 4.0b10 (Swofford, 2003) with Fitch parsimony (unordered characters with equal weights; Fitch, 1971), ACCTRAN optimization, and gaps treated as missing

data. Heuristic searches consisted of 1000 random taxon addition replicates of subtree-pruning-regrafting (SPR) and "keeping multiple trees" (MULTREES) with the number of trees limited to 10 per replicate to minimize extensive swapping on islands with many suboptimal trees. The resulting trees were then used as starting trees for tree-bisection-reconnection swapping (TBR, because this algorithm is sometimes able to reach shorter trees than SPR) with an upper limit of 10000 trees. Searches for shortest trees were also performed using parsimony ratchet as implemented in the program PAUPRat (Sikes and Lewis, 2001). Internal support was evaluated using 1000 bootstrap replicates using heuristic searches with random taxon-addition and the SPR algorithm; five trees were saved per replicate. Individual shortest trees, strict consensus trees, and bootstrap (BS) consensus trees were examined visually to assess congruence among data sets. Bootstrap support is categorized as weak (50–75%), moderate (76–90%), and strong (91–100%). Because of the large size of the data set, the incongruence length difference (ILD; Farris et al., 1995) and Bayesian and maximum likelihood analyses were not performed.

Two accessions were identified as natural hybrids based on their conflicting placements in shortest nrITS vs. plastid trees and on their intermediate morphology: *Blanco 2986* [putative *M. porrecta* Lindl. × *M. exaltata* (Kraenzl.) C. Schweinf.] and *Blanco 1661* [putative *M. strumata* (Endres & Rchb.f) Ames & Correll × *M. pseudoneglecta* J.T. Atwood]. Both were excluded from the combined analyses. No other cases of hard incongruence between data sets were detected. Data sets were analyzed individually and as a combined ITS/*matK/atpB-rbcL* matrix. A smaller combined four-region matrix (88 selected species) included *rpoC1* data.

RESULTS

General features of the DNA regions and tree statistics from separate and combined analyses are presented in Table 1. The number of species for each matrix is not equal because of amplification or sequencing failures in various species. Because of space limitations, trees from individual analyses are not presented.

**Analysis of nrITS**—Although nrITS is the shortest of the four regions utilized (833 aligned base pairs), it provided the greatest percentage of potentially parsimony-informative characters and the most resolution and the greatest number of clades with BS support ≥70% (N = 180; Table 1). All of the major clades found in the combined analyses (see Discussion) are monophyletic with BS ≥ 50% in the nrITS analysis except for *Trigonidium*, which forms three clades in the unresolved spine of the bootstrap consensus.

**Analysis of matK + trnK**—For *matK*, eight species repeatedly gave messy sequences, suggesting multiple copies or pseudogenes; other species sequenced cleanly but contained indels not in multiples of three, producing reading frameshifts. For this reason, we suspect that *matK* may be a pseudogene in at least some Maxillariinae. *Anthosiphon roseans* repeatedly produced messy sequences from several accessions. Because this monotypic genus is of special taxonomic interest, we cloned the *matK* PCR products and sequenced five of the longest clones. The five clones contained various numbers of indels, resulting in products ranging from ca. 1200 to 1850 bp. The longest (apparently intact) copy was selected for inclusion in the matrix.

Although the *matK + trnK* region yielded slightly more potentially parsimony-informative characters than nrITS and with slightly higher CI and similar RI values, the BS consensus is less resolved and has 50% fewer clades with support ≥70% (Table 1). Nevertheless, the supported clades are congruent with those found in the nrITS analysis.

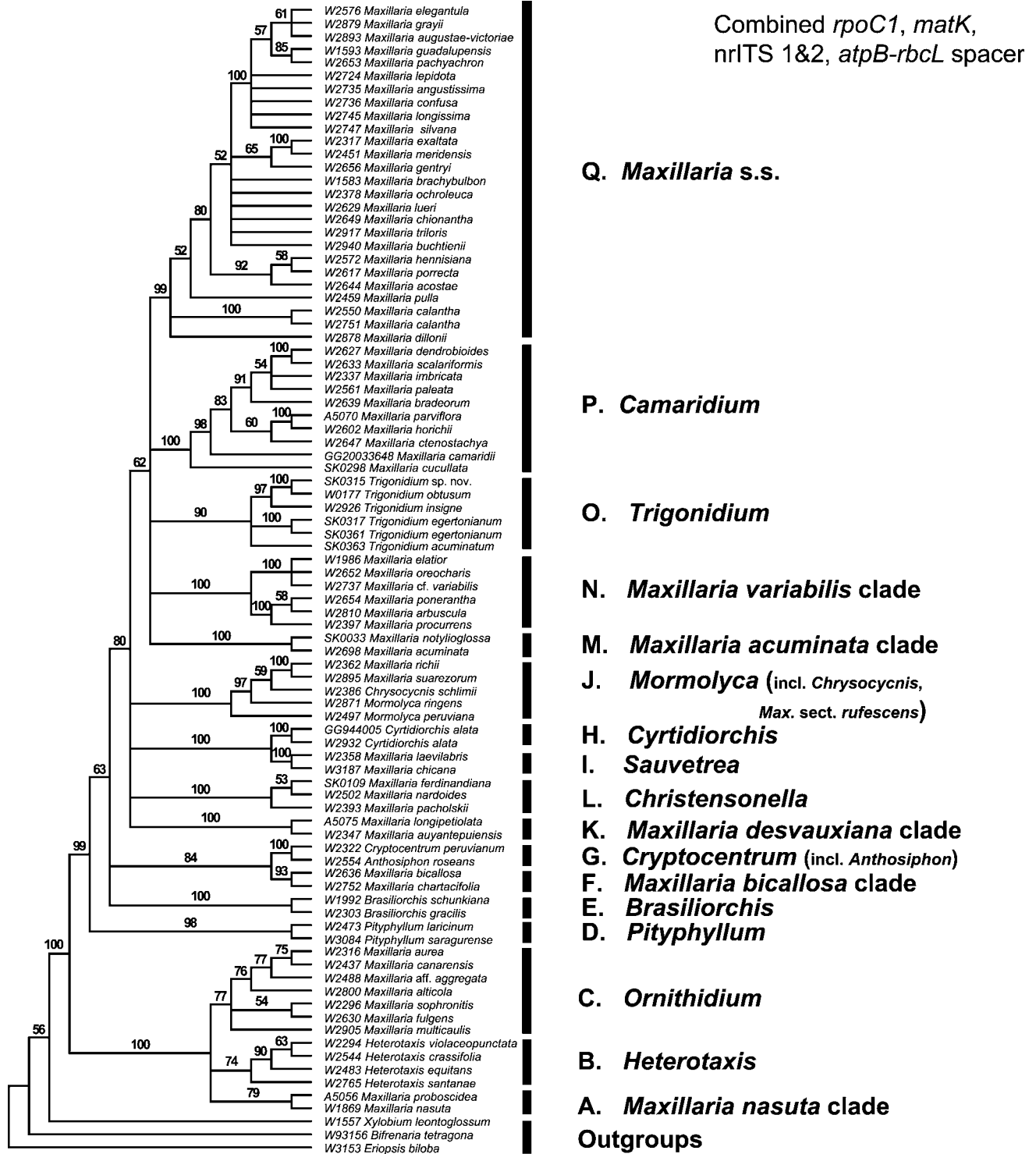


Fig. 8. Bootstrap consensus from a combined analysis of nrITS, *matK*+*trnK*, *atpB-rbcL* spacer, and *rpoC1* sequence data for Maxillariinae. Values above branches are bootstrap percentages  $\geq 50\%$ . Lettered clades correspond to those mentioned in Results/Discussion.

**Analysis of *atpB-rbcL* intergenic spacer**—The *atpB-rbcL* intergenic spacer proved difficult to sequence cleanly in some species because of multiple homopolymer A/T regions that caused stutter; consequently, the matrix includes only 580 individuals. The length of this region also varies greatly,

ranging from 449-1090 bp among species sampled, with many large indels, repeats, and some probable stem-loop regions. These features make this region very challenging to align. The total length of the aligned matrix was 2031 bp, but we judged almost half of it (1087 bp) to be unalignable; these regions

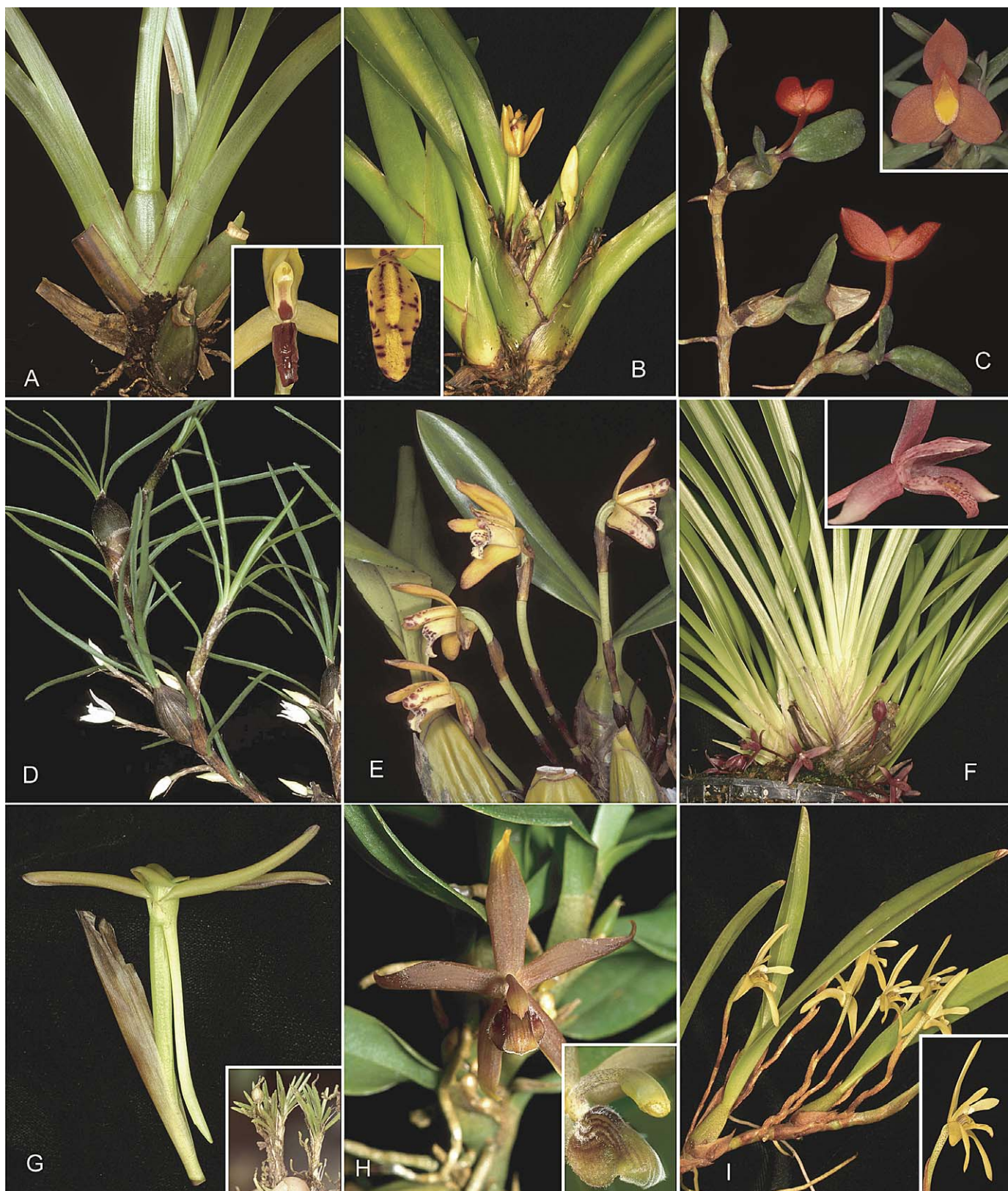


Fig. 9. Representatives of major clades of core Maxillariinae; letters correspond to clades in Figs. 1, 2, and 8. (A) *Maxillaria cymbidioides* Dodson, J.T. Atwood & Carnevali, *Whitten 1869* (inset: flower with labellum deflexed, showing callus); (B) *Heterotaxis sessilis* (Sw.) F. Barros [= *Maxillaria crassifolia* (Lindl.) Rchb.f.], *Whitten 2455* (inset: labellum showing callus); (C) *Maxillaria sophronitis* (Rchb.f.) Garay, *Whitten 2930* (inset: flower in frontal view); (D) *Pityphyllum larinum* (Kraenzl.) Schltr., *Whitten 1653*; (E) *Brasiliorchis phoicanthera* (Barb. Rodr.) R. Singer, S. Koehler & Carnevali, *Whitten 2304*;

were excluded from the analyses. This spacer region might be fully alignable within genera and species groups, but it turned out to be a less than optimal choice for subtribal level analyses. Nevertheless, the included aligned regions (944 bp) provided useful levels of variation congruent with the other data sets. The BS analysis yielded only 77 clades with BS support  $\geq 70\%$  and CI and RI values lower than for either the nrITS or *matK* analyses.

**Analysis of combined nrITS/matK/atpB-rbcL**—Figures 1–7 present one randomly chosen most parsimonious tree from the combined three-region analysis. Values above branches are Fitch branch lengths; values below the line are BS percentages  $\geq 50\%$ . Nodes that collapse in the strict consensus of all most parsimonious trees are marked with a black circle. Bifrenariinae sensu Dressler (1993) (*Bifrenaria-Hylaeorchis*) is highly supported (99% BS) and is basal to Lycastinae sensu Dressler (88% BS; *Neomoorea-Xylobium*), which is sister to core Maxillariinae (BS 99%). The spine of the tree within core Maxillariinae is poorly supported, but numerous clades (clades A–Q) often corresponding to recognized generic or subgeneric taxa received weak to strong BS support. The currently recognized minor genera of core Maxillariinae (*Anthosiphon*, *Chrysocycnis*, *Cyrtidiorchis*, *Mormolyca*, *Pityphyllum*, and *Trigonidium*) and the recent segregate genera (*Adamanthus*, *Brasiliorchis*, *Christensonella*, *Laricorchis*, and *Sauvetrea*) are embedded within a polyphyletic *Maxillaria* s.l. with moderate to high BS support.

**Nonmonophyly of species**—For species that include several samples per species, the individuals do not always form clades in the representative shortest tree (Figs. 1–7). Lineage sorting and introgression are possible explanations for such paraphyly, but in cases where branch lengths and support are substantial (e.g., *Christensonella*, clade L; *M. acutifolia* Lindl., clade J), this probably reflects poor alpha-taxonomy and unrecognized cryptic species. In other cases [e.g., *M. sigmoidea* (C. Schweinf.) Ames & Correll/*M. lutheri* J.T. Atwood, clade P; *M. flava* Ames, F. T. Hubb. & C. Schweinf./*M. microphyton* Schltr., clade P], we suspect a combination of short branch lengths and uncertain morphological species boundaries, plus possible ambiguous determination of specimens. For morphologically unambiguous species, the multiple samples nearly always formed clades, often revealing geographic structure.

**Analysis of rpoC1**—The *rpoC1* gene is the least variable of the regions utilized. The primers we used amplified about 85% of the gene (portions of the 5' and 3' ends were lacking, but an intron was included). The sequenced region ranged from 2365 to 2474 bp. Because of the length and consequent cost per individual, this gene was sequenced for only 88 accessions selected from all major clades revealed in the combined *matK*/ITS/*atpB-rbcL* analysis. Three species produced messy *rpoC1* sequences and are represented by missing data in the combined four-region analysis: *Cyrtidiorchis alata* (Lindl.) Rauschert (Whitten 2932 and Gerlach 944005), *Maxillaria calantha* Schltr. (Whitten 2550), and *M. chicana* Dodson (Whitten

3187). For the remaining 84 samples, the aligned matrix is 2843 bp with 387 bp of exon 1, 787 bp of intron, and 1319 bp of exon 2. The intron ranged in length from 729 to 769 bp. The matrix was easily aligned and contained few indels, ranging from 1 to 76 bp, mostly in the intron. Although branch lengths are short and BS support is low in the *rpoC1* analysis, the shortest trees (not shown) recovered the same clades and tree structure as the combined four-region analysis (Fig. 8).

**Analysis of combined rpoC1/nrITS/matK/atpB-rbcL**—The addition of data from the relatively conserved *rpoC1* gene in the limited 88-accession analysis results in increased resolution and support in the spine of the tree and in higher BS for most clades (Fig. 8). Clades A, B, and C (*M. nasuta* clade, *Heterotaxis*, and *Ornithidium*) still receive low to moderate BS, but the three are united in a basal clade with 100% BS. *Pityphyllum* (clade D) is successively sister to the remaining taxa; clades E–Q all receive BS greater than 90%. The *M. bicallosa* clade (F) is moderately supported as sister to *Cryptocentrum* + *Anthosiphon* (clade G). Clades H–L form a polytomy weakly sister to clades M–Q. *Trigonidium* is supported as monophyletic but with only 90% BS. Both *Camaridium* (clade P) and *Maxillaria* s.s. (clade Q) are strongly supported and together contain the majority of species in the subtribe.

## DISCUSSION

In the strict consensus of all shortest trees of all analyses, the currently recognized minor genera of core Maxillariinae (*Anthosiphon*, *Chrysocycnis*, *Cyrtidiorchis*, *Mormolyca*, *Pityphyllum*, and *Trigonidium*; Govaerts et al., 2005) and the five recent segregate genera (*Adamanthus*, *Brasiliorchis*, *Christensonella*, *Laricorchis*, and *Sauvetrea*) are embedded within a polyphyletic *Maxillaria* with moderate to high BS. In the following paragraphs, we discuss the morphological characteristics of well-supported clades that we feel warrant generic recognition. Some of these clades correspond to currently recognized or recently described genera; others represent novel segregates that are in the process of formal taxonomic circumscription. In the heading for each clade, two BS values are given; the first is that from the large three-region analysis, and the second is from the smaller four-region analysis. For simplicity throughout the discussion, figures, and appendix, we generally use the traditional species names in *Maxillaria* for those groups that are currently regarded as part of *Maxillaria* s.l. For each clade, we note the type of fruit dehiscence (apical vs. lateral) and the presence or absence of conspicuous perianth fibers (Fig. 10R).

### Clade descriptions—

**Clades A+B+C**—(100/100% BS) Fig. 1

This highly supported clade includes three morphologically distinctive subclades (the *M. nasuta* Rchb.f. clade, *Heterotaxis*, and *Ornithidium*) that receive moderate BS support; two of

←  
(F) *Maxillaria bicallosa* (Rchb.f.) Garay, Whitten 3339 (inset: flower in lateral view); (G) *Cryptocentrum latifolium* Schltr. flower showing labellar spur, Whitten 2733 [inset: plant habit of *C. peruvianum* (Cogn.) C. Schweinf., Whitten 2322]; (H) *Cyrtidiorchis frontinoensis* (Garay) Rauschert, Gerlach 94–4005 (inset: column and pubescent labellum); (I) *Maxillaria* aff. *alpestris* Lindl., Whitten 3113 (inset: flower, lateral view).

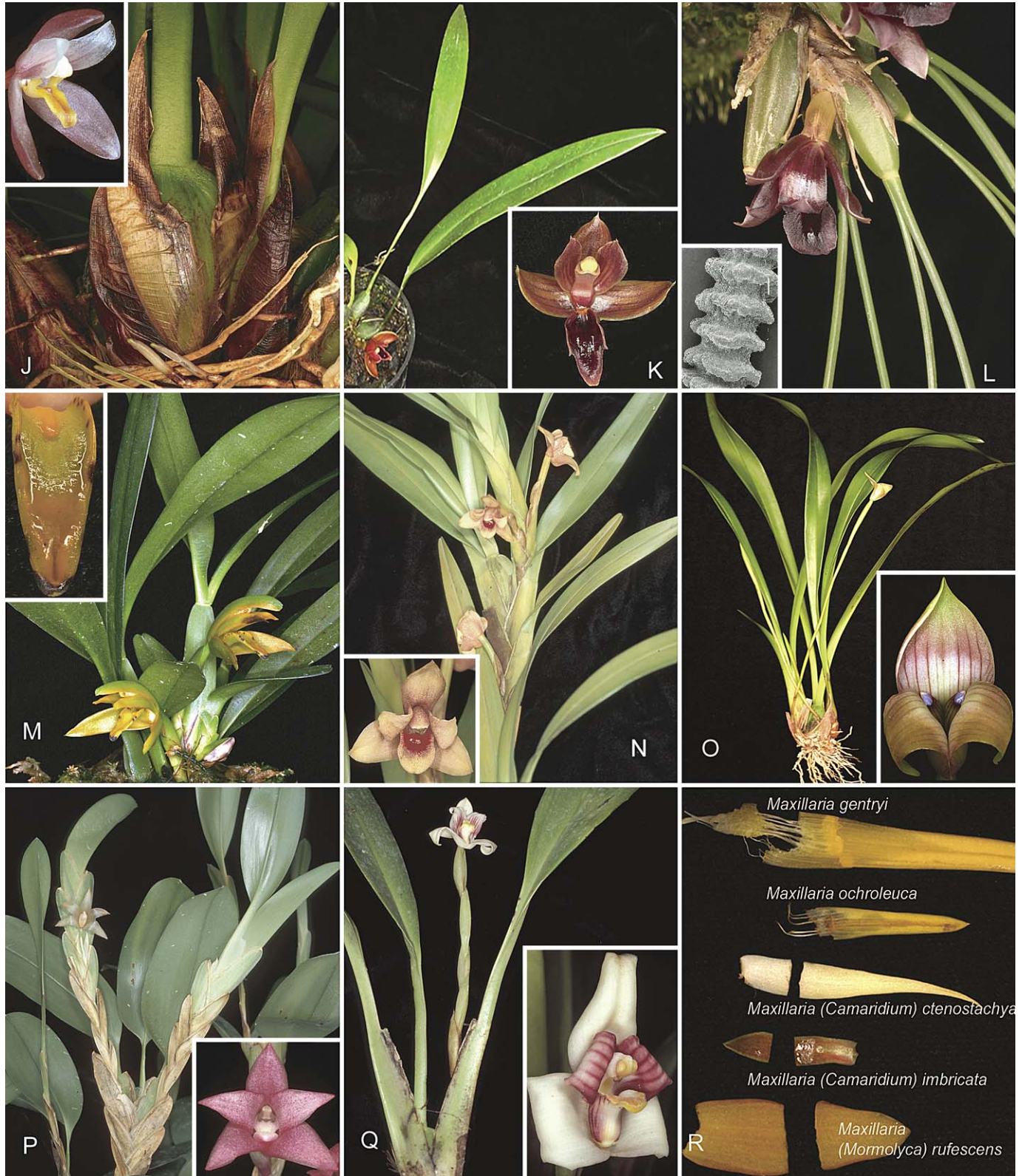


Fig. 10. Representatives of major clades of core Maxillariinae; letters correspond to clades in Figs. 2–8. (J) *Maxillaria richii* Dodson, Whitten 1975 (inset: flower, lateral view); (K) *Maxillaria longipetiolata* Ames & C. Schweinf., Whitten 2360 (inset: flower with labellum deflexed); (L) *Maxillaria acicularis* Herb. ex Lindl., Whitten 1994 (inset: SEM of root showing annular thickenings of velamen; scale bar = 100  $\mu$ m); (M) *Maxillaria scorpioidea* Kraenzl., Whitten 3335 (inset: labellum showing resinous secretion); (N) *Maxillaria procurrens* Lindl., Whitten 2438 (inset: flower showing shiny, dry callus); (O) *Trigonidium egertonianum* Bateman in Lindl., Whitten 3341 (inset: flower in frontal view showing shiny blue petal apices); (P) *Maxillaria paleata* (Rchb.f.)

TABLE 1. Features of DNA data sets used in this study in relation to one of the most parsimonious trees from each analysis (percentages calculated relative to aligned length).

DNA region	No. of species	Aligned length (bases)	No. of variable sites	No. of potentially parsimony-informative sites	Fitch tree length (steps)	No. of shortest trees	No. of nodes $\geq 70\%$ bootstrap (ingroup)	CI	RI	Transition/transversion ratio
<i>matK+trnK</i>	611	1852	795	476	2228	10 000+	86	0.46	0.84	0.68 (571/841)
nrITS 1&2	619	833	525	416	2691	10 000+	180	0.34	0.88	1.86 (1049/563)
18S	619	70	21	7	39	—	—	0.64	0.07	2.00 (8/4)
ITS1	619	260	197	167	1169	—	—	0.31	0.87	1.77 (462/260)
5.8S	619	164	39	28	112	—	—	0.43	0.93	3.60 (54/15)
ITS2	619	277	227	193	1263	—	—	0.34	0.90	1.96 (421/215)
26S	619	62	41	21	108	—	—	0.53	0.87	1.57 (44/28)
<i>atpB-rbcL</i> Spacer	580	944 (1087 excluded)	465	380	2579	10 000+	77	0.32	0.77	0.34 (682/1973)
Combined <i>matK</i> , ITS, <i>atpB-rbcL</i>	611	3629	1890	1267	7959	184	285	0.35	0.83	0.78 (2793/3579)
<i>rpoC1</i>	84	2843	350	149	565	10 000+	—	0.69	0.76	1.09 (176/162)
Exons	84	1704	170	63	245	—	—	0.74	0.84	1.29 (55/51)
Intron	84	787	180	86	326	—	—	0.50	0.67	0.83 (80/96)
Combined <i>matK</i> , ITS, <i>atpB-rbcL</i> , <i>rpoC1</i>	88	6127	1374	654	3178	216	—	0.56	0.66	0.93 (1289/1379)

these subclades have previously been recognized as genera. A detailed morphological and molecular analysis of this clade was performed by Ojeda (2003) and Ojeda et al. (2003) with recircumscription and addition of new species and combinations (Ojeda et al., 2005). Pseudobulbs are unifoliate. Pseudobulbless species with pseudomonopodial growth (presumably neotenic) also occur. The flowers in all three subclades provide some kind of floral reward: trichomes, resin-like secretions, or nectar. A putative synapomorphy for this clade is a greatly reduced column foot.

*Clade A*—(84/79% BS); *Maxillaria nasuta* clade, Figs. 1, 9; 3 spp.

Vegetatively, the three species in this clade (*M. nasuta*, *M. cymbidioides* Dodson, J.T. Atwood & Carnevali, *M. proboscidea* Rchb.f.) are similar to *Heterotaxis* (see next section) but have pseudobulbs with smooth, varnished surfaces rather than the minutely wrinkled, roughened surfaces of pseudobulbs of *Heterotaxis* and *Ornithidium*. Additional putative synapomorphies (within clade A+B+C) include relatively long inflorescences (ca. twice the length of pseudobulbs), fibrous sepals and petals, and papillae on the dorsal surface of the column. The labellar callus is ligulate and shiny and secretes an abundant reddish, sticky substance (probably resin) but lacks the raised pad of glandular trichomes present in *Heterotaxis* (Clade B). The fruits have lateral dehiscence; perianth fibers are present. *Maxillaria nasuta* is widely distributed in Central and South America south to Bolivia; the other two species are restricted to Ecuador, Colombia, and Venezuela.

*Clade B*—(76/74% BS) *Heterotaxis* Lindl., Figs. 1, 9; 11+ spp.; including *Dicrypta* Lindl., *Marsupiararia* Hoehne, *Pentulops* Raf., *Maxillaria* subgen. *Heterotaxis* (Lindl.) Brieger, *M. sect. Heterotaxis* (Lindl.) Brieger, *M. sect. Iridifoliae* Pfitz. Type: *Heterotaxis crassifolia* Lindl. [= *Heterotaxis sessilis* (Sw.) F. Barros]

*Heterotaxis* comprises about 11, primarily epiphytic species

distributed from southern Florida (USA) and the Greater Antilles to Brazil, with most of the species occurring in southern Central America and northern South America (Ojeda et al., 2005). Several inflorescences are produced sequentially from each leaf axil. Morphological cladistic analyses by Ojeda et al. (2003) of *Heterotaxis*, *Ornithidium*, and the *M. nasuta* Rchb.f. clade revealed three morphological synapomorphies for *Heterotaxis*: (1) the floral pedicel is wider than the other internodes of the peduncle; (2) the junction of the column and the pedicel is slanted at an angle of 45°; and (3) the sepals and petals have a subapical mucron. The flowers are yellow to orange-red, with the labellum in some species being mostly purple (or rarely pinkish) and with calli varying in size and texture; in most species the labellum is yellow or orange with purple or reddish spots or blotches. The labellum typically bears a linear pad of easily detached, glandular trichomes that secrete an unidentified reward (Singer et al., 2006); these trichomes are collected by meliponine bees. The fruits invariably have lateral dehiscence.

The distinctly fleshy flowers usually possess fiber bundles in the sepals and petals, a character shared with the *M. nasuta* clade (A) but absent in *Ornithidium* (clade C). *Heterotaxis* is characterized by short rhizomes and laterally compressed, oblong, minutely wrinkled, unifoliate pseudobulbs subtended by various leaf-bearing sheaths. Exceptions are *Maxillaria equitans* Schltr. and *M. valenzuelana* (A. Rich.) Nash that exhibit pseudomonopodial growth without pseudobulbs. Based on these characters, Hoehne (1947) created the genus *Marsupiararia* for these two species. Brieger and Illg (1972) included *M. nasuta* and *M. proboscidea* (as synonyms of each other) in the *Heterotaxis* group, but these two species form their own separate clade along with *M. cymbidioides* (see clade A). Brieger and Illg excluded *M. equitans* and *M. valenzuelana* from this group. The generic concept *Pentulops* Raf. (based on *M. discolor*) is also embedded within the *Heterotaxis* clade. Barros (2002) reinstated *Heterotaxis*, a decision supported and amplified by Ojeda et al. (2005), but the World Checklist of

←  
Ames & Correll, Whitten 2561 (inset: flower, frontal view); (Q) *Maxillaria irrorata* Rchb.f., Whitten 2571 (inset: flower, frontal view). (R) Sepals of various species of *Maxillaria*, torn to show presence/absence of fiber bundles. The top two (*M. gentryi* Dodson and *M. ochroleuca* Lodd. ex Lindl.) have fiber bundles and belong in *Maxillaria* s.s. (clade Q). The third and fourth (*M. ctenostachya* Rchb.f. and *M. imbricata* Barb.Rodr.) lack fiber bundles and belong in *Camaridium* (clade P). The fifth (*M. rufescens*) also lacks fiber bundles and belongs in *Mormolyca* (clade J).

Orchidaceae (Govaerts et al., 2005) still includes *Heterotaxis* as a synonym of *Maxillaria*.

*Clade C*—(57/77% BS) *Ornithidium* Salisb., Figs. 1, 9; 35+ spp.; including *Laricorchis* Szlach., *Neo-urbania* Fawc. & Rendle, *Siagonanthus* Poepp. & Endl., *Maxillaria* sect. *Ornithidium* (Salisb.) Christenson, *M.* sect. *Reflexae* Christenson, *M.* sect. *Siagonanthus* (Poepp. & Endl.) Christenson. Type: *Ornithidium coccineum* (Jacq.) Salisb. ex R. Br.

Species in this clade are widely distributed throughout the neotropics. Plants are characterized by the presence of either elongate rhizomes between erect to pendent growths with or without pseudobulbs, or erect, leafy, monopodial canes. The flowers are fleshy, often globose, tan, green, orange, yellow, red, pink, or mauve, lack perianth fibers, and usually produce nectar at the base of the labellum. Most brightly colored species are probably hummingbird-pollinated; those with more open, greenish flowers are probably bee- or wasp-pollinated. *Maxillaria haemathodes* (Ruiz & Pav.) Garay is remarkable for having deep royal blue flowers. Braga (1977) documented pollination of *M. pendens* Pabst by nectar-collecting wasps with attachment of the disclike viscidia to their compound eyes.

The surface of the pseudobulbs and stems of most species have a characteristic shiny, minutely cracked texture reminiscent of old varnish and are usually olive-green in life. Roots are usually orangish to brown. Some species [e.g., *M. multicaulis* (Poepp. & Endl.) C. Schweinf., *M. pendens* Pabst, *M. rigida* Barb. Rodr., *M. miniata* (Lindl.) L.O. Williams] typically produce caespitose juvenile plants that produce elongate rhizome segments as adults (Christenson, 2002a). This juvenile character, often missing in herbarium specimens, usually requires observation of populations in the field and may be more common within the clade. In contrast to the fruits of the previous two clades, the fruits of *Ornithidium* have apical dehiscence; perianth fibers are absent.

*Maxillaria multicaulis* (Poepp. & Endl.) C. Schweinf. and *M. coccinea* (Jacq.) L.O. Williams, the respective types of *Siagonanthus* and *Ornithidium*, are sister species in the combined analysis. The generic types of *Neo-urbania* [*Maxillaria adendrobium* (Rchb.f.) Dressler] and *Laricorchis* [*Maxillaria aggregata* (Kunth) Lindl.] are firmly nested within the *Ornithidium* clade. Christenson (2002a, b) included *Pleuranthium* as a generic synonym of *Maxillaria* s.l. (with *M. adendrobium* cited as the type), but this genus is typified by *Epidendrum dendrobii* Rchb.f., a true *Epidendrum* (Hágsater, 2005).

*Clade D*—(59/98% BS) *Pityphyllum* Schltr., Figs. 1, 9; 7 spp. Lectotype (designated by Sweet, 1972: 205): *Pityphyllum antioquiense* Schltr.

All species of *Pityphyllum* occur in the Andes from Venezuela to Peru; these inconspicuous epiphytes with diminutive flowers are rarely collected. Most *Pityphyllum* species produce small, bushy, pendent plants with needle-like or very narrow conduplicate leaves often clustered at the apex of the pseudobulb with a characteristic brown, scarious tunica (a leaf sheath fused to the pseudobulb and lacking a blade) tightly covering the ovoid to fusiform pseudobulb (Sweet, 1972; Whitten et al., 2006). In most species, the leaf sheaths (including the tunicae) each have a pair of ligules at the apex (Whitten et al., 2006); in *P. saragurensis* (Dodson) Whitten, these ligules form prominent recurved hooks. Flowers are

small, white or yellow/orange, and lack a column foot. The pollinarium consists of four small clavate pollinia attached to a delicate discoid or narrowly triangular viscidium. The tiny, narrow flowers of most species and the viscidium shape suggest attachment of pollinaria to the proboscis of small insects (rather than attachment to the scutellum), but no pollination records exist. The genus was recently broadened to include *Maxillaria huancabambae* (Kraenzl.) C. Schweinf. and *M. saragurensis* Dodson (Whitten et al., 2006) on the basis of our analyses. *Pityphyllum huancabambae* (Kraenzl.) Whitten is distinctive because of its broad conduplicate leaves and globose, bright-yellow flowers, but it also possesses a scarious tunica with small ligules. The bright-yellow flowers of this species are similar to those of many species of *Ornithidium* (clade C) and suggest hummingbird pollination. We are uncertain whether flowers of this genus secrete nectar. Fruit dehiscence is apical; perianth fibers are absent.

*Clade E*—(100/100% BS) *Brasiliorchis* R. Singer, S. Koehler & Carnevali, Figs. 2, 9; 13 spp.; *Maxillaria* sect. *Repentes* Pfitz. Type: *B. picta* (Hooker) R. Singer, S. Koehler & Carnevali

Most species of this clade are endemic to the Atlantic rain forest biome in southeastern Brazil; a few species reach northeastern Argentina [*B. chrysantha* (Barb. Rodr.) R. Singer, S. Koehler & Carnevali, *B. picta*]. This group is easily diagnosed by the sulcate to ridged bifoliate pseudobulbs; the campanulate, rewardless flowers; and pollinaria normally devoid of stipes. Most species have tightly aggregated pseudobulbs, but in a few species (*B. chrysantha*, *B. marginata*) they are separated by a conspicuous rhizome covered by scarious bracts. The pseudobulbs are not (or are only mildly) laterally flattened. The flowers are showy and long-lasting (10 d or more), fragrant, and devoid of secretions or multicellular trichomes. The pollinarium lacks a tegular stipe in most species and has a soft, hyaline, semilunar viscidium that readily collapses after pollinarium removal (Singer and Koehler, 2004). The flowers of most species combine cream or yellowish color with purplish dots or spotting, often more intense on the external surface of the sepals. The flowers of the diminutive *B. barbosa* (Loefgr.) R. Singer, S. Koehler & Carnevali and *B. schunkiana* (Campacci & Kautsky) R. Singer, S. Koehler & Carnevali are exceptional within the genus in displaying a dark, shining labellum, similar to those of the *Christensonella* clade (Pabst & Dungs, 1975). Fruit dehiscence is apical; perianth fibers are absent. Singer et al. (2007) include a more detailed characterization of the genus.

*Clade F*—(97/93% BS) *Maxillaria bicallosa* clade, Figs. 2, 9; 3 spp.; *M.* sect. *Polyphyllae* Christenson

This highly supported and easily recognized clade consists of only two described species, *M. bicallosa* (Rchb.f.) Garay and *M. chartacifolia* Ames & C. Schweinf., both from Costa Rica to Peru, and possibly one undescribed species from Colombia [E. Christenson (Botanical Research Institute of Texas) and G. Carnevali, personal communication]. Plants of this clade possess congested rhizomes bearing fan-shaped shoots with five to many (10–20) leaves, devoid of pseudobulbs. The leaves are relatively long, narrow, thin, and sessile. The flowers emerge from between the leaf bases and are pale yellow or spotted to uniformly dark maroon. The labellum is dark maroon, entire or obscurely three-lobed, and bears a small linear callus. In *M. chartacifolia*, the callus is

surrounded by a pad of dense, felt-like, swollen multicellular trichomes that are easily dislodged. These trichomes may represent a floral reward similar to pseudopollen, but their composition is unknown. The flowers usually have a fetid, cheese-like and/or fecal odor, suggesting dung-fly pollination. Fruits are elongate and narrow, with lateral dehiscence; perianth fibers are absent.

*Clade G*—(98/84% BS) *Cryptocentrum* Benth., Figs. 2, 9; 18+ spp.; including *Anthosiphon* Schltr., and *Pittierella* Schltr. Type: *Cryptocentrum jamesonii* Benth. [= *C. lehmannii* (Rchb.f.) Garay]

*Cryptocentrum* has been consistently recognized at the generic level because of its unique autapomorphies within Maxillariinae (Carnevali Fernandez-Concha, 1996). Plants are either monopodial (with distichous or polystichous phyllotaxy, depending on the species) or sympodial. Leaves are conduplicate to subterete; inflorescences are elongate with long peduncles. The flowers are green to tan, star-shaped, nocturnally fragrant, with a spur formed by the backward projecting bases of the lateral sepals and column foot that encloses a labellar spur, which is adaxially fused to the sepaline spur. The fruits apically dehisce; perianth fibers are absent. Species of *Cryptocentrum* are distributed from Costa Rica to Peru.

Garay (1962) created a separate subtribe for this genus (Cryptocentrinae) because of its unusual morphology, but Dressler (1961) and Carnevali (2001) reviewed the morphology of the genus and noted that most features are also found in various species of Maxillariinae. Within Maxillariinae, the presence of a long nectariferous spur and nocturnally fragrant flowers in *Cryptocentrum* are apomorphies probably associated with moth pollination. Some of the smaller species (e.g., *C. standleyi* Ames) have features of twig epiphytism, an extreme adaptation rare in Maxillariinae but more common in Oncidiinae (e.g., *Stellilabium*, *Tolumnia*; Chase et al., 2005). The *Cryptocentrum* clade has long branches relative to other Maxillariinae (Fig. 2), with accelerated rates of sequence divergence. Long branches also occur in Oncidiinae twig epiphytes, suggesting a correlation between adaptations to a stressful, rapid life cycle, accelerated divergence rates, and reduction in chromosome number (Chase et al., 2005). Morphological cladistic analyses (Carnevali Fernandez-Concha, 1996) indicate at least two origins of twig epiphytism from branch epiphytes within the genus. Schlechter created the genus *Pittierella* in 1906 based on *P. calcarata* Schltr., a species that clearly belongs in *Cryptocentrum*. Schlechter himself transferred *P. calcarata* to *Cryptocentrum* in 1914, and our molecular data confirm this generic placement (Fig. 2).

*Anthosiphon roseans* from Panama and Colombia was described by Schlechter in 1920, who correctly concluded that it was closely related to *Cryptocentrum*. It differs from most species of *Cryptocentrum* by the presence of pseudobulbs, a shorter spur, erect (not spreading) white to pinkish perianth parts, a shorter peduncle, and diurnal fragrance production. We are uncertain whether the spur produces nectar. Some authors have challenged the close relationship of *Anthosiphon* and *Cryptocentrum* (Dodson, 1993), but our molecular and morphological data strongly support sister status of these two genera, and we favor the lumping of *Anthosiphon* with *Cryptocentrum* to avoid the recognition of a monotypic genus based mostly on flower color. Hawkes (1953) transferred the sole species to *Cryptocentrum* as *C. roseans* (Schltr.) Hawkes.

*Maxillaria strumata* (Endres & Rchb.f) Ames & Correll (syn. *Sepalosaccus humilis* Schltr.) also has a spurlike structure formed by connate sepals, but the claw of the labellum is free from the column foot and lacks a labellar spur. Dressler (1961) concluded on the basis of morphology that this species is most closely related to *M. neglecta* (Schltr.) L.O. Williams (a member of *Camaridium*, clade P); our molecular data confirm Dressler's hypothesis. Brieger (1977) advocated the union of the four genera with a sepaline spur (*Anthosiphon*, *Cryptocentrum*, *Sepalosaccus*, and *Pseudomaxillaria* Hoehne) into a "generic series Cryptocentra," but our results do not support that classification.

*Clade H*—(65/100% BS) *Cyrtidiorchis* Rauschert, Figs. 2, 9; 5 spp.; *Cyrtidium* Schltr., non Vainio. Lectotype (designated by Ortiz, 1995: 70): *Cyrtidiorchis rhomboglossa* (F. Lehm. & Kraenzl.) Rauschert.

This small Andean genus ranges from Venezuela to Peru. Plants bear basal ovoid 1–2 foliate pseudobulbs and long leafy canes. Garay (1969) reports that plants in the field appear to have continuously growing (monopodial) stems, but these can be traced back to rhizomes with pseudobulbs. The transition from sympodial juvenile plants with pseudobulbs to adults with erect, monopodial shoots also occurs in a number of species in the *Camaridium* and *Ornithidium* clades. The inflorescences are supra-axillary, emerging immediately below the insertion of the next distal leaf, but opposite its axil. Supra-axillary inflorescences are rare in Orchidaceae but may also occur in *Chrysocynis* (clade J); more detailed observations are needed. Flowers are resupinate with flat, open perianth parts, a strongly arched column without a foot, and a vaguely insectlike labellum that is obscurely three-lobed and covered with patches of pilose trichomes. No observations of pollination have been published, but Dodson (1993) hypothesized that the flowers are sexually deceptive. The fruits have lateral dehiscence; perianth fibers are absent based on the few specimens examined.

The genus was first established in 1924 by Schlechter as *Cyrtidium*, an illegitimate homonym of the fungus genus *Cyrtidium* Vainio. Rauschert (1982) coined the new name *Cyrtidiorchis* to remedy the situation. Garay (1969) provided a synopsis of the genus (as *Cyrtidium*). We did not sample *C. rhomboglossa* (the generic lectotype), but all the species of *Cyrtidiorchis* have the same unusual vegetative modifications, and we are confident that they constitute a monophyletic group. *Cyrtidiorchis* is strongly supported (100% BS) as sister to *Sauvetea* (clade I), although the vegetative and floral morphology is very different in both groups. The trigonous ovary is a putative synapomorphy shared by these two clades.

*Clade I*—(100/100% BS) *Sauvetea* Szlach., Figs. 2, 9; ca. 10 spp.; *Maxillaria* sect. *Trigonae* Christenson. Type: *Sauvetea alpestris* (Lindl.) Szlach.

Most species in this predominately Andean clade possess elongate rhizomes with short, acutely triangular, two-ranked, strongly keeled papery bracts exposing the green internodes. The unifoliate, ancipitous pseudobulbs are subtended by similar acute papery bracts; plants of some species (e.g., *M. koehleri* Schltr., *M. laevilabris* Lindl.) are cespitose. The inflorescences are produced from the base of immature pseudobulbs; the scapes are covered with usually overlapping, two-ranked, strongly keeled bracts. Flowers are usually yellowish-green to tan with sepals not spreading widely and petals subparallel to the column. The three-lobed labellum



bears a ligulate callus with a sulcate depression along its length; no obvious reward is present. In most species, the ovary and fruit are strongly trigonous, but ovaries are terete in *M. koehleri* and *M. laevilabris*. *Maxillaria chicana* Dodson is distinctive for its diminutive, cespitose plants with terete leaves, but the inflorescence is clothed with keeled bracts and the fruit is apparently trigonous (Dodson, 1994). Fruit dehiscence in this clade is apical; perianth fibers are absent.

As circumscribed by Szlachetko and Śmiszek (2007), *Sauvetea* is polyphyletic. These authors included *Maxillaria acuminata* Lindl. in *Sauvetea*, but this species is morphologically different and appears firmly nested in a separate clade (M) in our analyses. Among the species that we did not sample but that Szlachetko and Śmiszek included in *Sauvetea*, we believe (based on their general morphology) that *Maxillaria grandimentum* C. Schweinf. actually belongs in *Maxillaria* s.s. (clade Q) and *M. planicola* C. Schweinf. (= *Camaridium latifolium* Schltr.) in *Camaridium* (clade P).

*Clade J*—(65/100% BS) *Mormolyca* Fenzl, Figs. 2, 10; 30+ spp.; including *Chrysocycnis* Linden & Rchb.f., *Cyrtoglottis* Schltr., *Maxillaria* sect. *Rufescens* Christenson. Type: *Mormolyca lineolata* Fenzl [= *M. ringens* (Lindl.) Gentil].

This clade includes a paraphyletic grade of *Mormolyca* species (with sexually deceptive flowers) sister to a clade composed of members of the *Maxillaria rufescens* Lindl. alliance (*M.* section *Rufescens*, with a diversity of floral fragrances, but probably not sexually deceptive), with *Chrysocycnis* (putatively sexually deceptive) nested within. Atwood and Mora de Retana (1999) had already suggested a close relationship between *Mormolyca* and the *Maxillaria rufescens* alliance based on vegetative morphology. Holtzmeier et al. (1998) also detected a close relationship between *Mormolyca ringens* and species of the *Maxillaria rufescens* alliance, based on an analysis of anatomical characters with a rather limited taxon sampling. Species in this clade range from southern Mexico and the Caribbean islands to Bolivia.

The six or seven species of *Mormolyca* vary in plant size, pseudobulb shape, and number of leaves per pseudobulb, but all bear flat, open flowers that lack a column foot (Garay and Wirth, 1959). The vaguely insect-like labellum bears a complex pattern of pilosity, reminiscent of labella in the Mediterranean orchid genus *Ophrys* L., which also has pseudocopulatory pollination. Under cultivation in Brazil (outside its native range), the flowers of *Mormolyca ringens* are pollinated by sexually excited drones of *Nannotrigona testaceicornis* and *Scaptotrigona* sp. (Apidae: Meliponini) that attempt to copulate with the labellum (Singer et al., 2004). The floral fragrance composition is complex, with large amounts of *n*-hexyl hexanoate and *n*-nonanal (Flach et al., 2004), and remarkably matches the pheromones of virgin queens of *Scaptotrigona* (Flach et al., 2006). The genus *Cyrtoglottis* Schltr., based on *C. gracilipes* Schltr., was merged with *Mormolyca* by Garay and Wirth (1959) due to their overall similarity. Their close relationship is confirmed by our results.

Species of the *Maxillaria rufescens* alliance are vegetatively similar to *Mormolyca ringens*, with cespitose, unifoliate pseudobulbs subtended by papery bracts and sessile, acute leaves (Carnevali Fernandez-Concha et al., 2001), but the inflorescences are much shorter. The flowers are morphologically similar among species, with a three-lobed labellum with acute lateral lobes, an arcuate column with a broad apex, and similar pollinaria. Flower color varies among species, ranging

from white, pink, yellow, and orange to brownish-purple, and floral fragrance composition also varies substantially among species (Flach et al., 2004). The labellum usually bears a linear pad of densely packed trichomes that produces an unidentified viscous secretion.

Plants of *Chrysocycnis* (two or three Andean species; Sweet, 1971) have elongate, erect rhizome segments between the pseudobulbs, and their leaves tend to be widely elliptic with prominent cross veins. The flowers have a strongly arcuate column (similar to that of *Cyrtidiorchis*), lack a well-developed column foot, and the insect-like labellum is markedly three-lobed (Sweet, 1971). The pollinators and fragrance composition of *Chrysocycnis* are unknown, but the flowers are thought to be sexually deceptive because of their similarity to those of *Cyrtidiorchis* and *Mormolyca* (Dodson, 1993). Atwood and Mora de Retana (1999) suggested that *Maxillaria tigrina* C. Schweinf. is a member of *Chrysocycnis*, but according to our data this species is well nested in *Camaridium* (see clade P).

A putative synapomorphy for this clade is the inflorescence production from the rhizome. In most Maxillariinae with sympodial growth, inflorescences are produced from the most current growth, either simultaneously with the emergence of a new shoot or from the sheathing bracts at the base of a recently matured pseudobulb. In species of *Chrysocycnis* and the *Maxillaria rufescens* alliance, inflorescences are produced from the rhizome between the second-, third-, and fourth-oldest pseudobulbs rather than from the terminal growth. In *Mormolyca*, inflorescences are produced from the rhizome between the terminal mature pseudobulb and the emerging vegetative shoot. These inflorescences are produced from the axils of rhizome bracts and therefore are not supra-axillary. In the few species of this clade we observed, fruit dehiscence is apical. Perianth fiber bundles are absent.

*Clade K*—(100/100% BS) *Maxillaria desvauxiana* clade, Figs. 3, 10; 4 spp.

This clade consists of four currently described, morphologically similar species: *M. desvauxiana* Rchb.f., *M. auyantepuiensis* Foldats, *M. foldatsiana* Carnevali & I. Ramírez, and *M. longipetiolata* Ames & C. Schweinf. (Carnevali and Ramírez, 1989). The superficially similar *Maxillaria neophylla* Rchb.f., previously hypothesized to belong in this group (Carnevali and Ramírez, 1989), is firmly nested in *Maxillaria* s.s. (clade Q, Fig. 6). The four species occur in the Guyana-northern Amazonas region, where two of them are endemic. Two species extend to the eastern slopes of the Andes and one (*M. longipetiolata*) into southern Central America. Two species are usually terrestrial on white sands (*M. auyantepuiensis* and *M. foldatsiana*). The plants have congested, ovoid, mildly laterally compressed pseudobulbs subtended by several chartaceous, fibrous, nonfoliaceous bracts. The single apical leaf has a distinct, usually long petiole and an oblong, apically acute blade. The peduncles are very short, and the flowers are clustered tightly among the pseudobulbs, often barely exceeding their height (a potential synapomorphy for the clade). The fleshy flowers are dull maroon with broadly triangular perianth parts. The labellum is three-lobed with rounded lateral lobes. The flowers lack any obvious reward, and the labellum callus is shiny and warty or verrucose, suggesting possible nectar, oil, or resin deceit. The mode of fruit dehiscence is unknown; perianth fibers are present.

*Clade L*—(98/100% BS) *Christensonella* Szlach., Mytnik, Górniak & Śmiszek, Figs. 3, 10; 11+ spp.; *Maxillaria* sect. *Urceolatae* Christenson. Type: *Christensonella nardoides* (Kraenzl.) Szlach., Mytnik, Górniak & Śmiszek.

This group of species, traditionally known as the *Maxillaria madida* Lindl. alliance, was recently elevated to generic rank as *Christensonella* by Szlachetko et al. (2006), although a few species still require to be formally transferred (in Fig. 3, we use the names in *Maxillaria* for all of them). This group comprises about 11 species with a dwarf (1–30 cm tall) sympodial growth habit. These plants generally grow as epiphytes in moist and seasonally dry forests of the Amazonian region and on rocky outcrops in southeastern Brazil, where most species are endemic. *Christensonella uncata* (Lindl.) Szlach., Mytnick, Górniak & Śmiszek is widely distributed from southern Mexico to Bolivia and has substantial vegetative variation.

Plants in this group are characterized by their roots with alternating thickenings and constrictions of their velamen, in an accordion-like fashion. The rhizome is rigid, very short to rarely elongate (e.g., *C. uncata*), and is usually covered in scarios, imbricate bracts. The pseudobulbs are usually aggregate, erect, subtended by several papery sheaths at the base, and bear 1–2, rarely 3–4, leaves at the apex. The number, shape, and size of leaves constitute the most important diagnostic character to distinguish the species, except for *M. neowiedii* Rchb.f. and *C. subulata* (Lindl.) Szlach., Mytnick, Górniak & Śmiszek, which have extremely polymorphic leaves. Other important characters traditionally used to delimit species include plant size, flower fragrance, length of the ovary-pedicel relative to the adjacent pseudobulb, and shape of the petals. The leaves are always sessile, erect to twisted, flat or conduplicate, and coriaceous to fleshy or rarely thin. In most species, the midlobe bears a conspicuous shiny purple to dark red spot covered by numerous trichomes and papillae, with no obvious reward. The callus is always glabrous and extends from the labellum base up to its median region, along the midvein, as a low, thick ridge. The pollinarium bears two pairs of laterally flattened, superposed, ovate to round pollinia, a small tegular stipe, and an arcuate viscidium. The stipe is unusually long in *M. pacholskii* Christenson and *C. uncata*. Fruit dehiscence in this group is apical; the fruits of *C. nardoides* extrude endocarpic trichomes along with the seeds, a unique mode of seed presentation among orchids (Blanco et al., 2006). Perianth fibers appear to be present in at least the larger species. Currently accepted species concepts within this clade are unsatisfactory, as evidenced by the nonmonophyly of many species in the cladogram (Fig. 3). A taxonomic revision and more detailed phylogenetic analyses of this clade based on combined molecular data sets and morphology will be published separately (S. Koehler, unpublished manuscript).

*Clade M*—(77/100% BS) *Maxillaria acuminata* clade, Figs. 4, 10; 12+ spp.

Plants of this clade are caespitose to straggly epiphytes with oblong, 2–4 foliate, shiny pseudobulbs that are laterally flattened with several conspicuous vertical ribs. The rhizomes are covered by overlapping, scarios brown bracts that transition into articulated foliaceous bracts subtending the pseudobulbs. Inflorescences are produced simultaneously with the emergence of new growths, but in most species they arise from bract axils between the second- and third-oldest pseudobulbs rather than at the base of the most recently matured pseudobulb. This trait is shared with the *Mormolyca*

clade (clade J), although it is unclear whether this represents a synapomorphy because these clades are not sister in the shortest trees (but without strong BS). Flowers are often greenish, not opening widely, with rigid, fibrous, acuminate to aristate sepals and petals. The column apex is usually conspicuously ciliate. The pollinarium is narrowly linear and oblong, with a prominent stipe whose margins curl inward upon removal from the column. The labellum is simple or obscurely three-lobed with a linear callus bearing a resinous/lipoidal secretion or waxy white crystals. Fruits have lateral dehiscence; perianth fibers are present. Species in this clade occur from Mexico to Bolivia.

Davies et al. (2003a) studied the histochemistry of labellar secretions and the ultrastructure of secretory tissues of *Maxillaria acuminata* Lindl., *M. cerifera* Barb.Rodr., and *M. notylioglossa* Rchb.f. They reported that the secretions were “lipoidal” and included aromatic amino acids and starch. Flach et al. (2004) used GC–MS and NMR analyses to identify the major secretions of *M. cerifera* and *M. scorpioidea* Kraenzl. (as *M. friedrichsthalii* Rchb.f.) as triterpenoid resins. These resins are likely collected by female bees for nest construction, as is the case for floral resins produced by other plant genera (Armbruster, 1984).

Embedded in this clade is the vegetatively anomalous *Maxillaria witsenioides* Schltr., which has long (to 0.8 m), pendent, monopodial stems and glaucous, ensiform, equitant leaves. The yellow-green flowers emerge on short peduncles from the leaf axils. The labellum bears a linear callus with a resinous secretion. Because of its pendent habit and equitant, glaucous leaves, it was hypothesized (Carnevali, 1991; Christenson, 2002a, b) to be a close relative of *M. valenzuelana* [= *Heterotaxis valenzuelana* (A. Rich.) I. Ojeda & Carnevali], and it was included in *Marsupiarina* or in *Maxillaria* sect. *Iridifoliae*. The molecular data refute this placement and indicate that the similarities between *M. witsenioides* and *H. valenzuelana* represent vegetative convergences. *Maxillaria witsenioides* is certainly a species with a very modified growth habit within the *M. acuminata* clade.

*Clade N*—(77/100% BS) *Maxillaria variabilis* clade, Figs. 4, 10; ca. 50 spp., including *M.* sect. *Ebulbes* Pfitz., and *M.* sect. *Erectae* Pfitz. sensu Christenson (2002a).

Most members of this clade have conspicuous rhizomes with moderately spaced, ovoid, unifoliate, bilaterally compressed pseudobulbs. These are subtended by scarios bracts, and in some species foliaceous bracts with persistent sheaths clothe the stem. Roots are smooth and white to brown. Leaves are light green, tough, and flexible, varying in width from 2–3 mm (*M. sanguinea* Rolfe) to several cm [*M. elatior* (Rchb.f.) Rchb.f.]. Flowers are produced from the basal bracts of emerging or recently matured growths; only one flower is produced from each leaf axil (no sequential bud development). Flowers are campanulate with broadly triangular sepals; the labellum is unlobed or obscurely three-lobed and bears a smooth, ligulate, glossy callus. The clinandrium and anther cap are smooth to minutely papillose. In some species, the glossy callus produces no obvious secretion but the flowers produce variously fruity fragrances (e.g., *M. sanguinea*, *M. tenuifolia* Lindl., *M. variabilis* Bateman ex Lindl.). *Maxillaria elatior* produces an abundant resin-like secretion on the callus, labellum base, and base of column, and the flowers have a terpenoid fragrance. Species in this clade are widely distributed throughout the neotropics. Fruits of species in this clade have

lateral dehiscence; perianth fibers are absent in most species but weakly present in larger-flowered species (e.g., *M. variabilis*).

There are two highly supported subclades in this group (Fig. 4): the *M. diuturna*/*M. arbuscula* subclade and the *M. variabilis*/*M. elatior* subclade. However, there are no clearly defined morphological differences between them.

Species of the *Maxillaria linearifolia*/*M. cassapensis* Rchb.f. group (*M.* section *Ebulbes* Pfitz., the “*M. graminifolia* suballiance” reviewed by Atwood, 2003) have long, erect or pendent, sparsely branched, monopodial stems; their placement in a clade of predominately sympodial, pseudobulbous plants has not been hypothesized before. However, they also share the single, nonsequential inflorescence per leaf axil, and some closely related species (e.g., *M. arbuscula*) appear to have monopodial mature shoots. A relationship of this “suballiance” with *M. dendrobioides* (Schltr.) L.O. Williams and relatives (in *Camaridium*, clade P) had been hypothesized by Atwood (2003) on the basis of their superficial vegetative similarity. Szlachetko and Śmiszek (2007) also held a similar view when they created the genus *Adamanthus* Szlach., comprising mostly species of *Maxillaria* section *Ebulbes*. However, these authors designated *Camaridium dendrobioides* Schltr. as the type and ignored the synonymy already worked out by Atwood (2003) for their generic transfers (further discussed under *Camaridium*, see the following section on clade P).

*Clade O*—(59/90% BS) *Trigonidium* Figs. 4, 10; 7 spp., type: *Trigonidium obtusum* Lindl.

This florally distinctive genus ranges from Mexico to Bolivia. Some authors estimate up to 13 species in the genus, but a recent study indicates that there are only seven (*M. Blanco*, unpublished manuscript). The monophyly of *Trigonidium* is only moderately supported by molecular data, although several clades within the genus (which correspond to different vegetative habits) receive high BS. Species vary in the pseudobulb shape, the number of apical leaves, and the length of the rhizomes, but the floral structure is very uniform throughout the genus. Pseudobulbs are cespitose to widely spaced on frequently branching rhizomes; ovoid, pyriform, or oblong; laterally compressed; slightly ridged; one-, two-, or up to five-foliate; subtended by several imbricate bracts. Leaves are thin to coriaceous, sublinear to oblanceolate, sessile or basally attenuate, and acute. Inflorescences originate from the base of developing or mature pseudobulbs (depending on the species). Flowers are erect, funnel-shaped, and trigonous, with the floral cavity facing upward. Sepals are similar to each other, often basally clawed, yellow to tan or cream with purple or reddish veins, reflexed at midpoint, basally forming a cup that encloses the petals, labellum, and column, with sepal apices spread flat or reflexed. The petals are much smaller than the sepals, lanceolate, asymmetric, with characteristic shiny thickened pads (often bluish) at the tips. The labellum is much shorter than the sepals. The column is erect, straight, wingless, and lacking a prominent column foot. The stipe is absent or transversely semilunate, with a semilunate viscidium. Fruit dehiscence is lateral; perianth fibers are absent.

Pseudocopulatory pollination has been documented in *T. obtusum*. The flowers are pollinated through sexual mimicry by males of *Plebeia droryana* (Apidae: Meliponini), which attempt copulation with the petals or lateral sepals and slip into the floral cavity (Singer, 2002).

*Clade P*—(100/100% BS) *Camaridium* Lindl., Figs. 5, 10; 80+ spp.; including *Adamanthus* Szlach., *Pseudomaxillaria* Hoehne, *Psittacoglossum* La Llave & Lex., *Sepalosaccus* Schltr., *Maxillaria* sect. *Camaridium* (Lindl.) Christenson, *M.* sect. *Cucullatae* Christenson, and *M.* sect. *Pseudomaxillaria* (Hoehne) Christenson. Type: *Camaridium ochroleucum* Lindl.

Lindley's (1824) original concept of *Camaridium*, based upon *Camaridium ochroleucum* Lindl. (= *Maxillaria camaridii* Rchb.f.), emphasized floral characters that distinguished it from *Ornithidium*. He stated (plate 844) that *Camaridium* is “principally distinguished from *Ornithidium* by not having the base of the labellum united with the base of the column, nor a connivent perianthium, nor a fleshy discus to the labellum, and especially characterized by its small labellum and expanded perianthium.” The clade recognized here as *Camaridium* is more florally diverse than Lindley's original concept, and many species [e.g., *M. neglecta* (Schltr.) L.O. Williams, *M. parviflora* (Poepp. & Endl.) Garay, *M. schlechteriana* J.T. Atwood] have been repeatedly transferred between *Camaridium* and *Ornithidium*, possibly reflecting homoplasious floral traits associated with pollination by nectar-foraging bees or hummingbirds (e.g., saccate and rigid labellums, abundant nectar, and yellow/orange colors).

Plants may be cespitose or scraggly epiphytes with widely spaced, unifoliate pseudobulbs or may form erect, monopodial, leafy canes. In some species (e.g., *M. scalariformis* J.T. Atwood, *M. inaudita* Rchb.f.), juvenile plants are sympodial and bear cespitose pseudobulbs, but the adult plants produce long, monopodial, leafy shoots. Inflorescences are usually produced from leafy new growths rather than from the base of mature pseudobulbs or mature canes. The floral bract is generally longer than the ovary. Floral morphology (especially labellum and callus shape) is variable, but many species lack a prominent column foot. The labellum is often much shorter than the sepals and petals; the perianth segments lack fibers and often have a minutely papillose epidermis that appears sparkling in direct sunlight. In some putatively hummingbird-pollinated species [e.g., *M. lutheri* J.T. Atwood, *M. sigmoidea* (C. Schweinf.) Ames & Correll], the labellum base is saccate and rigidly attached to the reduced column foot. Many species secrete abundant nectar at the labellum base, whereas others are apparently rewardless; no resin or pseudopollen production has been observed in this clade. *Maxillaria imbricata* Barb. Rodr. produces abundant nectar on the abaxial surfaces of the labellum, sepals, and petals and produces a foul, aminoid odor. Pollinarium morphology varies within this clade, possibly reflecting radiations to different classes of pollinators and sites of pollinarium attachment. As noted by Carnevali (1991), many putatively hummingbird-pollinated species (e.g., *M. scalariformis*, *M. sigmoidea*) produce relatively tiny pollinaria with cream or white pollinia and a broad, hyaline viscidium; these smaller pollinia are likely an adaptation to avoid removal by grooming of the bird's beak (Dressler, 1971). Fruit dehiscence appears to be always apical; perianth fibers are absent.

Traditionally, plants with pseudobulbs separated on long rhizomes were considered a trademark of the genus *Camaridium*. Therefore, many species in other clades (especially *Ornithidium*, *Maxillaria* s.s., and the *M. variabilis* clades) with this habit were at some point treated as part of *Camaridium*. This vegetative habit clearly evolved separately within core Maxillariinae and has little systematic value at the generic level. *Camaridium* is best distinguished by the combination of

apical fruit dehiscence, absence of fibers in floral segments, and a floral bract that often exceeds the ovary.

The recently described genus *Adamanthus* Szlach. (Szlachetko and Śmiszek, 2007) is grossly polyphyletic. It is typified by *Camaridium dendrobioides* Schltr. (a true *Camaridium*), but most of the other species are members of *Maxillaria* section *Ebulbes* Pfitz. (discussed in section *Clade N*). *Adamanthus nitidulus* (Rchb.f.) Szlach., not sampled by us, most likely belongs in the *Camaridium* clade; *A. pittieri* (Ames) Szlach. [*Maxillaria pittieri* (Ames) L.O. Williams] is clearly an *Ornithidium* (see section *Clade C*), and *A. exaltatus* (Kraenzl.) Szlach. [= *Maxillaria exaltata* (Kraenzl.) C. Schweinf.] is firmly nested in *Maxillaria* s.s. (see section *Clade Q*). Szlachetko and Śmiszek (2007) used the feminine gender for most of their new combinations even when they must be masculine; we use the correct gender here (McNeill et al., 2006: articles 62.1 and 62.2.c).

The genus *Pseudomaxillaria* Hoehne was originally erected to accommodate *Maxillaria parviflora* (Poepp. & Endl.) Garay, and later Brieger (1977) added most of its close relatives. This small species alliance is most diverse in Central America and was reviewed by Atwood (1993). It is also nested within *Camaridium*.

*Maxillaria strumata* (Endres & Rchb.f) Ames & Correll is unusual within *Camaridium* because of its small, caespitose plants and partially connate lateral sepals enclosing a subsaccate labellum (Brieger, 1977). The pollinarium has a discoid viscidium and a prominent stipe. This species was segregated as *Sepalosaccus humilis* Schltr. [= *S. strumatum* (Endres & Rchb.f.) Garay], but the molecular data show it is deeply embedded within *Camaridium*. *Maxillaria strumata* and *M. brevilabia* Ames & Correll are sister to the *Pseudomaxillaria* alliance, and all of them have subsaccate labella enclosed by the inflated bases of the lateral sepals. It is notable that *M. strumata* and *M. pseudoneglecta* (also in the *Pseudomaxillaria* alliance) hybridize in nature (see Materials and Methods, *Data analysis*).

Atwood and Mora de Retana (1999) suggested that *M. vittariifolia* L.O. Williams might deserve generic status because of its diminutive, caespitose plants and filiform peduncles and that *M. tigrina* C. Schweinf. might belong in *Chrysocynis* because of its superficial similarity to members of that genus (part of *Mormolyca*, see section *Clade J*). However, our data show both of these species nested within *Camaridium*.

Sister to the rest of *Camaridium* is a clade composed of members of the *Maxillaria cucullata* Lindl. alliance (*M. sect. Cucullatae*). This taxonomically difficult group of about 10 species is almost restricted to Mexico and Central America. The plants have caespitose pseudobulbs with nonfoliaceous subtending bracts. Inflorescences bear relatively large, inflated, green sheathing bracts, and the floral bract is cucullate and usually exceeds the length of the ovary. The flowers are yellow to purple, sometimes with lines of purple spots. The usually dark maroon labellum is three-lobed with rounded lateral lobes and an ovate midlobe, with an oblong or trapezoid callus thickened distally; its surface is usually verrucose, although Davies and Turner (2004) reported an absence of papillae on the labellar surface in this group. The perianth parts are generally fleshier and thicker than in other species of the *Camaridium* clade. There is a thickened, transverse ridge at the base of the column, just above the attachment of the labellum; its function is unknown, but this ridge is a putative

synapomorphy for this subclade. The type of the genus *Psittacoglossum* La Llave & Lexarza is part of this subclade. As traditionally recognized, the *M. cucullata* alliance is not monophyletic (*M. meleagris* Lindl. and *M. obscura* Lind. & Rchb.f. appear firmly nested among other members of *Camaridium*), and we prefer to consider *Psittacoglossum* as part of *Camaridium*.

*Clade Q*—(58/100% BS) *Maxillaria* s.s., Figs. 6, 7; 250+ spp.; including *M. subgen. Aggregatae* (Pfitz.) Brieger, *M. sect. Amazonicae* Christenson, *M. sect. Aggregatae* Pfitz., *M. sect. Arachnites* Christenson, *M. sect. Axilliflorae* Lindl., *M. sect. Maxillaria* Ruiz & Pav. (sensu Christenson, 2002a, b), *M. sect. Multiflorae* Christenson, *Dendrobium sect. Maxillaria* (Ruiz & Pav.) Pers., and *Menadena* Raf.; lectotype (designated by Brieger and Hunt, 1979: 602; Garay, 1997a): *Maxillaria platypetala* Ruiz & Pav.

This large clade includes many species with large, showy flowers, but also others with small plants and flowers (e.g., *M. acostae* Schltr.). Because of the large number of species in this clade and their morphological diversity, unambiguous diagnostic synapomorphies are difficult to identify. Plants of most species are caespitose with ovoid, unifoliate pseudobulbs and often one to several pairs of large foliaceous bracts that may equal the terminal leaf in size, although *M. grobyoides* Garay & Dunst. and *M. steyermarkii* Foldvats (not sampled, but tentatively included here) are bifoliate. The inflorescences usually emerge at the base of recently matured pseudobulbs, and the floral bract is often shorter than the ovary (contrasting with the longer floral bract of *Camaridium*). The flowers usually have a prominent column foot, and many species have a fringed or ciliate clinandrium margin. The flowers possess very tough perianth fibers. The anther cap is frequently crested or ornamented with trichomes. The labellum is usually three-lobed, with the lateral lobes rounded and much smaller than the midlobe. The labellum often bears trichomes (sparse to dense, depending on species), and the callus is usually linear or rectangular, sometimes broadly triangular. The pollinarium usually have a hard, brownish, horseshoe-shaped viscidium, lack a well-developed tegula (stipe), and have spheroidal to clavate pollinia. No species in this clade are known to produce a nectar or resin reward; they appear to be deceit pollinated or produce pseudopollen. In the *M. platypetala* alliance (*M. longissima* Lindl. to *M. striata* Rolfe, Fig. 7), flowers are usually large and showy, and the labellum always bears a dense indument of loose, deciduous moniliform trichomes (pseudopollen). In all known cases, the fruits have lateral dehiscence.

Another character found in many species of this clade, especially in the *M. platypetala* alliance, is a narrow projection from the pseudobulb apex that elevates the leaf abscission layer. When the leaf abscises, this projection persists on the pseudobulb and can vary in length from a few millimeters to several centimeters, depending on the species. A similar structure occurs in other orchids such as *Coelia* (Laeliinae), *Koellensteina* Rchb.f., and *Otostylis* Schltr. (Zygopetalinae). We adopt the term “phyllopodium” for this structure, in analogy to the phyllopodium of many species in the fern genera *Elaphoglossum* and *Oleandra* (Lellinger, 2002). In species with reduced pseudobulbs concealed by the foliaceous sheathing bracts (e.g., *M. angustissima* Ames, F. T. Hubb., & C. Schweinf., *M. breviscapa* Poepp. & Endl., *M. silvana* Campacci), a prominent phyllopodium is still present on the

apex of the pseudobulbs. The orchid phyllopodium probably represents the leaf sheath, which is extremely reduced in the pseudobulb apical leaves of most other orchids.

*Maxillaria exaltata* (Kraenzl.) C. Schweinf. and *M. meridensis* Lindl. have erect canes with the pseudobulbs reduced to swollen nodes or absent. Perhaps the most vegetatively atypical species in this clade is *M. lueri* Dodson with pendent growths, greatly reduced pseudobulbs concealed in the leaf sheaths, and long (up to 1 m), linear leaves.

Most internal clades within *Maxillaria* s.s. lack strong BS support because of short branch lengths, but it is clear that most of the sections defined by Christenson (2002a, b) are polyphyletic. An exception is *M.* section *Multiflorae* Christenson, which is morphologically distinctive (ancipitous, ridged pseudobulbs; leaves and foliaceous bracts abruptly narrowed above the abscission layer; and long, straight sepals and petals). Long, narrow, pendulous sepals and petals, a defining feature of *M.* section *Arachnites* Christenson, apparently have been gained and lost several times in *Maxillaria* and might represent an evolutionarily labile feature related to attraction of certain pollinators.

**Taxonomic implications**—The combined three- and four-region analyses demonstrate that *Maxillaria* as presently defined in the World Checklist of Orchidaceae (Govaerts et al., 2005) is polyphyletic and that all minor genera of core Maxillariinae are embedded within *Maxillaria* s.l. Although the spine of the tree is incompletely resolved with strong BS support, the bootstrap consensus (Fig. 8) does provide strong support for many clades that traditionally have been recognized as genera (e.g., *Cryptocentrum*, *Cyrtidiorchis*, *Pityphyllum*, *Trigonidium*), that correspond to recent generic segregates (e.g., *Brasiliorchis*, *Christensonella*, *Sauvetea*), or that have been recognized at generic level by previous workers (e.g., *Ornithidium*, *Camariidium*). The cladograms also include several strongly supported clades that represent novel assemblages of species whose relationships have not been previously hypothesized.

The polyphyly of *Maxillaria* s.l. (= core Maxillariinae) presents two alternatives: (1) lump all species into one extremely large and variable genus with a subgeneric classification that reflects phylogenetic relationships; or (2) divide *Maxillaria* s.l. into well-supported clades and create several new genera, together with redefined generic concepts of some existing minor genera. Both approaches would necessitate numerous nomenclatural transfers, but the existing generic classification is clearly misleading. As currently circumscribed, *Maxillaria* is not defined by a uniform set of character states; it is a true “catch-all” taxon.

We favor the division of *Maxillaria* s.l. into smaller genera (clades A–Q) that are more easily defined by morphological as well as molecular synapomorphies. A single mega-genus might require fewer nomenclatural transfers (although many would still be necessary), but it would be morphologically undiagnosable. We feel that recognition of the previously discussed clades as genera will produce a more predictive classification and will be more useful for field identification and floristic treatments. They will also facilitate more restricted analyses using more advanced phylogenetic methods and incorporating morphological characters. The majority of species will remain in *Maxillaria* s.s. (clade Q), thus keeping the necessary nomenclatural transfers to a minimum. Generic descriptions

and nomenclatural transfers will be made in separate publications.

A substantial number of unsampled species are known only from one or few herbarium specimens or from incomplete descriptions with destroyed types; assignment of these species to particular clades will be problematic on the basis of morphology alone. Increased sampling for molecular studies (especially for species from Bolivia, Peru, Colombia, and Venezuela) will be needed to clarify relationships within most of the clades. Clearly, the repeated loss of pseudobulbs, the evolution of monopodial stems, convergence in growth habit, and the simple floral plan has created taxonomic confusion within core Maxillariinae. The danger of erecting genera based upon a few, homoplasious morphological characters and/or incomplete molecular sampling is demonstrated by the recently described *Adamanthus*, *Laricorchis*, and *Sauvetea* (Szlachetko and Śmiszek, 2007). More subtle morphological or anatomical characters (e.g., presence/absence of fibers in sepals, fruit dehiscence) may prove phylogenetically informative, but more detailed morphological analyses are needed. Although these molecular data have greatly clarified relationships within the subtribe, we must echo Lindley's (1843, p. 16) comment: “With regard to the species that belong to true *Maxillaria*, now that it has been weeded of these species, I must take another opportunity of examining them.”

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APPENDIX 1. Voucher information and GenBank accession numbers for taxa used in this study. A dash indicates that the DNA region was not sampled. Herbarium acronyms: ESA = Universidade de São Paulo, São Paulo, Brazil; FLAS = University of Florida, Gainesville, FL, USA; M = Botanische Staatssammlung München, München, Germany; PMA = Universidad de Panamá, Panamá; QCA = Pontificia Universidad Católica del Ecuador, Quito, Ecuador; QCNE = Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador; SEL = Marie Selby Botanical Gardens, Sarasota, FL, USA; SP = Instituto de Botânica, São Paulo, Brazil; UEC = Universidade Estadual de Campinas, Brazil; USJ = Universidad de Costa Rica, San José, Costa Rica.

- Taxon**—GenBank accessions: *nrITS*, *matK+trnK*, *atpB-rbcL* spacer, *rpoC1*, *Collector and number*, Source, Herbarium.
- Anthosiphon roseans*** Schltr.—DQ210416, DQ210903, DQ209701, DQ872598, Whitten 2554, Panama, FLAS.
- Bifrenaria inodora*** Lindl.—DQ210217, DQ210744, —, —, Whitten 93189, Brazil, cult., FLAS. ***B. tetragona*** (Lindl.) Schltr.—AF239335, DQ210751, DQ209533, DQ872528, Whitten 93156, Brazil, cult., FLAS. ***B. tyrianthina*** (Loudon) Rchb.f.—DQ210235, DQ210752, —, —, Whitten 3008, Brazil, cult., FLAS.
- Brasiliorchis barbosa*** (Loefgr.) R.Singer, S.Koehler & Carnevali—DQ210150, DQ210682, DQ209460, —, Koehler 0140, Brazil, UEC. ***B. chrysantha*** (Barb.Rodr.) R.Singer, S.Koehler & Carnevali—DQ210113, DQ210644, DQ209424, —, Koehler 0029, Brazil, cult., UEC. ***B. gracilis*** (Lodd.) R.Singer, S.Koehler & Carnevali—DQ210108, DQ210639, DQ209420, —, Koehler 0017, Brazil, cult., UEC. ***B. gracilis***—DQ210154, DQ210686, DQ209464, —, Koehler 0147, Brazil, UEC. ***B. gracilis***—DQ210312, DQ210811, DQ209600, DQ872539, Whitten 2303, Brazil, cult., FLAS. ***B. kautskyi*** (Pabst) R. Singer, S.Koehler & Carnevali—DQ210115, DQ210646, DQ209426, —, Koehler 0035, Brazil, UEC. ***B. marginata*** (Lindl.) R.Singer, S. Koehler & Carnevali—DQ210156, DQ210688, —, Koehler 0152, Brazil, UEC. ***B. phoenicanthera*** (Barb.Rodr.) R.Singer, S.Koehler & Carnevali—DQ210173, DQ210703, DQ209480, —, Koehler 0274, Brazil, ESA. ***B. phoenicanthera***—DQ210313, DQ210812, DQ209601, —, Whitten 2304, Brazil, cult., FLAS. ***B. picta*** (Hook.) R.Singer, S.Koehler & Carnevali—DQ210084, DQ210624, DQ209396, —, Gerlach 1984–3140, cult., M. ***B. picta***—DQ210190, DQ210720, DQ209497, —, Koehler 0337, Brazil, UEC. ***B. picta***—DQ210522, DQ211002, DQ209804, —, Whitten 2755, Brazil, cult., FLAS. ***B. porphyrostele*** (Rchb.f.) R.Singer, S.Koehler & Carnevali—DQ210159, DQ210691, DQ209467, —, Koehler 0159, Brazil, UEC. ***B. porphyrostele***—DQ210294, DQ210793, DQ209584, —, Whitten 1972, Brazil, FLAS. ***B. schunkiana*** (Campacci & Kautsky) R.Singer, S.Koehler & Carnevali—DQ210300, DQ210799, DQ209589, DQ872537, Whitten 1992, Brazil, cult., FLAS. ***B. ubatubana*** (Hoehne) R.Singer, S.Koehler & Carnevali—DQ210158, DQ210690, —, Koehler 0155, Brazil, UEC. ***B. ubatubana***—DQ210205, DQ210735, DQ209512, —, Koehler 0373, Brazil, ESA. ***B. aff. ubatubana***—DQ210016, DQ210588, DQ209330, —, Atwood & Whitten 5099, Brazil, cult., SEL.
- Chrysocynis schlimii*** Linden & Rchb.f.—DQ210088, DQ210628, DQ209400, —, Gerlach 1992–763, Colombia, cult., M. ***C. schlimii***—DQ210350, DQ210847, DQ209637, DQ872547, Whitten 2386, Ecuador, cult., FLAS.
- Cryptocentrum calcaratum*** (Schltr.) Schltr.—DQ210487, DQ210970, DQ209771, —, Whitten 2651, Panama, FLAS. ***C. inaequisepalum*** C. Schweinf.—DQ210257, DQ210769, DQ209551, —, Whitten 1567, Ecuador, FLAS. ***C. inaequisepalum***—DQ210324, DQ210823, DQ209612, —, Whitten 2325, Ecuador, FLAS. ***C. inaequisepalum***—DQ210407, DQ210894, DQ209692, —, Whitten 2535, Ecuador, FLAS. ***C. inaequisepalum***—DQ210501, DQ210982, DQ209784, —, Whitten 2700, Ecuador, FLAS. ***C. latifolium*** Schltr.—DQ209999, DQ210578, DQ209315, —, Atwood & Whitten 5081, cult., SEL. ***C. latifolium***—DQ210332, DQ210831, DQ209619, —, Whitten 2349, Ecuador, FLAS. ***C. latifolium***—DQ210511, DQ210992, DQ209794, —, Whitten 2733, Ecuador, FLAS. ***C. lehmannii*** (Rchb. f.) Garay—DQ210365, DQ210859, DQ209652, —, Whitten 2408, Ecuador, FLAS. ***C. peruvianum*** (Cogn.) C.Schweinf.—DQ210279, DQ210786, DQ209572—Whitten 1796, Ecuador, cult., FLAS. ***C. peruvianum***—DQ210321, DQ210820, DQ209609, DQ872599, Whitten 2322, Ecuador, FLAS. ***C. pseudobulbosum*** C.Schweinf.—DQ210280, —, —, Whitten 1999, Ecuador, FLAS. ***C. pseudobulbosum***—DQ210367, DQ210861, DQ209654, —, Whitten 2411, Ecuador, cult. FLAS. ***C. standleyi*** Ames—DQ210309, DQ210808, DQ209597, —, Holst 8764, Costa Rica, SEL. ***C. standleyi***—DQ210322, DQ210821, DQ209610, —, Whitten 2323, Ecuador, FLAS. ***C. standleyi***—DQ210364, DQ210858, DQ209651, —, Whitten 2407, Ecuador, cult., FLAS. ***Cryptocentrum sp.***—DQ210323, DQ210822, DQ209611, —, Whitten 2324, Ecuador, FLAS.
- Cyrtidiorchis alata*** (Ruiz & Pav.) Rauschert—DQ210087, DQ210627, DQ209399, —, Gerlach 1994–4005, Colombia, M. ***C. alata***—DQ210569, DQ211044, DQ209849, —, Whitten 2932, Ecuador, cult., FLAS. ***C. frontinoensis*** (Garay) Rauschert—DQ210248, DQ210763, DQ209542, —, Whitten 2993, Colombia, cult., FLAS.
- Eriopsis biloba*** Lindl.—DQ210374, DQ210866, DQ209661, —, Whitten 2439, Ecuador, cult., FLAS. ***E. biloba***—DQ461788, DQ461806, DQ461770, DQ872521, Whitten 3153, Ecuador, QCA.
- Heterotaxis brasiliensis*** (Brieger & Illg) F. Barros—DQ210155, DQ210687, DQ209465, —, Koehler 0150, Brazil, UEC. ***H. discolor*** (Lodd. ex Lindl.) Ojeda & Carnevali—DQ210232, DQ210748, DQ209531, —, Atwood & Whitten 5063, Suriname, SEL. ***H. discolor***—DQ210052, DQ209899, DQ209367, —, Blanco 2098, Costa Rica, cult., USJ. ***H. discolor***—DQ210181, DQ210711, DQ209488, —, Koehler 0311, Brazil, ESA. ***H. discolor***—DQ210333, DQ209953, DQ209620, —, Whitten 2350, Ecuador, FLAS. ***H. equitans*** (Schltr.) Ojeda & Carnevali—DQ210151, DQ210683, DQ209461, —, Koehler 0141, Brazil, UEC. ***H. equitans***—DQ210389, DQ210877, —, DQ872595, Whitten 2483, Ecuador, cult., FLAS. ***H. fritzi*** Ojeda & Carnevali—DQ210497, DQ209969, DQ209781, —, Whitten 2672, Colombia, cult., FLAS. ***H. maleolens*** (Schltr.) Ojeda & Carnevali—DQ209978, DQ209856, DQ209295, —, Atwood & Whitten 5055, Honduras, SEL. ***H. maleolens***—DQ210525, DQ209972, DQ209807, —, Whitten 2764, cult., FLAS. ***H. santanae*** (Carnevali & I.Ramirez) Ojeda & Carnevali—DQ210526, DQ209973, DQ209808, DQ872582, Whitten 2765, Ecuador, cult., FLAS. ***H. sessilis*** (Sw.) F. Barros—DQ209986, DQ209862, DQ209303, —, Atwood & Whitten 5065, Jamaica, SEL. ***H. sessilis***—DQ210410, DQ210897, DQ209695, DQ872555, Whitten 2544, cult., FLAS. ***H. superflua*** (Rchb.f.) F. Barros—DQ210157, DQ210689, DQ209466, —, Koehler 0153, Brazil, UEC. ***H. superflua***—DQ210175, DQ210705, DQ209482, —, Koehler 0279, Brazil, ESA. ***H. superflua***—DQ461800, DQ461818, DQ461782, —, Whitten 3197, Ecuador, cult., QCA. ***H. valenzuelana*** (A. Rich.) Ojeda & Carnevali—DQ210170, DQ210700, DQ209477, —, Koehler 0263, Brazil, ESA. ***H. valenzuelana***—DQ210172, DQ210702, DQ209479, —, Koehler 0270, Brazil, ESA. ***H. valenzuelana***—DQ210466, DQ210950, DQ209749, —, Whitten 2620, Panama, FLAS. ***H. valenzuelana***—DQ210231, DQ209934, DQ209530, —, Whitten 3000, Panama, cult., FLAS. ***H. villosa*** (Barb.Rodr.) F. Barros—DQ210202, DQ210732, DQ209509, —, Koehler 0367, Brazil, ESA. ***H. villosa***—DQ210387, DQ209963, DQ209673, —, Whitten 2481, Ecuador, cult., FLAS. ***H. violaceopunctata*** (Rchb.f.) F. Barros—DQ210146, DQ210678, DQ209457, —, Koehler 0129, Brazil, cult., UEC. ***H. violaceopunctata***—DQ210308, DQ210807, DQ209596, DQ872538, Whitten 2294, Brazil, cult., FLAS.
- Hylaeorchis petiolaris*** (Schltr.) Carnevali & G. A. Romero—DQ210545, DQ211020, DQ209827, —, Whitten 3073, Ecuador, cult., QCA.
- Maxillaria acervata*** Rchb.f.—DQ210064, DQ210607, DQ209379, —, Blanco 2302, Costa Rica, cult., USJ. ***M. aciantha*** Rchb.f.—DQ210011, DQ209876, DQ209326, —, Atwood & Whitten 5094, Belize, SEL. ***M. aciantha***—DQ210296, DQ210795, DQ209585, —, Whitten 1978, Belize, FLAS. ***M. acicularis*** Herb. ex Lindl.—DQ210142, DQ210673, DQ209452, —, Koehler 0115, Brazil, SP.



- M. acicularis*—DQ210161, DQ210693, DQ209469, —, *Koehler 0237*, Brazil, UEC. *M. acicularis* —DQ210196, DQ210726, DQ209503, —, *Koehler 0352*, Brazil, cult., UEC. *M. acicularis* —DQ210204, DQ210734, DQ209511, —, *Koehler 0371*, Brazil, ESA. *M. acicularis* —DQ210301, DQ210800—, —, *Whitten 1994*, Brazil, cult., FLAS. *M. acostae* Schltr.—DQ210034, DQ210603, DQ209348, —, *Blanco 0938*, Costa Rica, USJ. *M. acostae*—DQ210067, DQ210610, DQ209381, —, *Blanco 2826*, Panama, FLAS. *M. acostae*—, —, DQ210965, DQ209766, DQ872566, *Whitten 2644*, Panama, cult., FLAS. *M. acostae*—DQ210532, DQ211008, DQ209814, —, *Whitten 2786*, Panama, cult., FLAS. *M. acuminata* Lindl.—DQ210408, DQ210895, DQ209693, —, *Whitten 2536*, Ecuador, FLAS. *M. acuminata*—DQ210447, DQ210932, DQ209731, —, *Whitten 2597*, Panama, cult., FLAS. *M. acuminata*—DQ210500, DQ210981, DQ209783, DQ872573, *Whitten 2698*, Ecuador, FLAS. *M. acutifolia* Lindl.—DQ210337, DQ210835, DQ209623, —, *Whitten 2361*, Ecuador, cult., FLAS. *M. cf. acutifolia*—DQ210829, DQ209617, —, *Whitten 2338*, Ecuador, FLAS. *M. adendrobium* (Rchb.f.) Dressler—DQ210214, DQ210741, DQ209519, —, *Dressler 4231*, Panama, FLAS. *M. adendrobium*—DQ210467, —, DQ209750, —, *Whitten 2621*, Panama, FLAS. *M. adolphi* (Schltr.) Ames & C.Schweinf.—DQ210066, DQ210609, DQ209380, —, *Blanco 2539*, Costa Rica, USJ. *M. aequiloba* Schltr.—DQ210273, DQ210784, DQ209567, —, *Whitten 1668*, Ecuador, cult., FLAS. *M. aequiloba*—DQ210564, DQ211039, DQ209844, —, *Whitten 2918*, Ecuador, cult., FLAS. *M. cf. aggregata* (Kunth) Lindl.—DQ210393, DQ210880, DQ209678, DQ872552, *Whitten 2488*, Ecuador, cult., FLAS. *M. cf. aggregata*—DQ461793, DQ461811, DQ461775, —, *Whitten 3180*, Ecuador, QCA. *M. cf. aggregata*—DQ461797, DQ461815, DQ461779, —, *Whitten 3189*, Ecuador, cult., QCA. *M. cf. aggregata*—DQ461799, DQ461817, DQ461781, —, *Whitten 3195*, Ecuador, cult., QCA. *M. cf. alba* (Hook.) Lindl.—DQ210000, DQ209873, DQ209316, —, *Atwood & Whitten 5082*, cult., SEL. *M. alba*—DQ209984, DQ210575, DQ209301, —, *Atwood & Whitten 5062*, Costa Rica, SEL. *M. alba*—DQ210171, DQ210701, DQ209478, —, *Koehler 0266*, Brazil, UEC. *M. alba*—DQ210315, DQ210814, DQ209603, —, *Whitten 2306*, Jamaica, cult., FLAS. *M. allenii* L.O.Williams—DQ210068, DQ210611, DQ209382, —, *Blanco 2836*, Panama, FLAS. *M. alpestris* Lindl.—DQ210414, DQ210901, DQ209699, —, *Whitten 2551*, Ecuador, cult., FLAS. *M. alticola* C.Schweinf.—DQ210399, DQ210886, DQ209684, —, *Whitten 2498*, Ecuador, cult., FLAS. *M. alticola*—DQ210535, DQ211010, DQ209817, DQ872584, *Whitten 2800*, Ecuador, cult., FLAS. *M. amparoana* Schtr.—DQ210005, DQ210583, DQ209321, —, *Atwood & Whitten 5087*, cult., SEL. *M. ampliflora* C.Schweinf.—DQ210069, DQ210612, DQ209383, —, *Blanco 2845*, Panama, FLAS. *M. ampliflora*—DQ210425, DQ210912, DQ209710, —, *Whitten 2566*, Panama, cult., FLAS. *M. ampliflora*—DQ210458, DQ210942, DQ209742, —, *Whitten 2608*, Panama, FLAS. *M. cf. anatomorum* Rchb.f.—DQ210483, DQ210966, DQ209767, —, *Whitten 2645*, Colombia, cult., FLAS. *M. anceps* Ames & C.Schweinf.—DQ210518, DQ209971, DQ209801, —, *Whitten 2750*, Nicaragua, cult., FLAS. *M. angustisegmenta* Ames & C.Schweinf.—DQ210012, DQ209877, DQ209327, —, *Atwood & Whitten 5095*, Costa Rica, cult., SEL. *M. angustisegmenta*—DQ210429, DQ210916—, —, *Whitten 2570*, Panama, FLAS. *M. angustissima* Ames, F.T.Hubb. & C.Schweinf.—DQ210054, DQ209901, DQ209369, —, *Blanco 2103*, Costa Rica, USJ. *M. angustissima*—DQ210479, DQ210961, DQ209762, —, *Whitten 2637*, Panama, FLAS. *M. angustissima*—DQ210512, DQ210993, DQ209795, DQ872575, *Whitten 2735*, Panama, FLAS. *M. arachnitiflora* Ames & C.Schweinf.—DQ210063, DQ209909, DQ209378, —, *Blanco 2262*, Costa Rica, cult., USJ. *M. arachnitiflora*—, —, DQ210758—, —, *Matthews s.n.*, Costa Rica, SEL. *M. arbuscula* (Lindl.) Rchb.f.—DQ210357, DQ210853, DQ209644, —, *Whitten 2395*, Ecuador, cult., FLAS. *M. arbuscula*—DQ210404, DQ210891, DQ209689, —, *Whitten 2508*, Ecuador, cult., FLAS. *M. arbuscula*—DQ210538, DQ211013, DQ209820, DQ872585, *Whitten 2810*, Ecuador, cult., FLAS. *M. arbuscula*—DQ210555, DQ211030, DQ209836, —, *Whitten 2902*, Ecuador, cult., FLAS. *M. aff. arbuscula*—DQ210401, DQ210888, DQ209686, —, *Whitten 2500*, Ecuador, cult., FLAS. *M. attenuata* Ames & C.Schweinf.—DQ210239, DQ209936, DQ209537, —, *Atwood s.n.*, Panama, SEL 1974-0030-113A, SEL. *M. atwoodiana* Pupulin—DQ210055, DQ209902, DQ209370, —, *Blanco 2104*, Costa Rica, cult., USJ. *M. augustae-victoriae* F.Lehm. & Kraenzl.—DQ210027, DQ210599, DQ209341, —, *Dressler & Atwood 6266*, Ecuador, cult., FLAS. *M. augustae-victoriae*—DQ210551, DQ211026, DQ209832, DQ872588, *Whitten 2893*, Ecuador, cult., FLAS. *M. auyantepuiensis* Foldats—DQ210331, DQ210830, DQ209618, DQ872543, *Whitten 2347*, Ecuador, FLAS. *M. auyantepuiensis*—DQ210336, DQ210834, DQ209622, —, *Whitten 2360*, Ecuador, cult., FLAS. *M. cf. bennettii* Christenson—DQ210352, DQ210849, DQ209639, —, *Whitten 2388*, Ecuador, cult., FLAS. *M. bicallosa* (Rchb.f.) Garay—DQ210233, DQ210749, DQ209532, —, *Atwood & Whitten 5058*, cult., SEL. *M. bicallosa*—DQ210277, DQ209946—, —, *Whitten 1677*, Ecuador, cult., FLAS. *M. bicallosa*—DQ210386, DQ209962, DQ209672, —, *Whitten 2480*, Ecuador, cult., FLAS. *M. bicallosa*—DQ210478, DQ210960, DQ209761, DQ872596, *Whitten 2636*, Panama, FLAS. *M. bicallosa*—DQ210517, DQ210998, DQ209800, —, *Whitten 2748*, Ecuador, cult., FLAS. *M. biolleyi* (Schltr.) L.O.Williams—DQ210050, DQ209897, DQ209365, —, *Blanco 2092*, Costa Rica, cult., USJ. *M. biolleyi*—DQ210019, DQ210591, DQ209333, —, *Dressler & Atwood 6241*, Panama, PMA. *M. bolivarensis* C.Schweinf.—DQ210341, DQ210838, DQ209627, —, *Whitten 2365*, Ecuador, cult., FLAS. *M. brachybulbon* Schltr.—DQ210262, DQ210773, DQ209556, DQ872533, *Whitten 1583*, Ecuador, FLAS. *M. bracteata* (Schltr.) Ames & Correll—DQ209988, DQ209864, DQ209305, —, *Atwood & Whitten 5068*, Costa Rica, cult., SEL. *M. bracteata*—DQ210180, DQ210710, DQ209487, —, *Koehler 0305*, Brazil, cult., ESA. *M. bracteata*—DQ210305, DQ210804, DQ209593, —, *Whitten 2198*, Costa Rica, FLAS. *M. bradei* Schltr. ex Hoehne—DQ210149, DQ210681, DQ209459, —, *Koehler 0138*, Brazil, UEC. *M. bradeorum* (Schltr.) L.O.Williams—DQ210443, DQ210928, DQ209727, —, *Whitten 2590*, Panama, cult., FLAS. *M. bradeorum*—DQ210481, DQ210963, DQ209764, DQ872565, *Whitten 2639*, Panama, FLAS. *M. bradeorum*—DQ210506, DQ210987, DQ209789, —, *Whitten 2716*, Ecuador, FLAS. *M. brevilabia* Ames & Correll—DQ210046, DQ209893, DQ209361, —, *Blanco 1717*, Costa Rica, USJ. *M. brevilabia*—DQ210456, DQ210940, DQ209740, —, *Whitten 2606*, Panama, cult., FLAS. *M. breviscapa* Poepp. & Endl. cf.—DQ210544, DQ211019, DQ209826, —, *Whitten 2873*, Ecuador, cult., FLAS. *M. buchtienii* Schltr.—DQ210572, DQ211047, DQ209852, DQ872592, *Whitten 2940*, Peru, cult., FLAS. *M. camaridii* Rchb.f.—DQ210086, DQ210626, DQ209398, DQ872583, *Gerlach 2003-3648*, Brazil, M. *M. camaridii*—DQ210193, DQ210723, DQ209500, —, *Koehler 0347*, Brazil, cult., UEC. *M. campanulata* C.Schweinf.—DQ210044, DQ209891, DQ209359, —, *Blanco 1679*, Costa Rica, USJ. *M. canarensis* J.T.Atwood—DQ210372, DQ209959, DQ209659, DQ872549, *Whitten 2437*, Ecuador, cult., FLAS. *M. candida* G. Lodd. ex Lindl.—DQ210189, DQ210719, DQ209496, —, *Koehler 0335*, Venezuela, ESA. *M. carinulata* Rchb.f.—DQ210263, DQ210774, DQ209557, —, *Whitten 1591*, Ecuador, FLAS. *M. carolinii* Christenson—DQ210573, DQ211048, DQ209853, —, *Whitten 2948*, Colombia, cult., FLAS. *M. cassapensis* Rchb.f.—DQ210256, DQ210768, DQ209550, —, *Whitten 1562*, Ecuador, FLAS. *M. cedralensis* J.T.Atwood & Mora-Ret.—DQ210097, DQ209916, DQ209409, —, *Mora & Warner s.n.*, Costa Rica, cult., USJ. *M. cerifera* Barb.Rodr.—DQ210117, DQ210648, DQ209428, —, *Koehler 0058*, Brazil, UEC. *M. cerifera*—DQ210307, DQ210806, DQ209595, —, *Whitten 2292*, Brazil, cult., FLAS. *M. chacoensis* Dodson—DQ210278, DQ210785, DQ209571, —, *Whitten 1693*, Ecuador, cult., FLAS. *M. chartacifolia* Ames & C.Schweinf.—DQ209981, DQ209859, DQ209298, —, *Atwood & Whitten 5059*, Ecuador, cult., SEL. *M. chartacifolia*—DQ210265, DQ209942, DQ209559, —, *Whitten 1597*, Ecuador, FLAS. *M. chartacifolia*—

- DQ210520, DQ211000, DQ209803, DQ872581, Whitten 2752, cult., FLAS. *M. chicana* Dodson—DQ461795, DQ461813, DQ461777, —, Whitten 3187, Ecuador, cult., QCA. *M. chionantha* J.T. Atwood—DQ210008, DQ210585, DQ209323, —, Atwood & Whitten 5091, Panama, SEL. *M. chionantha*—DQ210293, DQ210792, —, Whitten 1968, Panama, FLAS. *M. chionantha*—DQ210396, DQ210883, DQ209681, —, Whitten 2493, Ecuador, cult., FLAS. *M. chionantha*—DQ210476, DQ210958, DQ209759, —, Whitten 2634, Panama, FLAS. *M. chionantha*—DQ210486, DQ210969, DQ209770, DQ872568, Whitten 2649, Panama, FLAS. *M. coccinea* (Jacq.) L.O. Williams ex Hodge—DQ210009, DQ209875, DQ209324, —, Atwood & Whitten 5092, Puerto Rico, cult., SEL. *M. colemanii* Carnevali & Fritz—DQ209989, DQ209865, DQ209306, —, Atwood & Whitten 5069, Venezuela, SEL. *M. concavilabia* Ames & Correll—DQ210445, DQ210930, DQ209729, —, Whitten 2595, Panama, FLAS. *M. conduplicata* (Ames & C. Schweinf.) L.O. Williams—DQ209991, DQ210577, DQ209308, —, Atwood & Whitten 5071, Costa Rica, SEL. *M. conduplicata*—DQ210041, DQ209889, DQ209356, —, Blanco 1660, Costa Rica, USJ. *M. confusa* Ames & C. Schweinf.—DQ210001, DQ210579, DQ209317, —, Atwood & Whitten 5083, Costa Rica, SEL. *M. confusa*—DQ210343, DQ210840, DQ209629, —, Whitten 2367, Ecuador, cult., FLAS. *M. confusa*—DQ210513, DQ210994, DQ209796, DQ872576, Whitten 2736, Panama, cult., FLAS. *M. cf. confusa*—DQ210480, DQ210962, DQ209763, —, Whitten 2638, Panama, Bocas del Toro, Fortuna Dam site to Chiriquí Grande, FLAS. *M. consanguinea* Klotzsch—DQ210188, DQ210718, DQ209495, —, Koehler 0333, Brazil, ESA. *M. costaricensis* Schltr.—DQ210036, DQ209884, DQ209350, —, Blanco 1475, Costa Rica, cult., USJ. *M. costaricensis* Schltr.—DQ210288, DQ210788, DQ209579, —, Whitten 1910, Panama, FLAS. *M. crocea* Lindl.—DQ210103, DQ210634, DQ209415, —, Koehler 0005, Brazil, UEC. *M. crocea*—DQ210311, DQ210810, DQ209599, —, Whitten 2299, Brazil, cult., FLAS. *M. cryptobulbon* Carnevali & J.T. Atwood—DQ209982, DQ209860, DQ209299, —, Atwood & Whitten 5060, Ecuador, cult., SEL. *M. cryptobulbon*—DQ210397, DQ210884, DQ209682, —, Whitten 2494, Ecuador, cult., FLAS. *M. ctenostachya* Rchb.f.—DQ210098, DQ209917, DQ209410, —, Morales 1639, Costa Rica, USJ. *M. ctenostachya*—DQ210412, DQ210899, DQ209697, —, Whitten 2549, Panama, cult., FLAS. *M. ctenostachya*—DQ210484, DQ210967, DQ209768, DQ872567, Whitten 2647, Panama, FLAS. *M. cucullata* Lindl.—DQ210237, DQ210753, DQ209535, —, Atwood & Whitten 5066, Venezuela, cult., SEL. *M. cucullata*—DQ209997, DQ209871, DQ209313, —, Atwood & Whitten 5079, cult., SEL. *M. cucullata*—DQ210178, DQ210708, DQ209485, DQ872602, Koehler 0298, Costa Rica, cult., ESA. *M. cucullata*—DQ210411, DQ210898, DQ209696, —, Whitten 2546, cult., FLAS. *M. curvicolonna* M.A. Blanco & Neubig—DQ210474, DQ210956, DQ209757, —, Whitten 2632, Panama, FLAS. *M. cymbidioides* Dodson J.T. Atwood & Carnevali—DQ209987, DQ209863, DQ209304, —, Atwood & Whitten 5067, Ecuador, SEL. *M. dalessandroi* Dodson—DQ210366, DQ210860, DQ209653, —, Whitten 2409, Ecuador, cult., FLAS. *M. cf. dalessandroi*—DQ210549, DQ211024, —, Whitten 2889, Peru, cult., FLAS. *M. dendrobioides* (Schltr.) L.O. Williams—DQ210020, DQ210592, DQ209334, —, Dressler & Atwood 6243, Panama, PMA. *M. dendrobioides*—DQ210449, DQ210934, DQ209733, —, Whitten 2599, Panama, cult., FLAS. *M. dendrobioides*—DQ210469, DQ210952, DQ209752, DQ872561, Whitten 2627, Panama, FLAS. *M. dendrobioides*—DQ210491, DQ210974, DQ209775, —, Whitten 2655, Panama, FLAS. *M. densa* Lindl.—DQ209992, DQ209867, DQ209309, —, Atwood & Whitten 5072, Mexico, cult., SEL. *M. densa*—DQ210091, DQ210629, DQ209403, —, Higgins 1017, Mexico, FLAS. *M. densa*—DQ210290, DQ210790, DQ209581, —, Whitten 1964, cult., FLAS. *M. densifolia* (Poepp. & Endl.) Rchb.f.—DQ210253, DQ210767, DQ209547, —, Whitten 1554, Ecuador, FLAS. *M. desvauxiana* Rchb.f.—DQ210206, DQ210736, DQ209513, —, Koehler 1585, Brazil, ESA. *M. dichotoma* (Schltr.) L.O. Williams—DQ210441, DQ210926, DQ209725, —, Whitten 2584, Panama, FLAS. *M. dichotoma*—DQ210527, DQ211005, DQ209809, —, Whitten 2777, Panama, cult., FLAS. *M. dillonii* D.E. Benn. & Christenson—DQ210434, DQ209965, DQ209718, —, Whitten 2575, cult., FLAS. *M. dillonii*—DQ210546, DQ211021, DQ209828, DQ872586, Whitten 2878, Peru, cult., FLAS. *M. cf. disticha* (Lindl.) C. Schweinf.—DQ461791, DQ461809, DQ461773, —, Whitten 3165, Ecuador, QCA. *M. diuturna* Ames & C. Schweinf.—DQ210033, DQ209882, DQ209347, —, Blanco 0620, Costa Rica, cult., USJ. *M. diuturna*—DQ210022, DQ210594, DQ209336, —, Dressler & Atwood 6251, Panama, PMA. *M. diuturna*—DQ210314, DQ210813, DQ209602, —, Whitten 2305, Colombia, cult., FLAS. *M. diuturna*—DQ210473, DQ210955, DQ209756, —, Whitten 2631, Panama, FLAS. *M. diuturna*—DQ210530, DQ209975, DQ209812, —, Whitten 2780, Panama, cult., FLAS. *M. divaricata* (Barb. Rodr.) Cogn.—DQ210378, DQ210869, DQ209664, —, Whitten 2450, Ecuador, cult., FLAS. *M. dressleriana* Carnevali & J.T. Atwood—DQ209980, DQ209858, DQ209297, —, Atwood & Whitten 5057, Costa Rica, cult., SEL. *M. eburnea* Lindl.—DQ210454, DQ210938, DQ209738, —, Whitten 2604, Ecuador, cult., FLAS. *M. echiniphyta* Barb. Rodr.—DQ210197, DQ210727, DQ209504, —, Koehler 0353, Brazil, UEC. *M. echiniphyta* Barb. Rodr.—DQ210246, DQ210762, DQ209540, —, Whitten 2990, Brazil, cult., FLAS. *M. echiniphyta*—DQ210250, DQ210765, DQ209544, —, Whitten 1056, Brazil, cult., FLAS. *M. ecuadorensis* Schltr.—DQ210259, DQ210771, DQ209553, —, Whitten 1572, Ecuador, FLAS. *M. ecuadorensis*—DQ210508, DQ210989, DQ209791, DQ872574, Whitten 2724, Ecuador, FLAS. *M. elatior* (Rchb.f.) Rchb.f.—DQ210298, DQ210797, DQ209587, DQ872536, Whitten 1986, cult., FLAS. *M. elegantula* Rolfe—DQ210024, DQ210596, DQ209338, —, Dressler & Atwood 6262, Ecuador, cult., PMA. *M. elegantula*—DQ210025, DQ210597, DQ209339, —, Dressler & Atwood 6264, Ecuador, cult., PMA. *M. elegantula*—DQ210435, DQ210921, DQ209719, —, Whitten 2576, Ecuador, cult., FLAS. *M. elegantula*—DQ210437, DQ210923, DQ209721, —, Whitten 2578, Ecuador, cult., FLAS. *M. elegantula*—DQ210543, DQ211018, DQ209825, DQ872558, Whitten 2872, Ecuador, cult., FLAS. *M. encyclioides* J.T. Atwood & Dodson—DQ209983, DQ209861, DQ209300, —, Atwood & Whitten 5061, Ecuador, SEL. *M. endresii* Rchb.f.—DQ210010, DQ210586, DQ209325, —, Atwood & Whitten 5093, Costa Rica, SEL. *M. exaltata* (Kraenzl.) C. Schweinf.—DQ210029, DQ210601, DQ209343, —, Dressler & Atwood 6277, Panama, FLAS. *M. exaltata*—DQ210251, DQ209938, DQ209545, —, Whitten 1506, Ecuador, FLAS. *M. exaltata*—DQ210319, DQ210818, DQ209607, DQ872541, Whitten 2317, Ecuador, FLAS. *M. exaltata*—DQ210320, DQ210819, DQ209608, —, Whitten 2318, Ecuador, FLAS. *M. cf. exaltata*—DQ210325, DQ210824, DQ209613, —, Whitten 2332, Ecuador, FLAS. *M. cf. exaltata*—DQ210326, DQ210825, DQ209614, —, Whitten 2333, Ecuador, FLAS. *M. exaltata* × *M. porrecta*—DQ210080, DQ210623, DQ209393, —, Blanco 2986, Panama, FLAS. *M. falcata* Ames & Correll—DQ210079, DQ210622, DQ209392, —, Blanco 2975, Panama, cult., FLAS. *M. ferdinandiana* Barb. Rodr.—DQ210129, DQ210660, DQ209440, —, Koehler 0089, Brazil, SP. *M. ferdinandiana*—DQ210139, DQ210670, DQ209449, DQ872523, Koehler 0109, Brazil, SP. *M. ferdinandiana*—DQ210286, DQ209951, DQ209577, —, Whitten 1872, Brazil, cult., FLAS. *M. flava* Ames, F.T. Hubb. & C. Schweinf.—DQ210242, DQ210757, —, Dressler 5441, Panama, FLAS. *M. flava*—DQ210438, DQ210924, DQ209722, —, Whitten 2579, Panama, cult., FLAS. *M. flava*—DQ210460, DQ210944, DQ209744, —, Whitten 2611, Panama, cult., FLAS. *M. flava*—DQ210468, DQ210951, DQ209751, —, Whitten 2624, Panama, FLAS. *M. fletcheriana* Rolfe—DQ210209, DQ210739, —, Whitten 88028, Ecuador, FLAS. *M. fractiflexa* Rchb.f.—DQ210074, DQ210617, DQ209387, —, Blanco 2956, Ecuador, cult., FLAS. *M. friedrichsthalii* Rchb.f.—DQ210145, DQ210676, DQ209455, —, Koehler 0125, Brazil, UEC. *M. friedrichsthalii*—DQ210210, DQ209923, DQ209516, —, Whitten 1977, French Guiana, cult., FLAS. *M. cf. friedrichsthalii*—DQ210224, DQ209929, —, Whitten 1977, French Guiana, cult., FLAS. *M. fulgens* (Rchb.f.) L.O. Williams—DQ210225, DQ209930, DQ209525, —, Dressler 5452,

- Panama, FLAS. *M. fulgens*—DQ210472, DQ209968, DQ209755, DQ872563, Whitten 2630, Panama, FLAS. *M. galantha* J.T. Atwood & Carnevali—DQ210574, DQ211049, DQ209854, —, Whitten 2951, Panama, FLAS. *M. gentryi* Dodson—DQ210347, DQ210845, DQ209634, —, Whitten 2379, Ecuador, cult., FLAS. *M. gentryi*—DQ210400, DQ210887, DQ209685, —, Whitten 2499, Ecuador, cult., FLAS. *M. gentryi*—DQ210492, DQ210975, DQ209776, DQ872572, Whitten 2656, Panama, FLAS. *M. gigantea* (Lindl.) Dodson—DQ210260, DQ209941, DQ209554, —, Whitten 1579, Ecuador, FLAS. *M. gigantea*—DQ210318, DQ210817, DQ209606, DQ872540, Whitten 2316, Ecuador, FLAS. *M. gigantea*—DQ210359, DQ209956, DQ209646, —, Whitten 2398, Ecuador, cult., FLAS. *M. gomeziana* J.T. Atwood—DQ210297, DQ210796, DQ209586, —, Atwood s.n., SEL. *M. gomeziana*—DQ210228, DQ209932, DQ209527, —, Whitten 1985, Costa Rica, FLAS. *M. cf. grandiflora* (Kunth) Lindl.—DQ210026, DQ210598, DQ209340, —, Dressler & Atwood 6265, Ecuador, cult., PMA. *M. grayi* Dodson—DQ210547, DQ211022, DQ209829, DQ872587, Whitten 2879, Peru, cult., FLAS. *M. grisebachiana* Nir & Dod—DQ210542, DQ211017, DQ209824, —, Whitten 2841, Cuba, cult., FLAS. *M. guadalupensis* Cogn.—DQ210504, DQ210985, DQ209787, —, Whitten 2714, Ecuador, FLAS. *M. guadalupensis*—DQ210264, DQ210775, DQ209558, DQ872535, Whitten 1593, Ecuador, FLAS. *M. guadalupensis*—DQ210502, DQ210983, DQ209785, —, Whitten 2704, Ecuador, FLAS. *M. gualaquizensis* Dodson—DQ461796, DQ461814, DQ461778, —, Whitten 3188, Ecuador, cult., QCA. *M. guareimensis* Rchb.f.—DQ210565, DQ211040, DQ209845, —, Whitten 2920, Ecuador, cult., FLAS. *M. haberi* J.T. Atwood—DQ210032, DQ209881, DQ209346, —, Blanco 0496, Costa Rica, USJ. *M. hedwigiae* Hamer & Dodson—DQ209994, DQ209869, DQ209311, —, Atwood & Whitten 5074, Costa Rica, cult., SEL. *M. hedwigiae*—DQ210182, DQ210712, DQ209489, —, Koehler 0314, Guatemala, cult., ESA. *M. hedwigiae*—DQ210213—, —, Whitten 1961, Costa Rica, FLAS. *M. hennisiana* Schltr.—DQ210013, DQ209878—, —, Atwood & Whitten 5096, Ecuador, cult., SEL. *M. hennisiana*—DQ210431, DQ210918, DQ209715, DQ872557, Whitten 2572, Ecuador, cult., FLAS. *M. hennisiana*—DQ210529, DQ209974, DQ209811, —, Whitten 2779, Panama, cult., FLAS. *M. hennisiana*—DQ210536, DQ211011, DQ209818, —, Whitten 2808, Ecuador, cult., FLAS. *M. hennisiana*—DQ210537, DQ211012, DQ209819, —, Whitten 2809, Ecuador, cult., FLAS. *M. heterophylla* var. *acicularifolia* Hoehne—DQ210132, DQ210663, DQ209443, —, Koehler 0095, Brazil, SP. *M. heterophylla* var. *acicularifolia*—DQ210208, DQ210738, DQ209515, —, Koehler 1706, Brazil, SP. *M. heterophylla* var. *intermedia* Hoehne—DQ210162, —, DQ209470, —, Koehler 0240, Brazil, cult., UEC. *M. heterophylla* var. *magnifolia* Hoehne—DQ210165, DQ210695, DQ209473, —, Koehler 0245, Brazil, UEC. *M. heterophylla* var. *pygmaea* Hoehne—DQ210141, DQ210672, DQ209451, —, Koehler 0113, Brazil, SP. *M. heterophylla* var. *pygmaea*—DQ210174, DQ210704, DQ209481, —, Koehler 0278, Brazil, ESA. *M. heterophylla* var. *pygmaea*—DQ210176, DQ210706, DQ209483, —, Koehler 0292, Brazil, ESA. *M. hillsii* Dodson cf. —DQ210073, DQ210616, DQ209386, —, Blanco 2954, Ecuador, cult., FLAS. *M. horichii* Senghas—DQ210452, DQ210937, DQ209736, DQ872559, Whitten 2602, Panama, cult., FLAS. *M. horichii*—DQ210462, DQ210946, DQ209745, —, Whitten 2615, Panama, FLAS. *M. cf. horichii*—DQ210002, DQ210580, DQ209318, —, Atwood & Whitten 5084, Costa Rica, cult., SEL. *M. houtteana* Rchb.f.—DQ210559, DQ211034, DQ209839, —, Whitten 2910, Mexico, cult., FLAS. *M. huebschii* Rchb.f.—DQ210570, DQ211045, DQ209850, —, Whitten 2935, Ecuador, cult., FLAS. *M. imbricata* Barb.Rodr.—DQ210329, DQ210828, DQ209616, DQ872542, Whitten 2337, Ecuador, FLAS. *M. imbricata*—DQ210111, DQ210642, DQ209422, —, Koehler 0025, Brazil, UEC. *M. inaudita* Rchb.f.—DQ209977, DQ209855, DQ209294, —, Atwood & Whitten 5054, Panama, SEL. *M. inaudita*—DQ210524, DQ211004, DQ209806, —, Whitten 2763, Panama, FLAS. *M. irrorata* Rchb.f.—DQ210430, DQ210917, DQ209714, —, Whitten 2571, Ecuador, cult., FLAS. *M. johannis* Pabst—DQ210147, DQ210679, DQ209458, —, Koehler 0132, Brazil, UEC. *M. jostii* Dodson—DQ210092, DQ210630, DQ209404, —, Jost 3133, Ecuador, QCA. *M. jucunda* F. Lehm. & Kraenzl.—DQ210440, DQ210925, DQ209724, —, Whitten 2581, Ecuador, cult., FLAS. *M. jucunda*—DQ210455, DQ210939, DQ209739, —, Whitten 2605, Ecuador, cult., FLAS. *M. juergensii* Schltr.—DQ210120, DQ210651, DQ209431, —, Koehler 0069, Brazil, SP. *M. juergensii*—DQ210124, DQ210655, DQ209435, —, Koehler 0079, Brazil, cult., SP. *M. juergensii*—DQ210140, DQ210671, DQ209450, —, Koehler 0111, Brazil, cult., SP. *M. klugii* C. Schweinf.—DQ210354, DQ209955, DQ209641, —, Whitten 2390, Ecuador, cult., FLAS. *M. klugii*—DQ210395, DQ210882, DQ209680, —, Whitten 2492, Ecuador, cult., FLAS. *M. klugii*—DQ210533, DQ209976, DQ209815, —, Whitten 2787, Ecuador, cult., FLAS. *M. laevilabris* Lindl.—DQ210334, DQ210832, DQ209621, DQ872544, Whitten 2358, Ecuador, cult., FLAS. *M. cf. laevilabris*—DQ210345, DQ210842, DQ209631, —, Whitten 2372, Ecuador, cult., FLAS. *M. lankesteri* Ames—DQ210554, DQ211029, DQ209835, —, Whitten 2901, Costa Rica, cult., FLAS. *M. lankesteri*—DQ210243, DQ210759—, —, Whitten 2885, Costa Rica, cult., FLAS. *M. lawrenceana* (Rolfe) Garay & Dunst.—DQ210451, DQ210936, DQ209735, —, Whitten 2601, Colombia, cult., FLAS. *M. lehmannii* Rchb.f.—DQ210268, DQ210778, DQ209562, —, Whitten 1641, Ecuador, cult., FLAS. *M. lepidota* Lindl.—DQ210562, DQ211037, DQ209842, —, Whitten 2914, Ecuador, cult., FLAS. *M. aff. lepidota*—, —, DQ210783, DQ209566, —, Whitten 1665, Ecuador, cult., FLAS. *M. aff. lepidota*—DQ210351, DQ210848, DQ209638, —, Whitten 2387, Ecuador, cult., FLAS. *M. cf. lepidota*—DQ210363, DQ210857, DQ209650, —, Whitten 2406, Ecuador, cult., FLAS. *M. leucimata* Barb.Rodr.—DQ210107, DQ210638, DQ209419, —, Koehler 0015, Brazil, UEC. *M. linearifolia* Ames & C. Schweinf.—DQ210096, DQ209915, DQ209408, —, Mora 001–92, Costa Rica, cult., USJ. *M. loefgrenii* (Cogn.) Pabst—DQ210194, DQ210724, DQ209501, —, Koehler 0349, Brazil, UEC. *M. longibracteata* (Lindl.) Rchb.f.—DQ210353, DQ210850, DQ209640, —, Whitten 2389, Ecuador, cult., FLAS. *M. longicaulis* Schltr.—DQ210510, DQ210991, DQ209793, —, Whitten 2726, Ecuador, FLAS. *M. longicolumna* J.T. Atwood—DQ210495, DQ210978, DQ209779, —, Whitten 2667, Panama, FLAS. *M. longiloba* (Ames & C. Schweinf.) J.T. Atwood—DQ210432, DQ210919, DQ209716, —, Whitten 2573, cult., FLAS. *M. longipes* Lindl.—DQ210077, DQ210620, DQ209390, —, Blanco 2965, Ecuador, cult., FLAS. *M. longipes*—DQ210413, DQ210900, DQ209698, —, Whitten 2550, Ecuador, cult., FLAS. *M. longipes*—DQ210433, DQ210920, DQ209717, —, Whitten 2574, Ecuador, cult., FLAS. *M. longipes*—DQ210519, DQ210999, DQ209802, DQ872580, Whitten 2751, Ecuador, cult., FLAS. *M. longipetiolata* Ames & C. Schweinf.—DQ210229, DQ210747, DQ209528, DQ872529, Atwood & Whitten 5075, Costa Rica, SEL. *M. longipetiolata*—DQ210236, DQ209935, DQ209534, —, Whitten 1974, Costa Rica, FLAS. *M. longissima* Lindl.—DQ210269, DQ210779, DQ209563, —, Whitten 1642, Ecuador, cult., FLAS. *M. longissima*—DQ210360, DQ210855, DQ209647, —, Whitten 2399, Ecuador, cult., FLAS. *M. longissima*—DQ210515, DQ210996, DQ209798, DQ872578, Whitten 2745, Ecuador, cult., FLAS. *M. cf. loretoensis* C. Schweinf.—DQ210361, DQ210856, DQ209648, —, Whitten 2400, Ecuador, cult., QCA. *M. lueri* Dodson—DQ210003, DQ210581, DQ209319, —, Atwood & Whitten 5085, cult., SEL. *M. lueri*—DQ210303, DQ210802, DQ209591, —, Whitten 2051, Costa Rica, FLAS. *M. lueri*—DQ210471, DQ210954, DQ209754, DQ872562, Whitten 2629, Panama, FLAS. *M. lutheri* J.T. Atwood—DQ210422, DQ210909, DQ209707, —, Whitten 2563, Panama, FLAS. *M. lutheri*—DQ210426, DQ210913, DQ209711, —, Whitten 2567, Panama, cult., FLAS. *M. lutheri*—DQ210428, DQ210915, DQ209713, —, Whitten 2569, Panama, Chiriquí, cult., FLAS. *M. madida* Lindl.—DQ210119, DQ210650, DQ209430, —, Koehler 0065, Brazil, SP. *M. madida*—DQ210125, DQ210656, DQ209436, —, Koehler 0081, Brazil, SP. *M. madida*—DQ210138, DQ210669, DQ209448, —, Koehler 0107, Brazil, SP. *M. madida*—DQ210284, DQ209949, DQ209576, —, Whitten 1868, Brazil, cult., FLAS. *M. cf. madida*—DQ210498,

- DQ210980, DQ209782, —, Whitten 2673, Ecuador, cult., FLAS. *M. mapiariensis* (Kraenzl.) L.O. Williams—DQ210571, DQ211046, DQ209851, —, Whitten 2936, Ecuador, cult., FLAS. *M. marmoliana* Dodson—DQ210349, DQ209954, DQ209636, —, Whitten 2381, Ecuador, cult., FLAS. *M. meleagris* Lindl.—DQ210038, DQ209886, DQ209353, —, Blanco 1604, Guatemala, cult., FLAS. *M. meleagris*—DQ210539, DQ211014, DQ209821, —, Whitten 2816, Guatemala, cult., FLAS. *M. meridensis* Lindl.—DQ210037, DQ209885, DQ209351, —, Blanco 1562, Costa Rica, cult., USJ. *M. meridensis*—DQ210258, DQ210770, DQ209552, —, Whitten 1568, Ecuador, FLAS. *M. meridensis*—DQ210270, DQ210780—, —, Whitten 1647, Ecuador, cult., FLAS. *M. meridensis*—DQ210379, DQ210870, DQ209665, DQ872550, Whitten 2451, Ecuador, cult., FLAS. *M. meridensis*—DQ210427, DQ210914, DQ209712, —, Whitten 2568, Panama, cult., FLAS. *M. mexicana* J.T. Atwood—DQ210299, DQ210798, DQ209588, —, Whitten 1989, cult., FLAS. *M. microphyton* Schltr.—DQ210316, DQ210815, DQ209604, —, Whitten 2307, Costa Rica, cult., FLAS. *M. microphyton*—DQ210442, DQ210927, DQ209726, —, Whitten 2586, Panama, cult., FLAS. *M. microphyton*—DQ210493, DQ210976, DQ209777, —, Whitten 2659, Panama, FLAS. *M. cf. microphyton*—DQ210017, DQ210589, DQ209331, —, Dressler & Atwood 6238, Panama, PMA. *M. miniata* (Lindl.) L.O. Williams—DQ210062, DQ209908, DQ209377, —, Blanco 2261, Venezuela, cult., USJ. *M. minor* (Schltr.) L.O. Williams—DQ210448, DQ210933, DQ209732, —, Whitten 2598, Panama, cult., FLAS. *M. minor*—DQ210457, DQ210941, DQ209741, —, Whitten 2607, Panama, cult., FLAS. *M. minor*—DQ210470, DQ210953, DQ209753, —, Whitten 2628, Panama, FLAS. *M. minuta* Cogn.—DQ210133, DQ210664, DQ209444, —, Koehler 0097, Brazil, cult., SP. *M. minuta*—DQ210166, DQ210696, DQ209474, —, Koehler 0253, Brazil, UEC. *M. modesta* Schltr.—DQ210195, DQ210725, DQ209502, —, Koehler 0351, Brazil, UEC. *M. molitor* Rchb.f.—DQ210369, DQ210863, DQ209656, —, Whitten 2424, Ecuador, cult., FLAS. *M. molitor*—DQ210370, DQ210864, DQ209657, —, Whitten 2425, Ecuador, cult., FLAS. *M. moralesii* Carnevali & J.T. Atwood—DQ210051, DQ209898, DQ209366, —, Blanco 2097, Costa Rica, USJ. *M. moralesii*—DQ210295, DQ210794—, —, Whitten 1976, Costa Rica, FLAS. *M. mosonii* var. *echinochila* Hoehne—DQ210128, DQ210659, DQ209439, —, Koehler 0087, Brazil, SP. *M. mosonii* var. *echinochila*—DQ210177, DQ210707, DQ209484, —, Koehler 0294, Brazil, ESA. *M. mosonii* var. *hatschbachii* Hoehne—DQ210121, DQ210652, DQ209432, —, Koehler 0071, Brazil, UEC. *M. mosonii* var. *hatschbachii*—DQ210126, DQ210657, DQ209437, —, Koehler 0083, Brazil, SP. *M. multicaulis* (Poepp. & Endl.) C. Schweinf.—DQ210557, DQ211032, —, DQ872589, Whitten 2905, Ecuador, cult., FLAS. *M. multiflora* Barb.Rodr.—DQ210186, DQ210716, DQ209493, —, Koehler 0325, Brazil, ESA. *M. murilliana* Hoehne—DQ210548, DQ211023, DQ209830, —, Whitten 2883, Brazil, cult., FLAS. *M. nardoides* Kraenzl.—DQ210335, DQ210833—, —, Whitten 2359, Ecuador, cult., FLAS. *M. nardoides*—DQ210403, DQ210890, DQ209688, DQ872554, Whitten 2502, Ecuador, cult. Ecuagenera, FLAS. *M. nasuta* Rchb.f.—DQ210169, DQ210699, DQ209476, —, Koehler 0261, Brazil, ESA. *M. nasuta*—DQ210241, DQ210756, DQ209539, DQ872532, Whitten 1869, Ecuador, FLAS. *M. neglecta* (Schltr.) L.O. Williams—DQ210045, DQ209892, DQ209360, —, Blanco 1680, Costa Rica, USJ. *M. cf. neglecta*—DQ210383, DQ210874, DQ209669, —, Whitten 2466, Ecuador, cult., FLAS. *M. neophylla* Rchb.f.—DQ210550, DQ211025, DQ209831, —, Whitten 2891, Ecuador, cult., FLAS. *M. neowiedii* Rchb.f.—DQ210122, DQ210653, DQ209433, —, Koehler 0073, Brazil, SP. *M. neowiedii*—DQ210130, DQ210661, DQ209441, —, Koehler 0091, Brazil, SP. *M. neowiedii*—DQ210163, DQ209922, DQ209471, —, Koehler 0241, Brazil, UEC. *M. nicaraguensis* (Hamer & Garay) J.T. Atwood—, —, DQ210604, DQ209352, —, Blanco 1582, Costa Rica, USJ. *M. niesseniae* Christenson—DQ210560, DQ211035, DQ209840, —, Whitten 2911, Colombia, cult., FLAS. *M. notylioglossa* Rchb.f.—DQ210114, DQ210645, DQ209425, —, Koehler 0033, Brazil, UEC. *M. notylioglossa*—DQ210167, DQ210697, —, DQ872601, Koehler 0255, Brazil, UEC. *M. cf. nubigena* (Rchb.f.) C. Schweinf.—DQ210507, DQ210988, DQ209790, —, Whitten 2718, Ecuador, FLAS. *M. cf. nubigena*—DQ461789, DQ461807, DQ461771, —, Whitten 3160, Ecuador, QCA. *M. aff. nutans* Lindl.—DQ210561, DQ211036, DQ209841, —, Whitten 2912, Ecuador, cult., FLAS. *M. obscura* Linden & Rchb.f.—DQ210048, DQ209895, DQ209363, —, Blanco 1827, Costa Rica, cult., USJ. *M. ochroleuca* Lodd. ex Lindl.—DQ210105, DQ210636, DQ209417, —, Koehler 0011, Brazil, UEC. *M. ochroleuca*—DQ210346, DQ210844, DQ209633, DQ872546, Whitten 2378, Ecuador, cult., FLAS. *M. oreocharis* Schltr.—DQ210004, DQ210582, DQ209320, —, Atwood & Whitten 5086, Costa Rica, SEL. *M. oreocharis*—DQ210444, DQ210929, DQ209728, —, Whitten 2594, Panama, FLAS. *M. oreocharis*—DQ210465, DQ210949, DQ209748, —, Whitten 2619, Panama, FLAS. *M. oreocharis*—DQ210488, DQ210971, DQ209772, DQ872569, Whitten 2652, Panama, FLAS. *M. pacholskii* Christenson—DQ210355, DQ210851, DQ209642, DQ872600, Whitten 2393, Ecuador, cult., FLAS. *M. pacholskii*—DQ210382, DQ210873, DQ209668, —, Whitten 2464, Ecuador, cult., FLAS. *M. pacholskii*—DQ210402, DQ210889, DQ209687, —, Whitten 2501, Ecuador, cult., FLAS. *M. pachyacron* Schltr.—DQ210059, DQ209906, DQ209374, —, Blanco 2235, Costa Rica, USJ. *M. pachyacron*—DQ210021, DQ210593, DQ209335, —, Dressler & Atwood 6249, Panama, PMA. *M. pachyacron*—DQ210489, DQ210972, DQ209773, DQ872570, Whitten 2653, Panama, cult., FLAS. *M. pachyphylla* Schltr. ex Hoehne—DQ210015, DQ209879, DQ209329, —, Atwood & Whitten 5098, Brazil, cult., SEL. *M. pachyphylla*—DQ210137, DQ210668, —, DQ872522, Koehler 0105, Brazil, SP. *M. pachyphylla*—DQ210203, DQ210733, DQ209510, —, Koehler 0369, Brazil, cult., ESA. *M. pachyphylla*—DQ210285, DQ209950—, —, Whitten 1868, Brazil, cult., FLAS. *M. paleata* (Rchb.f.) Ames & Correll—DQ210420, DQ210907, DQ209705, DQ872556, Whitten 2561, Panama, FLAS. *M. paleata* (Rchb.f.) Ames & Correll—DQ210421, DQ210908, DQ209706, —, Whitten 2562, Panama, FLAS. *M. paleata*—DQ210424, DQ210911, DQ209709, —, Whitten 2565, Panama, cult., FLAS. *M. pardalina* Garay—DQ210065, DQ210608—, —, Blanco 2524, Ecuador, FLAS. *M. parkeri* Hook.—DQ210144, DQ210675, DQ209454, —, Koehler 0119, Brazil, UEC. *M. parviflora* (Poepp. & Endl.) Garay—DQ209990, DQ209866, DQ209307, DQ872530, Atwood & Whitten 5070, Costa Rica, SEL. *M. parviflora*—DQ210112, DQ210643, DQ209423, —, Koehler 0027, Brazil, UEC. *M. parviflora*—DQ210302, DQ210801, DQ209590, —, Whitten 2019, Haiti, FLAS. *M. parviflora*—DQ210541, DQ211016, DQ209823, —, Whitten 2822, Jamaica, cult., FLAS. *M. patens* Schltr.—DQ210261, DQ210772, DQ209555, —, Whitten 1580, Ecuador, FLAS. *M. patens* Schltr.—DQ210505, DQ210986, DQ209788, —, Whitten 2715, Ecuador, FLAS. *M. patens*—DQ210528, DQ211006, DQ209810, —, Whitten 2778, Panama, cult., FLAS. *M. aff. patens*—DQ210509, DQ210990, DQ209792, —, Whitten 2725, Ecuador, FLAS. *M. pauciflora* Barb.Rodr.—DQ210093, DQ210631, DQ209405, —, Jost 5002, Ecuador, QCA. *M. pauciflora*—DQ210344, DQ210841, DQ209630, —, Whitten 2368, Ecuador, FLAS. *M. pauciflora*—DQ210390, DQ209964, DQ209675, —, Whitten 2484, Ecuador, cult., FLAS. *M. pendens* Pabst—, —, DQ210677, DQ209456, —, Koehler 0128, Brazil, cult., UEC. *M. pendula* (Poepp. & Endl.) C. Schweinf.—DQ210405, DQ210892, DQ209690, —, Whitten 2513, Ecuador, cult., FLAS. *M. perryae* Dodson—DQ210006, DQ210584—, —, Atwood & Whitten 5088, Ecuador, SEL. *M. perryae*—DQ461786, DQ461804, DQ461768, —, Jost 8101, Ecuador, QCA. *M. perryae*—DQ210275, DQ209944, DQ209569, —, Whitten 1672, Ecuador, cult., FLAS. *M. aff. perryae*—DQ461801, DQ461819, DQ461783, —, Whitten 3200, Ecuador, cult., QCA. *M. pittieri* (Ames) L.O. Williams—DQ210060, DQ209907, DQ209375, —, Blanco 2237, Costa Rica, USJ. *M. pittieri*—DQ210439, DQ209966, DQ209723, —, Whitten 2580, Panama, FLAS. *M. platypetala* Ruiz & Pav.—DQ210558, DQ211033,

- DQ209838, —, *Whitten 2909*, Peru, cult., FLAS. *M. plebeja* Rchb.f.—DQ210127, DQ210658, DQ209438, —, *Koehler 0085*, Brazil, SP. *M. plebeja*—DQ210207, DQ210737, DQ209514, —, *Koehler 1653*, Brazil, SP. *M. plebeja*—DQ210281, DQ209947, DQ209573, —, *Whitten 1834*, Brazil, cult., FLAS. *M. ponerantha* Rchb.f.—DQ210339, DQ210837, DQ209625, —, *Whitten 2363*, Ecuador, cult., FLAS. *M. ponerantha*—DQ210417, DQ210904, DQ209702, —, *Whitten 2555*, Panama, FLAS. *M. ponerantha*—DQ210490, DQ210973, DQ209774, DQ872571, *Whitten 2654*, Panama, cult., FLAS. *M. aff. ponerantha*—DQ210418, DQ210905, DQ209703, —, *Whitten 2558*, Panama, cult., FLAS. *M. porrecta* Lindl.—DQ209985, DQ210576, DQ209302, —, *Atwood & Whitten 5064*, Ecuador, cult., SEL. *M. porrecta*—DQ210031, DQ209880, DQ209345, —, *Blanco 0337*, Costa Rica, cult., USJ. *M. porrecta*—DQ210100, DQ209919, DQ209412, —, *Pupulin 0978*, Costa Rica, USJ. *M. porrecta*—DQ210291, DQ210791, DQ209582, —, *Whitten 1966*, Costa Rica, cult., FLAS. *M. porrecta*—DQ210292, —, DQ209583, —, *Whitten 1967*, Ecuador, FLAS. *M. porrecta*—DQ210464, DQ210948, DQ209747, DQ872560, *Whitten 2617*, Panama, FLAS. *M. porrecta*—DQ210568, DQ211043, DQ209848, —, *Whitten 2931*, Venezuela, cult., FLAS. *M. proboscidea* Rchb.f.—DQ209979, DQ209857, DQ209296, DQ872531, *Atwood & Whitten 5056*, Venezuela, cult., SEL. *M. procurrens* Lindl.—DQ210272, DQ210782, DQ209565, —, *Whitten 1657*, Ecuador, cult., FLAS. *M. procurrens*—DQ210358, DQ210854, DQ209645, DQ872548, *Whitten 2397*, Ecuador, cult., FLAS. *M. procurrens*—DQ210373, DQ210865, DQ209660, —, *Whitten 2438*, Ecuador, cult., FLAS. *M. procurrens*—DQ210380, DQ210871, DQ209666, —, *Whitten 2452*, Ecuador, cult., FLAS. *M. pseudoneglecta* J.T.Atwood—DQ210007, DQ209874, DQ209322, —, *Atwood & Whitten 5089*, Costa Rica, cult., SEL. *M. pseudoneglecta*—DQ210222, DQ209927, DQ209523, —, *Whitten 2626*, Panama, FLAS. *M. pseudoreichenheimiana* Dodson—DQ209996—, —, —, *Atwood & Whitten 5078*, Ecuador, cult., SEL. *M. pseudoreichenheimiana*—DQ210328, DQ210827—, —, *Whitten 2335*, Ecuador, FLAS. *M. pulla* Linden & Rchb.f.—DQ210381, DQ210872, DQ209667, DQ872551, *Whitten 2459*, Ecuador, cult., FLAS. *M. pumila* Hook.—DQ210131, DQ210662, DQ209442, —, *Koehler 0094*, Brazil, cult., SP. *M. pumila*—DQ210135, DQ210666, DQ209446, —, *Koehler 0101*, Brazil, SP. *M. pumila*—DQ210164, DQ210694, DQ209472, —, *Koehler 0243*, Brazil, UEC. *M. pumila*—DQ210198, DQ210728, DQ209505, —, *Koehler 0355*, Brazil, UEC. *M. pumila*—DQ210083, DQ209912—, —, *Pupulin s.n.*, Costa Rica, cult., USJ. *M. punctostriata* Rchb.f.—DQ210056, DQ209903, DQ209371, —, *Blanco 2107*, Costa Rica, cult., USJ. *M. punctostriata*—DQ210409, DQ210896, DQ209694, —, *Whitten 2543*, Ecuador, cult., FLAS. *M. ramonensis* Schltr.—DQ210099, DQ209918, DQ209411, —, *Mora s.n.*, Costa Rica, cult., USJ. *M. reichenheimiana* Endres & Rchb.f.—DQ210053, DQ209900, DQ209368, —, *Blanco 2102*, Costa Rica, cult., USJ. *M. reichenheimiana*—DQ210463, DQ210947, DQ209746, —, *Whitten 2616*, Panama, FLAS. *M. reichenheimiana*—DQ210503, DQ210984, DQ209786, —, *Whitten 2713*, Ecuador, FLAS. *M. repens* L.O. Williams—DQ210070, DQ210613, DQ209384, —, *Blanco 2911*, Panama, FLAS. *M. richii* Dodson—DQ209995, DQ209870, DQ209312, —, *Atwood & Whitten 5077*, Ecuador, cult., SEL. *M. richii*—DQ210338, DQ210836, DQ209624, DQ872545, *Whitten 2362*, Ecuador, cult., FLAS. *M. cf. richii*—DQ461784, DQ461802, DQ461766, —, *Blanco 3108*, cult., FLAS. *M. rigida* Barb.Rodr.—DQ210104, DQ210635, DQ209416, —, *Koehler 0007*, Brazil, cult., UEC. *M. rigida*—DQ210116, DQ210647, DQ209427, —, *Koehler 0053*, Brazil, UEC. *M. ringens* Rchb.f.—DQ210047, DQ209894, DQ209362, —, *Blanco 1727*, Costa Rica, USJ. *M. robusta* Barb. Rodr.—DQ210192, DQ210722, DQ209499, —, *Koehler 0343*, Brazil, UEC. *M. rodrigueziana* J.T.Atwood & Mora-Ret.—DQ210061, DQ210606, DQ209376, —, *Blanco 2258*, Costa Rica, USJ. *M. rotundilabia* C.Schweinf.—DQ210406, DQ210893, DQ209691, —, *Whitten 2516*, Ecuador, FLAS. *M. rotundilabia*—DQ461792, DQ461810, DQ461774, —, *Whitten 3173*, Ecuador, QCA. *M. rubioi* Dodson—DQ210327, DQ210826, DQ209615, —, *Whitten 2334*, Ecuador, FLAS. *M. rufescens* Lindl.—DQ209993, DQ209868, DQ209310, —, *Atwood & Whitten 5073*, cult., SEL. *M. rufescens*—DQ210191, DQ210721, DQ209498, —, *Koehler 0339*, Brazil, UEC. *M. rufescens*—DQ210521, DQ211001—, —, *Whitten 2754*, cult., FLAS. *M. cf. rufescens*—DQ210168, DQ210698, DQ209475, —, *Koehler 0258*, Brazil, UEC. *M. cf. rufescens*—DQ210274, DQ209943, DQ209568, —, *Whitten 1669*, Ecuador, cult., FLAS. *M. rupestris* Barb.Rodr.—DQ210106, DQ210637, DQ209418, —, *Koehler 0013*, Brazil, UEC. *M. rupestris*—DQ210118, DQ210649, DQ209429, —, *Koehler 0063*, Brazil, UEC. *M. sanantonioensis* Christenson—DQ210415, DQ210902, DQ209700, —, *Whitten 2552*, Colombia, cult., FLAS. *M. sanderiana* Rchb.f. ex Sander—DQ210368, DQ210862, DQ209655, —, *Whitten 2422*, Ecuador, cult., FLAS. *M. sanderiana*—DQ210271, DQ210781, DQ209564, —, *Whitten 1652*, Ecuador, cult., FLAS. *M. sanderiana*—DQ210453, DQ209967, DQ209737, —, *Whitten 2603*, Ecuador, cult., FLAS. *M. sanguinea* Rolfe—DQ210081, DQ209910, DQ209394, —, *Blanco s.n.*, Costa Rica, cult., USJ. *M. scalariformis* J.T.Atwood—DQ210023, DQ210595, DQ209337, —, *Dressler & Atwood 6252*, Panama, PMA. *M. scalariformis*—DQ210419, DQ210906, DQ209704, —, *Whitten 2559*, Panama, FLAS. *M. scalariformis*—DQ210475, DQ210957, DQ209758, DQ872564, *Whitten 2633*, Panama, FLAS. *M. schlechteriana* (C.Schweinf.) J.T.Atwood—DQ210043, DQ209890, DQ209358, —, *Blanco 1662*, Costa Rica, USJ. *M. schlechteriana*—DQ210304, DQ210803, DQ209592, —, *Whitten 2157*, Costa Rica, FLAS. *M. scorpioidea* Kraenzl.—DQ210058, DQ209905, DQ209373, —, *Blanco 2143*, Costa Rica, cult., USJ. *M. cf. scorpioidea*—, —, DQ210843, DQ209632, —, *Whitten 2373*, Ecuador, cult., FLAS. *M. serrulata* Ames & Correll—DQ210082, DQ209911, DQ209395, —, *Blanco s.n.*, Costa Rica, USJ. *M. setigera* Lindl.—DQ210230, DQ209933, DQ209529, —, *Atwood s.n.*, cult., SEL. *M. setigera*—DQ210143, DQ210674, DQ209453, —, *Koehler 0117*, Brazil, cult., UEC. *M. sigmoidea* (C.Schweinf.) Ames & Correll—DQ210057, DQ209904, DQ209372, —, *Blanco 2141*, Costa Rica, cult., USJ. *M. sigmoidea*—DQ210072, DQ210615, DQ209385, —, *Blanco 2915*, Panama, FLAS. *M. sigmoidea*—DQ210018, DQ210590, DQ209332, —, *Dressler & Atwood 6240*, Panama, FLAS. *M. silvana* Campacci—DQ210516, DQ210997, DQ209799, DQ872579, *Whitten 2747*, Ecuador, FLAS. *M. cf. silvana*—DQ210391, DQ210878, DQ209676, —, *Whitten 2485*, Ecuador, cult., FLAS. *M. sophronitis* (Rchb.f.) Garay—DQ210310, DQ210809, DQ209598, DQ872593, *Whitten 2296*, Venezuela, cult., FLAS. *M. sophronitis*—DQ210461, DQ210945—, —, *Whitten 2613*, Venezuela, cult., FLAS. *M. speciosa* Rchb.f.—DQ210075, DQ210618, DQ209388, —, *Blanco 2957*, Colombia, cult., FLAS. *M. splendens* Poepp. & Endl.—DQ210152, DQ210684, DQ209462, —, *Koehler 0144*, Brazil, cult., UEC. *M. splendens*—DQ210289, DQ210789, DQ209580, —, *Whitten 1962*, Suriname, cult. FLAS. *M. cf. splendens*—DQ210388, DQ210876, DQ209674, —, *Whitten 2482*, Ecuador, cult., FLAS. *M. squamata* Barb.Rodr.—DQ461798, DQ461816, DQ461780, —, *Whitten 3193*, Ecuador, cult., QCA. *M. striata* Rolfe—DQ210267, DQ210777, DQ209561, —, *Whitten 1639*, Ecuador, cult., FLAS. *M. strumata* (Endres & Rchb.f.) Ames & Correll—DQ210179, DQ210709, DQ209486, —, *Koehler 0302*, Costa Rica, cult., ESA. *M. strumata*—DQ210245, DQ210761—, —, *Whitten 3021*, Guatemala, cult., FLAS. *M. strumata* × *M. pseudoneglecta*—DQ210042, DQ210605, DQ209357, —, *Blanco 1661*, Costa Rica, USJ. *M. suarezorum* Dodson—DQ210523, DQ211003, DQ209805, —, *Whitten 2758*, Ecuador, cult., FLAS. *M. suarezorum*—DQ210553, DQ211028, DQ209834, DQ872605, *Whitten 2895*, Ecuador, cult., FLAS. *M. synsepala* J.T.Atwood—DQ210076, DQ210619, DQ209389, —, *Blanco 2962*, Panama, FLAS. *M. tenuibulba* Christenson—DQ210552, DQ211027, DQ209833, —, *Whitten 2894*, Colombia, cult., FLAS. *M. tenuifolia* Lindl.—DQ210282, DQ210787, DQ209574, —, *Whitten 1843*, cult., FLAS. *M. tigrina* C.Schweinf.—DQ210085, DQ210625, DQ209397, —, *Gerlach 2001–2204*, Panama, cult., M. *M. tigrina*—DQ210244, DQ210760—, —, *Whitten 2991*, Panama, cult., FLAS. *M. tonduzii* (Schltr.) Ames & Correll—DQ210028, DQ210600, DQ209342, —,

- Dressler & Atwood 6276*, Panama, PMA. *M. trilobata* Ames & Correll—DQ210030, DQ210602, DQ209344, —, *Dressler & Atwood 6278*, Panama, PMA. *M. trilobata*—DQ210101, DQ209920, DQ209413, —, *Pupulin 2000*, Costa Rica, cult., USJ. *M. triloris* E. Morren—DQ210039, DQ209887, DQ209354, —, *Blanco 1640*, Colombia, cult., USJ. *M. triloris*—DQ210078, DQ210621, DQ209391, —, *Blanco 2967*, Colombia, cult., FLAS. *M. triloris*—DQ210255, DQ209940, DQ209549, —, *Whitten 1558*, Ecuador, FLAS. *M. triloris*—DQ210563, DQ211038, DQ209843, DQ872590, *Whitten 2917*, Colombia, cult., FLAS. *M. triloris*—DQ210567, DQ211042, DQ209847, —, *Whitten 2928*, Colombia, cult., FLAS. *M. cf. triloris*—DQ210342, DQ210839, DQ209628, —, *Whitten 2366*, Ecuador, cult., FLAS. *M. tubercularis* J.T. Atwood—DQ210446, DQ210931, DQ209730, —, *Whitten 2596*, Panama, FLAS. *M. aff. tubercularis*—DQ210540, DQ211015, DQ209822, —, *Whitten 2817*, Panama, cult., FLAS. *M. turkeliae* Christenson—DQ210276, DQ209945, DQ209570, —, *Whitten 1675*, Ecuador, cult., FLAS. *M. tutae* J.T. Atwood—DQ210071, DQ210614—, —, *Blanco 2913*, Panama, FLAS. *M. umbratilis* L.O. Williams—DQ210040, DQ209888, DQ209355, —, *Blanco 1642*, Costa Rica, USJ. *M. umbratilis*—DQ210049, DQ209896, DQ209364, —, *Blanco 1835*, Costa Rica, USJ. *M. umbratilis*—DQ210450, DQ210935, DQ209734, —, *Whitten 2600*, Panama, cult., FLAS. *M. umbratilis*—DQ210482, DQ210964, DQ209765, —, *Whitten 2643*, Panama, FLAS. *M. cf. umbratilis*—DQ210485, DQ210968, DQ209769, —, *Whitten 2648*, Panama, cult., FLAS. *M. uncata* Lindl.—DQ210123, DQ210654, DQ209434, —, *Koehler 0075*, Brazil, cult., SP. *M. uncata*—DQ210199, DQ210729, DQ209506, —, *Koehler 0359*, Brazil, UEC. *M. uncata*—DQ210356, DQ210852, DQ209643, —, *Whitten 2394*, Ecuador, cult., FLAS. *M. uncata*—DQ210459, DQ210943, DQ209743, —, *Whitten 2609*, Panama, cult., FLAS. *M. cf. uncata*—DQ210496, DQ210979, DQ209780, —, *Whitten 2670*, Ecuador, cult., FLAS. *M. aff. uncata*—DQ210223, DQ209928, DQ209524, —, *Atwood & Whitten 5076*, Ecuador, cult., SEL. *M. vaginalis* Rchb.f.—DQ210306, DQ210805, DQ209594, —, *Whitten 2259*, Costa Rica, cult., FLAS. *M. aff. vaginalis*—DQ210436, DQ210922, DQ209720, —, *Whitten 2577*, Panama, Chiriquí, cult., FLAS. *M. variabilis* Bateman ex Lindl.—DQ209998, DQ209872, DQ209314, —, *Atwood & Whitten 5080*, Nicaragua, cult. SEL. *M. variabilis*—DQ210035, DQ209883, DQ209349, —, *Blanco 1076*, Costa Rica, cult., USJ. *M. variabilis*—DQ210187, DQ210717, DQ209494, —, *Koehler 0327*, Mexico, cult., ESA. *M. cf. variabilis*—DQ210514, DQ210995, DQ209797, DQ872577, *Whitten 2737*, Panama, cult., FLAS. *M. vernicosa* Barb.Rodr.—DQ210134, DQ210665, DQ209445, —, *Koehler 0099*, Brazil, SP. *M. vernicosa*—DQ210136, DQ210667, DQ209447, —, *Koehler 0103*, Brazil, SP. *M. vernicosa*—DQ210287, DQ209952, DQ209578, —, *Whitten 1871*, Brazil, cult., FLAS. *M. vittariifolia* L.O. Williams—DQ210102, DQ209921, DQ209414, —, *Pupulin 2193*, Costa Rica, USJ. *M. vittariifolia*—DQ210283, DQ209948, DQ209575, —, *Whitten 1867*, Costa Rica, cult., FLAS. *M. wercklei* (Schltr.) L.O. Williams—DQ210477, DQ210959, DQ209760, —, *Whitten 2635*, Panama, FLAS. *M. cf. wercklei*—DQ210377, DQ210868, DQ209663, —, *Whitten 2443*, Ecuador, cult., FLAS. *M. whittenii* Dodson—DQ210340, —, DQ209626, —, *Whitten 2364*, Ecuador, cult., FLAS. *M. witsenioides* Schltr.—DQ210247, DQ209937, DQ209541, —, *Whitten 1600*, Ecuador, FLAS. *M. woytkowskii* C.Schweinf.—DQ210531, DQ211007, DQ209813, —, *Whitten 2782*, Bolivia, cult., FLAS. *M. yanganensis* Dodson—DQ461790, DQ461808, DQ461772, —, *Whitten 3161*, Ecuador, QCA. *Maxillaria* sp.—DQ210094, DQ210632, DQ209406, —, *Jost 6100*, Ecuador, QCA. *Maxillaria* sp.—DQ210095, DQ210633, DQ209407, —, *Jost 6406*, Ecuador, QCA. *Maxillaria* sp.—DQ210317, DQ210816, DQ209605, —, *Whitten 2310*, Peru, cult., FLAS. *Maxillaria* sp.—DQ210348, DQ210846, DQ209635, —, *Whitten 2380*, Ecuador, cult., FLAS. *Maxillaria* sp.—DQ210392, DQ210879, DQ209677, —, *Whitten 2486*, Ecuador, cult., FLAS. *Maxillaria* sp.—DQ210556, DQ211031, DQ209837, —, *Whitten 2904*, Ecuador, cult., FLAS. *Maxillaria* sp.—DQ461794, DQ461812, DQ461776, —, *Whitten 3186*, Ecuador, cult., QCA. *Maxillaria* sp.—DQ461785, DQ461803, DQ461767, —, *Jost 7921*, Ecuador, QCA.
- Mormolyca gracilipes* (Schltr.) Garay & Wirth—DQ210090, DQ209914, DQ209402, —, *Hirtz 8088*, Ecuador, cult., QCNE. *M. peruviana* C. Schweinf.—DQ210398, DQ210885, DQ209683, DQ872553, *Whitten 2497*, Ecuador, cult., FLAS. *M. polyphylla* Garay & Wirth—DQ210534, DQ211009, DQ209816, —, *Whitten 2789*, Ecuador, cult., FLAS. *M. ringens* (Lindl.) Gentil—DQ210148, DQ210680—, —, *Koehler 0134*, Brazil, cult., UEC. *M. ringens*—DQ210219, DQ209925, —, DQ872524, *Whitten 2871*, Mexico, cult. SEL. *M. schweinfurthiana* Garay & Wirth—DQ210234, DQ210750—, —, *Whitten 97085*, Peru, cult., FLAS. *M. schweinfurthiana*—DQ210249, DQ210764, DQ209543, —, *Whitten 3109*, Ecuador, cult., QCA.
- Neomoorea wallisii* (Rchb.f.) Schltr.—DQ210216, DQ210743, DQ209520, —, *Whitten 3010*, Panama, cult., FLAS.
- Pityphyllum antioquiense* Schltr.—DQ210371, DQ209958, DQ209658, —, *Whitten 2436*, Ecuador, cult., FLAS. *P. antioquiense*—DQ210384, DQ209961, DQ209670, DQ872594, *Whitten 2473*, Ecuador, cult., FLAS. *P. huancabambae* (Kraenzl.) Whitten—DQ210362, DQ209957, DQ209649, —, *Whitten 2402*, Ecuador, cult., FLAS. *P. pinoides* Sweet—DQ210089, DQ209913, DQ209401, —, *Whitten 2401*, Ecuador, cult., FLAS. *P. pinoides*—DQ210375, DQ209960, DQ209662, —, *Whitten 2440*, Ecuador, cult., FLAS. *P. saragurensis* (Dodson) Whitten—DQ461787, DQ461805, DQ461769, DQ872597, *Whitten 3084*, Ecuador, cult., QCA.
- Rudolfiella floribunda* (C.Schweinf.) Hoehne—DQ210394, DQ210881, DQ209679, —, *Whitten 2489*, Ecuador, cult., FLAS.
- Scuticaria salesiana* Dressler—DQ210385, DQ210875, DQ209671, —, *Whitten 2478*, Ecuador, cult., FLAS.
- Trigonidium acuminatum* Bateman in Lindl.—DQ210109, DQ210640—, —, *Koehler 0021*, Brazil, cult., UEC. *T. acuminatum*—DQ210153, DQ210685, DQ209463, —, *Koehler 0145*, Brazil, cult., UEC. *T. acuminatum*—DQ210201, DQ210731, DQ209508, DQ872604, *Koehler 0363*, Brazil, ESA. *T. acuminatum*—DQ210376, DQ210867—, —, *Whitten 2442*, Ecuador, cult., FLAS. *T. egertonianum* Bateman in Lindl.—DQ210184, DQ210714, DQ209491, DQ872527, *Koehler 0317*, Costa Rica, cult., ESA. *T. egertonianum*—DQ210200, DQ210730, DQ209507, DQ872603, *Koehler 0361*, Brazil, cult., UEC. *T. egertonianum*—DQ210211, DQ210740, DQ209517, —, *Whitten 2993*, cult., FLAS. *T. insigne* Rchb.f. in Benth. & Hook.f.—DQ210266, DQ210776, DQ209560, —, *Whitten 1599*, Ecuador, FLAS. *T. insigne*—DQ210423, DQ210910, DQ209708, —, *Whitten 2564*, cult., FLAS. *T. insigne*—DQ210494, DQ210977, DQ209778, —, *Whitten 2660*, Ecuador, cult., FLAS. *T. insigne*—DQ210566, DQ211041, DQ209846, DQ872591, *Whitten 2926*, Ecuador, cult., FLAS. *T. obtusum* Lindl.—DQ210110, DQ210641, DQ209421, —, *Koehler 0023*, Brazil, UEC. *T. obtusum*—DQ210220, DQ210746, DQ209521, DQ872525, *Whitten 2997*, cult., FLAS. *T. riopalenquense* Dodson—DQ210014, DQ210587, DQ209328, —, *Atwood & Whitten 5097*, Ecuador, cult., SEL. *T. riopalenquense*—DQ210252, DQ210766, DQ209546, —, *Whitten 1534*, Ecuador, FLAS. *Trigonidium* sp. nov.—DQ210183, DQ210713, DQ209490, DQ872526, *Koehler 0315*, Brazil, UEC. *Trigonidium* sp. nov.—DQ210185, DQ210715, DQ209492, —, *Koehler 0319*, Brazil, ESA.
- Xylobium leontoglossum* (Rchb.f.) Rolfe—DQ210499, DQ209970—, —, *Whitten 2683*, Ecuador, FLAS. *X. leontoglossum*—DQ210254, DQ209939, DQ209548, DQ872534, *Whitten 1557*, Ecuador, FLAS. *X. pallidiflorum* (Hook.) G. Nicholson—AF239338, AF239434—, —, *Whitten 1876*, Ecuador, FLAS. *X. subpulchrum* Dressler—DQ210218, DQ210745—, —, *Whitten 94013*, Peru, cult., FLAS. *X. zarumense* Dodson—AF239339, AF239435, DQ209578, —, *Whitten 1881*, Ecuador, FLAS. *Xylobium* sp.—DQ210160, DQ210692, DQ209468, —, *Koehler 0166*, Brazil, cult., UEC.