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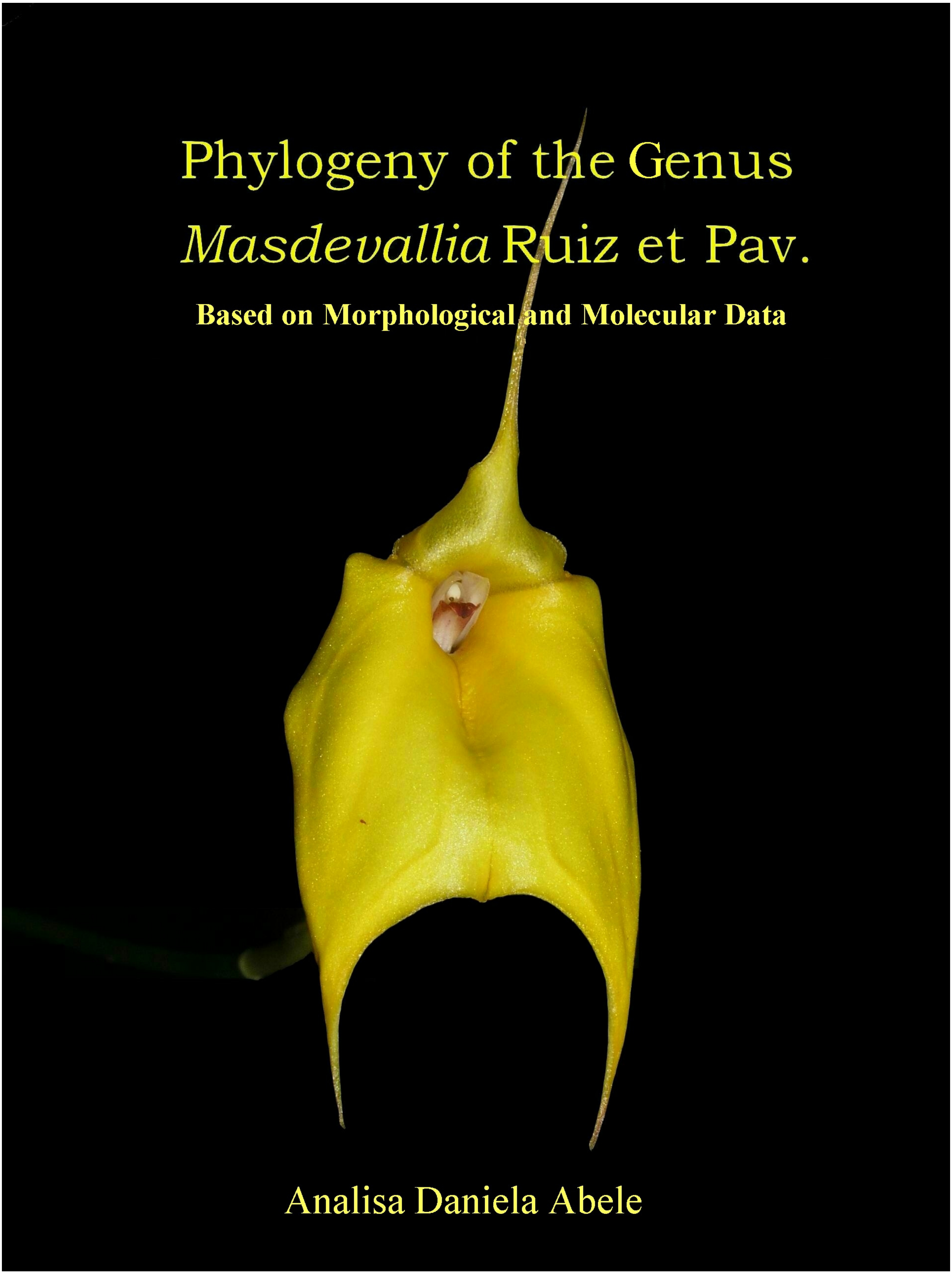
Based on Morphological and Molecular Data



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Phylogeny of the Genus *Masdevallia* Ruiz & Pav. (Orchidaceae) Based on Morphological and Molecular Data

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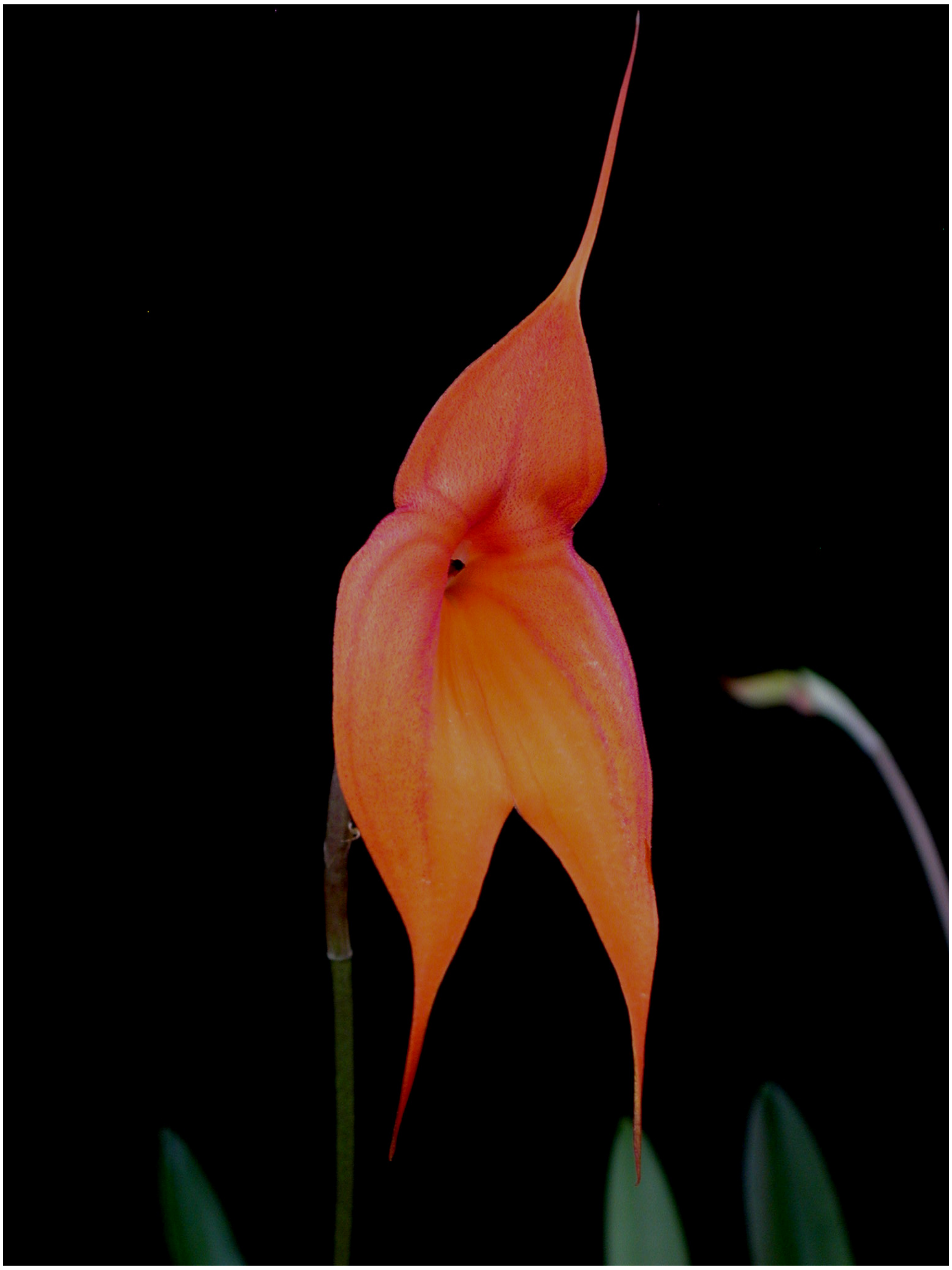

Masdevallia veitchiana Rchb. f.

CONTENTS

SUMMARY

The genus *Masdevallia* is one of 28 genera in subtribe *Pleurothallidinae*, with approximately 500 species. It is distributed from southern Mexico to southern Brazil, with main centers of diversity in the Andes of South America. Most species are epiphytes and occur in primary forests. *Masdevallia* species are characterized by coriaceous leaves borne on short ramicauls. The inflorescence emerges with an annulus a considerable distance below the abscission layer of the leaf; the sepals are variously connate and commonly have tails, and the lips are more or less ligulate. The taxonomy of *Masdevallia* is mainly based on floral structures. Although revisions of several sections of *Masdevallia* have been published during the last century, the delimitation of infrageneric taxa is still problematic, due to the lack of clear morphological synapomorphies. The naturalness and relationships of the subgenera, sections and subsections of *Masdevallia* was not previously examined in a phylogenetic context. Consequently, the aims of this study are to 1) address the subgeneric and sectional relationships in *Masdevallia* with molecular data, 2) to correlate molecular with morphological data in order to establish morphological synapomorphies for clades well supported by molecular data and, 3) to correlate molecular with geographical data in order to evaluate the possible speciation histories and processes. Macro-morphological and micro–morphological character (pollinia surface ornamentations) data were collected for 85 species of *Masdevallia*, chosen to represent the taxonomic, morphological, and geographic diversity within the genus. These data were subjected to a maximum parsimony analysis. Maximum parsimony analyses and Bayesian analyses were also performed with sequences of the non-coding internal transcribed spacer (ITS) of the nuclear ribosomal DNA for 104 species, representing all the subgenera, sections and subsections of the genus *Masdevallia*. Maximum parsimony analyses of combined data (molecular as well as macro and micro-morphological) were also performed. In the phylogenetic analysis of the genus *Masdevallia* based on morphological data, most groups are not supported by many characters. The lack of resolution obtained in this analysis suggests that detailed classifications at the infrageneric level are not well supported by morphological evidence. The phylogenetic relationships of the genus *Masdevallia* and of several groups within the genus are well resolved using ITS sequences. The strict consensus tree obtained from the maximum parsimony analysis and the 50% majority rule consensus of the 3000 trees obtained from the Bayesian analysis recovered essentially the same topology. The strict consensus tree of the combined data was partly congruent with the ITS topology and relationships among species of *Masdevallia* and outgroups were very similar in each tree.

The resulting phylogenetic tree obtained by maximum parsimony analyses of nuclear rDNA ITS sequences indicates that the genus *Masdevallia* is a well-supported monophyletic group that is unambiguously part of *Pleurothallidinae.* The infrageneric classification of the genus *Masdevallia* is only in part supported by the analysis of molecular data. Of the 11 subgenera of *Masdevallia* considered in this study, three forms strongly supported monophyletic groups in the analysis: subgenera *Cucullatia*, *Meleagris* and *Fissia*; the monospecific subgenera *Teagueia*, *Scabripes* and *Volvula* are of course monophyletic as well. Subgenera *Masdevallia*, *Pygmaeia* and *Polyantha* are not monophyletic. Subgenera *Nidificia* and *Amanda* form a clade with almost no internal resolution.

Four major clades were resolved within *Masdevallia*. Clade A included *Luerella pelecaniceps*, which is endemic to Panama, at an altitude of 800 to 1 000 m above the sea level, and *M. erinacea*, which is found throughout the whole geographical range. It shows no distinct morphological synapomorphy (and maybe due to long branch attraction). Clade B included subgenus *Pygmaeia* section *Zahlbrucknerae*, subgenus *Masdevallia* sections *Triotosiphon*, *Reichenbachianae*, *Minutae*, *Coriaceae*, and *Dentatae*, subgenus *Polyantha* sections *Alaticaules* and *Polyanthae*, *M. chimboensis* and *M. mentosa*. A synapomorphy of this group is a verrucose (to papillose) epichile. Species of this group are found throughout the whole geographical as well as altitudinal range. Clade C grouped subgenus *Pygmaeia* sections *Amaluzae* and *Aphanes*, subgenus *Masdevallia* section *Masdevallia* with all remaining subsections (*Caudatae*, *Coccinea*, *Masdevallia*, *Oscillantes* and *Saltatrices*), section *Durae*, section *Racemosae*, *M. caudivolvula* (subgenus *Volvula*), *M. macrura* (subgenus *Masdevallia* section *Coriaceae*), *M. hoeijeri* (subgenus *Pygmaeia* section *Aphanes*), and *M. bicornis* (subgenus *Scabripes*). Lateral sepals connate without the formation of a broad mentum or a secondary mentum with the column-foot are characteristic for most species of clade C. Species of this group are restricted to the southern part of the geographical range, with most species found at higher elevations (above 2 000 m above sea level). Clade D grouped subgenera *Teagueia*, *Cucullatia*, *Nidificia*, *Amanda*, *Fissia*, *Meleagris*, and *Dracula xenos*. Synapomorphies of the species grouped in this clade are the arcuate sepaline tubes and the featureless disc of the lip. Species of clade D grow mainly in the Andes, at an altitude of 450 to 3 100 m above sea level.

The characters that have been used as rapid identifiers for diagnosing subgenera, sections and subsections within *Masdevallia* (key characters) were plotted on one of the most parsimonious trees. The cross section of the peduncle (terete or triquetrous), the anthesis of the flowers (successively or simultaneous), the type of floral bract, the ovary smooth or with some external features such as crests or papillae, the grade of connation between the sepals, and the presence or absence of a division in the lip appear to be good synapomorphies for major clades in *Masdevallia*. Long tail-like appendages at the apex of the sepals appear to have evolved repeatedly in parallel and appear not to be phylogenetically informative.

ABBREVIATIONS

Alphabetical list of abbreviations used in text and figures.

ABI Applied Biosystems®
bp base pair
CG-... cytosine and guanosine, e.g. CG-content: amount of cytosine and guanosine in a certain region
cpDNA chloroplast DNA
CT-... cytosine and thymine (CG-...)
CTAB buffer; appendix
D. Dracula
DNA deoxyribonucleic acid
ETS external transcribed spacer
GA-... guanosine and adenine (CG-...)
GTR+Ã+I general substitution model ("general time reversible", substitution rates gamma-distributed, and proportion of sites are invariant)
HBG Botanischer Garten der Universität Hamburg
HHG Herrenhäuser Gärten Hannover
IGS 25S-18S intergenic spacer
ITS internal transcribed spacer
M. Masdevallia
ML maximum likelihood
MP maximum parsimony
MPR maximum parsimonious reconstruction
MPT most parsimonious tree(s)
mtDNA mitochondrial DNA
N unknown nucleic base (in alignments)
NEXUS data format used by common phylogenetic programs
NJ Neighbour-Joining algorithm
(n)rDNA (nuclear) ribosomal RNA gene
P. Porroglossum
PAUP Phylogenetic Analyses Using Parsimony, analyzing software
PCR polymerase chain reaction
pp posterior probability
RNA ribonucleic acid
rRNA ribosomal RNA
s.l. sensu latu, in a broad sense
s.s. sensu strictu, in a strict sense
sect. section (taxonomic unit)
sects. sections
sp. species (singular, taxonomic unit)
sp. subspecies (taxonomic unit)
spp. species (plural, taxonomic unit)
subg. subgenus (taxonomic unit)
subsect. subsection
subsects. subsections
T. Trisetella
TS Ton Sijm

Abbreviations used for nucleotides
Standard nucleotide code
A adenine
B "not A", i.e. C, G, or T
C cytosine (nucleic base)
D "not C", i.e. A, G, or T
G guanosine
H "not G", i.e. A, C, or T
K either G or T
M either A or C
N miscellaneous/unknown nucleotide
R purine (A or G)
S strong bond, i.e. C or G
T thymine
V "not T", i.e. A, C, or G
W weak bond, i.e. A or T
Y pyrimidine (C or T)

Standard colour code for alignments/oligonucleotide motives
Single nucleotides:

🟩 = A, 🟦 = C, ⬛ = G, 🟥 = T, ⁚ = gap

(site) variability comprising 2 possible nucleotides:

🟫 = K, 🟦 = M, 🟩 = R, 🟦 = S, 🟨 = W, 🟪 = Y

nucleotide state unknown = N

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INTRODUCTION

The most recent complete systematic treatment of Orchidaceae is that of DRESSLER (1993). This system originated 35 years ago (DRESSLER and DODSON, 1960) and has been altered and modified periodically by DRESSLER as the basic knowledge of orchid morphology, anatomy, and genetics has expanded (DRESSLER, 1979, 1981, 1986, 1993). The Orchidaceae, as defined by this system, comprise 850 genera and 20 000 species. These are arranged in five subfamilies, 22 tribes, and 70 subtribes (Table 1) principally based on anther number and position. The subfamilies are: Apostasioideae, containing the two orchid genera with either three fertile anthers or two fertile anthers and a filamentous staminode; Cypripedioideae, composed of the five genera with two fertile anthers (diandrous), a shield-shaped staminode, and a saccate labellum; Orchidoideae, containing the orchids with a single fertile anther (monandrous), which is erect and basifixed; Spiranthoideae, comprising the monandrous orchids with erect, acrotonic anther; and Epidendroideae, including all remaining monandrous orchids with an incumbent to suberect anther. This last subfamily is by far the largest (576 genera and approximately 15 000 species), encompassing more genera and species than all the others together, including the object of this study, the genus *Masdevallia*, which is one of 28 genera in subtribe *Pleurothallidinae*, subfamily Epidendreae I.

Table 1 Classification of the Orchid according to DRESSLER (1993)

Subfamily	Tribe	Subtribe
Apostasioideae Rchb. f.		
Cypripedioideae Lindl.		
Spiranthoideae Dressler	*Diceratosteleae* Dressler	
	Tropidieae Dressler	
	Cranichideae Endl.	*Goodyerinae* Klotsch *Prescottiinae* Dressler *Spiranthinae* Lindl. *Manniellinae* Schltr. *Pachyplectroninae* Schltr. *Cranichidinae* Lindl.
Orchidoideae	*Diurideae* Endl.	*Chloraeinae* Rchb. f. *Caladeniinae* Pfitzer *Drakaeinae* Schltr. *Acianthinae* Schltr. *Pterostylidinae* Pfitzer *Cryptostylidinae* Schltr. *Thelymitrinae* Lindl. *Rhizanthellinae* Rogers *Prasophyllinae* Schltr.
	Orchideae	*Orchidinae* *Habenariinae* Benth.

Table 1 Cont. Classification of the Orchids according to DRESSLER (1993)

	Diseae Dressler	*Huttonaeinae* Schltr. *Satyriinae* Schltr. *Coryciinae* Benth. *Disinae* Benth.
	Neottieae Lindl.	*Limodorinae* Benth. *Listerinae* Lindl.
Epidendroideae Lindl.	*Palmorchideae* Dressler	
	Triphoreae Dressler	
	Vanilleae Blume	*Galeolinae* Garay *Vanillinae* Lindl. *Lecanorchidinae* Dressler
	Gastrodieae Lindl.	*Gastrodiinae* Lindl. *Epipogiinae* Schltr. *Wullschlaegeliinae* Dressler
	Nervilieae Dressler	
	Malaxideae Lindl.	
	Calypsoeae Dressler	
	Cymbidieae Pfitzer	*Goveniinae* Dressler *Bromheadiinae* Dressler *Eulophiinae* Benth. *Thecostelinae* Schltr. *Cyrtopodiinae* Benth. *Acriopsidinae* Dressler *Catasetinae* Schltr.
	Maxillarieae Pfitzer	*Cryptarrheninae* Dressler *Zygopetalinae* Schltr. *Lycastinae* Schltr. *Maxillariinae* Benth. *Stanhopeinae* Benth. *Telipogoninae* Schltr. *Ornithocephalinae* Schltr. *Oncidiinae* Benth.
	Arethuseae Lindl.	*Arethusinae* Lindl. *Bletiinae* Benth. *Chysiinae* Schltr.
	Coelogyneae Pfitzer	*Thuniinae* Schltr. *Coelogyninae* Benth.
	Epidendreae I Dressler	*Sobraliinae* Schltr. *Arpophyllinae* Dressler *Meiracylliinae* Dressler *Coeliinae* Dressler *Laeliinae* Benth. ***Pleurothallidinae*** Lindl.
	Epidendreae II Dressler	*Glomerinae* Schltr. *Adrorhizinae* Schltr. *Polystachyinae* Pfitzer
	Podochileae Pfitzer	*Eriinae* Benth. *Podochilinae* Benth. & Hook. *Thelasiinae* Schltr. *Ridleyellinae* Dressler
	Dendrobieae Lindl. ex Endl.	*Dendrobiinae* Lindl. *Bulbophyllinae* Schltr.
	Vandeae Lindl.	*Aeridinae* Pfitzer *Angraecinae* Summerh. *Aerangidinae* Summerh.

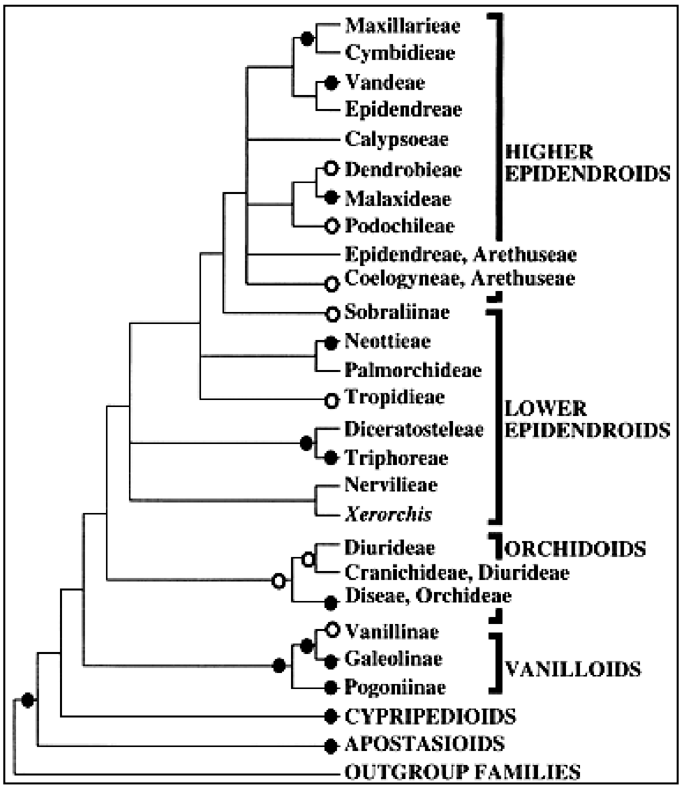

Fig. 1 Strict consensus summary of 6000 successively weighted *rbcL* trees for Orchidaceae from CAMERON et al. (1999). Informal subfamily names are indicated, as are tribes sensu DRESSLER (1993). Solid circles indicate clades with high bootstrap support (75-100%). Open circles indicate clades with weak bootstrap support (50-75%).

Cladistic parsimony analyses of *rbcL* nucleotide sequence data from 171 taxa representing nearly all tribes and subtribes of Orchidaceae (CAMERON et al., 1999), divide the family into five major monophyletic clades: apostasioid, cypripedioid, vanilloid, orchidoid, and epidendroid orchids, arranged in that order (Fig. 1). These clades, with exception of the vanilloids, essentially correspond to currently recognized subfamilies (DRESSLER, 1993). A distinct subfamily, based upon tribe *Triphoreae*, a clearly isolated group of monandrous orchids, is supported for *Vanilla* and its allies. The general tree topology is, for the most part, congruent with previously published hypotheses of intrafamilial relationships. However, there is no evidence supporting the previously recognized subfamilies *Spiranthoideae*, *Neottioideae* (now placed in the *Orchidoideae*), or *Vandoideae* (now included in *Epidendroideae*). Subfamily *Spiranthoideae* is embedded within a clade containing members of *Orchidoideae* which is sister to tribe *Diurideae*.

1.1 Subtribe *Pleurothallidinae* Lindl. ex G. Don (Epidendreae: Orchidaceae)

The subtribe *Pleurothallidinae* Lindl. ex G. Don is the largest in number of species of the subtribes with approximately 4 000 neotropical species in 28 genera (DRESSLER, 1993), accounting for 15 - 20% of the species in the entire family (Table 2).

Table 2 Genera of subtribe *Pleurothallidinae* (DRESSLER, 1993).

Acostaea Schltr.	*Dresslerella* Luer	*Octomeria* D. Don	*Restrepiopsis* Luer
Barbosella Schltr.	*Dryadella* Luer	*Ophidion* Luer	*Salpistele* Dressler
Barbrodria Luer	*Frondaria* Luer	*Platystele* Schltr.	*Scaphosepalum* Pfitzer
Brachionidium Lindl.	*Lepanthes* Sw.	*Pleurothallis* R. Br.	*Stelis* Sw.
Chamelophyton Garay	*Lepanthopsis* Ames	*Porroglossum* Schltr.	*Teagueia* (Luer) Luer
Condylago Luer	*Masdevallia* Ruiz & Pav.	*Restrepia* H. B. & K.	*Trichosalpinx* Luer
Dracula Luer	*Myoxanthus* Poepp. & Endl.	*Restrepiella* Garay & Dunsterv.	*Trisetella* Luer

The subtribe itself has as many species as major angiosperm families, such as the Cruciferae, Labiatae, Rosaceae or Palmae. However, members of the subtribe have been subjected to disproportionately less scientific scrutiny than these families because of their small size and the inaccessibility in the forest canopy. The subtribe ranges from southern Florida and Mexico to Argentina, but species richness is greatest in the montane cloud forests of Costa Rica, Panama, Colombia, Ecuador, Venezuela, Peru and Brazil.

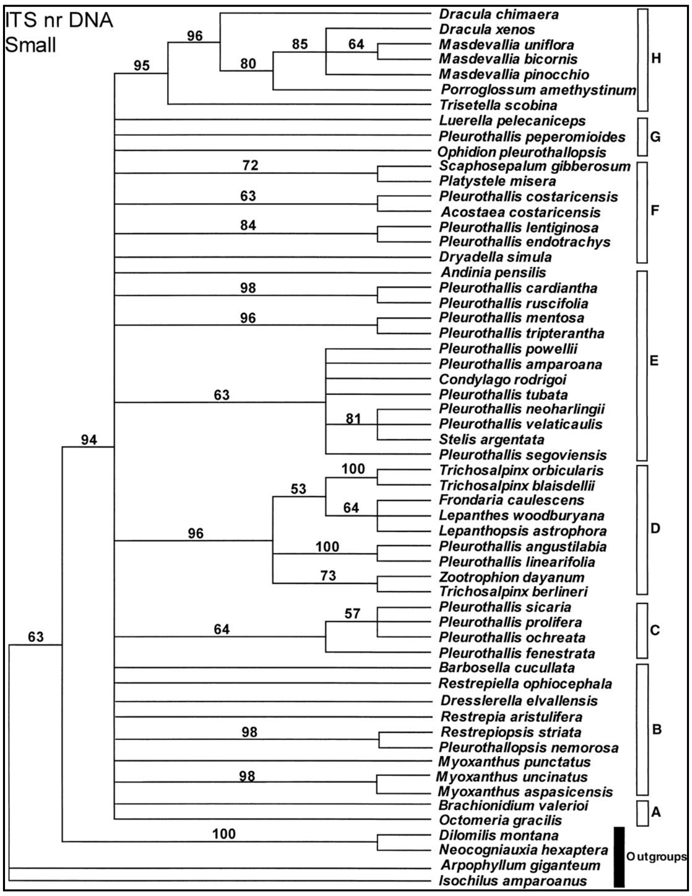

Fig. 2 Bootstrap consensus tree of ITS sequences of *Pleurothallidinae* (PRIDGEON et al. 2001).

Species of subtribe *Pleurothallidinae* are epiphytic or terrestrial; with a sympodial growth habit; leaves are duplicate, mostly coriaceous; ramicauls (secondary stems) are unifoliate, arise directly from the rhizome, and lack pseudobulbs; and the roots are velamenous (PRIDGEON, 1982). Inflorescences are usually terminal (rarely lateral) and flowers are either resupinate or non resupinate, dipteran-deceit-pollinated. One of the morphological features that unite all genera of this subtribe is the presence of an articulation between the ovary and the pedicel of the flowers. So that when flowers fall, the pedicels remain. In all other orchids the articulation occurs at the base of the pedicel (DRESSLER, 1981). Genera have been circumscribed primarily on the basis of the number of pollinia— eight, six, four, or two— although there can be either eight or six in *Brachionidium* Lindl. (LUER, 1986a) and two or four in *Myoxanthus* Poepp. & Endl. and *Lepanthes* Sw. (STENZEL, 2000). DRESSLER (1993) suggests that *Pleurothallidinae* are a diverse but very natural group that parallels the Old World *Bulbophyllinae* in floral evolution (both are pollinated by flies), and that the presence of the *Pleurothallis* seed type in the *Ponera* complex suggests an origin of the *Pleurothallidinae* from an ancestor similar to *Dilomilis* Raf. This supposition was confirmed in a first phylogenetic analysis of the *Pleurothallidinae* based on nuclear and plastid DNA sequences by PRIDGEON et al. (2001) (Fig. 2), which clearly showed that *Pleurothallidinae* is a monophyletic subtribe and that their sister group is *Dilomilis*, which has eight pollinia and reed stems with persistent leaf sheaths (ACKERMAN, 1995). It sister genus, *Neocogniauxia* Schltr., has sheathed stems terminated by a single leaf. The leaf anatomy of both, *Dilomilis* and *Neocogniauxia*, is similar in many aspects to that of most *Pleurothallidinae*: adaxial and abaxial hypodermis, helically thickened mesophyll cells, and absence of extravascular fibers (PRIDGEON, 1982). These two genera offered a stronger support for their inclusion in *Pleurothallidinae* in the ITS study of *Laeliinae* (VAN DEN BERG et al., 2000), the four-region study of *Epidendreae* and *Laeliinae* (VAN DEN BERG, 2000), and the mitochondrial DNA study by FREUDENSTEIN et al. (2000). There is only one morphological synapomorphy uniting the members of *Pleurothallidinae* as presently understood - an articulation between the ovary and pedicel - that *Dilomilis* and *Neocogniauxia* lack.

In a cladistic study of subtribe *Pleurothallidinae* using 45 morphological and anatomical characters, NEYLAND et al. (1995) also designated *Arpophyllum giganteum* Hartw. ex Lindl. as outgroup along with *Brassavola nodosa* (L.) Lindl. and *Epidendrum ciliare* L. of *Laeliinae*. Some of their results were similar to those obtained in a first molecular systematic analysis of the *Pleurothallidinae* (PRIDGEON et al., 2001). The genus *Porroglossum* Schltr., e.g., was sister to the genus *Masdevallia*, and *Trisetella* Luer was sister to both of them. Furthermore, *Lepanthes* was sister to subg. *Specklinia* of *Pleurothallis* R. Br. instead of *Lepanthopsis* Ames, which was part of a polytomy with *Pleurothallis* s.s. and *Restrepia* Garay & Dunsterv. *Brachionidium* Lindl. was sister to *Dracula* Luer, a relationship based in large part on the absence of a leaf hypodermis. Although the morphological analysis likewise clearly showed the polyphyly of *Pleurothallis*, the distribution of its various components differed from the highly bootstrap supported topology found by PRIDGEON et al. (2001).

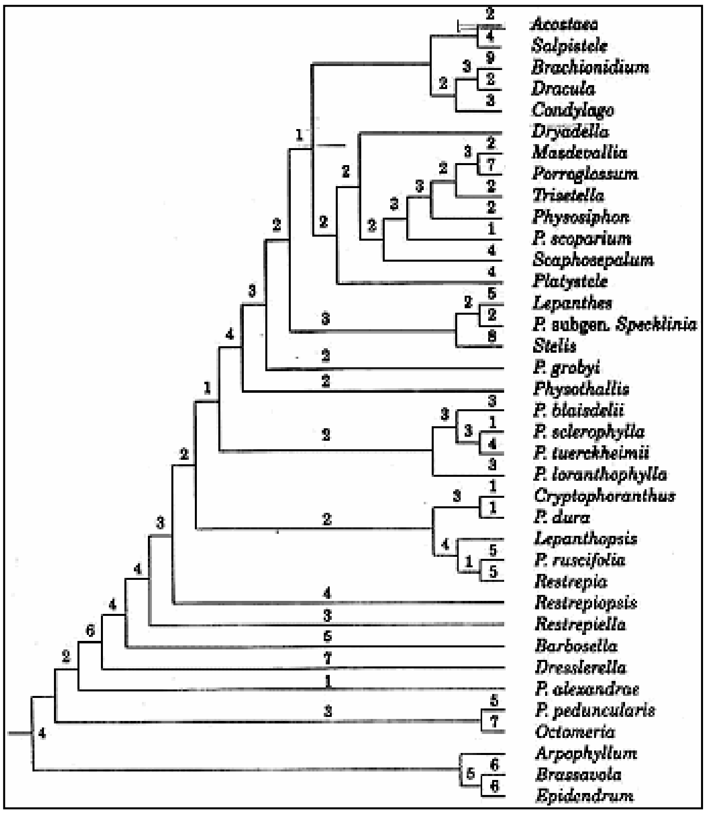

Fig. 3 One of the most parsimonious trees discovered in a cladistic study of subtribe Pleurothallidinae based on morphological and anatomical data (Neyland, 1995).

1.2 The genus *Masdevallia* Ruiz & Pav.

In the eighteenth century, one major scientific expedition, the renowned travel of Hipolito Ruiz and José Pavón to the Andes of Peru and to Chile (1778-1788), was organized by the government of Spain. During the extensive peregrination, the first *Masdevallia* known to science, *Masdevallia uniflora* Ruiz & Pav.= Typal species, was encountered in Huassahuassi, Peru. The genus *Masdevallia* was proposed in 1794 by Ruiz et Pav. in the first volume of Florae Peruvianae et Chilensis Prodromus and was named in honor of José Masdevall, physician in the court of Charles III of Spain. No other species of this genus were made known until 1809, when *Masdevallia infracta* was discovered in Brazil by Descourtilz, a French botanist and traveler. This species, of which living plants were imported to Europe in 1828, was the first to flower in cultivation.

The genus *Masdevallia* is currently estimated to include 500 to 600 species (LUER, 1986b to 2003). Prior to 1975, the genus consisted of 166 species, although 435 epithets had been attributed to the genus. This large number included those species that were subsequently removed to the genera *Dracula* Luer, *Dryadella* Luer, *Trisetella* Luer, *Porroglossum* Schltr. and *Scaphosepalum* Pfitzer (LUER, 2000), clearly recognized and distinguished by morphological and molecular data (see Figs. 2 and 3). In the last centuries, more than 400 species were described and the number of species increases quickly due the horticultural and botanical popularity, not only because of the attractive flowers, but also because of the relative ease of cultivation. *Masdevallia* is one of the largest genera in number of species of the *Pleurothallidinae*, exceeded by *Lepanthes*, *Pleurothallis* and *Stelis* Sw.

1.2.1 Distribution of species of *Masdevallia*

Species of *Masdevallia* are distributed from southern Mexico to southern Brazil with the main center of biodiversity in the high Andes of South America from Venezuela through Colombia, Ecuador, and Peru into Bolivia (Fig. 4). About 50 species occur in Central America, and less than 15 species occur in Brazil, including *M. infracta* Lindl., that occurs in the Mata Atlantica of Brazil, some 2 500-3 500 kilometers away from the "*Masdevallia* area".

1.2.2 Habitats and growth habit of species of *Masdevallia*

Most *Masdevallia* species are epiphytes, occurring in tropical montane rainforest, in higher altitudes between 1 500 and 2 500 meters above sea level, in environments subject to daily mist, rain, or fog and a relative air humidity of 80 - 90%. Some species, such as *M. veitchiana* Rchb. f., *M. coccinea* Linden ex Lindl. etc., may also grow as terrestrial or lithophytic plants.

Fig. 4 Distribution of *Masdevallia* species

1.2.3 Morphology of species of *Masdevallia*

Species of the genus *Masdevallia* are perennial plants and very small and weak up to large and robust. They are characterized by short ramicauls (aerial leaf-bearing stems) (Figs. 6 and 8) produced successively from a stout rhizome. The ramicauls have several nodes and internodes (homoblastic), each node bearing a single, tubular sheath or bract (Figs. 6 and 8). The term “ramicaul” was suggested by STERN and PRIDGEON (1984) as substitute for “secondary stem” that may be used for any leaf- and inflorescence-bearing stems. The term “secondary stem”, found in many taxonomic descriptions, seems to refer to the vegetative shoot above the rhizome, but this use is inaccurate and confusing (DRESSLER, 1993).

The rhizome, or primary stem, is usually short, so that a densely caespitose habit is formed (Fig. 5), even when the rhizome is a little longer and ascending. In a few species the rhizome is significantly elongated (i.e. *M. assurgens* Luer & R. Escobar, *M. paivaeana* Rchb. f., *M. racemosa* Lindl., and *M. scandens* Rolfe). Ramicauls of *Masdevallia* species are unifoliate, erect or suberect (truly pendent in only one species, *M. caesia* Roezl) and partially or completely enclosed by 2 or 3 thin, imbricating sheaths near the base (Figs. 6 and 8).

Leaves of *Masdevallia* species are thick and fleshy, and they show a great variation in shape, from elliptical to narrowly elliptical or obovate to narrowly obovate (Figs. 6 and 8). Sizes of *Masdevallia* leaves can vary considerably; for example, the leaves of the Central American *M. hoeijeri* Luer & Hirtz are 5 - 10 mm long, where those of the Ecuadorian *M. ova-avis* Luer are 15 - 20 cm long. Most species are subpetiolate but petiolate leaves are present in a few species. The apices or tips are acute, obtuse to rounded, shallowly notched with a mucro in the sinus. The base is rounded, cuneate or narrowly cuneate, with or without a channeled petiole; the surface is smooth and the venation parallel. Leaves are commonly green or dark green, rarely purplish.

Species of *Masdevallia* are single flowered (Fig. 6) or the inflorescence is a raceme (Fig. 8) that may be shorter or longer than the leaves, few to many flowered with the flowers produced simultaneously or successively, densely or distantly on the rachis, longer or shorter than the leaves. The peduncle emerges laterally from an ill definite ring, the annulus, usually near or at the base of the ramicaul, or occasionally higher near the middle, but always a considerable distance below the apex, the leaf stem abscission layer. Peduncles are terete in cross-section in most species (Fig. 6); a triquetrous peduncle (Fig. 8) occurs in a large group of interrelated species of subgenus *Polyantha*, and four species produce both round and triangular peduncles (*M. garciae* Luer, *M. infracta* Lindl., *M. richarsoniana* Luer, and *M. sprucei* Rchb. f.). The peduncle is smooth in all species except in *M. bicornis* Luer in which it is scabrous. The pedicel varies in length. In some instances it is thicker and longer than the peduncle that bears it.

The flowers are borne by a subtending floral bract (Figs. 6 and 8), which is usually tubular, but some species are characterized by inflated (e. g. *M. caloptera* Rchb. f., *M. dimorphotricha* Luer & Hirtz, *M. lehmanii* Rchb. f.) or cucullate floral bracts (i. e. *M. cerastes* Luer & Escobar, *M. corniculata* Rchb. f., *M. cucullata* Lindl., *M. delhierroi* Luer & Hirtz, *M. hercules* Luer & Andreetta, and *M. vidua* Luer & Andreetta). In some species there are several imbricate floral bracts (e. g. *M. cuprea* Lindl., *M. deceptrix* Luer & Würstle, *M. impostor* Luer & Escobar, *M. medusa* Luer & Escobar, *M. sanctae-fidei* Kraenzl.). *Masdevallia* flowers are zygomorphic, with an articulation between ovary and pedicel (Fig. 8), and variable in size, from 7 mm (*M. bangii* Schltr.) to 50 mm (*M. veitchiana* Rchb. f.) including the tail length. The ovaries of all species are trivalvate and each valve is ribbed to some degree. The ovaries can be smooth or verrucose to papillose or pitted, with the ribs smooth, carinate or crested.

The sepals are conspicuous, membranous to thickly fleshy, variously colored, smooth to verrucose or pubescent, broad or narrow, acute to obtuse (Figs. 6 and 8). Sepals are variously connate, from barely connate at the base to form a cup, to deeply connate to form a cylindrical tube; in a few species the dorsal sepal is free from the laterals. The degree of connation between the sepals is used to define some infrageneric taxa. The apices of sepals are commonly contracted into elongated segments (tails) (Fig. 6); tailless sepals characterize some infrageneric taxa (e. g. *M. mentosa* Luer, *M. henniae* Luer & Dalström, *M. expers* Luer & Andreetta). Sepals display the greatest diversity in size, shape, texture and color of all the floral parts and are almost always the most important features in specific diagnoses.

The petals are considered the hallmark of the genus (LUER, 1986b). They are usually callous, small and inconspicuous, usually about the length of the column they flank, more or less waxy or cartilaginous in consistency, commonly thickened along the labellar margin, usually forming a carina or a tooth (Fig. 6), often producing a marginal angle or a kind of process or tooth somewhere between the middle and the base. In some species (e.g., *M. chaetostoma* Luer) a callus is missing. The shape of petals varies from oblong to elliptic and obovate. The apex varies from truncate to acute and rounded. Verrucose petals characterize some infrageneric taxa.

The lip (Figs. 6 and 8), which is usually not much larger than the lateral petals, is more or less ligulate, smooth or verrucose and entire or denticulate at the apex. It is usually sulcate to some degree between a pair of longitudinal calli; the absence of calli is used to define some infrageneric taxa. In some taxa the calli are developed into oblique, marginal folds that divide the lip into an epichile and a hypochile.

The base of the lip is truncate or cordate and attached to a curved extension from the base of the column-foot.

The column is very much the same in all species of *Masdevallia* (Figs. 6 and 8). It is semiterete, with a ventral anther, the apical margins entire to lightly toothed. The base of the column is prolonged into a thickened foot at the apex of the ovary (Figs. 6 and 8), and from the apex of the foot there is a free incurved extension to which the lip is attached. The rostellum is retrorse and two pollinia are present.

Characters of the anther have been among the most important in orchid systematics since the beginning of the 19th century. This is especially true for the greater than 99% of orchids that have only a single anther (Vanilloideae, Orchidoideae, Epidendroideae), because their anthers exhibit the greatest degree of variation. In spite of this importance, relatively little study has been devoted to understanding the variation encountered in these characters. Some of these characters are related to the orientation of the anther, others to the nature of pollinia themselves or of their associated structures (stalks). Variation in pollinia includes differences in numbers and packaging. FREUDENSTEIN and RASMUSSEN (1996) studied pollinium development with particular reference to how different numbers are produced and examined differences among sectile pollinia (FREUDENSTEIN and RASMUSSEN, 1997). RASMUSSEN (1985, 1986a) has characterized some of the variation observed in pollinium stalks. The surface topology and wall anatomy of the pollinia surface provide a substantial set of data, which appears to have great phylogenetic value in Orchidaceae. Pollinia structure has been described by WILLIAMS and BROOME (1976), SCHILL and PFEIFFER (1977), BURNS-BALOGH (1983), HESSE, BURNS-BALOGH, and WOLFF (1989), ZAVADA (1990), SCHLAG and HESSE (1993) and STENZEL (2000). The pollen is aggregated into sectile pollinia, which is typical of the subfamily (LINDLEY, 1830-1840; BURNS-BALOGH & FUNK, 1986). The pollen tetrads are combined into massulae, and the massulae are united into the pollinium.

Fig. 5 Morphology of *Masdevallia glandulosa* Königer, painted by Joubert Da Silva.

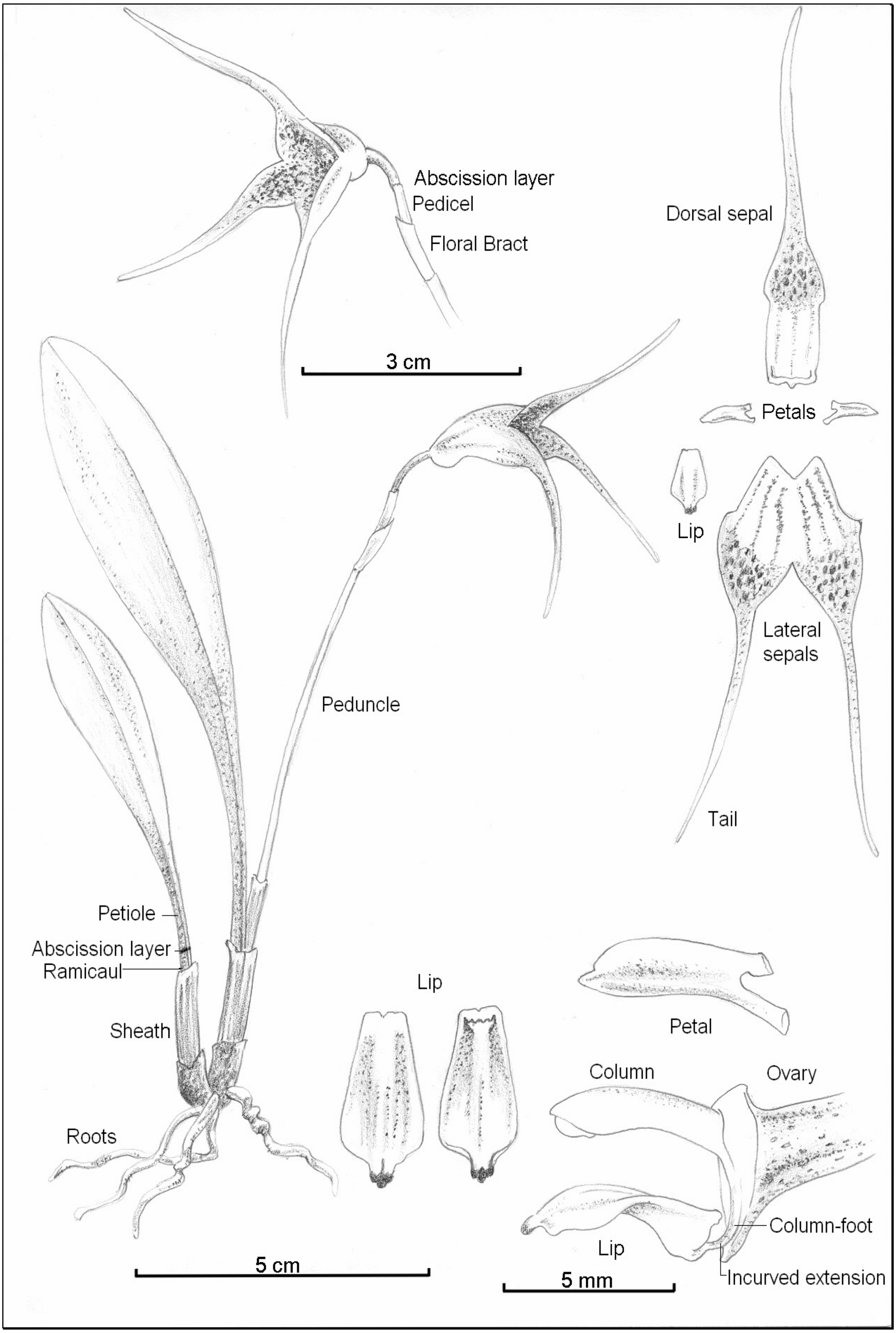

Fig. 6 Morphology of *Masdevallia glandulosa* Königer

Fig. 7 *Masdevallia melanoxantha* Linden & Rchb. f. painted by Joubert Da Silva.

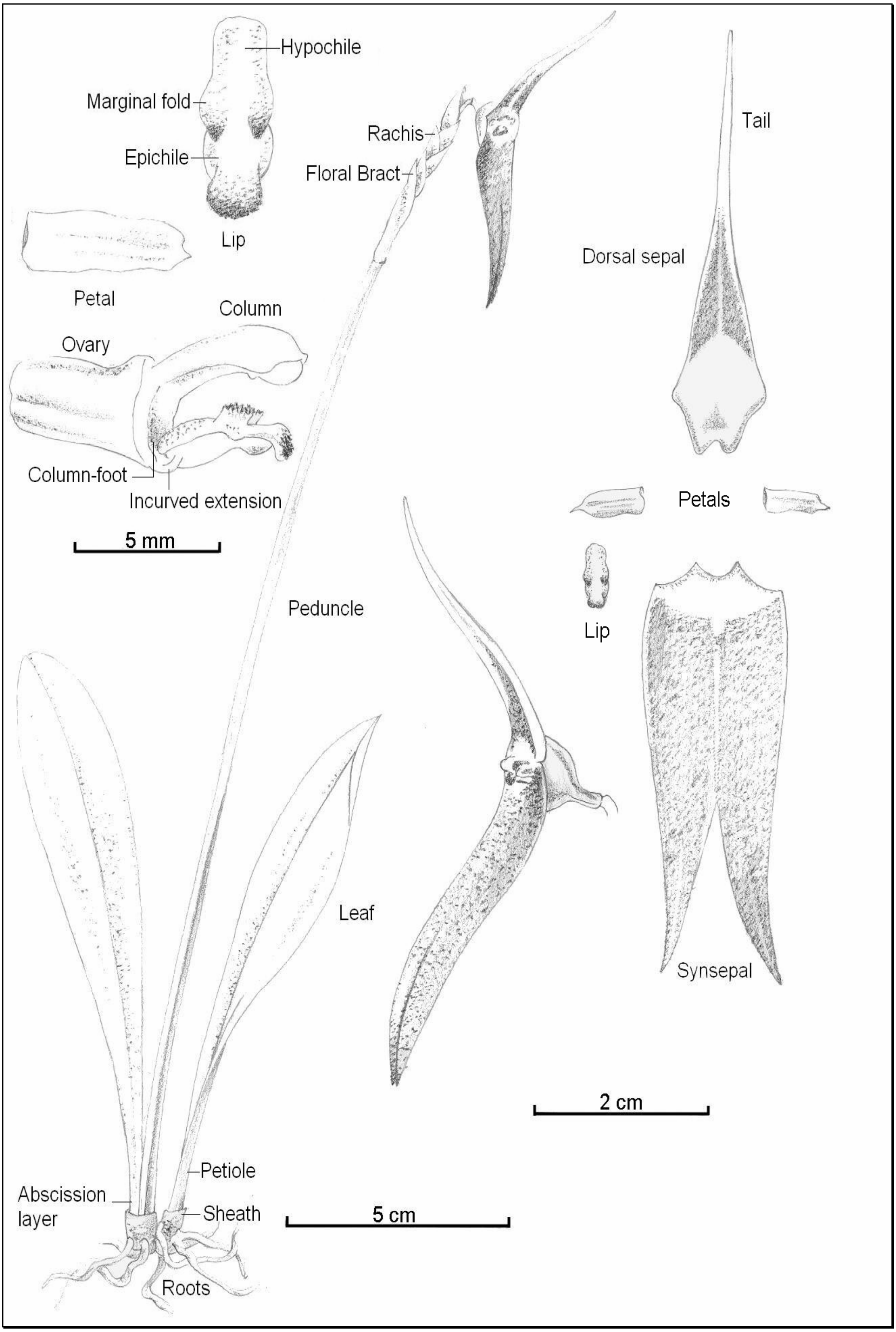

Fig. 8 Morphology of *Masdevallia melanoxantha* Linden & Rchb. f.

Masdevallia fruits (Fig. 9) are capsules that consist of three carpels, as are all Orchidaceae fruits.

Fig. 9 *Masdevallia* capsules: a) Capsules of *Masdevallia herradurae* F. Lehm. & Kraenzl., b) Capsules of *Masdevallia infracta* Lindl. Scale bars= 1 cm (A, B).

Masdevallia seeds are exceedingly small, almost dustlike, consisting of a tiny embryo suspended inside a reticulate or netlike testa and surrounded by a large volume of air space. In *Masdevallia*, they can range in weight from 3 to 14 µg and may be 0.4 – 1.25 mm long and 0.08 – 0.27 wide.

Their shapes can be very variable. The seed coat may be hard and coriaceous or papery. Observations through a scanning electron microscope (Fig. 10) have shown that the seed coats may have transverse, longitudinal, and netlike reticulations.

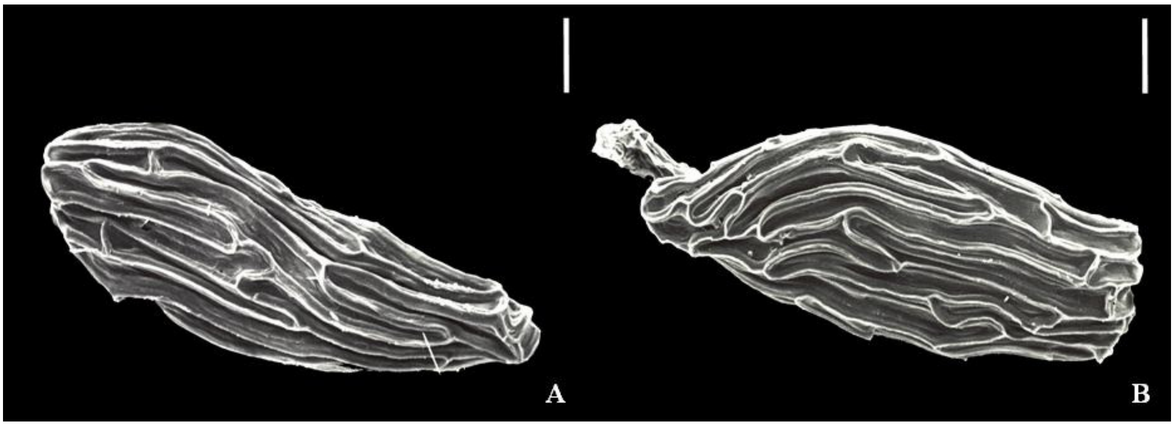

Fig 10 *Masdevallia* seeds: a) Seed of *Masdevallia herradurae* F. Lehm. & Kraenzl. b) Seed of *Masdevallia infracta* Lindl. Scale bars= 20 µm (A, B).

1.2.4 Infrageneric relationships of *Masdevallia* based on molecular data

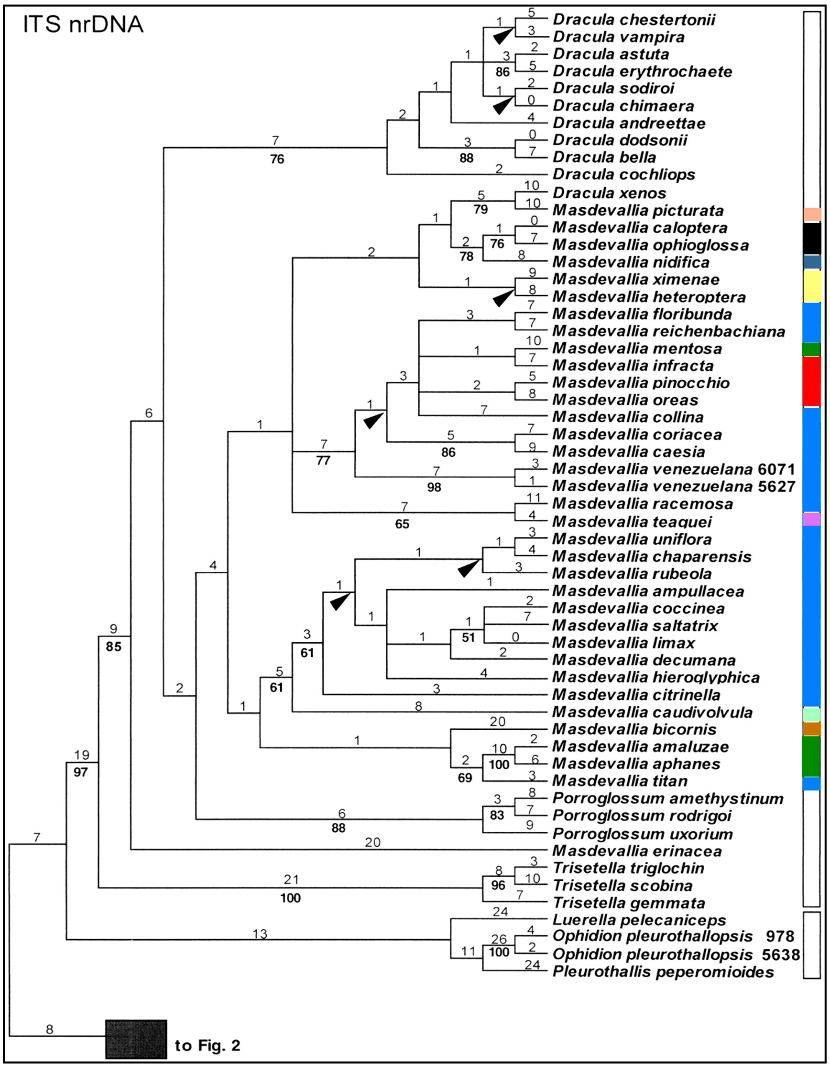

Fig. 11 A portion of one of the 10 0001 most parsimonious trees of the complete ITS nrDNA of *Pleurothallidinae* from PRIDGEON et al. (2001). Subgenera are represented by different colours.

Masdevallia is a distinctive genus in the subtribe *Pleurothallidinae* and its delimitation has never been a problem, although in the last 20 years, four genera (*Dracula* Luer, *Dryadella* Luer, *Trisetella* Luer, and *Porroglossum* Schltr.) have been segregated from *Masdevallia*. In a cladistic analysis of the subtribe *Pleurothallidinae* based on morphological and anatomical data (NEYLAND et al., 1995), the genus *Masdevallia* appears as sister to *Porroglossum* (see Fig. 3, p. 5). In a first molecular systematic analysis of the subtribe *Pleurothallidinae* by PRIDGEON et al. (2001) based on nuclear and plastid DNA sequences, the genus *Masdevallia* was not monophyletic, however most of the species grouped together in a clade. The phylogenetic relationship of the genus *Masdevallia* relative to outgroup taxa is well resolved using ITS sequences (PRIDGEON et al., 2001); species of *Masdevallia* appears as sister to *Dracula, Trisetella* and *Porroglossum* (see Fig. 2 p. 4 and 11). *Dracula xenos* Luer & R. Escobar came out as sister to *Masdevallia picturata* Rchb. f., and *Masdevallia erinacea* Rchb. f. resulted sister to the genera *Dracula* Luer, *Masdevallia,* and *Porroglossum* Schltr. (Fig. 11). The naturalness and relationships of the subgenera, sections and subsections of *Masdevallia* were not previously examined in a phylogenetic context. A glance at Fig.11 has shown that that most of the proposed subgenera are not monophyletic and that the infrageneric classification of the genus *Masdevallia* should be reconsidered.

1.2.5 Classification history of *Masdevallia* and nomenclatural implications

Although revisions of several sections of *Masdevallia* were published in the last century, a comprehensive treatment of all species is still lacking. This is partly caused by the problematic delimitation of groups within the genus due to the absence of diagnostic morphological characters, and the great number of species. The proposed infrageneric classifications for the genus *Masdevallia* are shown in Table 3.

Infrageneric classification of *Masdevallia* proposed by Heinrich Gustav Reichenbach (1873 - 1878)

The earliest attempt to indicate subdivisions of the genus was made by Reichenbach. Usually he did not mention the rank of the subdivisions, but in a few instances he indicated groups or "sections". In the whole 14 groups/sections were recognized by Reichenbach:

Section *Amandae* Rchb. f., Gard. Chron. 2: 290. 1874.

Type: *Masdevallia amanda* Rchb. f. & Warsc. Bonplandia 2: 115.

Characterized by stems producing several small flowers, by the serrate wings or ridges on the ovary, the inflated floral bracts and the petals that are toothed on both margins.

Section *Clausae-porrectae* Rchb. f., Gard. Chron. 2: 338. 1875.

Type: *Masdevallia ionocharis* Rchb. f., Gard. Chron., 4: 388. 1875.

Characterized by single-flowered peduncles, tubular floral bracts, and cartilaginous petals with a well-developed, retrorse tooth from the callus near the base on the labellar margin.

Section *Coriacea*e Rchb. f., Gard. Chron. 1: 240. 1874.

Type: *Masdevallia coriacea* Lindl., Ann. Mag. Nat. Hist. 15: 257. 1845.

Syn.: Section *Leontoglossae* Rchb. f., Otia Bot. Hamburg. 1: 15. 1878.

Type: *Masdevallia leontoglossa* Rchb. f., Bonplandia 3: 69. 1855.

Characterized by rigid (coriaceous) leaves and thick succulent flowers.

Section *Cucullatae* Rchb. f., Gard. Chron. 1: 72. 1878.

Type: *Masdevallia cucullata* Rchb. f., Orchid. Linden. 4. 1846.

Characterized by the extreme shortness of the pedicel, which causes the large cucullate bract to conceal the ovary and the base of the flower.

Table 3 Infrageneric classification of *Masdevallia* Ruiz & Pav. from Reichenbach (1873) to Luer (2003).

Reichenbach (1873-1878)	**Pfitzer (1888)**	**H. J. Veitch (1889)**	**Woolward (1896)**	**Kraenzlin (1925)**	**Luer (1986)**	**Luer (2000-2003)**
Sect. *Amandae*	Sect. *Cupulatae*	Sect. *Eumasdevallia*	Sect. *Amandae*	Sect. *Alaticaules*	Subg. *Amanda*	Subg. *Amanda*
Sect. *Clausae-porrectae*	Sect. *Polyanthae*	Subsect. *Coriaceae*	Sect. *Coccineae*	Sect. *Chimaeroideae*	Sect. *Fissae*	Subg. *Cucullatia*
Sect. *Coriaceae*	Sect. *Saccilabiatae*	Subsect. *Cucullatae*	Sect. *Coriaceae*	Sect. *Coccineae*	Sect. *Nidificae*	Subg. *Fissia*
Sect. *Cucullatae*	Sect. *Triaristellae*	Subsect. *Polyanthae*	Sect. *Cucullatae*	Sect. *Echidna*	Sect. *Ophioglossae*	Subg. *Masdevallia*
Sect. *Echidnae*	Sect. *Tubulosae*	Subsect. *Coccineae*	Sect. *Fissae*	Sect. *Fissae*	Sect. *Pygmaeae*	Sect. *Amaluzae.*
Sect. *Fissae*		Subsect. *Caudatae*	Sect. *Minutae*	Sect. *Floribundae*	Subg. *Masdevallia*	Subsect. *Amaluzae*
Sect. *Minutae*		Subsect. *Amandae*	Sect. *Muscosae*	Sect. *Leontoglossae*	Sect. *Amaluzae*	Subsect. *Zahlbrucknerae*
Sect. *Polyanthae*		Sect. *Saccolabiatae*	Sect. *Polyanthae*	Sect. *Polystictae*	Sect. *Aphanes*	Sect. *Coriaceae*
Sect. *Saccilabiatae*		Sect. *Triaristellae*	Sect. *Racemosae*	Sect. *Reichenbachianae*	Sect. *Caudivolvulae*	Sect. *Dentatae*
Sect. *Saltatrices*			Sect. *Reichenbachianae*	Sect. *Rhombopetalae*	Sect. *Coriacea*	Sect. *Durae*
Sect. *Triangulares*			Sect. *Saccolabiatae*	Sect. *Triangulares*	Subsect. *Coriaceae*	Sect. *Masdevallia*
Sect. *Triaristellae*			Sect. *Saltatrices*	Sect. *Triaristellae*	Subsect. *Durae*	Subsect. *Caudatae*
Sect. *Tubulosae*			Sect. *Triangulares*	Sect. *Tubulosae*	Sect. *Cucullatae*	Subsect. *Coccinea*
Sect. *Verrucosae*			Sect. *Triaristellae*	Sect. *Urceolares*	Sect. *Ligiae*	Subsect. *Masdevallia*
			Sect. *Tubulosae*		Sect. *Masdevallia*	Subsect. *Oscillantes*
					Subsect. *Caudatae*	Subsect. *Saltatrices*
					Subsect. *Coccinea*	Sect. *Minutae*
					Subsect. *Masdevallia*	Sect. *Racemosae*
					Subsect. *Oscillantes*	Sect. *Reichenbachianae*
					Subsect. *Saltatrices*	Sect. *Triotosiphon*
					Subsect. *Tubulosae*	Subg. *Meleagris*
					Sect. *Mentosae*	Subg. *Nidificia*
					Sect. *Minutae*	Subg. *Polyantha*
					Sect. *Polyantha*	Sect. *Alaticaules*
					Subsect. *Alaticaules*	Subsect. *Alaticaules*
					Subsect. *Polyanthae*	Subsect. *Coaetaneae*
					Sect. *Racemosae*	Sect. *Polyanthae*
					Sect. *Reichenbachianae*	Subsect. *Polyanthae*
					Subsect. *Dentatae*	Subsect. *Successiviflorae*
					Subsect. *Reichenbachianae*	Subg. *Pygmaeia*
					Subg. *Meleagris*	Sect. *Aphanes*
					Subg. *Pelecaniceps*	Subsect. *Aphanes*
					Subg. *Teagueia*	Subsect. *Pterigophorae*
						Sect. *Pygmaeae*
						Subg. *Scabripes*
						Subg. *Teagueia*
						Subg. *Volvula*

Section *Echidna* Rchb. f., Linnaea 41: 11. 1877.

Type: *Masdevallia echidna* Rchb. f., Bonplandia 3: 69. 1855.

Characterized by pubescent sepals, bivalvate petals, and by a three-nerved lip.

Section *Fissae* Rchb. f., Otia Bot. Hamburg. 1: 16. 1878.

Type: *Masdevallia picturata* Rchb. f., Otia Bot. Hamburg. 1: 16. 1878.

In the unique species included in this section, *M. picturata* Rchb. f., the dorsal sepal is not united to the lateral sepals. Reichenbach´s name for this group, *Fissae* = the cleft, is based on this peculiarity.

Section *Minutae* Rchb. f., ex Woolward. Gen. Masdevallia. 1896.

Type: *Masdevallia minuta* Lindl., Ann. Mag. Nat. Hist. 12:396. 1842.

Reichenbach simply indicated the subgeneric category *Minutae* for *Masdevallia minuta*.

Section *Polyanthae* Rchb. f., Gard. Chron. 1: 372. 1874.

Type: *Masdevallia polyantha* Lindl., Orchid. Linden. 6. 1846.

Species of this section produce more than one flower upon each peduncle, the flowers of some species expand at the same time and others in succession. With the exception of *M. schlimii*, all species have triquetrous or three angled stems.

Section *Saccilabiatae* Rchb. f., Gard. Chron. 37: 1238. 1873.

Type: *Masdevallia chimaera* Rchb. f., Gard. Chron. 463. 1872.

Lectotype designated by Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 15: 23. (1986b).

Characterized by a saccate or cochleate lip; the club-shaped petals, which are keeled and papillose near the apex, and the short and open perianth tube, which is generally more or less hairy.

Section *Saltatrices* Rchb. f., Linnaea 41: 10. 1877.

Type: *Masdevallia saltatrix* Rchb. f., Linnaea 41: 10. 1877.

Characterized by species with the sepals deeply connate into a long sepaline tube that is more or less constricted above the middle or below the free segments, and more or less ventricose below the constriction.

Section *Triangulares* Rchb. f., Gard. Chron. 1: 372. 1874.

Type: *Masdevallia triangularis* Lindl., Orchid. Linden. 5. 1846.

Characterized by the widely spreading, more or less similar, long-tailed sepals that are basally connate into a shallow sepaline cup which exposes the petals, and column and lip standing more or less erect in the centre.

Section *Triaristellae* Rchb. f., Gard. Chron. 6 (138): 226. 1876.

Type: *Masdevallia triaristella* Rchb. f., Gard. Chron. 6 (138): 226. 1876.
Characterized by their inflorescence, a succession of single flowers borne in a congested raceme; the petals small and membranous; and the simple, longitudinally callous lip which is sagittate or cordate at the base, the retrorse basal lobes projecting behind to either side of the central hinge to the wedge-shaped column-foot. The column is elongate with a hooded ventral anther with two pollinia, and a large ventral stigma.

Section *Tubulosae* Rchb. f., Otia Bot. Hamburg. 1: 14. 1878.

Type: *Masdevallia tubulosa* Lindl., Orchid. Linden. 4. 1846.
Composed of very small species characterized by solitary, white to yellowish or greenish tubular flowers often with more or less similar free parts of the sepals. The callus of the petals is usually poorly developed. The lip is ligulate, usually with a pair of calli.

Section *Verrucosae* Rchb. f., Gard. Chron. 1: 8. 1876.

Type: *Masdevallia verrucosa* Rchb. f., Linnaea 22: 819. 1849.
Characterized by their inflorescence, a raceme that produces a succession of non-resupinate flowers, usually with caudate sepals. A usually prominent, more or less flat callus occupies the inner surface of the lateral sepals toward the apex. The petals are fleshy, broad and multiangular. The lip is deflexed and crested near the middle. The elongated, thick-footed column is winged with a toothed apex partially covering the ventral anther.

Infrageneric classification of *Masdevallia* proposed by Ernst Hugo Heinrich Pfitzer (1888)

The second proposed infrageneric classification was those of Pfitzer published in “Die natürlichen Pflanzenfamilien”. It included five sections, of which four sections: *Tubulosae*, *Polyanthae*, *Saccilabiatae*, and *Triaristellae*; were previously recognized by Reichenbach (1873-1878). One new section was described and species of section *Verrucosae* were placed into a higher rank.

Section II. *Cupulatae* Pfitzer, Nat. Pflanzenfam. 2(6): 136. 1888.

Type: *Masdevallia shuttleworthii* Rchb. f., Gard. Chron. 1: 170. 1875.
Species of this section are characterized by one flowered peduncles, and flat flowers with the sepals connate into a cup and the flat labellum.

Genus *Scaphosepalum* Pfitzer, Nat. Pflanzenfam. 2(6): 136. 1888.

Lectotype: *Masdevallia ochthodes* Rchb. f., Bonplandia 3: 70. 1855. Lectotype designated by Garay. Orquideología 9: 124 (1974).
Syn.: *Pleurothallis* section *Racemosae*. Rchb., Bonplandia 2: 24. 1854.
= sect. *Verrucosae* Rchb. f., Gard. Chron. 1: 8. 1876.
Type: *Masdevallia verrucosa* Rchb. f., Linnaea 22: 819. 1849. = *Scaphosepalum verrucosum* (Rchb. f.) Pfitzer, Nat. Pflanzenfam. 2(6): 139. 1888.

Reichenbach attributed the earliest species of this genus to *Masdevallia*, probably because of the vegetative similarity and the sepaline tails.

Infrageneric classification of *Masdevallia* proposed by Harry James Veitch (1889)

In the “Manual of Orchidaceous plants cultivated under glass in Great Britain”, H. J. Veitch described the principal genera, species and varieties cultivated under glass to supply amateurs and cultivators of exotic orchids. H. J. Veitch proposed for the genus *Masdevallia* an infrageneric classification based on Reichenbach´s classification. The infrageneric classification comprises 3 sections and 6 subsections, these last ones demoted from the rank of section in Reichenbach´s classification to subsections of *Eumasdevallia*.

Section I. *Eumasdevallia* H. J. Veitch, Man. Orchid. Pl. 5: 17. 1889.

According with Article 11 of the International Code of Botanical Nomenclature (IBCN; GREUTER et al., 2000), Veitch´s name for section *Eumasdevallia* is illegitimate.

The very large section *Eumasdevallia* comprised the great bulk of the genus and was not easily differentiated from with the remaining sections. The section comprised species with the lip generally ligulate or linear-oblong, usually nearly flat, more or less fleshy; petals flat, often somewhat oblique; sepals united below into a tube which is generally but not always longer than broad, the sepaline tails variable in length, breadth, and colour. It included subsections *Amandae*, *Caudatae*, *Coccineae*, *Coriaceae*, *Cucullatae*, and *Polyanthae*.

Section II. *Saccolabiatae* Rchb.f., Gard. Chron. 37: 1238. 1873.

Type: *Masdevallia chimaera* Rchb. f., Gard. Chron. 463. 1872.

It was not clear if the section name was Saccolabiatae or Saccilabiatae, because Reichenbach used in most places Saccilabiatae, but in one or two instances Saccolabiatae. H. J. Veitch retained the name Saccolabiatae because it is formed more in accordance with classical usage. H. J. Veitch described the section as “a most distinct section, including the species that are sometimes called by horticulturists the Chimaeroid group”. It includes the following:

M. astuta Rchb. f.
M. bella Rchb. f.
M. carderi Rchb. f.
M. chestertonii Rchb. f.
M. chimaera Rchb. f.
M. erythrochaete Rchb. f.
M. gaskelliana Rchb. f.
M. houtteana Rchb. f.
M. nycterina Rchb. f.
M. radiosa Rchb. f.
M. troglodytes E. Morren
M. vespertilio Rchb.

Section III *Triaristellae* Rchb. f., Gard. Chron. 6 (138): 226. 1876.

Type: *Masdevallia triaristella* Rchb. f., Gard. Chron. 6 (138): 226. 1876.

The species included in this section are characterized by extremely short perianth tube, the lateral sepals, that are united almost to the apex, the lateral tails, i.e., not a prolongation of the sepals, but inserted below their apex on the lateral margin. The peduncles of the species included in this section are slender and the leaves small and narrow. H. J. Veitch described this section as a “very natural group of exceptional interest, consisting of dwarf-tufted plants, bearing minute gem-like flowers”. It includes *M. gemmata* Rchb. f., *M. triaristella* Rchb. f. and *M. tridactylites* Rchb. f.

Infrageneric classification of *Masdevallia* proposed by Florence Helen Woolward (1896)

In her monograph of the genus *Masdevallia*, Florence Woolward in 1896 assembled a collection of her paintings, numbered the sections, and placed them as well as the species contained in them in alphabetical order. Woolward (1896) used the classification of Reichenbach with minor changes. The species were grouped into 15 sections, of which three sections, *Muscosae*, *Racemosae* and *Reichenbachianae*; were newly proposed by Woolward. The remaining sections were *Amandae*, *Coccineae*, *Coriaceae*, *Cucullatae*, *Fissae*, *Minutae*, *Polyanthae*, *Saccolabiatae*, *Saltatrices*, *Triangulares*, *Triaristellae*, and *Tubulosae*.

Section VII *Muscosae* Woolward, Gen. Masdevallia. 1896.

Type: *Masdevallia muscosa* Rchb. f., Gardener's Chronicle & Agricultural Gazette 1: 460. 1875.

The species included in this section were segregated into a new genus, *Scaphosepalum* Pfitzer, but in the absence of a final decision, Woolward omitted this genus and placed the unique species, *M. muscosa* Rchb. f., into Section *Muscosae*.

Section IX *Racemosae* Woolward, Gen. Masdevallia. 1896.

Type: *Masdevallia racemosa* Lindl., Ann. Mag. Nat. Hist. 15: 256. 1845.

This section was proposed by Woolward because *M. racemosa* Lindl. was impossible to classify with any other species. *Masdevallia racemosa* Lindl. is characterized by the creeping rhizomes, producing leaves at intervals and bearing two or three flowers upon one peduncle.

Fig 12 Florence Woolward´s painting of *Masdevallia coccinea* (Section II Coccineae). Source: J. Stewart. 1992. HMSO, London.

Fig 13 Florence Woolward´s painting of *Masdevallia macrura* (Section IV *Cucullatae*). Source: J. Stewart. 1992. HMSO, London.

Section X *Reichenbachianae* Woolward, Gen. Masdevallia. 1896.

Type: *Masdevallia reichenbachiana* Endres ex Rchb. f., Gard. Chron. 4(87): 257. 1875.

This section included all the species allied with *M. reichenbachiana* Endres, a plant which Reichenbach temporally included among the *Coriaceae*. The species included in section *Reichenbachianae* are distinguished from the *Coriaceae* by the fleshy texture of their flowers and leaves, by the deep narrow tube and by the carinate veins upon the inner surface of the lateral sepals. This section comprised seven species:

- *M. calura* Rchb. f.
- *M. demissa* Rchb. f.
- *M. fulvescens* Rolfe
- *M. marginella* Rchb. f.
- *M. reichenbachiana* Endres
- *M. rolfeana* Kraenzl.
- *M. schroederiana* hort. Sander.

The genus *Porroglossum* Schltr.

In 1920 Schlechter proposed to segregate *Masdevallia echidna* Rchb. f. into a new genus, *Porroglossum* (from the Greek porro, “far, far off”, and glossa, “tongue”) referring either to the position of the lip in relation to the column or elongated column-foot, or to the fact that the lip was far from the usual. The peculiar sensitive lip was noted by Oliver in 1888, who described the mechanism of movement and its influence on the pollination.

Porroglossum Schltr., Repert. Spec. Nov. Regni Veg. Beih. 7: 82. 1920.

Type: *Porroglossum colombianum* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 7: 83. 1920.

Syn.: sect. *Echidnae* Rchb. f., Linnaea 41: 11. 1876.

Type: *Masdevallia echidna* Rchb. f., Bonplandia 3: 69. 1855. (*Porroglossum echidnum* (Rchb. f.) Garay, Svensk. Bot. Tidskr. 47: 201. 1953.

= *Masdevallia* section *Muscosae* Woolward, Gen. Masdevallia. 1896.

Type: *Masdevallia muscosa* Rchb. f., Gardener's Chronicle & Agricultural Gazette 1: 460. 1875.

= *Lothania* Kraenzl., Gard. Chron. ser. 3, 75: 173. 1924.

Type: *Lothania mordax* Rchb. f., Gard. Chron. ser. 3, 75: 173. 1924.

Infrageneric classification of *Masdevallia* proposed by Friedrich Wilhelm Ludwig Kraenzlin (1925)

The next treatment of the genus was assembled in 1925 by Kraenzlin. The infrageneric classification proposed by Kraenzlin included 14 sections, two of them, *Urceolares* and *Floribundae*, were new sections proposed by Kraenzlin. Five sections, *Polystictae*, *Leontoglossae*, *Alaticaules*, *Chimaeroideae*, and *Rhombopetalae*, were renamed, and two sections; *Racemosae* and *Minutae*, were merged into other sections. Some species were merged into different sections:

Section *Tubulosae* Rchb. f., Otia Bot. Hamburg. 1: 14. 1878.

Type: *Masdevallia tubulosa* Lindl., Orchid. Linden.4. 1846.

Seven species were included by Kraenzlin in this section. *Masdevallia saltatrix* Rchb. f. (prior sect. *Saltatrices* Rchb. f.) was placed in this section:

- *M. angulifera* Rchb. f.
- *M. constricta* Poepp. et Endl.
- *M. olivacea* Kraenzl.
- *M. saltatrix* Rchb. f.
- *M. tubulosa* Lindl
- *M. ventricularia* Rchb. f.
- ***M. tridentata*** Lindl

Section *Coccineae* (H. J. Veitch) Woolward, Gen. Masdevallia. 1896.

Type: *Masdevallia coccinea* Linden ex Lindl., Orchid. Linden. 5 (26). 1846.

12 species were placed by Kraenzlin in this section, including *M. racemosa* (Section *Racemosae* Woolward). The other species were:

- *M. amabilis* Rchb. f.
- *M. barleana* Rchb. f.
- *M. coccinea* Lind. ex Lindl.
- *M. crescenticola* Kraenzl.
- *M. davisii* Rchb. f.
- *M. deformis* Kraenzl.
- *M. eduardii* Rchb. f.
- *M. militaris* Rchb. f.
- *M. racemosa* Lindl.
- *M. rosea* Lindl. (prior section *Tubulosae* sensu Woolward)
- *M. tuerckheimii* O. Ames
- *M. veitchiana* Rchb. f.

Section *Polystictae* Kraenzl., Repert. Spec. Nov. Regni Veg. Beih. 34: 32. 1925.

Type: *Masdevallia polysticta* Rchb. f., Gard. Chron. 1: 338. 1874.

Syn.: sect. *Eumasdevallia* subsect. *Amandae* (Rchb. f.) H. J. Veitch, Man. Orchid. Pl. 5: 18. 1889.

Type: *Masdevallia amanda* Rchb. f. & Warsc., Bonplandia 2: 115

In accordance with Article 11 of the International Code of Botanical Nomenclature (IBCN; GREUTER et al., 2000), Kraenzlin´s name for section *Polystictae* is illegitimate.

The section was renamed because the most representative species for this section, according to Kraenzlin, was *M. polysticta* Rchb. f. The "new" name for this section described the characteristic colour. Eleven species and six putative hybrids were included in this section:

- *M. abbreviata* Rchb. f.
- *M. amanda* Rchb. f.
- *M. caloptera* Rchb. f.
- *M. densiflora* Schltr.
- *M. gustavi* Rchb. f.
- *M. lehmanni* Rchb. f.
- *M. pachyura* Rchb. f.
- *M. polysticta* Rchb. f.
- *M. sodiroi* Schltr.
- *M. spathulifolia* Kraenzl.
- *M. tridens* Rchb. f.

Hybrids according to Kraenzlin:

- *M. calopterocarpa* Rchb. f.
- *M. melanopus* Rchb. f.
- *M. sphenopetala* Kraenzl.
- *M. huebschiana* Kraenzl.
- *M. bulbophyllopsis* Kraenzl.
- *M. corazonica* Schltr.

Section *Urceolares* Kraenzl., Repert. Spec. Nov. Regni Veg. Beih. 34: 32. 1925.

Type: *Masdevallia urceolaris* Kraenzl., Notizbl. Bot. Gart. Berlin-Dahlem 8: 132. 1922.

Section *Urceolares* included mainly newly described species or species "section indeterminate or confused" that were characterized by the connation of sepals very similar as in section *Polysticta*, the tails of sepals very short, and single flowers or inflorescences with 2 or 3 flowers produced successively. Thirteen species in two informal groups were placed in this section:

Caudatae
M. erinacea Rchb. f.
M. molossoides Kraenzl.
M. ophioglossa Rchb. f. (prior section *Minutae*)
M. rhopalura Schlechter
M. stenantha Lehm.
M. urceolaris Kraenzl.

Ecaudatae
M. antioquensis Lehm.
M. ecaudata Schltr.
M. anura Kraenzl.
M. schmidtchenii Kraenzl.
M. molossus Rchb. f. (prior section *Saltatrices*)
M. yauaperyensis Barb. Rodr.
M. chloracra Rchb. f. (prior section *Coriaceae*).

Section *Reichenbachianae* Woolward, Gen. Masdevallia. 1896.

Type: *Masdevallia reichenbachiana* Endres ex Rchb. f., Gard. Chron. 4(87): 257. 1875.

Seven species were included in this section by Kraenzlin:

M. demissa Rchb. f.
M. rolfeana Kraenzl.
M. calura Rchb. f.
M. aspera Rchb. f.
M. schroederiana hort.
M. reichenbachiana Endres
M. marginella Rchb. f

Section *Leontoglossae* (Rchb. f.) Kraenzl., Repert. Spec. Nov. Regni Veg. Beih. 34: 32. 1925.

Type: *Masdevallia leontoglossa* Rchb. f., Otia Bot. Hamburg. 1: 15. 1878.

Syn.: sect. *Coriaceae* Rchb. f., Gard. Chron. 1: 240. 1874.

= sect. *Eumasdevallia* subsect. *Coriaceae* (Rchb. f.) H. J. Veitch, Man. Orchid. Pl. 5: 18. 1889.

Type: *Masdevallia coriacea* Lindl., Ann. Mag. Nat. Hist. 15: 257. 1845.

In accordance with Article 11 of the International Code of Botanical Nomenclature (IBCN; GREUTER et al., 2000), Kraenzlin´s name for section *Leontoglossae* is illegitimate.

This section was renamed because the name "Coriaceae" applied, according to Kraenzlin, to most *Masdevallia* species. The name Leontoglossae was considered more descriptive for the labellum with a verrucose apex, characteristic for members of this section. Some species of section *Cucullatae* were transferred to this section. The section included seven informal groups: Gargantuae, Cupulares, Peristeriiformes, Civiles, Cucullatae, Microleontoglossae, and Lepidae. The section comprised 42 species, the great majority in culture:

Gargantuae
M. angulata Rchb. f.
M. deorsum Rolfe
M. elephanticeps Rchb. f.
M. gargantua Rchb. f.
M. mooreana Rchb. f.
M. stenorhynchos Kraenzl.
M. velifera Rchb. f.

Cupulares
M. chimboensis Kraenzl.
M. coriacea Lindl.
M. cupularis Rchb. f.
M. sulphurea F. Lehm. & Kraenzl.

Peristeriiformes
M. peristeria Rchb. f.
M. macroglossa Rchb. f.
M. pachyantha Rchb. f
M. corderoana Lehm
M. haematosticta Rchb. f.
M. fragans Woolward

Species imperfecte nota:
M. inaequalis Rchb. f.
M. fractiflexa Lehm. & Kraenzl.

Civiles
M. aequatorialis Kraenzl.
M. civilis Rchb. f.
M. dermatantha Kraenzl.
M. leontoglossa Rchb. f. Rchb. f.
M. rechingeriana Kraenzl. (= *M. sceptrum* Rchb. f.)
M. torta Rchb. f.

Cucullatae
M. macrura (prior section Cucullatae according to H. J. Veitch and Woolward)
M. metallica Lehm.
M. corniculata Rchb. f. (section *Cucullatae*)
M. cucullata Lindl. (section Cucullatae)

Microleontoglossae
M. laevis Lindl.
M. ortgiesiana Rchb. f.
M. pardina Rchb. f.
M. platyglossa Rchb. f.
M. porcelliceps Rchb. f.
M. trionyx Kraenzl.
Lepidae
M. affinis Lindl.
M. cayenensis Rchb. f.
M. ellipes Rchb. f.
M. endotrachys Kraenzl.
M. ensata Rchb. f.
M. lepida Rchb. f.
M. xiphium Rchb. f.

Section *Floribundae* Kraenzl., Repert. Spec. Nov. Regni Veg. Beih. 34: 84. 1925.

Type: *Masdevallia floribunda* Lindl., Edward´s Bot. Reg. 29: 72. 1843.

This section also comprised 31 species, including part of the species from sections *Triangulares* Rchb. f., *Minutae* Rchb. f. and *Clausae-porrectae* Rchb. f. The section was divided into three informal groups: Longicaudae, Brevicaudae and Ecaudatae. Species included in this section were:

Longicaudae
M. copiosa Kraenzl.
M. flaveola Rchb. f.
M. hians Lindl. & Rchb. f.
M. nidifica Rchb. f.
M. pteroglossa Schltr.
M. strumifera Rchb. f.
M. tenuipes Schltr.

Brevicaudae
M. anachaete Rchb. f.
M. chontalensis Rchb. f.
M. cyathogastra Schltr.
M. diantha Schltr.
M. floribunda Lindl.
M. guianensis Lindl.
M. heterotepala Rchb. f.
M. muriculata Kraenzl.
M. pygmaea Kraenzl.
M. schizopetala Kraenzl.
M. sprucei Rchb. f.
M. striatella Rchb. f.
M. trigonopetala Kraenzl.
M. ulei Schltr.
M. wendlandiana Rchb. f.

Ecaudatae
M. campyloglossa Rchb. f.
M. fertilis Kraenzl.
M. lansbergii Rchb. f.
M. liliputana Cogn.
M. minuta Lindl.
M. paulensis Barb. Rodr.
M. sanctae-rosae Kraenzl.
M. sarcophylla Kraenzl.
M. tubuliflora Ames

Section *Alaticaules* Kraenzl., Repert. Spec. Nov. Regni Veg. Beih. 34: 84. 1925.

Type: *Masdevallia melanoxantha* Linden & Rchb. f., Bonplandia 2: 283.1854.

Syn.: sect. *Polyanthae* Rchb. f., Gard. Chron. 1: 372. 1874.

= sect. *Eumasdevallia* subsection *Polyanthae* H. J. Veitch, Man. Orchid. Pl. 5: 18. 1889.

Type: *Masdevallia polyantha* Lindl., Orchid. Linden. 6. 1846.

According with Article 11 of the International Code of Botanical Nomenclature (IBCN; Greuter et al., 2000), Kraenzlin´s name for section *Alaticaules* is illegitimate.

Most species of section *Alaticaules* were members of the section *Polyanthae*. The section was renamed. Species of section *Alaticaules* are characterized by the peduncles that are triangular in cross section. The section is divided into four informal groups, Longiscapae, Succedaneae, Breviscapae and Brevicaudae: Members of section *Alaticaules* were:

Longiscapae
M. buccinator Rchb. f. & Warsz.
M. cinnamomea Rchb. f.
M. schlimii Linden ex Lindl.
M. subumbellata Kraenzl.
M. xylina Rchb. f.

Succedaneae
M. carruthersiana F. Lehm. & Kraenzl.
M. ephippium Rchb. f.
M. guttulata Rchb. f.
M. infracta Lindl.
M. jalapensis Kraenzl.
M. lawrenci Kraenzl.
M. melanoxantha Linden & Rchb. f.
M. remotiflora Kraenzl.
M. sanctae-fidei Kraenzl.
M. weberbaueri Schltr.

Breviscapae
M. bicolor Poepp. & Endl.
M. maculata Klotzsch & H. Karst.

Brevicaudae
M. auropurpurea Rchb. f. & Warsz.
M. brachyura F. Lehm. & Kraenzl.
M. cuprea Lindl.
M. lata Rchb. f.
M. mastodon Rchb. f.
M. parvula Schltr.
M. peruviana Rolfe
M. platyrhachis Rchb. f.
M. tovarensis Rchb. f.
M. aurantica Lindl.

Section C*himaeroideae* Kraenzl., Repert. Spec. Nov. Regni Veg. Beih. 34: 125. 1925.

Syn.: sect. *Saccilabiatae* Rchb. f., Gard. Chron. 37: 1238. 1873.

Type: *Masdevallia chimaera* Rchb. f., Gard. Chron. 463. 1872.

According with Article 11 of the International Code of Botanical Nomenclature (IBCN; GREUTER et al., 2000), Kraenzlin´s name for section *Chimaeroideae* is illegitimate.

This section was renamed because the old name characterized, according to Kraenzlin, only five of the 32 species. This section is characterized by the commonly pendent racemes, which originate from the ramicaul with an annulus a considerable distance below the abscission layer. The petals are small and usually verrucose between a pair of valvelike laminae. The lip is divided into a cleft hypochile and a more or less rounded, concave epichile often with lamellate, radiating veins. The section was divided into five informal groups. To this section belong:

Saccatae
M. chimaera Rchb. f.

Erythrochaetae
M. astuta Rchb. f.
M. erythrochaete Rchb. f.
M. gaskelliana Rchb. f.
M. microglochin Rchb. f.

Radiosae
M. benedicti Rchb. f.
M. callifera Schltr.
M. gorgo Rchb. f. ex Kraenzl.
M. houtteana Rchb. f.
M. lactea Kraenzl.
M. pusilla Rolfe
M. radiosa Rchb. f.
M. velutina Rchb. f.
Carderianae
M. carderi Rchb. f.
M. carderiopsis F. Lehm. & Kraenzl.
M. platycrater Rchb. f.
M. trinema Rchb. f.
M. trinemoides Kraenzl.
M. woolwardiae F. Lehm. ex. Kraenzl.

Nycterinae
M. bella Rchb. f.
M. chestertonii Rchb. f.
M. medellinensis Kraenzl.
M. nycterina Rchb. f.
M. tubeana Rchb. f.
M. venosa Rolfe
M. vespertilio Rchb. f.

Chimaeroideae spuriae
M. alismifolia Kraenzl.
M. johannis Schltr.
M. mopsus F. Lehm. & Kraenzl.
M. pachygne Kraenzl.
M. pantherina F. Lehm. & Kraenzl.
M. quilichaoensis F. Lehm. & Kraenzl.

Section *Triangulares* Rchb. f., Gard. Chron. 1: 372. 1874.

Type: *Masdevallia triangularis* Lindl., Orchid. Linden. 5. 1846.

Section *Triangulares* was divided into three informal groups. To this section belong:

Tridentatae
M. caudata Lindl.
M. caudivolvula Kraenzl.
M. chlorotica Kraenzl.
M. chrysochaete F. Lehm.
M. chrysoneura F. Lehm. & Kraenzl.
M. confusa Kraenzl.
M. cucutillensis Kraenzl.
M. estradae Rchb. f.
M. expansa Rchb. f.
M. klabochorum Rchb. f.
M. macropus F. Lehm. & Kraenzl.
M. tonduzii Woolward
M. triangularis Lindl.

Jonocharides
M. arminii Linden & Rchb. f.
M. casta Kraenzl.
M. chiquindensis Kraenzl.
M. filamentosa Kraenzl.
M. herradurae F. Lehm. & Kraenzl.
M. ionocharis Rchb. f.
M. laucheana Kraenzl. ex Woolward
M. leucantha F. Lehm. & Kraenzl.
M. pastensis Kraenzl.
M. tricolor Rchb. f.

Campanulatae
M. bonplandi Rchb. f.
M. hymenantha Rchb. f.
M. kalbreyeri Rchb. f. ex Kraenzl.
M. paiveana Rchb. f.
M. scandens Rolfe
M. uniflora Ruiz & Pav.
M. xerophila F. Lehm. & Kraenzl.
M. zahlbruckneri Kraenzl.

Section *Fissae* Rchb. f., Otia Bot. Hamburg. 1: 16. 1878.

Type: *Masdevallia picturata* Rchb. f., Otia Bot. Hamburg. 1: 16. 1878.

In the section *Fissae*, Kraenzlin included 22 species, some species prior members of the section *Clausae-porrectae* sensu Reichenbach:

M. bathychista Schltr.
M. cryptocopis Rchb. f. ex Kraenzl.
M. diversifolia Kraenzl.
M. falcago Rchb. f.
M. fasciata Rchb. f.
M. fissa Kraenzl.
M. flaccida Kraenzl.
M. frontinoensis Kraenzl.
M. heteroptera Rchb. f.
M. hieroglyphica Rchb. f.
M. iricolor Rchb. f. ex Kraenzl.
M. longiflora Kraenzl.
M. ocanensis Kraenzl.
M. paisbambae F. Lehm. & Kraenzl.
M. palmensis Kraenzl.
M. picturata Rchb. f.
M. restrepioidea Kraenzl.
M. schizantha Kraenzl.
M. wageneriana Linden ex Lindl.
M. xanthina Rchb. f.
M. meleagris Lindl. ex Rchb. f.
M. uncifera Rchb. f.

Section *Echidna* Rchb. f., Linnaea 41: 11. 1877.

Type: *Masdevallia echidna* Rchb. f., Bonplandia 3: 69. 1855.

Syn.: sect. *Muscosae* Woolward, Gen. Masdevallia. 1896.

Type: *Masdevallia muscosa* Rchb. f., Gard. Chron. 1: 460. 1875.

According with Article 11 of the International Code of Botanical Nomenclature (IBCN; GREUTER et al., 2000), Kraenzlin´s name for section Echidna is illegitimate.

Echidna is a small section with two species, *M. echidna* Rchb. f. and *M. xipheres* Rchb. f., characterized by the sensitive lip.

Section *Rhombopetalae* Kraenzl., Repert. Spec. Nov. Regni Veg. Beih. 34: 188. 1925.

Type*: Masdevallia simula* Rchb. f., Gard. Chron. 3: 8. 1875.

Syn.: sect. *Saltatrices* Woolward, Gen. Masdevallia. 1896.

Type*: Masdevallia simula* Rchb. f., Gard. Chron. 3: 8. 1875.

According with Article 11 of the International Code of Botanical Nomenclature (IBCN; GREUTER et al., 2000), Kraenzlin´s name for section *Rhombopetalae* is illegitimate.

To this section belong:

M. amethystina Rchb. f.
M. aviceps Rchb. f.
M. auriculigera Rchb. f.
M. pumila Poepp. & Endl.
M. simula Rchb. f.
M. sessilis Rchb. f.
M. edwallii Cogn.
M. perpusilla Kraenzl.
M. pusiola Rchb. f.
M. meiracyllium Rchb. f.
M. simulatrix Kraenzl.
M. popayanensis F. Lehm. & Kraenzl.
M. zebrina Porsch.
M. plantaginea (Poepp. & Endl.) Cogn.

Section *Triaristellae* Rchb. f., Gard. Chron. 6 (138): 226. 1876.

Type: *Masdevallia triaristella* Rchb. f., Gard. Chron. 6 (138): 226. 1876.

To this section belong:

M. anaristella Kraenzl.
M. gemmata Rchb. f.
M. triaristella Rchb. f.
M. trichaete Rchb. f.
M. tridactylites Rchb. f.
M. triglochin Rchb. f.
M. triseta Rchb. f. ex Kraenzl.

The genus *Dracula* Luer

Dracula Luer, Selbyana 2: 190. 1978.

Syn.: sect. *Saccilabiatae* Rchb. f., Chron. 37: 1238. 1873.
Type: *Masdevallia chimaera* Rchb. f., Gard. Chron. 463. 1872.
Lectotype designated by Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 15: 23. 1986.
= sect. *Chimaeroideae* Kraenzl., Repert. Spec. Nov. Regni Veg. Beih. 34: 125. 1925. (nom. illeg.).
Type: *Masdevallia chimaera* Rchb. f., Gard. Chron. 463. 1872.

The genus *Dracula* Luer was proposed in 1978. Species of the genus *Dracula* had been attributed to *Masdevallia* because of the sepaline tails. Recently molecular analysis (PRIDGEON et al., 2001) confirms that *Dracula* constitutes a well-defined taxon. Over 80 species are known from Central America and the northwestern Andes.

Infrageneric classification of *Masdevallia* proposed by Luer (1986b)

In his first monograph of the genus *Masdevallia* (LUER, 1986b), LUER proposed a new infrageneric classification for the genus *Masdevallia*. At this time, more than 350 species were attributed to the genus, most of them described by LUER. The infrageneric classification proposed by LUER included 5 subgenera, 17 sections, and 12 subsections.

Subgenus *Amanda* (Rchb. f.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 10. 1986.

Bas.: sect. *Amandae* Rchb. f., Gard. Chron. 2: 290. 1874.
Type: *Masdevallia amanda* Rchb. f. & Warsc., Bonplandia 2: 115.

This subgenus corresponds to Reichenbach´s section *Amandae*. The subgenus comprises five sections characterized by the single-flowered or simultaneously two- to many flowered inflorescence; the peduncle round in cross section; the ovaries carinate or crested; the sepals more or less membranous; the petals relatively thin, often denticulate or serrate; and a lip more or less divided into a hypochile and an epichile by marginal folds.

Section *Amandae* Rchb. f., Gard. Chron. 2: 290. 1874.

Syn.: sect. *Eumasdevallia* subsect. *Amandae* (Rchb. f.) H. J. Veitch, Man. Orchid. Pl. 5: 18. 1889.
Type: *Masdevallia amanda* Rchb. f. & Warsc., Bonplandia 2: 115
= sect. *Polystictae* Kraenzl., Repert. Spec. Nov. Regni Veg. Beih. 34: 32. 1925 (nom. illeg.).
Type: *Masdevallia polysticta* Rchb. f., Gard. Chron. 1: 338. 1874.

This section included 27 species and has been clearly delimited since Reichenbach

M. abbreviata Rchb.f
M. alvaroi Luer & Escobar
M. amanda Rchb. f. & Warsc.
M. bulbophyllopsis Kraenzl.
M. caloptera Rchb. f.
M. chaetostoma Luer
M. corazonica Schltr.
M. dalstroemii: Luer

- *M. delphina* Luer
- *M. graminea* Luer
- *M. huebschiana* Kraenzl.
- *M. hydrae* Luer
- *M. invenusta* Luer
- *M. lehmanii* Rchb. f.
- *M. leptoura* Luer
- *M. melanopus* Rchb. f.
- *M. microsiphon* Luer
- *M. ova-avis* Luer
- *M. pachyura* Rchb. f.
- *M. polysticta* Rchb. f.
- *M. porphyrea* Luer & Malo
- *M. pulcherrima* Luer & Andreetta
- *M. rafaeliana* Luer
- *M. spathulifolia* Kraenzl.
- *M. tentaculata* Luer
- *M. tridens* Rchb. f.
- *M. zygia* Luer & Malo

Section *Fissae* Rchb. f. Rchb. f., Otia Bot. Hamburg. 1: 16. 1878.

Type: *Masdevallia picturata* Rchb. f., Otia Bot. Hamburg. 1: 16. 1878.

This section, clearly delimited since Reichenbach, included three species. Two of these species, *M. mutica* Luer & R. Escobar and *M. pleurothalloides* Luer, have been described in 1977 and 1978.

Section *Nidificae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 12. 1986.

Type: *Masdevallia nidifica* Rchb. f., Otia Bot. Hamburg. 1: 18. 1878.

The species of section *Nidificae* are characterized by single flowers; more or less inflated floral bracts; carinate or crested ovaries; sepals connate into a short or cylindrical sepaline tube with a bulbous or broad base; and a lip divided into a hypochile and an epichile. The section included five species, of which three, *M. molossus* and *M. molossoides* (prior section *Saltatrices* according to Woolward and section *Urceolares* according to Kraenzlin) and *M. nidifica* (prior section *Minutae* according to Woolward and *Floribundae* according to Kraenzlin), have been transferred to this section.

- *M. dynastes* Luer
- *M. molossoides* Kraenzl.
- *M. molossus* Rchb. f.
- *M. nidifica* Rchb. f.
- *M. ventricosa* Schltr.

Section *Ophioglossae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 15. 1986.

Type: *Masdevallia ophioglossa* Rchb. f., Otia Bot. Hamburg. 1: 17. 1878.

Masdevallia ophioglossa (prior section *Minutae* according to Woolward and *Urceolares* according to Kraenzlin) was segregated as a section of its own based on morphological characters that present a unique combination according to Luer (1986b).

Section *Pygmaeae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 15. 1986.

Type: *Masdevallia pygmaea* Kraenzl., Repert. Spec. Nov. Regni Veg. Beih. 34: 92. 1925.

This section is distinguished by the carinate ovaries, more or less echinate or papillose; the sepals are connate into a short tube or cup; the callus of the petals is usually produced into a basal tooth; and the lip is entire or indistinctly divided by marginal folds. According to Luer, this section could be separated as a new subgenus on the basis of the lips, but in spite of this difference, appears to be more or less allied to subgenus *Amanda*. The section included five small species:

- *M. anachaeta* Rchb. f.
- *M. hoeijeri* Luer & Hirtz
- *M. pterigophora* Luer & Escobar
- *M. erinacea* Rchb. f.
- *M. pygmaea* Kraenzl.(prior section *Floribundae* Kraenzlin)

Subgenus *Masdevallia*

Syn.: sect. *Eumasdevallia* H. J. Veitch, Man. Orchid. Pl. 5: 18. 1889.

Type: *Masdevallia uniflora* Ruiz & Pav., Fl. Peruv. 1: 122, pl. 27. 1794.

The subgenus *Masdevallia* consists of the majority of the species of the genus. Luer divided this subgenus into twelve sections. According to Luer all species of subgenus *Masdevallia* seem to be related whereas the boundaries of some species are not well defined. The subgenus includes some forms with peculiar combinations of features that represent a problem for the delimitation of infrageneric taxa.

Section *Amaluzae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 18. 1986.

Type: *Masdevallia amaluzae* Luer & Malo, Phytologia 39(4): 185. 1978.

Species of this section are characterized by a horizontal or descending raceme of successive flowers with slender sepaline tails; the petals are usually callous; the lip is entire with a pair of low calli. The section includes four closely allied species found in south-eastern Ecuador, one in west-central Ecuador, and one widely distributed from Central America to Bolivia:

M. amaluzae Luer & Malo
M. naranjapatae Luer
M. zahlbruckneri Kraenzl.
M. carmenesis Luer & Malo
M. patula Luer & Malo
M. sanchezii Luer & Andreetta

Section *Aphanes* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 18. 1986.

Type: *Masdevallia aphanes* Königer, Die Orchidee 30: 196. 1979.

Section *Aphanes* comprises three very small species, *M. aphanes* Königer, *M. capillaris* Luer, and *M. scopaea* Luer & Vasquez, found in Ecuador, Peru and Bolivia. The species of this section are characterized by a raceme of successively, tailless flowers with more or less papillose or verrucose ovaries and ligulate lips.

Section *Caudivolvulae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 19. 1986.

Type: *Masdevallia caudivolvula* Kraenzl., Notizbl. Bot. Gart. Berlin-Dahlem 8: 128. 1922.

This section includes only *M. caudivolvula* Kraenzl., a species that could not be accomodated into another section because of its sepals, markedly thickened along the veins on the inner surface, and the apices that are continued into thick and twisted tails.

Section *Coriaceae* Rchb. f., Gard. Chron. 1: 240. 1874.

Syn.: sect. *Masdevallia* subsect. *Coriaceae* (Rchb. f.) H. J. Veitch, Man. Orchid. Pl. 5: 18. 1889.

Type: *Masdevallia coriacea* Lindl., Ann. Mag. Nat. Hist. 15: 257. 1845.

= sect. *Leontoglossae* Rchb. f., Otia Bot. Hamburg. 1: 15. 1878. (nom. illeg.).

Type: *Masdevallia leontoglossa* Rchb. f., Bonplandia 3: 69. 1855.

The section *Coriaceae* is divided into two subsections:

Subsection *Coriaceae* (Rchb. f.) H. J. Veitch, Man. Orchid. Pl. 5: 18. 1889.

Type: *Masdevallia coriacea* Lindl., Ann. Mag. Nat. Hist. 15: 257. 1845.

Subsection *Coriaceae* included 35 species and one variety, all Andean in origin except for one species (*M. cupularis* Rchb. f.) occurring in Costa Rica:

M. angulata Rchb. f.
M. atahualpa Luer
M. cacodes Luer & Escobar
M. caesia Roezl.
M. campyloglossa Rchb. f.
M. civilis Rchb. f.
M. colossus Luer
M. coriacea Lindl.
M. coriacea var. *bonplandii*
M. cupularis Rchb. f.
M. elephanticeps Rchb. f.
M. foetens Luer & Escobar
M. fractiflexa Lehm. & Kraenzl.
M. fragans Woolward
M. hylodes Luer & Escobar
M. hystrix Luer & Hirtz
M. leontoglossa Rchb. f.
M. macroglossa Rchb. f.
M. maloi Luer
M. misasii Braas
M. mooreana Rchb. f.
M. murex Luer
M. oscarii Luer & Escobar
M. pachyantha Rchb. f.
M. pardina Rchb. f.
M. peristeria Rchb. f.
M. picea Luer
M. platyglossa Rchb. f.
M. pyxis Luer
M. rigens Luer
M. sanctae-rosae Kraenzl.
M. semiterete Luer & Escobar
M. sorocula Rchb. f.
M. sumapazensis Ortiz
M. torta Rchb. f.
M. velifera Rchb. f

Subsection *Durae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 23. 1986.

Type: *Masdevallia dura* Luer, Phytologia 39: 197. 1978.

This subsection is composed of the *M. ayabacana* Luer, *M. dura* Luer, *M. utriculata* Luer, and *M. panguiensis* Luer & Andreetta, that flower successively.

Section *Cucullatae* Rchb. f., Gard. Chron. 1: 72. 1878.

Syn.: subsect. *Cucullatae* (Rchb. f.) H. J. Veitch, Man. Orchid. Pl. 5: 18. 1889.

Type: *Masdevallia cucullata* Rchb. f., Orchid. Linden. 4. 1846.

This small section is clearly delimited since Reichenbach. It includes four species:

M. cerastes Luer & Escobar
M. corniculata Rchb. f.
M. cucullata Rchb. f.
M. macrura Rchb. f.

Section *Ligiae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 26. 1986.

Type: *Masdevallia ligiae* Luer & Escobar, Orquideologia 15: 131. 1982.

This section comprises a unique Colombian species, *M. ligiae* Luer & Escobar, that is, according to Luer, probably a hybrid between a species of *Masdevallia* subsect. *Saltatrices* and a species of sect. *Polyanthae*.

Section *Masdevallia*

Type: *Masdevallia uniflora* Ruiz & Pav., Fl. Peruv. 1: 122, pl. 27. 1794.

This section consists of a large number of closely interrelated species, characterized by single-flowered peduncles; the petals are cartilaginous with a well-developed, retrorse tooth from the callus near the base on the labellar margin; the disc of the lip is smooth or with a low pair of parallel calli.

Subsection *Caudatae* H. J. Veitch, Man. Orchid. Pl. 5: 18. 1889.

Type: *Masdevallia caudata* Lindl., Gen. Sp. Orch. 193. 1833.

Syn.: sect. *Cupulatae* Pfitzer, Nat. Pflanzenfam. 2(6): 136. 1888.

Type: *Masdevallia shuttleworthii* Rchb. f., Gard. Chron. 1: 170. 1875.

= sect. *Triangulares* Rchb. f., Gard. Chron. 1: 372. 1874.

Type: *Masdevallia triangularis* Lindl., Orchid. Linden. 5. 1846.

The section comprises 28 species, widespread in the Andes but absent from Central America:

M. apparitio Luer & Escobar
M. boliviensis Schltr.
M. bottae Luer & Andreetta
M. caudata Lindl.
M. cyclotega Königer
M. decumana Königer
M. discolor Luer & Escobar
M. estradae Rchb. f.
M. expansa Rchb. f.
M. hubeinii Luer & Würstle
M. instar Luer & Andreetta
M. iris Luer & Escobar
M. klabochorum Rchb. f.
M. leucophaea Luer & Vasquez
M. ludibunda Rchb. f.
M. lynchniphora Königer
M. pileata Luer & Würstle
M. prodigiosa Königer
M. purpurella Luer & Escobar
M. replicata Königer
M. sanctae-inesae Luer & Malo
M. setacea Luer
M. triangularis Lindl.
M. tricolor Rchb. f.
M. valenciae Luer & Escobar
M. venatoria Luer & Malo
M. wurdackii C. Schweinf.
M. xanthina Rchb. f.

Subsection *Coccineae* H. J. Veitch, Man. Orchid. Pl. 5: 18. 1889.

Syn.: sect. *Coccineae* (H. J. Veitch) Woolward, Gen. Masdevallia. 1896.

Type: *Masdevallia coccinea* Linden ex Lindl., Orchid. Linden. 5 (26). 1846.

Twelve species distributed in the Andes of Colombia, Ecuador and Peru are included in this section:

M. amabilis Rchb. f. & Warsc.
M. barleana Rchb. f.
M. coccinea Lind. ex Lindl.
M. davisii Rchb. f.
M. deformis Kraenzl.
M. echinata Luer
M. ignea Rchb. f.
M. rosea Lindl.
M. stumpflei Braas
M. veitchiana Rchb. f.
M. venusta Schltr.
M. welischii Luer

Subsection *Masdevallia*

Type: *Masdevallia uniflora* Ruiz & Pav., Fl. Peruv. 1: 122, pl. 27. 1794.

Syn.: sect. *Clausae-porrectae* Rchb. f., Gard. Chron. 2: 338. 1875.

Type: *Masdevallia ionocharis* Rchb. f., Gard. Chron., 4: 388. 1875.

= sect. *Urceolares* Kraenzl., Repert. Spec. Nov. Regni Veg. Beih. 34: 32. 1925. (nom. illeg.)

Type: *Masdevallia urceolaris* Kraenzl., Notizbl. Bot. Gart. Berlin-Dahlem 8: 132. 1922.

This large group of species contains those with a colorful sepaline cup more deeply connate than that of subsect. *Caudatae*. To this subsection belong:

M. affinis Lindl.
M. agaster Luer
M. arminii Rchb. f.
M. assurgens Luer & Escobar
M. calocodon Luer & Vasquez
M. chaparensis Hashimoto
M. cinnamomea Rchb. f. (prior sect. *Polyanthae* Woolward and *Alaticaules* Kraenzl.)
M. clandestina Luer & Escobar
M. condorensis Luer & Hirtz
M. corderoana Lehm. & Kraenzl.
M. datura Luer & Vasquez
M. elachys Luer
M. elegans Luer & Escobar
M. encephala Luer & Escobar
M. ensata Rchb. f.
M. falcago Rchb.f.
M. figueroae Luer
M. gilbertoi Luer & Escobar
M. glandulosa Königer
M. helenae Luer
M. hians Rchb. f.
M. hieroglyphica Rchb. f.
M. hymenanthe Rchb. f.
M. ionocharis Rchb. f.
M. laevis Lindl.
M. lamprotyria Königer
M. lepida Rchb. f.
M. leucantha Lehm. & Kraenzl.
M. lineolata Königer
M. lucernula Königer
M. macropus Lehm. & Kraenzl.
M. mastodon Rchb. f.

M. mejiana Garay
M. midas Luer
M. nebulina Luer
M. nitens Luer
M. norops Luer & Andreetta
M. notosibrica Maekawa & Hashimoto
M. odontocera Luer & Escobar
M. paivaeana Rchb. f.
M. pandurilabia C. Schweinf.
M. patriciana Luer
M. picta Luer
M. pumila Poepp. & Endl.
M. rimarima-alba Luer
M. roseola Luer
M. scandens Rolfe
M. schmidt-mummii Luer & Escobar
M. selenites Königer
M. strumifera Rchb. f.
M. trigonopetala Kraenzl.
M. uncifera Rchb. f.
M. uniflora Ruiz & Pav.
M. urceolaris Kraenzl.
M. ustulata Luer
M. vasquezii Luer
M. verecunda Luer
M. yungasensis Hashimoto

Subsection *Oscillantes* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 32. 1986.

Type: *Masdevallia wageneriana* Lindl. ex Lindl, Paxton´s Fl. Gard. 3: 74. 1852.

This section was created on the basis of the oscillating lip. The lip is held more or less horizontally and loosely, seemingly balanced by a very fine extension from the column-foot to within the cavity beneath the convex base of the more or less pandurate lip. The subsection includes twelve species:

M. andreettana Luer
M. ariasii Luer
M. catapheres Königer
M. citrinella Luer & Malo
M. dalessandroi Luer
M. pernix Königer
M. persicina Luer
M. phasmatodes Königer
M. pteroglossa Schltr.
M. rodolfoi (Braas) Luer
M. rubiginosa Königer
M. wageneriana Lind. ex Lindl.

Subsection *Saltatrices* (Rchb. f.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 36. 1986.

Bas.: sect. *Saltatrices* Rchb. f., Linnaea 41: 10. 1877.

Type: *Masdevallia saltatrix* Rchb. f., Linnaea 41: 10. 1877.

This subsection, closely related to section *Masdevallia* according to Luer (1986b), includes 14 species and one subspecies:

M. ampullacea Luer & Andreetta
M. anemone Luer
M. angulifera Rchb. f. (prior sect. *Tubulosae*)
M. aurea Luer
M. constricta Poepp. & Endl. (prior sect. *Tubulosae*)
M. fuchsii Luer
M. limax Luer
M. marthae Luer & Escobar
M. mendozae Luer
M. os–draconis Luer & Escobar
M. saltatrix Rchb. f. (prior sect. *Tubulosae*)
M. strobelii Sweet & Garay
M. urosalpinx Luer
M. ventricularia Rchb. f. (prior sect. *Tubulosae*)
M. vetricularia subsp. *filaria* (Luer & Escobar) Luer

Subsection *Tubulosae* (Rchb. f.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 38. 1986.

Bas.: sect. *Tubulosae* Rchb. f., Otia Bot. Hamburg. 1: 14. 1878.

Type: *Masdevallia tubulosa* Lindl., Orch. Lind. 4. 1846.

= subg. *Triotosiphon* Schltr., Repert Spec. Nov. Regni Veg. Beih. 10: 42. 1922.

= sect. *Triotosiphon* (Schltr.) Sweet., Bot. Mus. Leafl. 26: 40. 1978.

Type: *Masdevallia bangii* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 10: 41. 1922.

A subsection composed of very small to medium-sized species characterized by solitary, white to yellowish or greenish tubular flowers. The most widely distributed species is the variable *M. tubulosa* Lindl. known from Venezuela to Peru. From Ecuador is a form with short, thick tails, segregated as *M. syringodes* by Luer & Andreetta. This subsection includes seven species and one subspecies:

M. bangii Schltr.
M. irapana Sweet.
M. kyphonantha Sweet.
M. lansbergii Rchb. f.
M. pseudominuta Sweet.
M. tubulosa Lindl.
M. tubulosa subsp. *syringodes* (Luer & Andreetta) Luer
M. venezuelana Sweet

Section *Mentosae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 38. 1986.

Type: *Masdevallia mentosa* Luer, Phytologia 39: 212. 1978.

A section consisting of a single, unusual, little Ecuadorian species characterized by a slender, successively flowering peduncle, triquetrous in cross section, which would place it in *Masdevallia* sect. *Polyanthae* if it didn't have an entire and smooth lip.

Section *Minutae* Rchb. f. ex Woolward, Gen. Masdevallia. 1896.

Type: *Masdevallia minuta* Lindl., Ann. Mag. Nat. Hist. 12: 396. 1842.

Syn.: sect. *Floribundae* Kraenzl., Repert. Spec. Nov. Regni Veg. Beih. 34: 84. 1925.

Type: *Masdevallia floribunda* Lindl., Edward´s Bot. Reg. 29: 72. 1843.

A section with 21 species distributed from Mexico to Bolivia, related to subsect. *Masdevallia* according to Luer but the flowers are distinguished by the small, short, usually pointed tooth arising between the middle and the lower third of the petal from a longitudinal callus above the labellar margin. It includes:

M. arangoi Luer & Escobar
M. attenuata Rchb. f.
M. chontalensis Rchb. f.
M. crescenticola Lehm. & Kraenzl.
M. flaveola Rchb. f.
M. floribunda Lindl.
M. geminiflora Ortiz
M. guayanensis Lindl. ex Benth.
M. gutierrezii Luer
M. herradurae Lehm. & Kraenzl.
M. laucheana Kraenzl.
M. livingstoneana Roezl. & Rchb. f.
M. minuta Lindl.
M. nicaraguae Luer
M. pescadoensis Luer & Escobar
M.plantaginea Poepp. & Endl.
M. scabrilinguis Luer
M. schizopetala Kraenzl.
M. tonduzii Woolward
M. tubuliflora Ames
M. wendlandiana Rchb. f.

Section *Polyanthae* Rchb. f., Gard. Chron. 1: 372. 1874.

Syn.: *Masdevallia* sect. *Polyanthae* (Rchb. f.) H. J. Veitch, Man. Orchid. Pl. 5: 18. 1889.

Type: *Masdevallia polyantha* Lind. ex Lindl., Orchid. Lind. 6. 1846.

Species of section *Polyanthae* are characterized by successive or simultaneous racemes of flowers, with smooth petals and lips divided near the middle by marginal folds into an epichile and a hypochile. This section was divided into two subsections.

Subsection *Alaticaules* (Kraenzl.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 43. 1986.

Lectotype designated by Luer: *Masdevallia melanoxantha* Lindl. & Rchb. f., Bonplandia 2: 283. 1854.

Bas.: sect. *Alaticaules* Kraenzl., Repert. Spec. Nov. Regni Veg. Beih. 34: 84. 1925. (nom. illeg.)

(Kraenzlin designated both *M. melanoxantha* Lindl. & Rchb. f., and *M. polyantha* Lind. ex Lindl., as the type of the section Alaticaules. *Masdevallia polyantha* is the type of section *Polyanthae*)

This large subsection comprises species with peduncles triangular in cross section:

M. aenigma Luer & Escobar
M. auropurpurea Rchb. f.
M. bicolor Poepp. & Endl.
M. brachyura Lehm. & Kraenzl.
M. brenneri Luer
M. buccinator Rchb. f.
M. calagrasalis Luer
M. cardiantha Königer
M. carolloi Luer & Andreetta
M. carruthersiana Lehm. & Kraenzl.
M. cinnamomea Rchb. f. (prior section *Masdevallia*)
M. cuprea Lindl.
M. don-quijote Luer & Andreetta
M. dunstervillei Luer
M. echo Luer
M. empusa Luer
M. excelsior Luer & Andreetta
M. guerrieroi Luer & Andreetta
M. guttulata Rchb. f.
M. hepatica Luer
M. impostor Luer & Escobar
M. infracta Lindl.
M .isos Luer
M. kuhniorum Luer
M. maculata Kl. & Karst.
M. medusa Luer & Escobar
M. megaloglossa Luer & Escobar
M. melanoxantha Rchb. f.
M. mezae Luer
M. monogona Königer
M. navicularis Garay & Dunster.
M. odontopetala Luer
M. phoenix Luer
M. pinocchio Luer & Andreetta
M. portillae Luer & Andreetta
M. posadae Luer & Escobar
M. prosartema Königer
M. receptrix Luer & Vasquez
M. rechingeriana Kraenzl.
M. sanguinea Luer & Andreetta
M. sceptrum Rchb. f. (prior sect. Leontoglossae Rchb. f.)
M. scitula Königer
M. scobina Luer & Escobar
M. sernae Luer & Escobar
M. sprucei Rchb. f.
M. stenorhynchos Kraenzl.
M. theleüra Luer
M. tovarensis Rchb. f.
M. trochilus Lind. & André
M. vargasii C. Schweinf.
M. virens Luer & Andreetta
M. virgo-cuencae Luer & Andreetta
M. weberbaueri Schltr.
M. whiteana Luer

Subsection *Polyanthae* (Rchb. f.) H. J. Veitch, Man. Orchid. Pl. 5: 18. 1889.

Type: *Masdevallia polyantha* Lind. ex Lindl., Orchid. Linden. 6. 1846.

This small subsection contains those species with the peduncles round in cross section:

M. curtipes Barb. Rodr.
M. dioscoidea Luer & Würstle
M. lata Rchb. f.
M. menatoi Luer & Vasquez
M. oreas Luer & Vasquez
M. schlimii Lind. ex Lindl.
M. thienii Dodson

Section *Racemosae* Woolward, Gen. Masdevallia. 1896.

Type: *Masdevallia racemosa* Lindl., Ann. Mag. Nat. Hist. 15: 256. 1845.

Section *Reichenbachianae* Woolward, Gen. Masdevallia. 1896.

Type: *Masdevallia reichenbachiana* Endres ex Rchb. f., Gard. Chron. 4(87): 257. 1875.

Section *Reichenbachianae* includes two subsections. The petals of the species includes in this section are callous along the lower margin without forming a tooth except in two species (*M. collina* L. O. Williams and *M. macrogenia* (Arango) Luer & Escobar), the basis for creating the two subsections.

Subsection *Dentatae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 48. 1986.

Type: *Masdevallia collina* L. O. Williams., Amer. Orchid Soc. Bull. 11: 93. 1942.

Subsection *Dentatae* include two species, *M. collina* L. O. Williams and *M. macrogenia* (Arango) Luer & Escobar. According to Luer (1986b), the species included in this subsection are not closely allied to section *Reichenbachianae* but it shown very similar floral and vegetative characters.

Subsection *Reichenbachianae* (Woolward) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 48. 1986.

Bas.: sect. *Reichenbachianae* Woolward, Gen. Masdevallia. 1896.

Type: *Masdevallia reichenbachiana* Endres ex Rchb. f., Gard. Chron. 4(87): 257. 1875.

Subsection *Reichenbachianae* includes eleven species, all distributed in Central America:

M. calura Rchb. f.
M. chasei Luer
M. demissa Rchb. f.
M. fulvescens Rolfe
M. garciae Luer
M. marginella Rchb. f.
M. reichenbachiana Endres ex Rchb. f.
M. rolfeana Kraenzl.
M. schroederiana Veitch
M. striatella Rchb. f.
M. walteri Luer

Subgenus *Meleagris* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 51. 1986.

Syn.: *Rodrigoa* Braas, Die Orchidee 30: 203. 1979.

Type: *Masdevallia meleagris* Lindl., Ann. Mag. Nat. Hist. ser. 1 15: 257. 1845.

This subgenus consists of seven closely related species characterized by the successively flowering raceme of attractive, colorful flowers with widely spreading sepals; the ovaries of most species are crested, and the sepals are free near their bases, similar to many species in subgen. *Amanda*. Braas proposed the genus *Rodrigoa* for this subgenus in 1979. To this subgenus belong:

M. alexandri Luer
M. anisomorpha Garay
M. heteroptera Rchb. f.
M. hortensis Luer & Escobar
M. meleagris Lindl.
M. parvula Schltr.
M. segurae Luer & Escobar

Subgenus *Pelecaniceps* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 53. 1986.

Syn.: *Luerella* Braas, Die Orchidee 30: 108. 1979.

Type: *Masdevallia pelecaniceps* Luer, Selbyana 3: 22. 1976.

The monotypic subgenus *Pelecaniceps* is characterized by the single-flowered peduncle, the thick rugose sepals without tails, callous petals that are subcarinate externally, and a lip with acute, erect lateral lobes and an excavate base. In his monograph of the genus *Masdevallia*, Luer (1986b) indicated that this species is probably not closely related to the genus *Masdevallia*, as shown by Braas in 1979. This supposition was confirmed in a first molecular analysis of the subtribe *Pleurothallidinae* (PRIDGEON et al., 2001), and the name proposed by Braas was accepted.

Subgenus *Teagueia* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 53. 1986.

Type: *Masdevallia teaguei* Luer, Selbyana 2: 381. 1978.

Masdevallia teaguei Luer, the unique species of subgenus *Teagueia*, is characterized by flowers produced successively in congested racemes; the sepals are connate into a gibbous cup; the callus of the thick petals is produced into a tooth above the base; the lip is divided into a cleft hypochile forming a pair of prostrate lamellae, and a decurved, tricarinate epichile. The column is typical for *Masdevallia*.

Infrageneric classification of *Masdevallia* proposed by Luer (2000-2003)

Subgenus *Amanda* (Rchb. f.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 10. 1986.

Bas.: sect. *Amandae* Rchb. f., Gard. Chron. 2: 290. 1874.

Syn.: subsect. *Amandae* (Rchb. f.) Veitch, Man. Orchid. Pl. 5: 18, 1889.

Type: *Masdevallia amanda* Rchb. f. & Warsc., Bonplandia 2: 115. 1854.

= sect. *Polystictae* Kraenzl., Repert. Spec. Nov. Regni Veg. Beih. 34: 32. 1925. (nom. illeg.)

Type: *Masdevallia polysticta* Rchb. f., Gard. Chron. 1: 338. 1874.

Subgenus *Amanda* is a clearly delimited group since Reichenbach. This subgenus previously contained the sections *Fissia*, *Nidificae* and *Pygmaeae*, which have been raised to the rank of subgenera here. Since the latest infrageneric classification of Luer (1986b) eight new species have been described, and one *M.* X*alvaroi*, previously recognized as a species, is, according to Luer, a natural hybrid between *M. picturata* and a *M. amanda*:

- *M. anceps* Luer & Hirtz
- *M. dimorphotricha* Luer & Hirtz
- *M. pozoi* Königer
- *M. segrex* Luer & Hirtz
- *M. sertula* Luer & Andreetta
- *M. staaliana* Luer & Hirtz
- *M. vittatula* Luer & Escobar
- *M. xanthodactyla* Rchb. f.

Subgenus *Cucullatia* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 77: 10. 2000.

Syn.: sect. *Cucullatae* Rchb. f., Gard. Chron. 1: 72. 1878.

= sect. *Eumasdevallia* subsect. *Cucullatae* (Rchb. f.) H. J. Veitch, Man. Orchid. Pl. 5: 18. 1889.

Type: *Masdevallia cucullata* Rchb. f., Orchid. Linden. 4. 1846.

Species included in this subgenus were previously treated as members of subgenus *Masdevallia*. The section was raised to a higher category, due to the large cucullate floral bract, a character not present into any other group. Since the latest infrageneric classification of Luer (1986b) three new species were described: *M. delhierroi* Luer & Hirtz, *M. hercules* Luer & Andreetta and *M. vidua* Luer & Andreetta. One species, *M. macrura* Rchb. f., was transferred to sect. *Coriaceae*.

Subgenus *Fissia* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 77: 10. 2000.

Syn.: sect. *Fissae* Rchb. f., Otia Bot. Hamburg. 1: 16. 1878.

Type: *Masdevallia picturata* Rchb. f., Otia Bot. Hamburg. 1: 16. 1878.

The subgenus *Fissia* was previously recognized as section of subgenus *Amanda.* It included species that according to Luer display a unique combination of characters: a single-flowered inflorescence, free sepals and a divided lip showing. This combination of characters is not present in any other subgenera of *Masdevallia*, therefore the group has been raised to a higher rank. Since the latest monograph of *Masdevallia* (LUER, 1986), no new species have been described.

Subgenus *Masdevallia* Ruiz & Pav., Ann. Mag. Nat. Hist. 12: 396. 1842.

Syn.: sect. *Eumasdevallia* H. J. Veitch, Man. Orchid. Pl. 5: 18. 1889.

Type: *Masdevallia uniflora* Ruiz & Pav., Fl. Peruv. 1: 122, pl. 27. 1794.

The subgenus *Masdevallia* comprises the majority of species of the genus. It is divided into eight sections and five subsections:

Section *Coriaceae* Rchb. f., Gard. Chron. 1: 240. 1874.

Syn.: subsect. *Coriaceae* (Rchb. f.) H. J. Veitch, Man. Orchid. Pl. 5: 18. 1889.

Type: *Masdevallia coriacea* Lindl., Ann. Mag. Nat. Hist. 15: 257. 1845.

= sect. *Leontoglossae* Rchb. f., Otia Bot. Hamburg. 1: 15. 1878. (nom. illeg.)

Type: *Masdevallia leontoglossa* Rchb. f., Bonplandia 3: 69. 1855.

A clearly delimited group related to subgenus *Masdevallia* since Reichenbach. Two species, *M. pyxis* Luer and *M. cupularis* Rchb. f., were transferred to subgenus *Polyantha*. *Masdevallia gargantua* Rchb. f. was not included in the first monograph of the genus *Masdevallia* from Luer (1986b) and is now included into section *Coriaceae*. The following new species were described since 1986:

M. belua Königer & D'Alessandro
M. bourdetteana Luer
M. lilianae Luer
M. pachysepala (Rchb. f.) Luer
M. rigens Luer
M. spilantha Königer

Section *Dentatae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 77: 10. 2000.

Bas.: subg. *Masdevallia* sect. *Reichenbachianae* subsect. *Dentatae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 48. 1986.

Type: *Masdevallia collina* L. O. Williams, Amer. Orchid Soc. Bull. 11: 93. 1942.

Species of section *Dentatae* were previously recognized to be closely related with species of section *Reichenbachianae*. Two new species for this section were described since 1986: *M. dryada* Luer & Escobar and *M. zapatae* Luer & Escobar.

Section *Durae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 23. 1986.

Bas.: subg. *Masdevallia* sect. *Coriaceae* subsect. *Durae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 23. 1986.

Type: *Masdevallia dura* Luer, Phytologia 39: 197. 1978.

Section *Durae* was previously recognized as subsection of section *Coriaceae*. Since the latest monograph of *Masdevallia* (LUER, 1986) six new species were described:

M. goliath Luer
M. newmaniana Luer
M. princeps Luer
M. regina Luer
M. robusta Luer
M. titan Luer

Section *Masdevallia*

Type: *Masdevallia uniflora* Ruiz & Pav., Fl. Peruv. 1: 122, pl. 27. 1794.

Section *Masdevallia* is divided into five subsections. Most species of the previously recognized subsection *Tubulosae* were segregated into section *Triotosiphon*. The type species of that subsection, *M. tubulosa* Lindl., is included into subsection *Masdevallia* now.

Subsection *Caudatae* H. J. Veitch, Man. Orchid. Pl. 5: 18. 1889.

Type: *Masdevallia caudata* Lindl., Gen. Sp. Orchid. Pl. 193. 1833.

= sect. *Cupulatae* Pfitzer, Nat. Pflanzenfam. 2(6): 136. 1888.

Type: *Masdevallia shuttleworthii* Rchb. f., Gard. Chron. 1: 170. 1875.

= sect. *Triangulares* Rchb. f., Gard. Chron. 1: 372. 1874.

Type: *Masdevallia triangularis* Lindl., Orchid. Linden. 5. 1846.

Since 1986 more than 30 species were described or transferred to subsection *Caudatae*:

M. alismifolia Kraenzl. (prior section *Chimaeroidea* sensu Kraenzl.)
M. antonii Königer
M. arminii Linden & Rchb. f. (prior subsect. *Masdevallia* sensu Luer)
M. asterotricha Königer
M. brockmuelleri Luer
M. cloesii Luer
M. cordeliana Luer
M. cyclix Luer & Malo
M. ephelota Luer & Cloes
M. eucharis Luer
M. eumeliaea Luer
M. harlequina Luer
M. icterina Königer
M. immensa Luer
M. leonii D. E. Benn & Christenson
M. ludibundella Luer
M. mandarina (Luer & Escobar) Luer
M. marizae Luer
M. nivea Luer & Escobar
M. pandurilabia C. Schweinf. (prior subsect. *Masdevallia* sensu Luer)
M. papillosa Luer
M. pernix Königer
M. phlogina Luer
M. polychroma Luer
M. renzii Luer
M. rhinophora Luer & Escobar
M. rufescens Königer
M. schmidt mummii Luer & Escobar
M. schizantha Kraenzl.
M. tricallosa Königer
M. venatoria Luer & Malo
M. vexillifera Luer
M. wuelfinghoffiana Luer & J. Portilla
M. zamorensis Luer & J. Portilla

Subsection *Coccineae* H. J. Veitch, Man. Orchid. Pl. 5: 18. 1889.

Syn.: sect. *Coccineae* (H. J. Veitch) Woolward, Gen. Masdevallia. 1896.

Type: *Masdevallia coccinea* Linden ex Lindl., Orchid. Linden. 5(26). 1846.

Since 1986 (LUER) two new species, *M. idae* Luer & Arias and *M. niesseniae* Luer were described.

Subsection *Masdevallia*

Syn.: sect. *Clausae-porrectae* Rchb. f., Gard. Chron. 2: 338. 1875.

Type: *Masdevallia ionocharis* Rchb. f., Gard. Chron., 4: 388. 1875.

Syn.: sect. *Urceolares* Kraenzl., Repert. Spec. Nov. Regni Veg. Beih. 34: 32. 1925.

Type: *Masdevallia urceolaris* Kraenzl., Notizbl. Bot. Gart. Berlin-Dahlem 8: 132. 1922.

Since 1986, more than 30 species were newly described or transferred to this subsection:

M. burianii Luer & Dalström
M. carpishica Luer & Cloes
M. cleistogama Luer
M. cranion Luer
M. crassicaulis Luer & J. Portilla
M. deniseana Luer & J. Portilla
M. dreisei Luer
M. dudleyi Luer
M. exquisita Luer &Hirtz
M. glomerosa Luer & Andreetta
M. guayanensis Lindl. ex Benth (prior sect. *Minutae* sensu Luer)
M. hartmanii Luer
M. heideri Königer
M. ishikoi Luer
M. juan-albertoi Luer & Arias
M. karinae Nauray ex Luer
M. leonardoi Luer
M. lilacina Königer
M. lewisii Luer & Vasquez
M. lilacina Königer
M. manoloi Luer & Arias
M. medinae Luer & J. Portilla
M. melanoglossa Luer
M. os-viperae Luer & Andreetta
M. patriciana Luer & Malo
M. phacopsis Luer & Dalström
M. popowiana Königer & J. G. Weinm.
M. quasimodo Luer & Teague
M. schoonenii Luer
M. soennemarkii Luer & Dalström
M. solomonii Luer & Vasquez
M. suinii Luer & Hirtz
M. terborchii Luer
M. tinekeae Luer & Vasquez
M. trautmanniana Luer & J. Portilla
M. truncata Luer
M. tubulosa Lindl.
M. zebracea Luer

Subsection *Oscillantes* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 32. 1986.

Type: *Masdevallia wageneriana* Lindl. ex Lindl., Paxton´s Fl. Gard. 3: 74. 1852.

Subsection *Oscillantes* is currently estimated to contain 29 species, of which 18 were described between 1986 and 2004, including a natural hybrid, *M.* X*wubbenii* Luer, probably between *M. wageneriana* Lind. ex Lindl.and *M. triangularis* Lindl.:

M. albella Luer & Teague
M. amoena Luer
M. castor Luer & Cloes
M. cretata Luer
M. ejiriana Luer & J. Portilla
M. formosa Luer & Cloes
M. josei Luer
M. manta Königer
M. microptera Luer & Würstle
M. nikoleana Luer & J. Portilla
M. ortalis Luer
M. pollux Luer & Cloes
M. rhodehameliana Luer
M. rubeola Luer & Vasquez
M. sulphurella Königer
M. tricycla Luer
M. zongoënsis Luer & Hirtz

Natural hybrids
M. X*wubbenii*

Subsection *Saltatrices* (Rchb. f.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 36. 1986.

Bas.: sect. *Saltatrices* Rchb. f., Linnaea 41: 10. 1877.

Type: *Masdevallia saltatrix* Rchb. f., Linnaea 41: 10. 1877.

For this subsection 13 new species and one natural hybrid (*M.* X*mystica*) were described in the last two decades. One species, *M. notosibrica* Mekawa & Hashimoto (prior subsection *Masdevallia*) and one recognized natural hybrid, *M.* X*ligiae* (prior the type of the monotypic section *Ligiae*), were transferred to this subsection:

M. agaster Luer
M. calosiphon Luer
M. chuspipatae Luer & Teague
M. erynogaster Luer & Andreetta
M. filaria Luer & Escobar
M. hirtzii Luer & Andreetta
M. maxilimax (Luer) Luer
M. morochoi Luer & Andreetta
M. rex Luer & Vasquez
M. ricii Luer & Vasquez
M. siphonantha Luer
M. tubata Schltr.
Natural hybrids
M. X*mystica*
M. X*lygiae*

Section *Minutae* Rchb. f. ex Woolward, Gen. Masdevallia. 1896.

Type: *Masdevallia minuta* Lindl., Ann. Mag. Nat. Hist. 12: 396. 1842.

Syn.: sect. *Floribundae* Kraenzl., Repert. Spec. Nov. Regni Veg. Beih. 34: 84. 1925.

Type: *Masdevallia floribunda* Lindl., Edward´s Bot. Reg. 29: 72. 1843.

Two new species, described in 1994 and 1991, are now included in this section: *M. adamsii* Luer and *M. tokachiorum* Luer.

Section *Racemosae* Woolward, Gen. Masdevallia. 1896.

Type: *Masdevallia racemosa* Lindl., Ann. Mag. Nat. Hist. 15: 256. 1845.

Section *Reichenbachianae* Woolward, Gen. Masdevallia. 1896.

Type: *Masdevallia reichenbachiana* Endres ex Rchb. f., Gard. Chron. 4(87): 257. 1875.

This section was previously divided into two subsections: *Reichenbachianae* and *Dentatae*. This last one was excluded from *Reichenbachianae* and now is forming a separate section in subgenus *Masdevallia*. Four new species were described for this section: *M. enallax* Königer, *M. lankesteriana* Luer, *M. mejiana* Garay, and *M. polita* Luer & Sijm. *Masdevallia garciae* Luer and *M. striatella* were transferred to subgenus *Polyantha.*

Section *Triotosiphon* (Schltr.) Sweet, Bot. Mus. Leafl. 26: 40. 1978.

Type: *Masdevallia bangii* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 10: 41. 1922.

Syn.: subg. *Triotosiphon* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 10: 42. 1922.

This taxon was suggested by Schlechter as subgenus *Triotosiphon*. According to Luer (2003), however it meets the criteria for subgenus *Masdevallia*. The species included in this section were previously members of section *Tubulosae*. However, the type of section *Tubulosae*, *M. tubulosa* Lindl., was transferred to subsection *Masdevallia*. Section *Triotosiphon* includes six species. Vegetatively, the small to very small, caespitose plants bear single, more or less tubular flowers; the free portion of the sepals is short and the lips are simple and channeled between longitudinal calli:

M. bangii Schltr.
M. gnoma Sweet
M. irapana Sweet
M. kyphonantha Sweet
M. lansbergii Rchb. f.
M. venezuelana Sweet

Subgenus *Meleagris* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 51. 1986.

Syn.: *Rodrigoa* Braas, Die Orchidee 30: 203. 1979.

Type: *Masdevallia meleagris* Lindl., Ann. Mag. Nat. Hist. ser. 1 15: 257. 1845.

Five new species were described for this subgenus since 1986 and one species, *M. fasciata*, were reclassified:

M. fasciata Rchb. f. (prior sect. *Fissae* sensu Kraenzl.)
M. milagroi Luer & Hirtz
M. pantomima Luer & Hirtz
M. planadensis Luer & Escobar
M. ximenae Luer & Hirtz

Subgenus *Nidificia* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 77: 10. 2000.

Syn.: sect. *Nidificae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 12. 1986.

Type: *Masdevallia nidifica* Rchb. f., Otia Bot. Hamburg. 1: 18. 1878.

Syn.: sect. *Ophioglossae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 15. 1986.

Type: *Masdevallia ophioglossa* Rchb. f., Otia Bot. Hamburg. 1: 17. 1878.

Reichenbach described *M. molossus* Rchb. f., the first species attributable to this subgenus in 1877, and included it in the unranked, infrageneric category *Saltatrices*. The second described species attributable to this subgenus, *M. nidifica* Rchb. f., was included into section *Clausae-porrectae*. The section *Nidificae* was proposed in 1986 as section of the subgenus *Amanda*. According to Luer (2000), this section can be raised to a higher rank, because its members are not closely related to subgenus *Amanda*. Three new species of this subgenus were described during the past 20 years: *M. bucculenta* Luer & Hirtz, *M. lamia* Luer & Hirtz, and *M. strigosa* Königer. *Masdevallia ophioglossa* Rchb. f. (prior section *Ophioglossae*) is now included in this subgenus.

Subgenus *Polyantha* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 77: 10. 2000.

Bas.: sect. *Polyanthae* Rchb. f., Gard. Chron. 1: 372. 1874.

Type: *Masdevallia polyantha* Lind. ex Lindl., Orch. Lind. 6. 1846.

Subgenus *Polyantha* was previously recognized as section of subgenus *Masdevallia*. It includes now 2 sections and 4 subsections.

Section *Alaticaules* Kraenzl., Repert. Spec. Nov. Regni Veg. Beih. 34: 105. 1925.

Lectotype: *Masdevallia melanoxantha* Linden & Rchb. f., Bonplandia 2: 283. 1854.

Syn.: subsect. *Alaticaules* (Kraenzl.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 43. 1986.

Section *Alaticaules* was proposed by Kraenzlin (1925, see page 30) and was divided in two subsections based on the length of the raceme. Presently it is divided according to the mode of flowering, simultaneously or successively.

Subsection *Alaticaules* (Kraenzl.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 43. 1986.

Lectotype: *Masdevallia melanoxantha* Linden & Rchb. f., Bonplandia 2: 283. 1854.

Syn.: subsect. *Longiscapae* Kraenzl., Repert. Spec. Nov. Regni Veg. Beih. 34: 105. 1925.

Lectotype: *Masdevallia melanoxantha* Linden & Rchb. f., Bonplandia 2: 283. 1854.

Syn.: subsect. *Breviscapae* Kraenzl., Repert. Spec. Nov. Regni Veg. Beih. 34: 106. 1925.

Lectotype: *Masdevallia maculata* Klotsch & H. Karsten, Allg. Gartenzeitung 15: 330. 1847.

Syn.: subsect. Alaticaules (Kraenzl.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 43. 1986.

This subsection comprises the majority of species of this section. They are characterized by a successively flowering raceme with a triquetrous peduncle. Species that produce partially terete peduncles are included in both sections, *Alaticaules* and *Polyanthae*. For this subsection 43 new species have been described. Several species that had been placed here earlier have now been segregated as subsect. *Coaetanae*.

M .isos Luer
M. adrianae Luer
M. aguirrei Luer & Escobar
M. amplexa Luer
M. anfracta Königer & J.J. Portilla
M. benettii Luer
M. bicolor Poepp. & Endl.
M. brachyura Lehm. & Kraenzl
M. brenneri Luer
M. bryophila Luer
M. buccinator Rchb. f.
M. calagrasalis Luer
M. cardiantha Königer
M. carruthersiana Lehm. & Kraenzl.
M. cocapatae Luer, Teague & Vásquez
M. cuprea Lindl.
M. deceptrix Luer & Würstle
M. descendens Luer & Andreetta
M. don-quijote Luer & Andreetta
M. dorisae Luer
M. draconis Luer & Andreetta
M. echo Luer
M. empusa Luer
M. excelsior Luer & Andreetta
M. fosterae Luer
M. garciae Luer (prior section *Reichenbachianae*)
M. guerrieroi Luer & Andreetta
M. guttulata Rchb. f.
M. helgae Königer & J. Portilla
M. impostor Luer & Escobar
M. infracta Lindl.
M. kuhniorum Luer
M. lenae Luer & Hirtz
M. lintricula Königer
M. maculata Kl. & Karst.
M. martineae Luer
M. martiniana Luer
M. mascarata Luer & R. Vásquez
M. melanoxantha Rchb. f.
M. monogona Königer
M. navicularis Garay & Dunster.
M. recurvata Luer & Dalström
M. obscurans (Luer) Luer
M. odontopetala Luer
M. omorenoi Luer & R. Vásquez
M. oscitans (Luer) Luer
M. patchicutzae Luer & Hirtz
M. phoenix Luer
M. pinocchio Luer & Andreetta
M. portillae Luer & Andreetta
M. posadae Luer & Escobar
M. sanguinea Luer & Andreetta
M. revoluta Königer & J.J. Portilla
M. receptrix Luer & Vasquez
M. richardsoniana Luer
M. sanctae-fidei Kraenzl.
M. schudelii Luer
M. scitula Königer
M. scobina Luer & Escobar
M. serendipita Luer & Teague
M. sernae Luer & Escobar
M. sprucei Rchb. f.
M. stenorhynchos Kraenzl.
M. stirpes Luer
M. synthesis Luer
M. theleüra Luer
M. trochilus Lind. & André
M. tsubotae Luer
M. vargasii C. Schweinf.
M. vargasii C. Schweinf.
M. virens Luer & Andreetta
M. virgo-cuencae Luer & Andreetta
M. vomeris Luer
M. weberbaueri Schltr.
M. whiteana Luer
M. xylina Rchb. f.
M. norae Luer
M. pastinata Luer
M. zumbae Luer
M. prosartema Königer

Subsection *Coaetaneae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 77: 10. 2000.

Type: *Masdevallia sceptrum* Rchb. f., Gard. Chron. n. s. 7: 653. 1877.

A small subsection characterized by the simultaneously flowering raceme. It includes:

M. aenigma Luer & Escobar
M. bicolor Poepp. & *Endl*
M. buccinator Rchb. f.
M. cinnamomea Rchb. f.
M. concinna Königer
M. dunstervillei Luer
M. empusa Luer
M. infracta Lindl. (species included in the two sections of *Polyantha*)
M. isos Luer
M. medusa Luer & Escobar
M. mezae Luer
M. sceptrum Rchb. f.
M. sernae Luer & Escobar
M. tovarensis Rchb. f.

Section *Polyanthae* Rchb. f., Gard. Chron. n.s. 1: 372. 1874.

Bas: sect. *Polyanthae* Rchb. f., Gard. Chron. n.s. 1: 372. 1874.

Type: *Masdevallia schlimii* Lind. ex Lindl., Orchid. Lind. 5. 1846.

This section is characterized by a simultaneously or successively flowering inflorescence with a terete peduncle. It includes two subsections.

Subsection *Polyanthae* (Rchb. f.) Veitch, Man. Orchid. Pl. 5: 18. 1889.

Type: *Masdevallia polyantha* Linden ex Lindl., Orchid. Linden. 6. 1846.

This subsection includes only few species, characterized by the simultaneously flowered inflorescence. To this section belong:

M. wuerstlei Luer
M. oreas Luer & R. Vásquez
M. menatoi Luer & R. Vásquez
M. schlimii Linden ex Lindl.
M. striatella (prior Sect. *Reichenabachianae*)

Subsection *Successiviflorae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 77: 10. 2000.

Type: *Masdevallia lata* Rchb. f., Gard. Chron. n. s. 7(178): 653. 1877.

Species of subsection *Succesiviflorae* are characterized by the successively flowering, or occasionally a single flowered inflorescence. To this subsection belong:

M. cosmia Königer
M. curtipes Barb. Rodr.
M. dioscoidea Luer & Würstle
M. eumeces Luer
M. garciae Luer
M. infracta Rchb. f.
M. jarae Luer
M. lata Rchb. f.
M. maduroi Luer
M. mayaycu Luer & Andreetta
M. menatoi Luer & Vásquez
M. oreas Luer & Vásquez (included into *Polyanthae* too)
M. pyxis Luer
M. striatella Rchb. f. (included into *Polyanthae* too)
M. richardsoniana Luer (included into *Alaticaules* too)
M. schlimii Lind. ex Lindl. (included into *Polyanthae* too)
M. sprucei Rchb. f. (included into *Alaticaules* too)
M. thienii Dodson

Subgenus *Pygmaeia* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 77: 10. 2000.

Type: *Masdevallia pygmaea* Kraenzl., Rep. Spec. Nov. Regni Veg. Beih. 34: 92. 1925.

Bas.: sect. *Pygmaeae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 12. 1986.

Type: *Masdevallia pygmaea* Kraenzl., Rep. Spec. Nov. Regni Veg. Beih. 34: 92. 1925.

Syn.: sect. *Amaluzae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 18. 1986.

Type: *Masdevallia amaluzae* Luer & Malo, Phytologia 39(4): 185. 1978.

= sect. *Aphanes* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 18. 1986.

Type: *Masdevallia aphanes* Königer, Die Orchidee 30: 196. 1979.

Subgenus *Masdevallia* sections *Amaluzae* and *Aphanes*, and subgenus *Amanda* section *Pygmaeae* (Luer, 1986) were united to form subgenus *Pygmaeia*. Luer indicated that all the species of this proposed subgenus probably are not closely related, but treating these three sections in a single, loosely related, more easily recognized taxon , seems preferable to maintainig several small subgenera. All the species included in this subgenus are united by their small, caespitose habit. Subgenus *Pygmaeia* is divided into four sections.

Section *Amaluzae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 18. 1986.

Bas.: subgen. *Masdevallia* sect. *Amaluzae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 18. 1986.

Type: *Masdevallia amaluzae* Luer & Malo, Phytologia 39(4): 185. 1978.

Section *Amaluzae* is distinguished by a small to very small, caespitose habit with a successively flowered raceme, borne by a slender, ascending, and horizontal to descending peduncle; the ovaries are smooth with low ribs; the lips are more or less oblong with variations of a pair of longitudinal calli. To this section belong:

M. amaluzae Luer & Malo
M. audax Königer
M. aurorae Luer & M. W. Chase
M. carmenensis Luer & Malo
M. chimboensis Kraenzl.
M. manchinazae Luer & Andreetta
M. mataxa Königer & H. Mend.
M. merinoi Luer & J. J. Portilla
M. paquishae Luer & Hirtz
M. sanchezii Luer & Andreetta
M. patula Luer & Malo
M. schizostigma Luer

Section *Aphanes* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 18. 1986.

Bas.: subgen. *Masdevallia* sect. *Aphanes* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 18. 1986.

Type: *Masdevallia aphanes* Königer, Die Orchidee 30: 196. 1979.

Syn.: subg. *Masdevallia* subsect. *Pterigophorae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 77: 10. 2000.

Type: *Pleurothallis pterygiophora* Luer & Escobar, Lindleyana 4: 50. 1988.

Species of section *Aphanes* show the same habit as those of section *Amaluzae*, but the ovaries are costate, crested or verrucose. The section includes:

M. aphanes Königer
M. berthae Luer & Andreetta
M. collantesii D.E. Benn. & Christenson
M. expers Luer & Andreetta
M. henniae Luer & Dalström
M. hoeijeri Luer & Hirtz
M. indecora Luer & R. Escobar
M. scopaea Luer & R. Vásquez
M. plantaginea (Poepp. & Endl.) Cogn. (prior sect. *Minutae* sensu Luer)
M. pterygophora Luer & R. Escobar
M. pyknosepala Luer
M. scalpellifera Luer
M. mentosa Luer
M. setipes Schltr
M. trifurcata Luer

Section *Pygmaeae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 12. 1986.

Bas.: subgen. *Masdevallia* sect. *Pygmaeae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 12. 1986.

Type: *Masdevallia pygmaea* Kraenzl., Rep. Spec. Nov. Regni Veg. Beih. 34: 92. 1925.

The species included in this section are characterized by papillose or spiculate ovaries. It includes:

M. erinacea Rchb. f.
M. anachaeta Rchb. f.
M. pygmaea Kraenzl.

Section *Zahlbrucknerae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 82: 432. 2000.

Bas.: subsect. *Zahlbrucknerae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 77: 10. 2000.

Type: *Masdevallia zahlbruckneri* Kraenzl., Rep. Spec. Nov. Regni Veg. Beih. 17: 413. 1921.

Species of this section are characterized by smooth or slightly costate ovaries and callous petals with a distinct, retrorse process at the base. This section includes four species:

- *M. schizopetala* Kraenzl. (prior section *Minutae* sensu Luer)
- *M. zahlbruckneri* Kraenzl.
- *M. vieirana* Luer & R. Escobar
- *M. naranjapatae* Luer

Subgenus *Scabripes* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 77: 10. 2000.

Type: *Masdevallia bicornis* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 128. 1997.

This monotypic subgenus is characterized by a successively flowering inflorescence with a scabrous peduncle, and a minute hornlike process on either side of the lip above the base.

Subgenus *Teagueia* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 16: 53. 1986.

Type: *Masdevallia teaguei* Luer, Selbyana 2: 381. 1978.

Syn.: *Jostia* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 79: 2. 2000.

Masdevallia teaguei was segregated into a new genus (*Jostia*) in 2000. A first molecular analysis of the subtribe *Pleurothallidinae* (PRIDGEON et al, 2001), indicate a relationship with *Masdevallia.* For this reason *M. teagueia* was reincluded into the genus *Masdevallia*.

Subgenus *Volvula* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 77: 10. 2000.

Type: *Masdevallia caudivolvula* Kraenzl., Notizbl. Bot. Gart. Berlin-Dahlem 8: 128. 1922.

This monotypic subgenus is characterized by single flowers, a lip divided by marginal folds, and thick sepals that are carinate internally with thick-twisted tails.

Reclassification of *Masdevallia* proposed by Luer (2006)

Sensu Luer (2006), on the basis of "marked morphological differences among some of the subgenera," the genus *Masdevallia* was divided 19 smaller genera, 16 of which are validated as new. "Recent DNA analyses" are barely mentioned, and no cladogram is reproduced. In an attempt to pacify horticulturists and others who might be upset by these sweeping name changes, the author indicates that "the majority of species remain in the sections of *Masdevallia*."While this may well be true over the entire geographic range of the group, it does not hold for Costa Rica. Indeed, according to this new system, not a single one of the 31 spp. treated under the name *Masdevallia* in the Manual will remain in *Masdevallia* s. str.; instead, they will be apportioned among eight of the splinter genera, as follows: *Acinopetala* Luer, with *Masdevallia attenuata* Rchb. f., *M. chontalensis* Rchb. f., *M. flaveola* Rchb. f., *M. floribunda* Lindl., *M. laucheana* J. Fraser, *M. livingstoneana* Roezl ex Rchb. f., *M. scabrilinguis*

Luer, *M. schizopetala* Kraenzl., and *M. tubuliflora* Ames; *Alaticaulia* Luer, with *M. lata* Rchb. f.; *Buccella* Luer, with *M. molossoides* Kraenzl. and *M. nidifica* Rchb. f.; *Diodonopsis* Pridgeon & M. W. Chase, with *M. erinacea* Rchb. f. and *M. pygmaea* Kraenzl.; *Fissia* (Luer) Luer, with *M. picturata* Rchb. f.; *Spilotantha* Luer, with *M. rafaeliana* Luer; *Zahleria* Luer, with *M. zahlbruckneri* Kraenzl.; and *Reichantha* Luer, with all the rest.

1.2.6 Natural hybrids of *Masdevallia*

Orchidaceae are well known as a family in which wide crosses are possible; interspecific and intergeneric hybrids are the basis for a thriving commercial market. This reputation is based on the great ease and frequency of artificial crosses, but, because of mechanical barriers and pollinator specificity, no parallel exists in nature. If one examines orchid floras, such as that of North America (Luer, 1975), documented hybrids at either the generic or specific level are not particularly frequent. No data exist to substantiate the claim that natural hybrids are more frequent in Orchidaceae than in other families.The occurrence of natural hybridization in *Masdevallia* has been commented on for many years, beginning with REICHENBACH (1879), H. J. VEITCH (1902) and KRAENZLIN (1925), although the frequency with which putative hybrids are recognized depends greatly on how finely the species delimitations are drawn. Few hybrids have ever been reported from South America, primarily because of the lack of material and field examination. REICHENBACH (1879) proposed *Masdevallia* X *splendida* as a possible hybrid between *Masdevallia veitchiana* and *Masdevallia barleana*, and his supposition was proven correct by artificial recreation of the hybrid (LUER, 2003). LUER (2002) reported *Masdevallia* X *ligiae* as a possible hybrid between a species of subsection *Saltatrices* and a species of section *Polyanthae*, as a product of random pollination of various species by tiny fruit-flies. The majority of natural hybrids have a morphology intermediate between the two parents and are often characterized by reduced pollen stainability and seed set. Seven combinations are supposed to form possible natural hybrids: *M.* X *alvaroi, M.* X *ligiae, M.* X *mystica, M.* X *parlatoreana, M.* X *splendida, M.* X *strumella,* and *M.* X *wubbenii.*

1.2.7 Intergeneric hybrids of *Masdevallia*

The first *Dracuvallia* hybrid was made in 1902 by H. J. Veitch when he crossed *Dracula chimaera* with *Masdevallia tovarensis*. At this time only about twelve *Dracuvallia* hybrids have been registered. Another large stumbling block appears to be that the resultant hybrids are sterile. The *Draculas* will breed with *Masdevallia* hybrids, put the *Dracuvallia* hybrids will not breed back to the parental species. Most of these hybrids exhibit rippling or pleating on the surface of the lip and some severe reflexing.

1.3

AIMS

Although revisions of several sections of *Masdevallia* were published in the last century, a comprehensive treatment of all species is still lacking. The delimitation of infrageneric taxa is problematical and complex. These difficulties result not only from the large species number, but in addition, the identification of morphological and anatomical synapomorphies in the subtribe *Pleurothallidinae* is complicated by the homoplasy rife in vegetative and floral features (PRIDGEON, 1982), as shown in the cladistic study by NEYLAND et al. (1995). Morphological features such as fleshy or terete leaves, variously connate sepals, and ornamented ovaries occur in clearly unrelated species (LUER, 1986b). The same is true for anatomical features such as thickenings in the foliar hypodermis, differentiation of a foliar collenchyma, and presence of spirally thickened idioblasts (PRIDGEON, 1982; NEYLAND et al. 1995). Most of these features are either xeromorphic adaptations or adaptative responses to selection pressures imposed by pollinators with similar behaviors. Thus, in the absence of reliable homologous morphological and anatomical characters to be interpreted as synapomorphies, no satisfactory phylogenetic treatment of this large genus has been published to date. A first molecular systematic analysis of subtribe *Pleurothallidinae* revealed that *Masdevallia* is not monophyletic (PRIDGEON et al., 2001), however most species grouped together in a large clade which is sister, in descending order, to the genera *Porroglossum*, *Dracula,* and *Trisetella*. The naturalness and relationships of the subgenera, sections and subsections of *Masdevallia* were not previously examined in a phylogenetic context.

Consequently, the aims of this study are to use molecular data to

1) address the subgeneric and sectional relationships in *Masdevallia* with molecular data

2) to correlate molecular with morphological data in order to establish morphological synapomorphies for clades well supported by molecular data and

3) to correlate molecular with geographical data in order to evaluate the possible speciation histories and processes.

For these analyses, the non-coding internal transcribed spacer (ITS) of nuclear ribosomal DNA was sequenced. Internal transcribed spacer sequence variation has been previously used in phylogenetic studies of orchids to identify monophyletic groups at genus level and below and to provide a molecular basis for taxonomic restructuring, particularly in *Cypripedioideae* (COX et al., 1997), *Orchidinae* (PRIDGEON et al., 1997; BATEMAN, PRIDGEON and CHASE, 1997), *Catasetinae* (PRIDGEON and CHASE, 1998), *Diseae* (DOUZERY et al., 1999), *Pogoniinae* (CAMERON and CHASE, 1999), *Lycastinae* (RYAN et al., 2000), *Laeliinae* (VAN DEN BERG et al., 2000), *Maxillarieae* (WHITTEN, WILLIAMS, and CHASE, 2000), *Coelogyninae* (GRAVENDEEL et al., 2001), *Pleurothallidinae* (PRIDGEON, SOLANO and CHASE, 2001), and *Cranichideae* (SALAZAR et al, 2003).

2

MATERIAL AND METHODS

2.1 Morphological analysis

2.1.1 Sampling

This analysis includes 85 species of *Masdevallia*, chosen to represent the taxonomic, morphological, and geographic diversity within the genus. Living material was obtained from the botanical garden of the University of Hamburg (Germany) (HBG), the “Herrenhäuser Gärten” in Hannover (Germany) (HHG) and the private collection from Ton Sijm in Hem-Venhuizen (Netherlands) (TS). Plant material was herbarized and deposited at the Herbarium Hamburgense (HBG). Reproductive structures were preserved in 70% alcohol. Herbaria specimens as well as literature were used to confirm the correct determination of the species. All of the segregate subgenera/sections/subsections recognized by Luer (2000-2003) are represented with multiple species (Table 4). From among the subgenera of *Masdevallia* recently established new genera (Luer, 2006) were not considered in this study. Because no single taxonomy of *Masdevallia* includes an exhaustive enumeration of species, information from the available taxonomic treatments was combined and the latest sectional circumscriptions (LUER 2000-2003) were adopted to dictate sampling. As a result: (1) assignment of many of the listed species to subgenus, sections and subsections required inference based on sectional descriptions; and (2) the listing of sections sampled should not be taken as endorsement of their validity, as these were adopted simply to ensure the broadest possible representation from within segregate subgeneric groups.

Table 4 Reference of source information for the analyzed taxa. The infrageneric classification follows LUER (2000-2003).

Subgenus	Section	Subsection	Taxon	Source
Amanda			*M. abbreviata* Rchb. f.	HBG A3-G-236
			M. caloptera Rchb. f.	HBG A3-G-113
			M. chaetostoma Luer	HBG 98-G-21
			M. pachyura Rchb. f.	HBG A3-G-112
			M. ophioglossa Rchb. f.	HBG A3-G-248
			M. ova-avis Luer	HBG A3-G-402
Cucullatia			*M. delhierroi* Luer & Hirtz	TS s.n.
			M. cerastes Luer & R. Escobar	TS s.n.
			M. corniculata Rchb. f.	HBG A3-G-296
Fissia			*M. picturata* Rchb. f.	HBG 98-G-9
			M. pleurothalloides Luer	TS s.n.
Masdevallia	*Coriaceae*		*M. campyloglossa* Rchb. f.	HBG A3-G-326
			M. civilis Rchb. f.	HBG A3-G-408
			M. macrura Rchb. f.	HBG A3-G-243
			M. peristeria Rchb .f.	HBG A3-G-125
			M. picea Luer	HBG A3-G-353

Table 4 Cont. Reference of source information for the analyzed taxa. The tribal classification follows Luer (2000-2003).

Subgenus	Section	Subsection	Taxon	Source
Masdevallia	*Dentatae*		*M. collina* L.O. Williams	HHG s.n.
	Durae		*M. goliath* Luer & Andreetta	HBG 00-G-258
			M. panguiensis Luer & Andreetta	HHG s.n.
			M. princeps Luer	HBG 98-G-326
	Masdevallia	*Caudatae*	*M. antonii* Königer	TS s.n.
			M. decumana Königer	HBG 98-G-11
			M. estradae Rchb. f.	HBG A3-G-85
		Coccineae	*M. coccinea* Linden ex Lindl.	HBG A3-G-107
			M. davisii Rchb. f.	HBG A3-G-332
			M. deformis Kraenzl.	HBG 97-G-71
			M. veitchiana Rchb. f.	HBG A3-G-100
		Masdevallia	*M. glandulosa* Königer	HBG A3-G-339
			M. lamprotyria Königer	HBG 96-G-146
			M. patriciana Luer	HBG 98-G-10
			M. uniflora Ruiz & Pav.	HBG 98-G-26
			M. paivaeana Rchb. f.	HBG 97-G-230
		Oscillantes	*M. persicina* Luer	HBG 98-G-22
			M. rubiginosa Königer	HBG 98-G-323
		Saltatrices	*M. ampullacea* Luer & Andreetta	HBG 98-G-321
			M. hirtzii Luer & Andreetta	HBG 98-G-12
			M. notosibrica Maekawa & Hashimoto	HBG 00-G-313
			M. X *mystica* Luer	HBG 02-G-077
	Minutae		*M. floribunda* Lindl.	HBG A3-G-368
			M. gutierrezii Luer	HBG 97-G-65
			M. herradurae Lehm. & Kraenzl.	HHG s.n.
			M. pescadoensis Luer & R. Escobar	HBG A3-G-314
			M. scabrilinguis Luer	HBG A3-G-334
			M. wendlandiana Rchb. f.	HBG 97-G-64
	Racemosae		*M. racemosa* Lindl.	TS s.n.
	Reichenbachiana		*M. reichenbachiana* Endres ex Rchb. f.	HBG A3-G-282
			M. fulvescens Rolfe	HBG A3-G-105
			M. walteri Luer	HBG A3-G-386
	Triotosiphon		*M. bangii* Schltr.	HHG
			M. lansbergii Rchb. f.	TS s.n.
			M. kyphonantha H.R. Sweet	TS s.n.
			M. venezuelana H.R. Sweet	HBG
Meleagris			*M. alexandri* Luer	HHG s.n.
			M. meleagris Lindl. ex Rchb. f.	TS s.n.
			M. parvula Schltr.	TS s.n.
Nidificia			*M. molossus* Rchb. f.	HHG s.n.
			M. nidifica Rchb. f.	HBG A3-G-400
Polyantha	*Alaticaules*	*Alaticaules*	*M. cardiantha* Königer	HBG A3-G-352
			M. echo Luer	HBG A3-G-26
			M. garciae Luer	HBG 00-G-158
			M. guttulata Rchb. f.	HBG A3-G-185
			M. infracta Lindl.	HBG A3-G-24
			M. melanoxantha Linden & Rchb. f.	HBG A3-G-65
			M. pinocchio Luer & Andreetta	HBG 97-G-66
	Polyanthae	*Polyanthae*	*M. schlimii* Linden ex Lindl.	HBG A3-G-241
			M. striatella Rchb. f.	HHG s.n.
			M. oreas Luer & Vásquez	HHG s.n.
		Successiviflorae	*M. lata* Rchb. f.	HBG 02-G-80
			M. pyxis Luer	HBG 99-G-47
			M. cupularis Rchb. f.	HHG s.n.
	Amaluzae		*M. carmenesis* Luer & Malo	HBG 99-G-80
			M. chimboensis Kraenzl.	TS s.n.
			M. patula Luer & Malo	HBG 99-G-78
			M. sanchezii Luer & Andreetta	HBG 00-G-280
	Aphanes		*M. hoeijeri* Luer & Hirtz	HBG 98-G-16
			M. aphanes Königer	TS s.n.
			M. mentosa Luer	J & L Orchids s.n.
	Pygmaeae		*M. erinacea* Rchb. f.	HBG 98-G-17
	Zahlbrucknerae		*M. zahlbruckneri* Kraenzl.	HHG s.n.
			M. vieirana Luer & R. Escobar	TS s.n.

Table 4 Cont. Reference of source information for the analyzed taxa. The tribal classification follows Luer (2000-2003).

Subgenus	Section	Subsection	Taxon	Source
Pygmaeia	*Zahlbrucknerae*		*M. naranjapatae* Luer	TS s.n.
Scabripes			*M. bicornis* Luer	TS s.n.
Teagueia			*M. teaguei* Luer	TS s.n.
Volvula			*M. caudivolvula* Kraenzl.	TS s.n.

2.1.2 Outgroups

Eight species of the genera *Dracula* and *Porroglossum* were chosen as outgroups (Table 5) because these genera are the traditional candidates for a sister group relationship with *Masdevallia* (PRIDGEON et al., 1982), and molecular analysis (sequences from nuclear ribosomal ITS and *mat*K) confirm this supposition (PRIDGEON et al., 2001) (Fig. 2, p. 4). A cladistic study with morphological and anatomical data showed that *Dracula*, *Porroglossum*, and *Trisetella*, are closely related with the genus *Masdevallia* (NEYLAND et al., 1995).

Table 5 List of outgroup species analyzed, arranged by (sub) genera and (sub) sections according to Luer (2000-2003).

Genus	Subgen.	Sect.	Subsect.	Series	Taxon	Source
Dracula	*Dracula*	*Dracula*	*Dracula*	*Parviflorae*	*D. astuta* (Rchb.f.) Luer	HBG
					D. houtteana (Rchb. f.) Luer	HBG
				Dracula	*D. chimaera* (Rchb. f.) Luer	HBG
		Cochliopsia			*D. cochliops* Luer & R.Escobar	HBG
	Sodiroa				*D. sodiroi* (Schltr.) Luer	HBG
	Xenosia				*D. xenos* Luer & R.Escobar	TS
Porroglossum	*Porroglossum*	*Porroglossum*			*P. amethystinum* (Rchb. f.) Garay	HBG
		Tortae			*P. uxorium* Luer	HBG

2.1.3 Characters and character states

Whenever possible, morphological data were derived from observations of living material from the botanical garden of the University of Hamburg (Germany), the "Herrenhäuser Gärten" in Hannover (Germany) and the private collection from Ton Sijm in Hem-Venhuizen (Netherlands). Herbarium specimens were used to supplement living material and to confirm characters that were initially scored from fresh material. A few character states were extracted from the literature, as noted below in the discussion of individual characters. The criteria for character inclusion were:

- The states were mutually exclusive, with a fixed order of evolution so that each state is derived directly from just one other state, and there is a unique state from which every other state is eventually derived (FARRIS et al., 1970).
- The character states did not vary within terminals.

STEVENS (1991) and GIFT and STEVENS (1997) have shown that the assignment of character states to continuously varying characters are arbitrary and artificial, such characters were ignored. Characters used to construct the morphological data matrix were discrete and did not show continuous variation. Variation for each quantitative character under consideration was graphed and only characters with non-overlapping variation (those with distinct morphological gaps) were included in the phylogenetic data matrix (GIFT and STEVENS, 1997). The morphological data matrix was constructed and edited using DELTA 1.04 (2000).

2.1.5 Macro-morphological characters included

In total, 49 multi-state and 48 binary characters were scored. Of these 97 characters, ten (1-10) relate to vegetative and 85 (11-85) to reproductive features. The morphological characters included are listed below. All multistate characters were treated as unordered (Table 6). Plesiomorphic characters are listed first, followed by apomorphic ones (polarity decisions based on trees rooted with *Dracula*). Unknown characters were coded as ?, and not applicable characters were coded as -.

2.1.4 Micro–morphological characters

The pollinia surface ornamentations were scored using SEM. Pollinia were broken apart and mounted on aluminums stubs using a colloidal-graphite glue (Witcomb, 1985). Stubs were sputter coated with gold, examined using a Cambridge S200 scanning electron microscope at an accelerating voltage of 5 KV and photographed at magnifications of 1 000 and 3 000 times. The descriptive terminology for surface sculpturing is adapted from that of PUNT et al. (1994). The observed variation in exine sculpture was coded as characters and character states (Table 6).

Table 6 Characters and character states used in the cladistic analysis of the genus *Masdevallia.* Plesiomorphic characters are listed first, followed by apomorphic ones.

Character n°	Character states
1	Growth habit: 1=terrestrial, 2=epiphyte
2	Habit: 1=caespitose, 2=repent or scandent
3	Ramicaul, length: 1=≤ 15 mm, 2=between 16 and 25 mm, 3=≥ 35 mm
4	Leaf, shape: 1=oblong, 2=elliptic 3=obovate
5	Leaf, apex: 1=acute, 2=obtuse
6	Leaf, base: 1=base cuneate into the petiole, 2=base decurrent into the petiole
7	Leaf, petiole: 1=petiolate, 2=subpetiolate (petiole not defined)
8	Leaf, texture: 1=coriaceous, 2=chartaceous, 3=thinly coriaceous
9	Leaf, including the petiole: 1=≤ 5 cm, 2= between 5.1 and 15 cm, 3=≥ 20 cm
10	Leaf, wide: 1=≤8 mm, 2=between 8.1 and 29 mm 3=≥35 mm
11	Inflorescence: 1=a solitary flower, 2=racemose
12	Inflorescence, emergence: 1=basal (from low on the ramicaul), 2=suprabasal (from near the middle of the ramicaul)
13	Raceme: 1=congested, 2=distantly flowered
14	Raceme: 1=few-flowered, 2=4 to many flowered

Table 6 Cont. Characters and character states used in the cladistic analysis of the genus ***Masdevallia*.** Plesiomorphic characters are listed first, followed by apomorphic ones.

Character n°	Character states
15	Flowers,anthesis: 1=in succession over a long period, 2=in periodic clusters
16	Peduncle: 1=erect, 2=descending to horizontal
17	Peduncle: 1=with more than 2 internodes/bracts, 2=without internodes
18	Peduncle: 1=peduncle longer than the leaves, 2=peduncle shorter or as long as the leaves
19	Peduncle in cross section: 1=terete, 2=triquetrous
20	Peduncle, surface: 1=glabrous, 2=scabrous
21	Floral bracts, type: 1=tubular, 2=inflated, 3=cucullate 4=imbricate
22	Floral bracts, indument: 1=glabrous, 2=papillose, 3=pubescent
23	Pedicel: 1=thicker and longer than the peduncle that bears it, 2=shorter than the peduncle
24	Ovary: 1=carinate, 2=with undulating crest, 3=with undulate carinae, *4=twisted
25	Ovary, indument: 1=glabrous, 2=papillose, 3=echinate, 4=verrucose
26	Sepals, connation: 1=dorsal sepal free from the laterals, 2=dorsal sepal connate with the laterals
27	Lateral sepals, connation: 1=connate, 2=free but connate to the column foot
28	Dorsal and lateral sepals, connation: 1=connate for similar lengths, 2=different connate
29	Sepals, connate to form: 1=a cylindrical tube, 2= a sepaline cup, 3= a flat, widely spreading flower
30	Sepals connate to form a cylindrical tube: 1=constricted above the middle, 2=not constricted above the middle
31	Sepaline tube: 1=arcuate, 2=not arcuate
32	Dorsal sepal, connation (not including the tail length): 1=connate with the lateral sepals above the middle, 2=connate with the lateral sepals below or at the middle, 3=connate with the lateral sepals in the total length
33	Lateral sepals, connation: 1=connate into a synsepal or lamina (above the middle), 2=connate at the middle, 3=connate below the middle
34	Lateral sepals, connate to form a broad mentum or a secondary mentum with the column-foot: 1=yes, 2=no
35	Dorsal sepal, shape: 1=oblong, 2=elliptic, 3=ovate, 4=obovate
36	Dorsal sepal, inner surface: 1=glabrous, 2=pubescent, 3=verrucose, 4=echinate, 5=cellular – glandular, 6=papillose
37	Dorsal sepal, texture: 1=fleshy, 2=membranous
38	Dorsal sepal, margin: 1=entire, 2=dentate to serrate, 3=erose, 4=revolute, 5=ciliate
39	Dorsal sepal, apex: 1=acute, 2=obtuse, 3=acuminate, 4=rounded, 5=truncate, 6=attenuate
40	Dorsal sepal, apex with the free portion produced into a tail: 1=yes, 2=no
41	Tail from the dorsal sepal: 1=retrorse, 2=antrorse, 3=erect, 4=curled
42	Tails: 1=clavate, 2=not clavate
43	Tail from the dorsal sepal: 1=less than half as long as the lamina, 2=more than half as long to as long as the lamina, 3=longer than lamina.
44	The tail from the dorsal sepal: 1=longer than the tails from the lateral sepals, 2=similar than the tails from the lateral sepals, 3=shorter than the tails from the lateral sepals
45	Lateral sepals (or synsepal) shape: 1=oblong, 2=elliptic, 3=ovate (lanceolate), 4=obovate, 5=falcate
46	Lateral sepals, inner surface: 1=glabrous, 2=pubescent, 3=verrucose, 4=echinate, 5=cellular-glandular, 6=papillose
47	Lateral sepals, consistency: 1=fleshy, 2=membranous
48	Lateral sepals, margin: 1=entire, 2=erose, 3=revolute, 4=ciliate
49	Lateral sepals, apex: 1=acute, 2=obtuse, 3=retuse, 4=acuminate, 5=rounded, 6=truncate, 7=attenuate
50	Lateral sepals, the free portion produced into a tail: 1=yes, 2=no
51	Tails from the lateral sepals: 1=retrorse, 2=antrorse, 3=erect, *4=curled
52	Lateral sepals, apex: 1=with apices diverging (with the angle between obtuse), 2=with apices approximate (the angle between acute)
53	Tails from the lateral sepals: 1=clavate, 2=not clavate
54	Tails from the lateral sepals: 1=less than half as long as the lamina, 2=more than half as long to as long as the lamina, 3=longer than lamina
55	Petals and lip: 1=petals and lip are out of sight deep within the sepaline tube, 2=petals and lip are not out of sight deep within the sepaline tube
56	Petals, shape: 1=oblong, 2=elliptic, 3=ovate, 4=obovate, 5=triangular, 6=panduriform
57	Petals, margin: 1=entire, 2=dentate to serrate, 3=revolute, 4= erose,
58	Petals: 1=arcuate, 2=not arcuate
59	Petals, apex: 1=bivalvate with an inner and outer lamina, 2=not the above combination
60	Petals, apex: 1=acute, 2=obtuse, 3=rounded, 4=truncate, 5=attenuate, 6=clavate
61	Petals, apex: 1=entire, 2=bilobed, 3=denticulate, 4=tridentate, 5=apiculate, 6=longitudinally channeled, twisted and curved up, 7=decurved

Table 6 Cont. Characters and character states used in the cladistic analysis of the genus *Masdevallia.* Plesiomorphic characters are listed first, followed by apomorphic ones.

Character n°	Character states
62	Petals, base: 1=truncate, 2=cordate
63	Petals, indument: 1=smooth, 2=verrucose, 3=papillose
64	Petals, consistency: 1=membranous, 2=cartilaginous
65	Petals, margin: 1=callous at the margins, 2=ecallous at the margins
66	Petals, margin: 1=both margins (anterior or labellar and upper) with a longitudinal callus, 2=only the labellar margin with a longitudinal callus
67	Petals, margin: 1=both margins callous and shallowly sulcate centrally, 2=both margins callous but not sulcate centrally
68	Longitudinal callus from the labellar margin: 1=ending in a broad, rounded thick process, 2=ending in an acute-uncinate process, 3=ending in an obtuse angle, 4=not ending in a process or angle
69	Process: 1=retrorse, 2=not retrorse
70	Callus ending: 1=at or below the base, 2= above the base, 3=between the middle and the lower third
71	Lip, shape: 1=oblong, 2=elliptic, 3=ovate, 4=obovate, 5=spathulate, 6=trapeziform
72	Lip, margin: 1=entire, 2=serrate to dentate, 3=crenate, 4=erose
73	Lip, apex: 1=recurved, 2=not recurved, 3=involute
74	Lip, base: 1=truncate, 2=cordate-semicordate, 3=retuse, 4=concave
75	Lip, base: 1=with elevated margins, 2=not as above
76	Lip, indument: 1=smooth, 2=verrucose, 3=papillose, 4=glandulose, 5=pubescent
77	Lip, callus at the apex: 1=present, 2=ecallous at the apex
78	Lip: 1=oscillating, 2=not oscillating
79	Lip: 1=divided by marginal folds into an epichile and a hypochile, 2=not divided
80	Disc: 1=with a central, flat callus below the middle, 2=with a pair of calli near the middle, 3=featureless, 4=longitudinally thickened, 5=with 3 lamellae and several, radiating, elevated veins
81	Disc: 1=sulcate, 2=not sulcate,
82	Epichile, shape: 1=oblong, 2=elliptic, 3=ovate, 4=obovate
83	Epichile, margin: 1=entire, 2=dentate to serrate, 3=crenate, 4=erose, 5=decurved
84	Epichile, indument: 1=glabrous, 2=verrucose, 3=papillose, 4=cellular-glandular
85	Hypochile, shape: 1=oblong, 2=elliptic, 3=ovate, 4=obovate
86	Hypochile, margin: 1=entire, 2=dentate to serrate, 3=crenate, 4=erose
87	Hypochile: 1=with a pair of acute, uncinate processes, 2=not as above, 3=with erect, rounded, marginal angles
88	Lip: 1=sensitive, 2=not as above
89	Column: 1=longer than the labellum, 2=similar or shorter
90	Column-foot: 1=much longer than the column, 2=shorter or similar than the column
91	Rostellum: 1=apical, 2=retrorse
92	Pollinia, shape: 1=drop-like, 2=lentiform, 3=clavate
93	Exine, sculpture: 1=psilate, 2=fossulate, 3=verrucate to scabrate-gemmate, 4=rugulate
94	Exine, margin: 1=normal, 2=prominent
95	Pollinia: 1=shorter than 500 µm, 2=between 550 and 800 µm long, 3=more than 900 µm long
96	Pollinia, wide: 1=shorter than 300 µm, 2=between 300 and 600 µm wide, 3=more than 700 µm wide
97	Caudicles: 1=present, 2=absent

2.2 Molecular analysis

2.2.1 Material

2.2.1.1 Chemicals

Chemicals were purchased from the companies VWR International GmbH (Darmstadt, Germany), AppliChem (Darmstadt, Germany), Carl Roth GmbH + Co. KG. (Karlsruhe, Germany), Life Technology (Paisley, Scotland), Sigma-Aldrich Chemie GmbH (Taufkirchen, Germany), Gene Craft (Münster, Germany), Applied Biosystems (Foster City, USA), Aldrich Chemical Company (Milwaukee, USA) and Eurogentec (Searing, Belgium).

Deionized water (Milli Q Water System, Millipore, Bedford, USA) was used for preparation of all solutions. According to different requirements, solutions were sterilized (20 min, 120 °C, 2 x 105 Pa) or filter sterilized with 0.2 µm filters (Nalgene, Rochester, USA).

2.2.1.2 Taxon sampling

In this study 104 species were included, representing all the subgenera, sections and subsections of the genus *Masdevallia* according to LUER (2000-2003). Eleven species of the genera *Dracula*, *Luerella*, *Trisetella* and *Porroglossum* were used as outgroups based on the results of PRIDGEON et al. (2001), NEYLAND et al. (1995) and PRIDGEON et al. (1982). For species such as *M. macrura, M. corniculata*, *M. racemosa*, *M. caudivolvula* and *Dracula xenos*, which presented an unresolved position in the phylogenetic analysis, more than two specimens from different collections were analyzed. About 10% of the sequences were obtained from the Gen Bank (PRIDGEON et al., 2001) and the remaining 90% were produced for this study. Voucher specimens are listed in Table 7 and 8.

Table 7 Reference of source information for the sequenced taxa. The infrageneric classification follows LUER (2000-2003). Accession numbers for sequences of the GenBank data base are listed in the last column (PRIDGEON et al, 2001).

Subgenus	**Section**	**Subsection**	**Taxon**	**Source**	**Database Acces. n°**
Amanda			*M. abbreviata* Rchb. f.	HBG A3-G-236	
			M. caloptera Rchb. f.	HBG A3-G-113	
			M. chaetostoma Luer	HBG 98-G-21	
			M. pachyura Rchb. f.	HBG A3-G-112	
			M. ophioglossa Rchb. f.	HBG A3-G-248	
			M. ova-avis Luer	HBG A3-G-402	
Cucullatia			*M. delhierroi* Luer & Hirtz	TS s.n.	
			M. cerastes Luer & R. Escobar	TS s.n.	
			M. corniculata Rchb. f.	HBG A3-G-296	
			M. corniculata Rchb. f.	HHG s.n.	
Fissia			*M. picturata* Rchb. f.	HBG 98-G-9	
			M. pleurothalloides Luer	TS s.n.	

Table 7 Cont. Reference of source information for the sequenced taxa. The infrageneric classification follows LUER (2000-2003). Accession numbers for sequences of the GenBank data base are listed in the last column (PRIDGEON et al, 2001).

Subgenus	**Section**	**Subsection**	**Taxon**	**Source**	**Database Acces. n°**
Masdevallia	*Coriaceae*		*M. caesia* Roezl.	Hermans 1257 (K)	AF262786
			M. campyloglossa Rchb. f.	HBG A3-G-326	
			M. civilis Rchb. f.	HBG A3-G-408	
			M. coriacea Lindl.	Kew 1977-4593 (K)	AF262781
			M. macrura Rchb. f.	HBG A3-G-243	
			M. macrura Rchb. f.	HHG s.n.	
			M. peristeria Rchb. f.	HBG A3-G-125	
			M. picea Luer	HBG A3-G-353	
	Dentatae		*M. collina* L.O. Williams	HHG s.n.	
			M. collina L.O. Williams	Manning 890809 (K) Kew Spirit 60913	AF262784
	Durae		*M. goliath* Luer & *Andreetta*	HBG 00-G-258	
			M. panguiensis Luer & *Andreetta*	HHG s.n.	
			M. princeps Luer	HBG 98-G-326	
			M. titan Luer	J & L Orchids s.n.	AF262803
	Masdevallia	*Caudatae*	*M. antonii* Königer	TS s.n.	
			M. cyclotega Königer	HBG 98-G-324	
			M. decumana Königer	HBG 98-G-11	
			M. estradae Rchb. f.	HBG A3-G-85	
		Coccineae	*M. coccinea* Linden ex Lindl.	HBG A3-G-107	
			M. davisii Rchb. f.	HBG A3-G-332	
			M. deformis Kraenzl.	HBG 97-G-71	
			M. veitchiana Rchb. f.	HBG A3-G-100	
		Masdevallia	*M. glandulosa* Königer	HBG A3-G-339	
			M. lamprotyria Königer	HBG 96-G-146	
			M. chaparensis T. Hashim.	Manning 900908 (K) Kew Spirit 61344	AF262797
			M. hieroglyphica Rchb. f.	Kew 1997-5335 (K)	AF262798
			M. patriciana Luer	HBG 98-G-10	
			M. uniflora Ruiz & Pav.	HBG 98-G-26	
			M. paivaeana Rchb. f.	HBG 97-G-230	
		Oscillantes	*M. persicina* Luer	HBG 98-G-22	
			M. rubiginosa Königer	HBG 98-G-323	
			M. citrinella Luer & Malo	Kew 1997-5325 (K)	AF262774
			M. rubeola Luer & R. Vásquez	J & L Orchids s.n.	AF262791
		Saltatrices	*M. ampullacea* Luer & Andreetta	HBG 98-G-321	
			M. hirtzii Luer & Andreetta	HBG 98-G-12	
			M. notosibrica Maekawa & Hashimoto	HBG 00-G-313	
			M. limax Luer	Kew 1997-5427 (K)	AF262796
			M. saltatrix Rchb. f.	J & L Orchids s.n.	AF262793
			M. X mystica Luer	HBG 02-G-077	
	Minutae		*M. floribunda* Lindl.	HBG A3-G-368	
			M. gutierrezii Luer	HBG 97-G-65	
			M. herradurae Lehm. & Kraenzl.	HHG s.n.	
			M. pescadoensis Luer & R. Escobar	HBG A3-G-314	
			M. scabrilinguis Luer	HBG A3-G-334	
			M. wendlandiana Rchb. f.	HBG 97-G-64	
	Racemosae		*M. racemosa* Lindl.	TS s.n.	
	Reichenbachianae		*M. reichenbachiana* Endres ex Rchb. f.	HBG A3-G-282	
			M. fulvescens Rolfe	HBG A3-G-105	
			M. walteri Luer	HBG A3-G-386	
	Triotosiphon		*M. lansbergii* Rchb. f.	TS s.n.	
			M. kyphonantha H.R. Sweet	Kew 1997-5335 (K)	AF262780
			M. venezuelana H.R. Sweet	Manning 96106 (K)	AF262782
Meleagris			*M. heteroptera* Rchb. f.	Beckendorf s. n.	AF262800
			M. alexandri Luer	HHG	
Meleagris			*M. parvula* Schltr.	TS s.n.	
			M. ximenae Luer & Hirtz	J & L Orchids s.n.	AF262794

Table 7 Cont. Reference of source information for the sequenced taxa and for out groups. The infrageneric classification follows Luer (2000-2003). Accession numbers for sequences of the GenBank data base are listed in the last column (Pridgeon et al, 2001).

Subgenus	**Section**	**Subsection**	**Taxon**	**Source**	**Database Acces. n°**
Nidificia			*M. molossus* Rchb. f.	HHG s.n.	
			M. nidifica Rchb. f.	HBG A3-G-400	
Polyantha	*Alaticaules*	*Alaticaules*	*M. cardiantha* Königer	HBG A3-G-352	
			M. echo Luer	HBG A3-G-26	
			M. garciae Luer	HBG 00-G-158	
			M. guttulata Rchb. f.	HBG A3-G-185	
			M. infracta Lindl.	HBG A3-G-24	
			M. melanoxantha Linden & Rchb.f.	HBG A3-G-65	
			M. pinocchio Luer & Andreetta	HBG 97-G-66	
	Alaticaules	*Coaetanae*	*M. mezae* Luer	HBG A3-G-354	
	Polyanthae	*Polyanthae*	*M. schlimii* Linden ex Lindl.	HBG A3-G-241	
			M. striatella Rchb. f.	HHG s.n.	
			M. oreas Luer & Vásquez	Manning 891127 (K) Kew Spirit 62102	AF262779
		Successiviflorae	*M. lata* Rchb. f.	HBG 02-G-80	
			M. pyxis Luer	HBG 99-G-47	
			M. cupularis Rchb. f.	HHG s.n.	
Pygmaeia	*Amaluzae*		*M. carmenensis* Luer & Malo	HBG 99-G-80	
			M. chimboensis Kraenzl.	TS s.n.	
			M. amaluzae Luer & *Malo*	Manning 941040 (K) Kew Spirit 60912	AF262799
			M. patula Luer & *Malo*	HBG 99-G-78	
			M. sanchezii Luer & Andreetta	HBG 00-G-280	
	Aphanes		*M. hoeijeri* Luer & Hirtz	HBG 98-G-16	
			M. aphanes Königer	J & L Orchids s.n.	AF262802
			M. aphanes Königer	TS s.n.	
			M. mentosa Luer	J & L Orchids s.n.	AF262777
	Pygmaeae		*M. erinacea* Rchb. f.	HBG 98-G-17	
	Zahlbrucknerae		*M. zahlbruckneri* Kraenzl.	HHG s.n.	
			M. vieirana Luer & R. Escobar	TS s.n.	
			M. naranjapatae Luer	TS s.n.	
Scabripes			*M. bicornis* Luer	TS s.n.	
Teagueia			*M. teaguei* Luer	TS s.n.	
Volvula			*M. caudivolvula* Kraenzl.	TS s.n.	

Table 8 Reference of source information for the sequenced outgroups taxa. The infrageneric classification follows Luer (1989 -1993). Accession numbers for sequences of the GenBank data base are listed in the last column (Pridgeon et al, 2001).

Genus	**Subgen.**	**Sect.**	**Subsect.**	**Series**	**Taxon**	**Source**	**Database Acces. n°**
Dracula	*Dracula*	*Dracula*	*Dracula*	*Parviflorae*	*D. astuta* (Rchb.f.) Luer	Hermans 2055 (K) Kew Spirit 24	AF262762
					D. houtteana (Rchb. f.) Luer	HBG 99-G-335	
				Dracula	*D. chimaera* (Rchb. f.) Luer	Hermans 1357 (K) Kew Spirit 58741	AF262966
		Cochliopsia			*D. cochliops* Luer & R.Escobar	Hermans 889 (K)	AF262767
	Sodiroa				*D. sodiroi* (Schltr.) Luer	Hermans 2836 (K) Kew Spirit 59696	AF262764
	Xenosia				*D. xenos* Luer & R.Escobar	TS	
Luerella					*L. pelecaniceps* (Luer) Braas	Hermans 3662 (K)	AF262810
Porroglossum	*Porroglossum*	*Porroglossum*			*P. amethystinum* (Rchb. f.) Garay	HBG A3-G-139	
		Tortae			*P. uxorium* Luer	Hermans 2213 (K) Kew Spirit 56966	AF262806
Trisetella		*Trisetella*	*Triaristella*		*T. gemmata* (Rchb. f.) Luer	Kew 1997-5447 (K)	AF262809
			Calvicaulis		*T. scobina* Luer	Kew 1997-5449 (K)	AF262808

2.2.2 Molecular methods

2.2.2.1 DNA isolation

Total DNA was extracted using the CTAB (hexadecyltrimethylammonium bromide) method of Dumolin et al. (1995), with slight modifications according to Rohwer & Rudolph (2005).

Leaf tissue (0.5 - 1.0 g fresh leaf tissue, approx. 0.3 g silica gel dried leaf material) was ground in liquid nitrogen in a mortar and a pestle to a fine powder. Leaf tissue was transferred into a 2 ml reaction tube containing 1 ml of the extraction buffer and 50 µl 1 M DTT and swirled to suspend the slurry. The suspension was incubated at 65° C for 10 minutes with occasional swirling (every two minutes). The suspension was cooled at room temperature for 10 min, 400 µl of dichloromethane were added and the suspension mixed gently but thoroughly to form an emulsion and centrifuged at 13 000 rpm (Biofuge Fresco, Heraeus n° 3325B, Sanyo, Bad Neuendorf, Germany) for 10 minutes at 4 °C to separate the phases. The aqueous (top) phase containing DNA was transferred into a 1.5 ml reaction tube, and 2/3 volume of - 20° C cold isopropanol was added. Tubes were spun for 10 minutes at 13 000 rpm (Heraeus n° 3325B) at 4 °C and the liquid poured off and drained upside down for 5 minutes or longer to evaporate the alcohol. To wash the precipitated DNA, 1 ml of 70% ethanol was added and mixed gently to remove the pellet from the bottom. Tubes were again spun for 10 minutes at 13 000 rpm (Heraeus n° 3325B) at 4 °C and the liquid poured off. The pellet was dried for approx. 60 minutes or longer on air, resuspended in 50 µl TE puffer and stored at 4°C.

1x Extraction Buffer (pH 7.5)

ATMAB (Alkyltrimethylammoniumbromide)	20 g
PVP 40 000 MW	10 g
EDTA (pH 8.0) 0.5 M	40 ml
Tris HCl (pH 8.0) 1 M	100 ml
NaCl 5 M	280 ml
H_2O dest.	add. to 1 l

1x TE Buffer (pH 8.0)

Tris HCl (pH 8.0) 10 mM	2 ml
1 mM EDTA	0.4 ml
H_2O dest.	add 200 ml

- Adjust to pH 8.0 (with concentrated HCl or NaOH) and sterilize.

2.2.2.2 Gel electrophoresis

The quality and quantity of DNA was checked on a 0.8% agarose gel (Gibco, Life Technology, Paisley, Scotland). For this, 2 µl DNA and 2 µl bromophenol loading buffer were mixed before loading the agarose gel. Gels were run in 0.5x TBE for ~30 min at 70 V in a mini sub cell (Bio-Rad, Germany) until the bromophenol blue marker dye migrated to the end of the 10 cm gel. Smart DNA ladder (Eurogentec, Searing, Belgium) was used as marker. Gels were stained with 0.5 mg/L ethidium bromide for approx. 15 min and photographed under UV light with a digital camera (Camedia C5050, Olympus Optical, Tokyo, Japan).

Bromophenol loading buffer:

• bromophenol	0,25 g
• H_2O	100 ml
• Mix 700 µl bromophenol with 300 µl glycerol.	

10x TBE (pH 8.4)

• 890 mM Tris HCl	108 g
• 890 mM boric acid	55 g
• 20 mM EDTA	40ml
• H_2O	add. to 1 l
• Adjust to pH 8.4	

2.2.2.3 Selection of molecular markers

The ITS region including the 5.8 S nrDNA gene and partial sequences of the 18 S and 26 S nrDNA genes were chosen as molecular marker. This marker is part of an operon being highly and tandemly repeated in the plant genome. This operon is composed of three ribosomal DNAs described above, an external transcribed spacer (ETS) and an intergenic region (IGS, see Fig. 14). The ITS region itself is flanking the 5.8S rDNA and consists of ITS I lying between the 18S and the 5.8S DNA and ITS II between the 5.8S gene and the 26S gene. In angiosperms, the whole internal transcribed spacer is less than 700 bp in length (Baldwin et al. 1995) exhibiting approx. 187 – 305 bp within the ITS I region, 163 – 164 bp in the 5.8S rDNA and approx. 187 – 252 bp in the ITS II region.

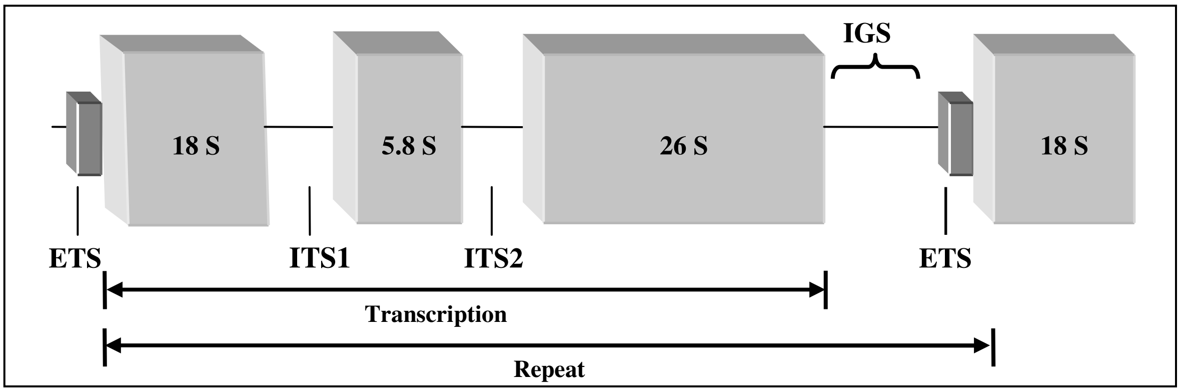

Fig. 14 Schematic diagram of rDNA repeat in plants. 18S, 5.8S, and 26S refer to the ribosomal rRNA genes. ITS1 and ITS2 are the two internal transcribed spacer regions. IGS is the intergenic spacer; ETS is the external transcribed spacer (according to SOLTIS and SOLTIS, 2000).

Several factors make the ITS region valuable for use in phylogenetic analyses on genus and species level (BALDWIN et al., 1995): 1) The high copy number of this gene family simplifies the amplification and sequencing of this region. 2) Whereas the ITS itself is highly variable, the flanking ribosomal genes are strongly conserved, which allows the use of universal primers designed by BALDWIN et al. (1995) or SUN et al. (1994) to investigate this highly variable region. 3) This nuclear multigene family undergoes concerted evolution described by BALDWIN et al. (1995) unifying the individual repeats. These properties turn the ITS region to one of the most important molecular markers for phylogenetic analysis promoting an accurate reconstruction of species relationships from sequencing. So far 66% of published molecular phylogenies are based on ITS sequences (ALVAREZ and WENDEL, 2002). However, non-homologous copies are occasionally present with point mutations and/ or insertion/ deletion events, causing small variation among the copies within a species (ALVAREZ and WENDEL, 2002). Nevertheless, this region is the most important marker used so far and was chosen in this study.

The internal transcribed spacer sequence variation has been previously used in phylogenetics studies of orchids to identify monophyletic groups at the genus level and below to provide a molecular basis for taxonomic reconstruction, particularly in *Cypripedioideae* (COX et al., 1997), *Orchidinae* (PRIDGEON et al., 1997; BATEMAN, PRIDGEON and CHASE, 1997), *Catasetinae* (PRIDGEON and CHASE, 1998), *Diseae* (DOUZERY et al., 1999), *Pogoniinae* (CAMERON and CHASE, 1999), *Lycastinae* (RYAN et al., 2000), *Laeliinae* (VAN DEN BERG et al., 2000), *Maxillarieae* (WHITTEN, WILLIAMS, and CHASE, 2000), *Coelogyninae* (GRAVENDEL et al., 2001), and *Pleurothallidinae* (PRIDGEON, SOLANO and CHASE, 2001).

2.2.2.4 Amplification

ITS amplification: The ITS1 - 5.8 S - ITS2 rDNA region was amplified using the following primer pairs described by SUN et al. (1994):

- ITS 18 (5´- GTC CAC TGA ACC TTA TCA TTT AGA GG –3´)
- ITS 26 (5´- GCC GTT ACT AAG GGA ATC CTT GTT AG –3´)

Amplifications were carried out in a 10 µl reaction volume containing ≈ 50 ng template DNA, 1x Taq-buffer, 20 mM $MgCl_2$, 20µM dNTPs and 2µM of each primer, 0.25 u of Taq DNA polymerase (Genecraft, Germany), and in addition 10% DMSO to dissolve secondary structures.

A BIOMETRA Tgradient DNA thermal cycler (Germany) was used with the following PCR profile: an initial denaturation step for 4 min at 95° C followed by 38 thermal cycles of 95° C for 30 sec denaturation, 50° C for 30 sec annealing and 72° C for 4 min elongation (THIEDE, J. submitted). As closing extension step a final incubation for 6 min at 72° C was carried out. The quality and quantity of PCR samples was checked on a 0.8% agarose gel following the method described in Gel electrophoresis (pp. 60 - 61). The amplified DNA was purified by differential filtration using Millipore columns (Ultrafree-MC Filter Unit, 30 000 NMWL, Millipore, Bedford, Massachusetts) following manufacturer's instructions.

2.2.2.5 Sequencing

Cycle sequencing was carried out directly with the purified PCR product using the ABI Prism Big Dye Terminator Cycle Sequencing Ready Reaction kit (Applied Biosystems, Foster City, California, USA). A reaction volume of 20µl included 0.6 mM primer, 5.7 µl of sequence dilution buffer, 2.3 µl reaction mix and 1 – 6 µl PCR product. Cycle sequencing conditions were as follows: 30 cycles of 50 sec. denaturation (96°C), 15 sec. annealing (50°C), and 4 min. elongation (60°C) using a Tgradient thermal cycler (BIOMETRA, Germany).

Sequencing reactions were purified by ethanol precipitation. For each reaction a 1.5 ml centrifuge tube was prepared by adding 80 µl 0.3 M Na acetate (pH 5.2) and 300 µl 96% ethanol. The entire 20µl contents of reaction tubes were transferred to the microcentrifuge tubes containing ethanol solutions. The solution was mixed and incubated at room temperature for 20 min. After incubation, the solution was centrifuged in a microcentrifuge (Biofuge Fresco, Heraeus n° 3325B, Sanyo, Bad Neuendorf, Germany) at 13 000 rpm and 4° C for 60 min. All liquid was carefully removed. The pellet was washed by adding 100 µl 70% ethanol and spinned again under the same conditions (13 000 rpm and 4° C for 60 min). The liquid was removed and the pellet was dried in a heat block at 65 °C for 10 min.

The purified sequence reaction was run on an ABI Prism 377 automated sequencer (PE-Applied Biosystems) in the Universitäts Klinikum Eppendorf (UKE) "Institut für Zellbiochemie und klinische Neurobiologie", Hamburg, Germany.

Sequence alignment: Electropherograms were assembled and edited with Sequencher 3.1 software (GeneCodes, Ann Arbor, Michigan, USA). The ITS sequences were aligned with subsequent manual editing using the sequence editing program Sequencher.

2.3 Phylogenetic analysis

2.3.1 Morphological data set

Parsimony analysis was performed using PAUP* 4.0b10 (SWOFFORD, 2002). All morphological characters were assessed as independent, unordered, and equally weighted (Fitch parsimony; FITCH, 1971). Unknown characters were coded as **?**, and not applicable characters were coded as **-**. A heuristic search was conducted with 100 random addition replicates, rearrangements limited to 100 000 per replicate, tree bisection-reconnection swapping (TBR) with MULPARS on (i.e., saving all shortest trees). Five hundred bootstrap replicates were performed with TBR and MulTrees on, MaxTrees set to 1000, simple addition and up to 1 000 000 rearrangements per replicate.

2.3.2 Molecular data set

2.3.2.1 Parsimony

Parsimony analysis was performed using PAUP* 4.0b10 (SWOFFORD, 2002). All molecular characters were assessed as independent, unordered, and equally weighted (Fitch parsimony; FITCH, 1971). Indels were coded as missing data. A heuristic search was conducted with 1 000 random addition replicates, rearrangements limited to 10 000 per replicate, tree bisection-reconnection swapping (TBR) with MULPARS on (i.e., saving all shortest trees). Because of an inadequate number of informative characters and the high number of taxa, heuristic searches could not be completed. A first alternative strategy was employed to explore tree space. One thousand random addition sequence replicates were conducted using tree bisection-reconnection (TBR) branch swapping, with MULTREEs in effect, but holding only one tree per step and saving no more than 10 trees per replicate to minimize swapping time on suboptimal trees. A second round of TBR branch swapping was performed on trees collected in the first analysis saving up to 10 000 trees. Once this limit was reached, these trees were swapped to completion. Successive weighting (SW) (FARRIS, 1969) of resulting trees was carried out according to the rescaled consistency index using the maximum value (best fit) criterion and a base weight of 1.0. The SW strategy is a useful tool employed to reduce the global effect of highly homoplasious base positions on the resulting topologies (WENZEL, 1997; LLEDÓ et al., 1998). SW was followed by a heuristic search with 1000 random sequence addition replicates, TBR branch swapping, and again saving no more than 10 trees per replicate. All trees from these 1 000 replicates were then swapped to completion, after which another round of weighting was implemented. This process was repeated until the same tree length/rescaled consistency index was obtained twice in succession. Internal clade support was evaluated both with and without weighting with 100 bootstrap replicates (FELSENSTEIN, 1985), using simple sequence addition and TBR branch swapping. No more than 15 trees were saved in each replicate and only groups that appeared in >50% of the trees were retained (bootstrap procedure).

2.3.2.2 Bayesian inference

Bayesian analyses (BAYES, 1763) were performed using MrBayes 3.0b4 (RONQUIST and HUELSENBECK, 2003). Calculations of likelihood were based on a general time reversible nucleotide substitution model (GTR; LANAVE et al., 1984; TAVARÉ, 1986; RODRÍGUEZ et al., 1990). The ML parameters in MrBayes were set as follows: “lset nst=6”, and “rates=invigamma” (site specific rate variation such that some sites are invariant and the rates of others are drawn from the gamma distribution). The Markov chain Monte Carlo process was set so that four chains ran simultaneously for 1 000 000 generations, with tress being sampled every 100 generations for a total of 10 000 trees in the initial sample. The \`burn - in´ time was estimated from the plot of likelihoods generated using the \`sump´ command in MrBayes. Majority rule consensus trees were generated by importing the sets of individual trees into PAUP* 4.0b10 (SWOFFORD, 2002), excluding trees generated during the burn-in time. Each analysis was repeated five times to check that runs converged on the same topology and 95% confidence interval of likelihood scores. HILLIS and BULL (1993) and SUZUKI et al. (2002) showed that bootstrap analyses are generally conservative, while SUZUKI et al. (2002) found that the posterior probabilities in Bayesian analysis can be excessively bounteous. For the purpose of our discussion in the case of Bayesian, clade credibility values for good support was estimated as ≥ 90% clade credibility value and poor support below 70% clade credibility value. Trees were edited using the program Treeview 1.6.6. All trees were rooted with *Porroglossum amethystinum* as outgroup taxon.

2.3.3 Combined data set

Congruence between taxonomically equivalent ITS and morphological data sets was evaluated by comparing tree topologies. This approach enabled clades in strongly supported agreement or disagreement to be identified before data sets were combined. An incongruence length difference (ILD) test (FARRIS et al., 1995) was also conducted to investigate character congruence between taxonomically equivalent ITS and morphologial partitions. This was implemented as the "partition-homogeneity test" in PAUP* 4.0b10 (SWOFFORD, 2002). All parsimony-uninformative characters were removed from each data set prior to conducting the partition-homogeneity test (WIENS and HOLLINGSWORTH, 2000). A thousand replicates were analyzed, with each repartitioned data set subject to a heuristic search of one hundred random stepwise addition replicates and TBR branch swapping.

2.3.3.1 Parsimony

The data were arranged in two major partitions, ITS sequences and morphology. A heuristic search was conducted on the data in combination with 100 random addition replicates, rearrangements limited to 100 000 per replicate, tree bisection-reconnection swapping (TBR) with MULPARS on (i.e., saving all shortest trees). Five hundred bootstrap replicates were performed with TBR and MulTrees on, MaxTrees set to 1000, simple addition and up to 1 000 000 rearrangements per replicate.

2.3.3.2 Character-state reconstruction

The distribution of each morphological character state on several randomly selected most parsimonious trees was investigated by unambiguous character state changes using MacClade version 4.0 (MADDISON and MADDISON, 2000).

2.4 Biogeographical analysis

Geographical distributions of species of *Masdevallia* were obtained from the monograph of the genus *Masdevallia* by Luer (2000-2004). Distribution maps were created using ArcView GIS, version 3.0 (ESRI, 1992-1997). Analysis of ITS sequences was then used to frame a phylogenetic hypothesis for comparasion with species distribution. The altitudinal range of each species was investigated by unambiguous character state changes using MacClade version 4.0 (MADDISON and MADDISON, 2000).

3

RESULTS

3.1 Morphological analysis

3.1.1 Description of the analyzed morphological characters

The morphological characters included or excluded from the phylogenetical analyses are described below. Enclosed in parenthesis is the character number (indicated in Table 6, chapter 2.1.5, p. 58-59).

1) Growth habit

Most species are epiphytes [1(2)], some species may also grow as terrestrial plants [1(1)] (e.g. *M. veitchiana*, *M. coccinea*) and a few may also grow terrestrial as well as epiphytic (e.g. *M. persiteria*).

2) Rhizome

The rhizome, or primary stem, is usually short so that a densely caespitose habit is formed [2(1)], even when the rhizome is a little longer and ascending. In a few species, the rhizome is significantly elongated (e.g. *M. paivaeana*, and *M. scandens*) [2(2)].

3) Ramicaul

All the species of *Masdevallia* are characterized by aerial leaf-bearing stems produced successively from a stout rhizome. The stems have several nodes and internodes (homoblastic); each node bears a single, tubular sheath or bract. Ramicauls are unifoliate. A diagram of all taxa examined in this study is shown in Fig. 15. The gap present in ramicaul length is not considered to be distinct enough to recognize the proposed character states and was therefore omitted.

4-10) Leaves

Leaf shape (character 4) varies considerably within the genus *Masdevallia*. Most species show elliptical leaves [4(2)], while obovate [4(3)] and oblong [4(1)] leaves are present in a few species. The apices or tips (character 5) are acute [5(1)] or obtuse to rounded [5(2)] and shallowly notched with a mucro in the sinus. The base of leaves [6(1-2)] is mostly cuneate into the (sub)petiole [7(1-2)]. Leaves of *Masdevallia* are dorsiventral, the petiole is merely the constricted base of the lamina.

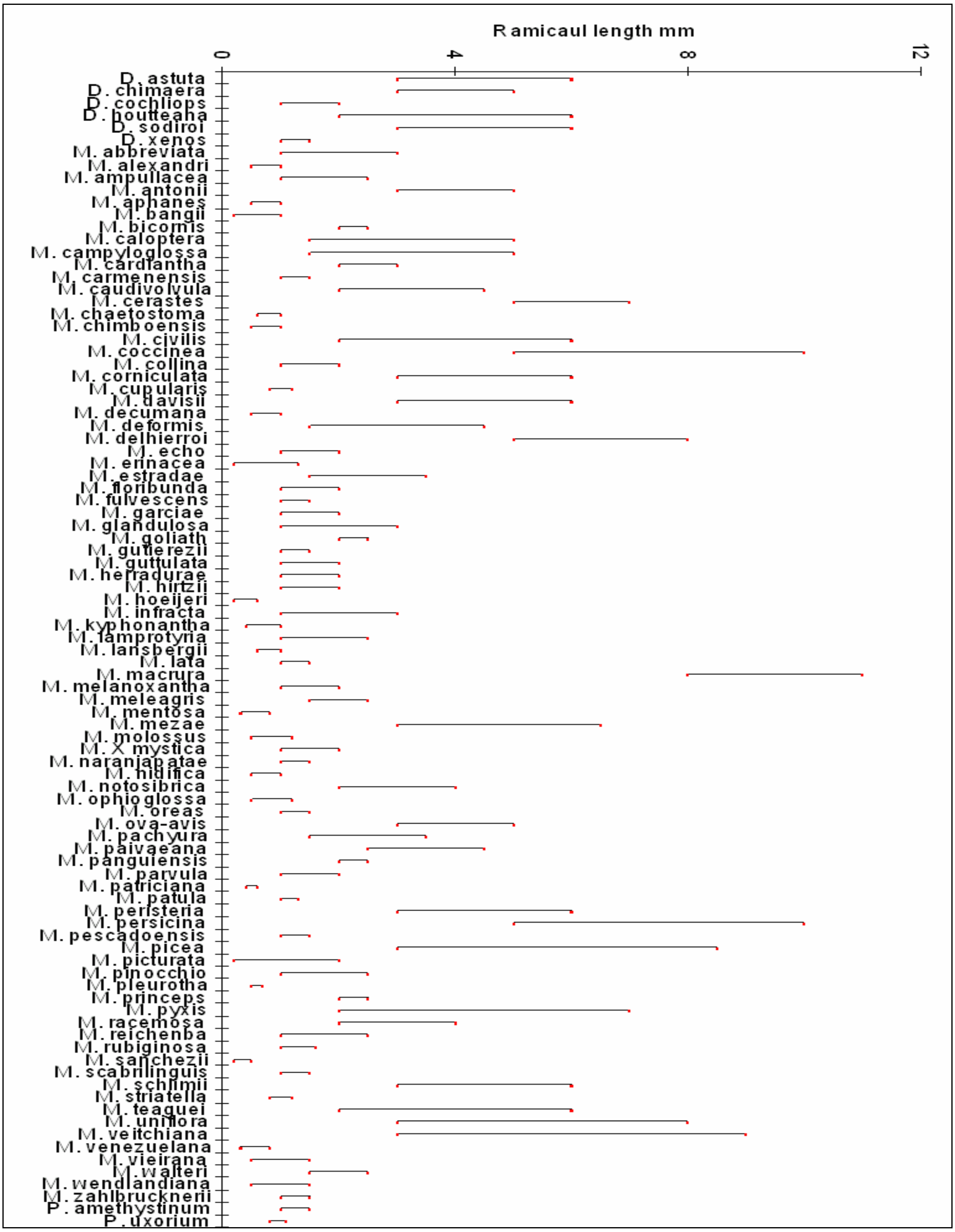

Fig. 15 Vegetative morphology: ramicaul length (character 3).

The leaf consistency is coriaceous [8(1)], from relatively thin [8(2)] to very thick and fleshy, or extremely rigid [8(3)]. The texture of dried leaves varies considerably within subtribe *Pleurothallidinae* and the genus *Masdevallia* from thin papery to decidedly leathery; this character could not be divided unambiguously into discrete, non-overlapping states as recommended by PIMENTEL & RIGGINS (1987) and was therefore omitted. Leaf size (characters 9-10) varies considerably within the genus *Masdevallia*. A diagram of the length of leaves for all taxa examined in this study is shown in Fig. 16A. The gap presented in the leaves length is considered to be not distinct enough to recognize states in this character; the same occurs with the leaf width (Fig. 16B) and both were therefore omitted.

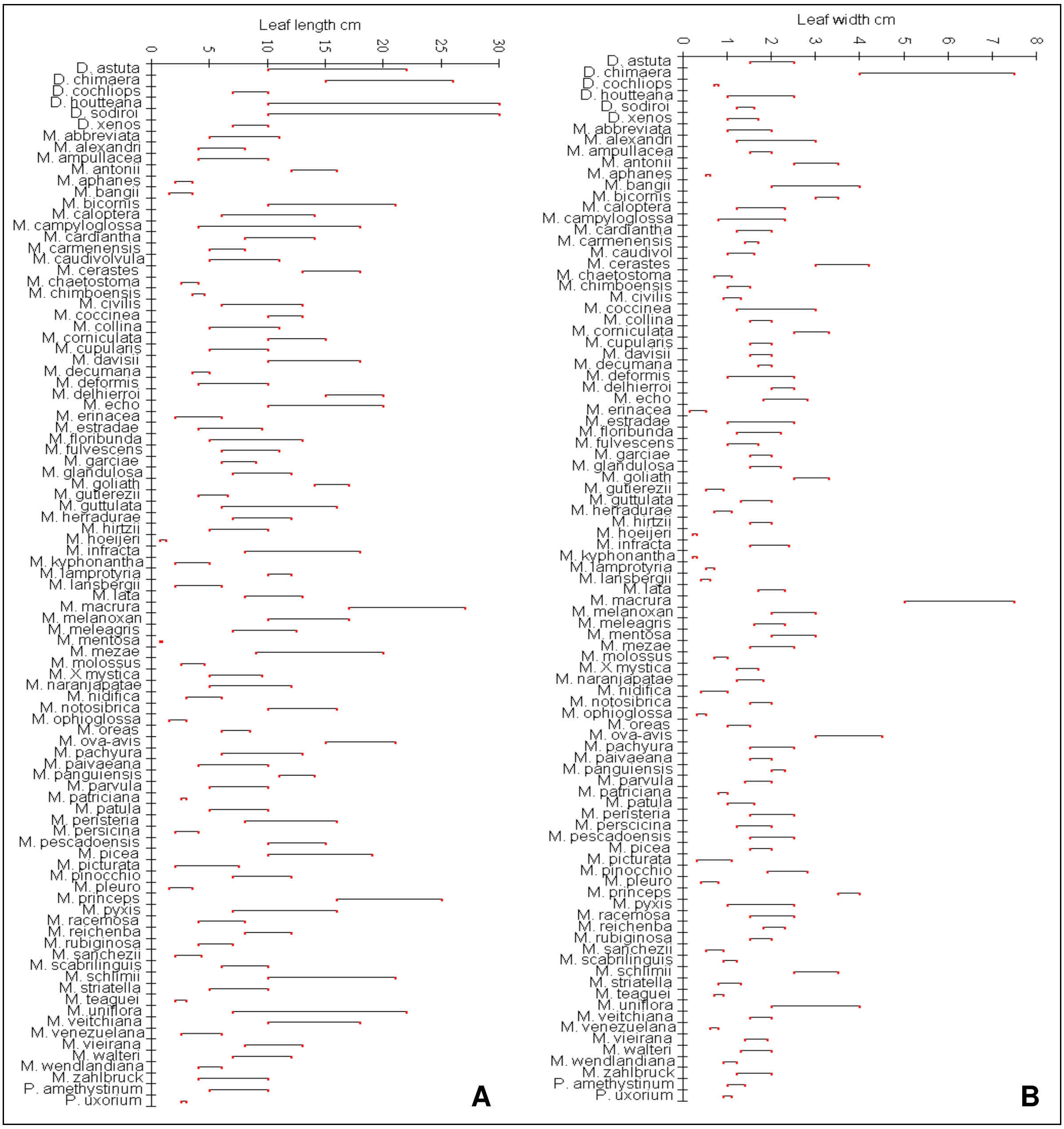

Fig. 16 Vegetative morphology: leaf length (a)and leaf width (b) (characters 9 and 10).

11-15) Inflorescence

Single-flowers [11(1)] characterize subgenera *Cucullatia*, *Fissia*, *Nidificia*, *Volvula*, and *Masdevallia* sections *Masdevallia*, *Coriaceae* and *Triotosiphon* (LUER, 2001). Subgenera *Masdevallia* sections *Minutae* and *Reichenbachianae*, *Polyantha* section *Polyanthae* and *Pygmaeia* sections *Aphanes* and *Pygmaeae* exhibit both: solitary flowers and/or racemose inflorescences. The inflorescences of all species emerge laterally with an annulus usually near or at the base of the ramicauls [12(1)], or occasionally higher, near the middle [12(2)]. Distantly flowered racemes [13(2)] characterize subgenus *Amanda* (LUER, 2001). Congested racemes are present in most subgenera/sections [13(1)]. The following character states were recognized for the number of flowers in the inflorescence: few flowered raceme (flower number <4) [14(1)] and many – flowered raceme (flower number ≥4) [14(2)]. Flowers opening either successively [15(1)] or simultaneously [15(2)] have been used to characterize some infrageneric taxa. In inflorescences with more than 4 flowers, flowers are considered to be opening simultaneously when all flowers are expanded before the first starts to wither. Erect peduncles [16(1)] characterize most species of *Masdevallia*. Ascending or horizontal to descending peduncles [16(2)] characterize subgenus *Pygmaeia* sections *Pygmaeae* and *Zahlbrucknerae* (LUER, 2000).

Peduncles with more than two internodes [17(1)] can be considered as a reduction of a raceme. For the purpose of this work, peduncles with more than two internodes are considered only when there is not an emergence of a pedicel. Peduncles shorter than [18(2)] or of similar length as the leaves [18(1)], have not been used for infrageneric diagnosis. The gap present in Fig. 17 is considered to be distinct enough to recognize two character states: peduncle longer than the leaves [18(1)] and peduncle shorter than or as long as the leaves [18(2)].

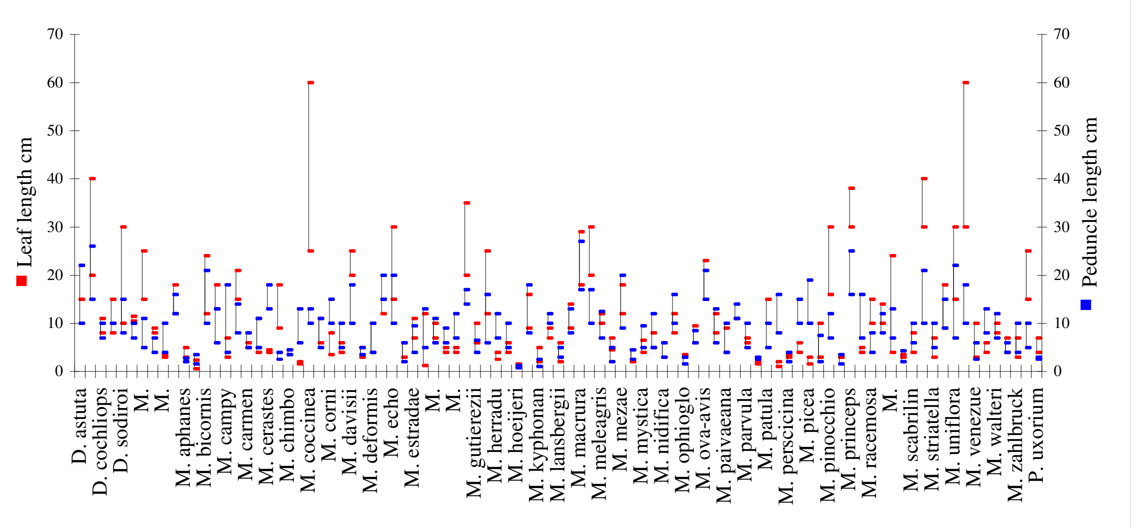

Fig. 17 Correlation between leaf length and peduncle length (character 18)

Peduncles triquetrous in cross section characterize subgenus *Polyantha* section *Alaticaules* (LUER, 2000). However, individuals of some species (e.g. *M. garciae*, *M. infracta*, *M. sprucei*) occasionally produce terete peduncles (character 19). Scabrous peduncles (character 20) are present in *M. bicornis* (subgenus *Scabripes*).

The floral bract (character 21) is an important character for the delimitation of some infrageneric taxa (REICHENBACH, 1888; LUER, 1986-2003). Cucullate floral bracts [21(3)] characterize subgenus *Cucullatia*, inflated floral bracts [21(2)] are commonly present in species of subgenus *Amanda*, and tubular floral bracts [21(1)] characterize the remaining subgenera/sections. The types of floral bracts are shown in Fig. 18.

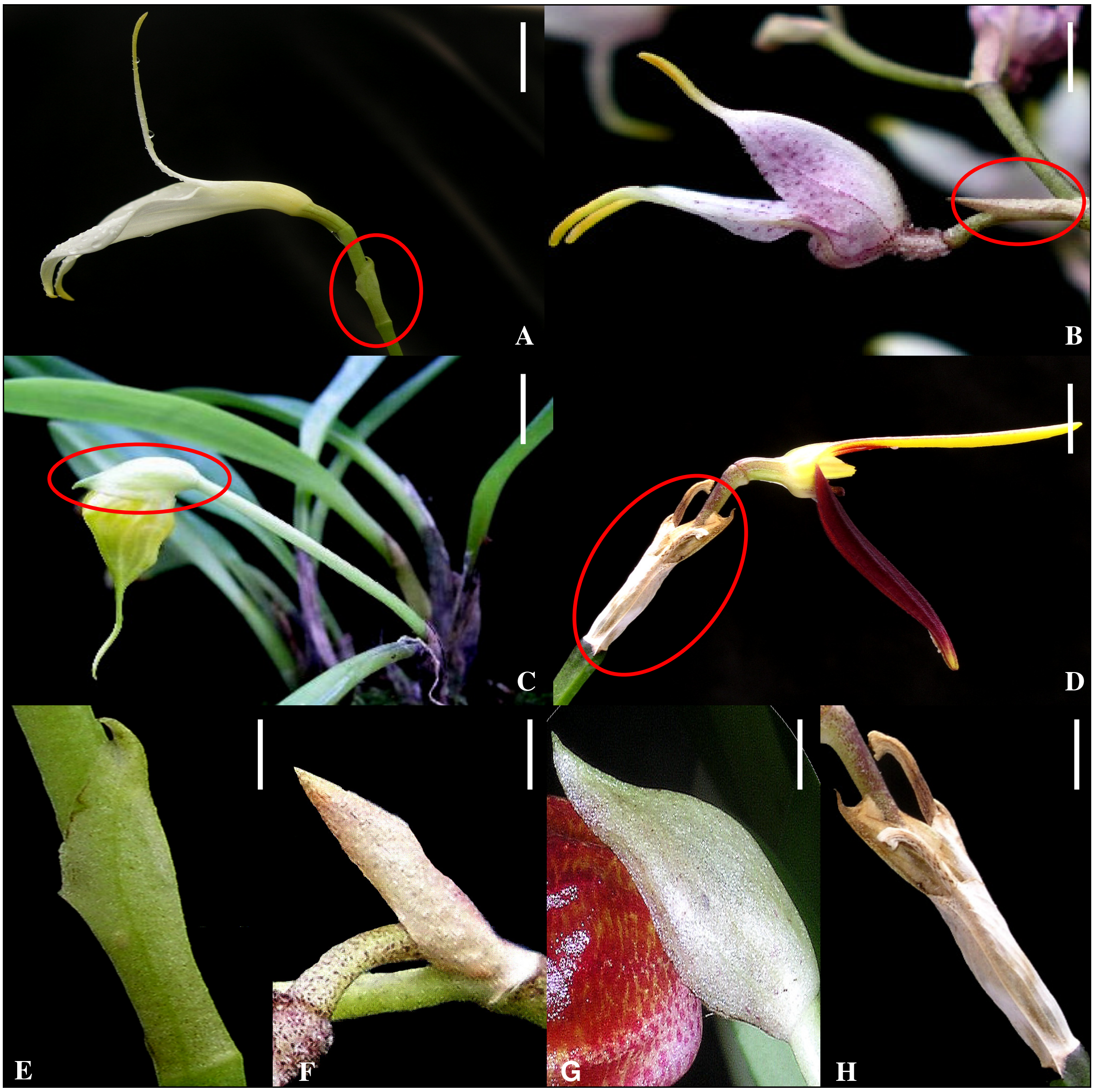

Fig. 18 Types of floral bracts: (A, E) tubular in *M. coccinea* Lind. ex Lindl, (B-F) inflated in *M. caloptera* Rchb. f., (C, G) cucullate in *M. delhierroi* Luer & Hirtz, (D, H) imbricate in *M. melanoxantha* Lind. & Rchb. f. Scale bars= 1cm (A, C, D); 5 mm (B); 2mm (E, F, G, H).

Pedicels thicker and longer than the peduncles (character 23) characterize species of the subgenus *Masdevallia* section *Coriaceae* according to LUER (1986b-2003).

24-25) Ovary

In many species the ovary is smooth, the ribs being only barely visible externally, or as shallow grooves between valves. Species with the ribs manifested by crests or some other external features such as papillae are characteristic for subgenera *Amanda*, *Fissia* and *Pygmaeia*, (characters 24 and 25) (Fig. 19) LUER (2000).

Fig. 19 Ovary: (A) ovary carinate in *M. echo* Luer, (B-C) ovary with undulating crest in *M. ventricosa* Schltr. and *M. caloptera* Rchb. f., (D) ovary scabrous in *M. erinacea* Rchb. f. Scale bars= 1.5 mm (A); 1 mm (B, C, D).

26-40) Sepals

The dorsal sepal free from the laterals [26(1)] characterizes subgenera *Fissia* and *Meleagris*. The lateral sepals free at the basis, only connate to the column foot (character 27), characterizes subgenus *Meleagris* (e.g. *M. alexandri*). The grade of connation between the sepals is variable among species of *Masdevallia*, although two character states are clearly delimited: connation between dorsal and lateral sepals similar to the connation between lateral sepals [28(1)], and connation between dorsal and lateral sepals different from the connation between lateral sepals [28(2)]. Sepals barely connate at the base to form a shallow cup characterize subgenus *Amanda* (LUER, 2003); sepals deeply connate forming a cylindrical tube the subsection *Coccinea* of section *Masdevallia*. The shape of connation has not been discussed previously in a phylogenetic context; however this feature could be related to the pollinator. In the absence of morphometrical analysis, the following character states were designed: sepals connate forming a tube [29(1)], sepals connate forming a cup [29(2)], and sepals connate forming a flat, widely spread flower [29(3)] (Fig. 20). Sepals connate forming a tube constricted above the middle characterizes subgenus *Masdevallia* section *Saltatrices* (LUER, 1986b-2003) (Fig. 20D); two states were designed: sepals connate forming a tube constricted above the middle [30(1)] and sepals connate forming a tube not constricted above the middle [30(2)].

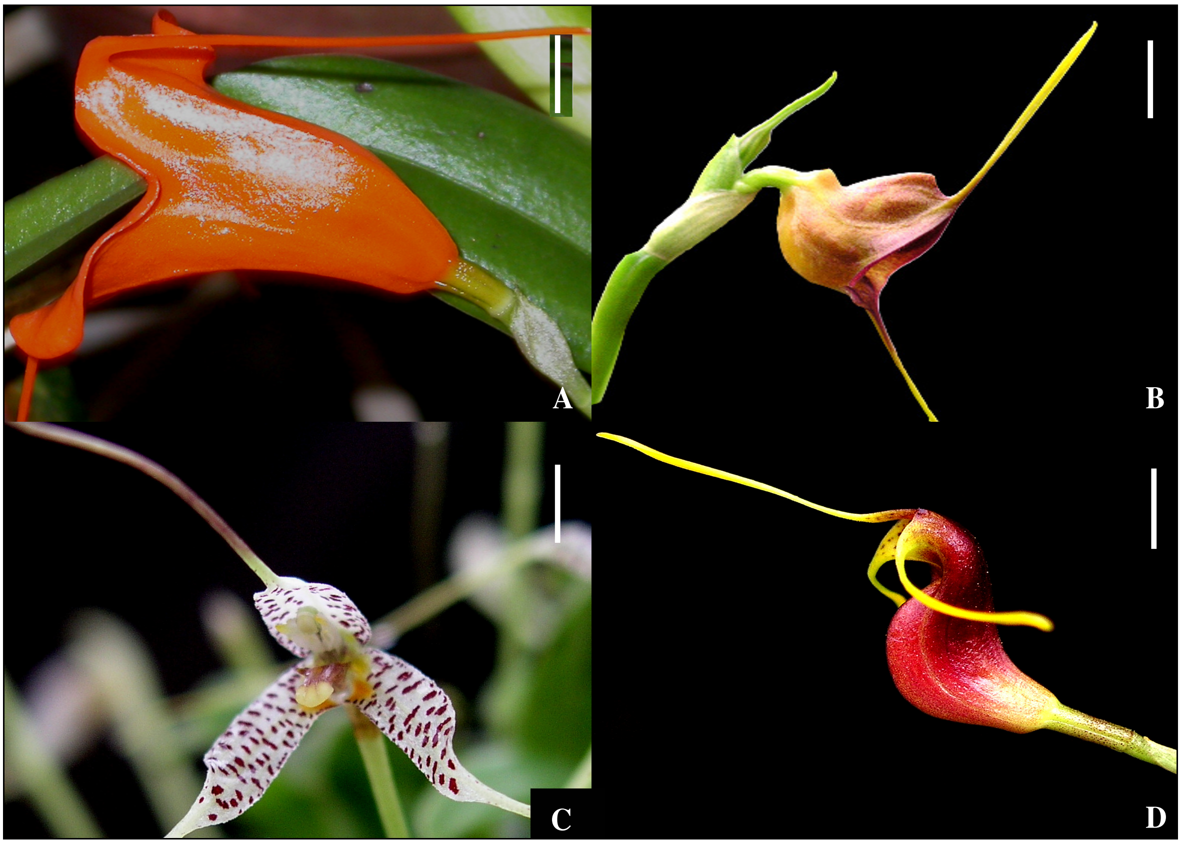

Fig. 20 Connation of sepals: (A) connate into a tube in *M. hirtzii* Luer & Andreetta, (B) connate into a cup in *M. echo* Luer, (C) connate to form a flat, widely spreading flower in *M. picturata* Rchb. f., (D) connate into a tube constricted above the middle in *M. saltatrix* Rchb. f. Scale bars= 4 mm (A, C); 5mm (D); (B) 1.5 cm.

Sepaline arcuate tubes (character 31) are present in a few species (e.g. *M. coccinea*, *M. veitchiana*, *M. ophioglossa*).

The gap present in the degree of connation between dorsal and lateral sepals (character 32) is considered to be distinct enough to recognize three character states: dorsal sepal connate with the lateral sepals above the middle [32(1)], dorsal sepal connate with the lateral sepals below or at the middle [32(2)], and dorsal sepal connate with the lateral sepals for the total length [32(3)] (Fig. 21A). For the connation among lateral sepals (character 33), three character states were assigned: connate into a synsepal or lamina (above the middle), connate at the middle, and connate below the middle. The gap shown in Fig. 21b is considered to be distinct enough to recognize the previously mentioned character states.

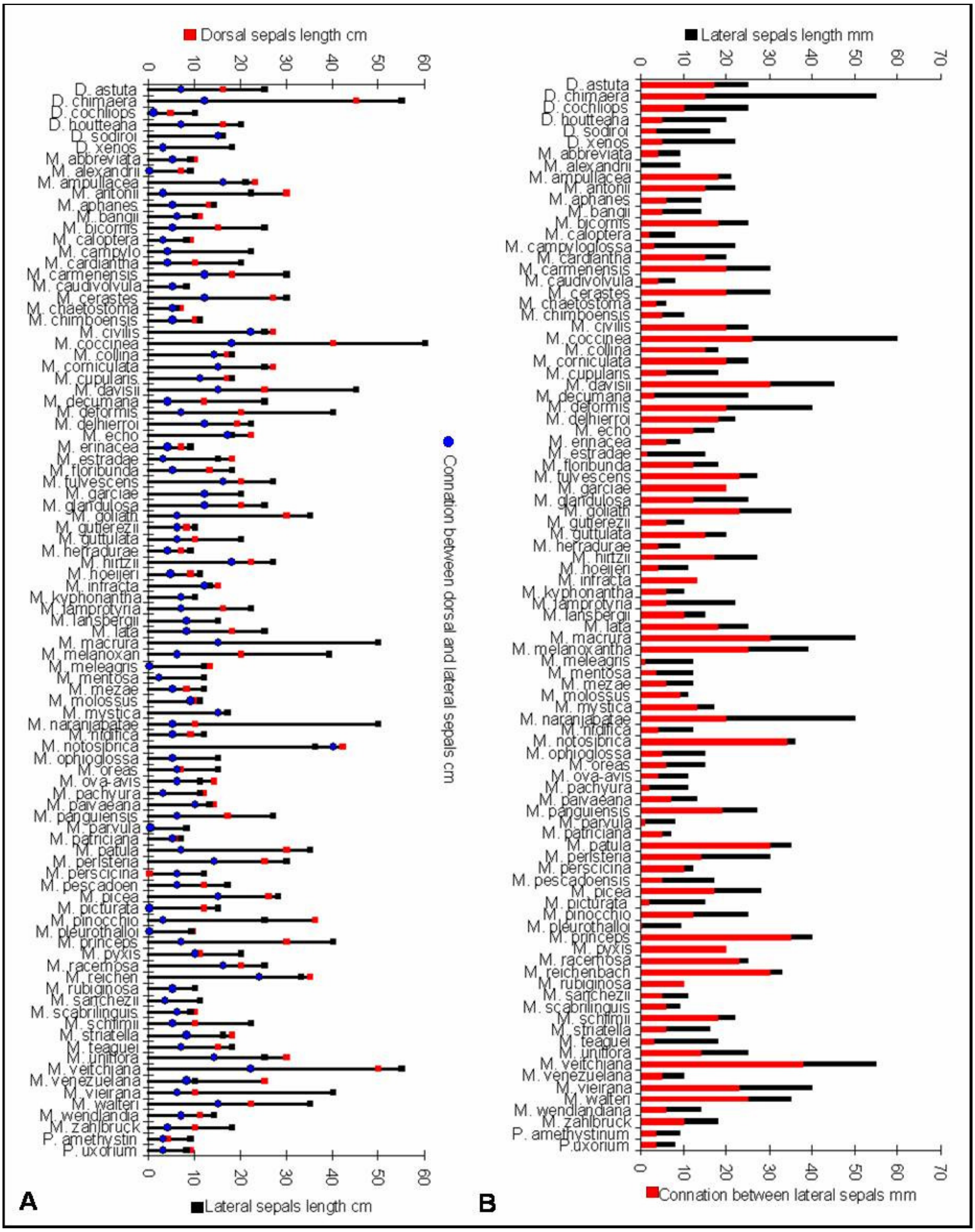

Fig. 21 Connation of sepals: (A) connation of the dorsal sepal with lateral sepals, (B) connation of lateral sepals (characters 32 and 33).

The lateral sepals connate to form a broad mentum (character 34) characterize some species such as *M. patriciana* and *M. abbreviata*, etc. (Fig. 22).

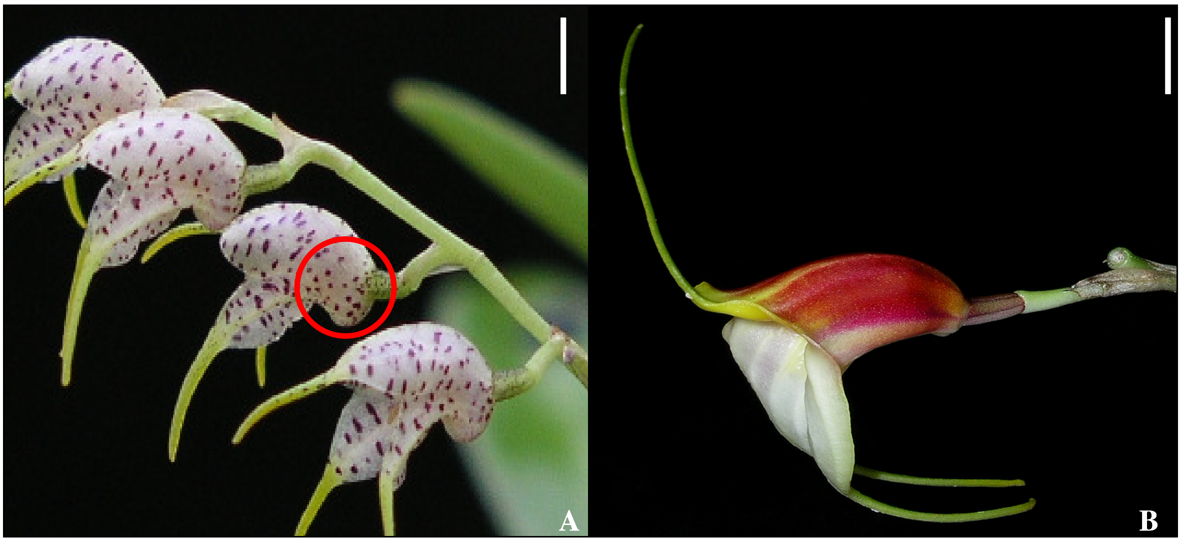

Fig. 22 Connation of lateral sepals: (A) lateral sepals connate forming a mentum with the column-foot in *M. abbreviata* Rchb. f., (B) lateral sepals connate without the formation of a mentum in *M. reichenbachiana* Endres ex Rchb. f. Scale bars= 5.5 mm (A); 7.5 mm (B).

Four character states were assigned for the shape of dorsal and lateral sepals (characters 35 and 45). About a 45% of the analyzed species displayed obovate dorsal and lateral sepals, followed of ovate sepals (~ 30%), oblong sepals (~ 20%) and elliptical sepals (~ 3%). Few species showed more than one character state for the shape of dorsal and lateral sepals (e.g. *M. infracta*, *M. hirtzii*, *M. herradurae*).

The surface of the dorsal and lateral sepals (characters 36 and 46) is mainly smooth, some species showed pubescent (e. g. *M. ampullacea*), verrucose (e.g. *M. peristeria*), echinate (e.g. *M erinacea*), glandulous (e.g. *M. glandulosa*), and papillose sepals (e.g. *M. veitchiana*) (Fig. 23).

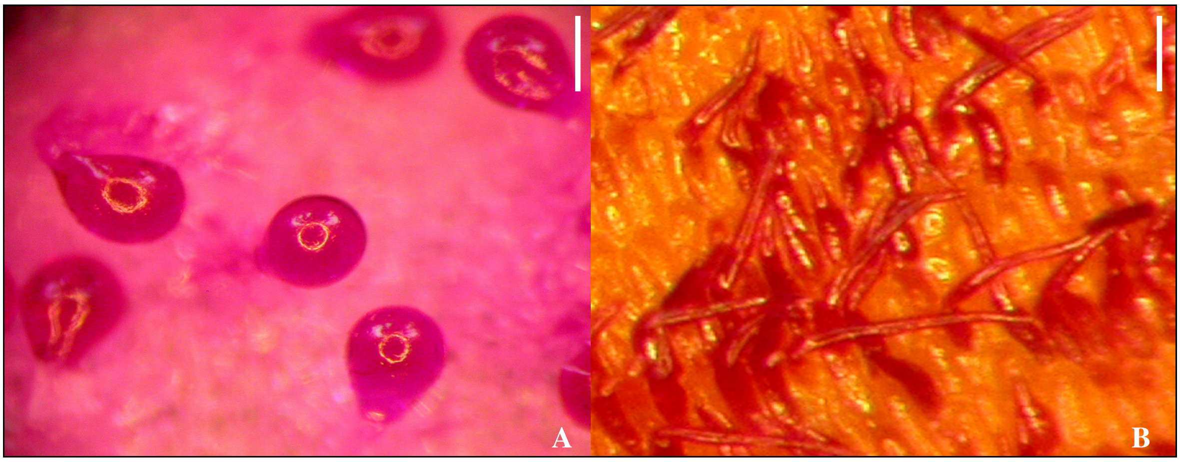

Fig. 23 Vestiture of sepals: (A) glandulous in *M. glandulosa* Königer, (B) pubescent in *M. echo* Luer. Scale bars= 0.5 mm (A, B).

Coriaceous (characters 37 and 47), very thick and fleshy sepals characterize species of sections *Coriaceae*, *Polyanthae*, and some species of the subgenus *Pygmaeia*; membranous sepals characterize most species of the subgenera *Amanda*, *Nidificia*, and *Meleagris*. Two character states were recognized: dorsal or lateral sepal membranous and dorsal or lateral sepal coriaceous.

The margin of the sepals (characters 38 and 48) is mostly entire; species of subgenera *Amanda* and *Nidificia* presented sepals with erose or dentate to serrate margins. *Masdevallia carmenensis* showed sepals with ciliate margin. The sepal apex (characters 39 and 49) varies from acute to obtuse, rounded and attenuate. The free portion of the apex produced into tails (characters 40 and 50) has been used to define some groups, e.g. tailless flowers characterize subgenus *Pygmaeia* section *Aphanes* (LUER, 2000) (Fig. 24).

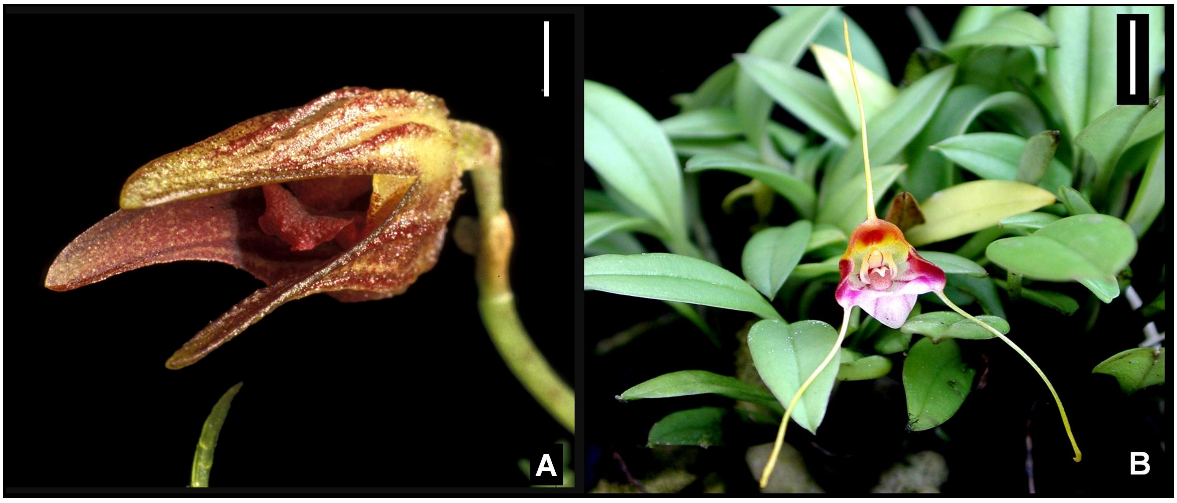

Fig. 24 Apex of sepals: (A) sepals tailless in *M. aphanes* Königer (photo courtesy of T. Sijm), (B) sepals with tails in *M. patriciana* Luer. Scale bars= 5 mm (A, B).

The exposure of sepaline tails (characters 41 and 51) has not been used to define infrageneric groups. In order to evaluate this character, three character states were designed: sepaline tails antrorse, sepaline tails retrorse, and sepaline tails erect. The sepaline tails of lateral sepals (character 52) are in some species approximate (with the angle between them acute), but in other instances they are divergent (with the angle between them obtuse). Sepaline tails are clavate (characters 42 and 53) in a few species (e.g. *M. erinacea*). Two states were designed: sepaline tails clavate and sepaline tails not clavate. The length of sepaline tails (characters 43 and 54) was not previously discussed in a phylogenetic context, however, species of e.g. subgenus *Polyantha* show short to very short sepaline tails, and species of e.g. subgenus *Masdevallia* section *Durae* show very long sepaline tails. The gap present in the lengths of dorsal (Fig. 25a) and lateral sepaline tails (Fig. 25b) is considered to be distinct enough to define three character states: (1) less than half as long as the lamina, (2) more than half as long to as long as the lamina, and (3) longer than lamina.

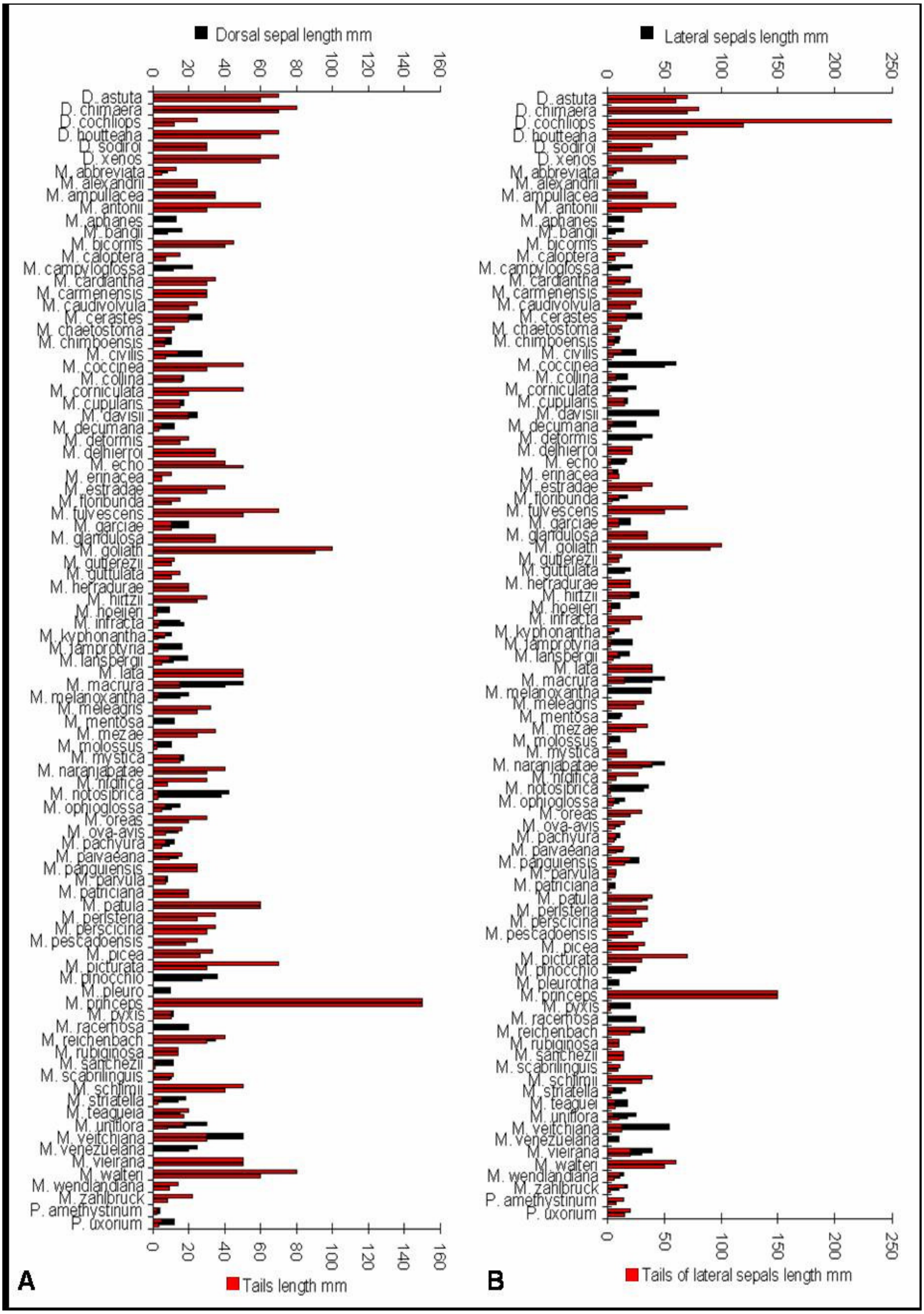

Fig. 25 Tails of sepals: (A) comparison between the length of the dorsal sepals and the length of the tails from the dorsal sepals, (B) comparison between the length of the lateral sepals and the length of the tails of lateral dorsal sepals (characters 43 and 54).

Sepaline tails of the dorsal sepal (character 44) (Fig. 26) can be longer, shorter or of similar length as the sepaline tails of the lateral sepals. In order to evaluate this character, three character states were postulated: longer than the tails of the lateral sepals, similar to the tails of the lateral sepals, and shorter than the tails of the lateral sepals.

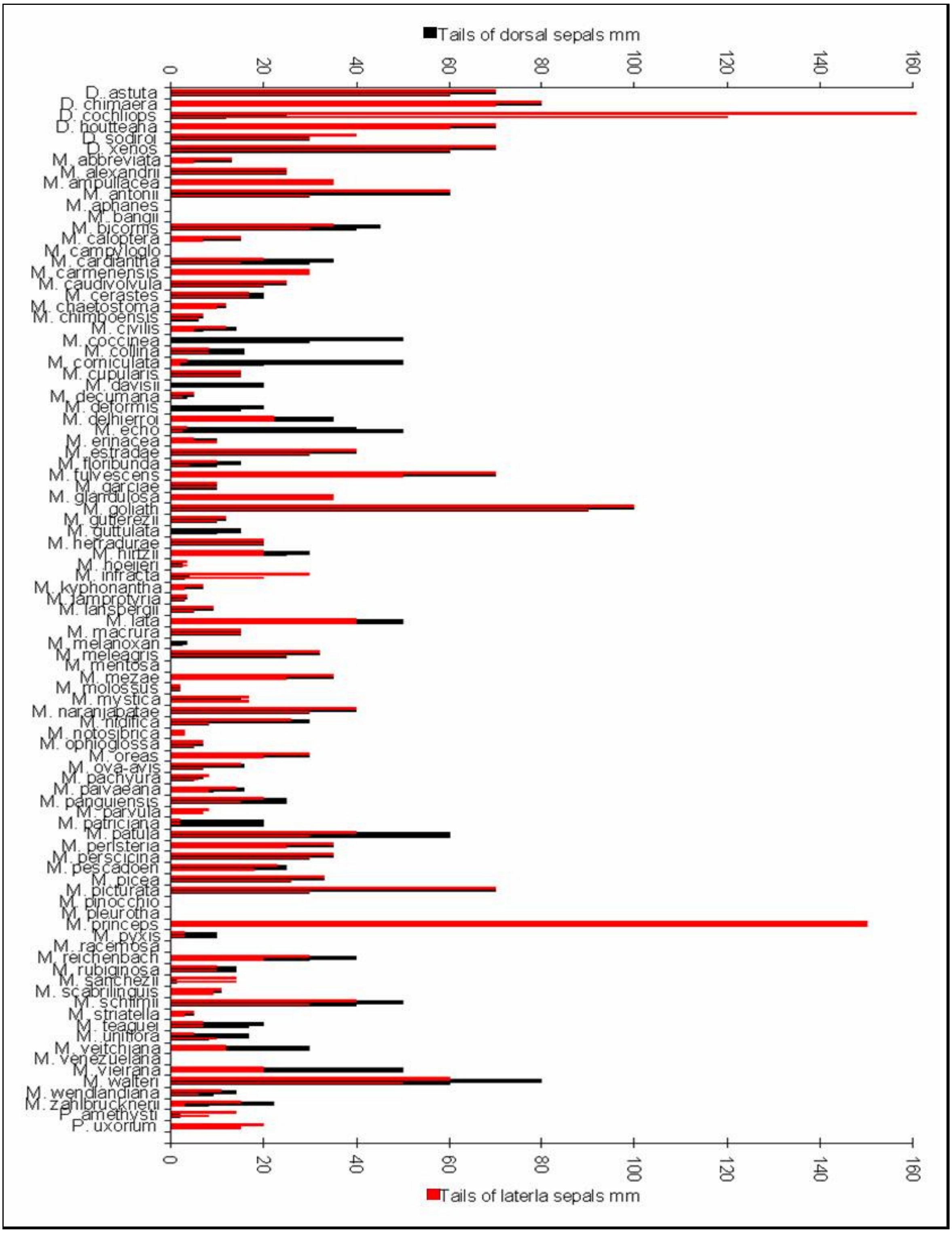

Fig. 26 Comparison between the tails of the dorsal and lateral sepals (character 44).

55-70) Petals

Petals and lip completely hidden within the sepaline tube (character 55) have been used to define subgenus *Masdevallia* section *Masdevallia* subsection *Caudatae* (LUER, 1986b-2000). The shape of the petals (character 56) varies considerably. Four discrete, non overlapping character states are recognizable: oblong, elliptic, ovate, and obovate. Petals (character 57) with denticulate to serrate margin characterize species of subgenus *Amanda* (LUER, 2000), while erose margins are present in *M. sanchezii*, *M. molossus*, and *M. ampullacea*. Three character states were designed: entire, dentate to serrate, and erose. Some species show arcuate petals (character 58). Two character states were designed: petals arcuate [58(1)], and petals not arcuate [58(2)] (Fig. 27).

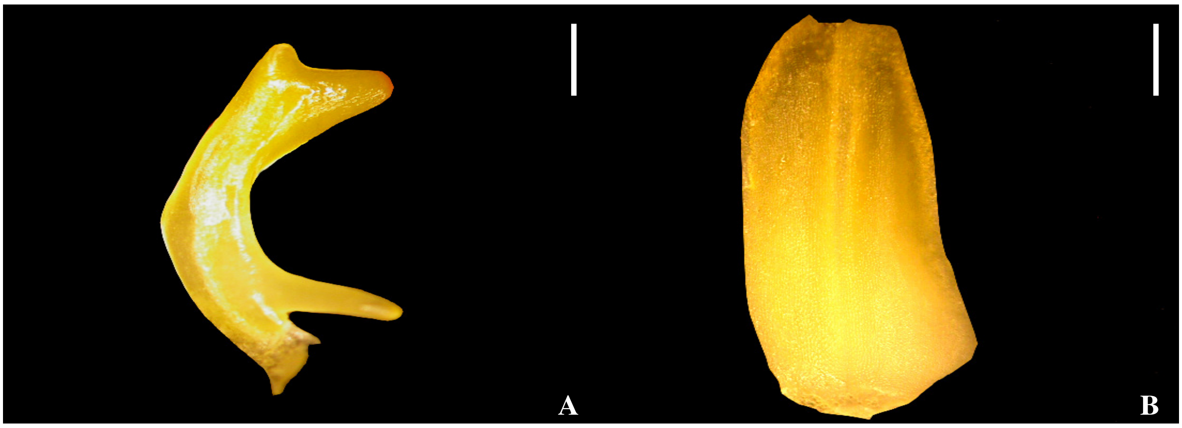

Fig. 27 Petals: (A) arcuate in *M. bicornis* Luer, (B) not arcuate in *M. cardiantha* Königer. Scale bars= 1mm (A, B).

The apex of petals (character 59) varies from truncate to acute and rounded. Bivalvate petals with an inner and an outer lamina (character 60) characterize the genus *Dracula* (Fig. 28).

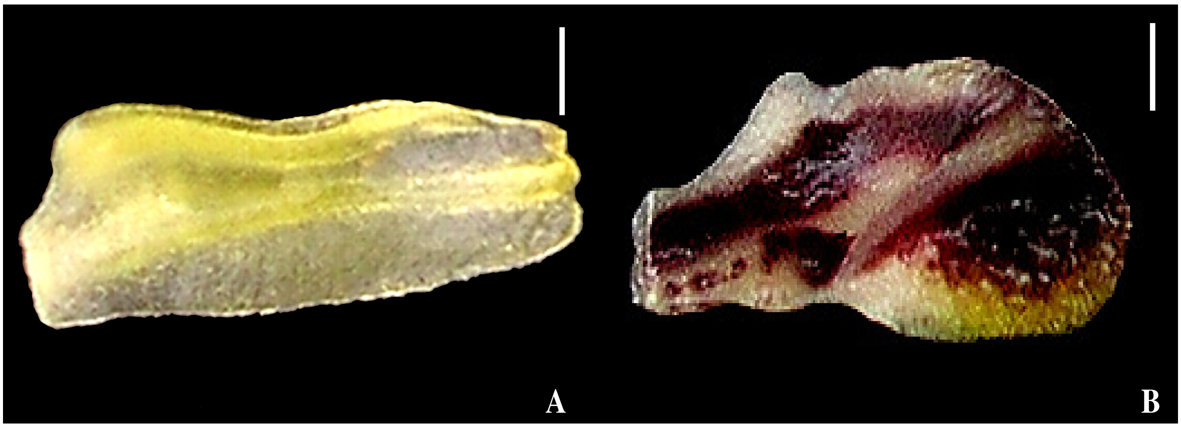

Fig. 28 Petals: (A) a typical *Masdevallia* petal in *M. ventricosa* Schltr., (B) petal bivalvate in *Dracula velutina* Luer. Scale bars= 1mm.

For the margin of the petal apex five states were designed: entire [61(1)], bilobed [61(2)], dentate to denticulate [61(3)], apiculate [61(4)], and longitudinally channeled, twisted and curved up [61(5)]. The base of petals (character 62) is mostly truncate and in few species, such as *M. coccinea,* cordate. The vestiture of petals could be used to define some infrageneric groups; e.g. verrucose petals characterize most analyzed species of subgenus *Masdevallia* section *Durae*. Three states were designed: smooth [63(1)], verrucose [63(2)], and papillose [63(3)], (the last one is mostly present in the genus *Dracula*). The consistency of petals (character 64) has been used to define some infrageneric groups; e.g. membranous petals characterize subgenus *Amanda*. Two character states were designed: petals membranous and petals cartilaginous.

Most *Masdevallia* species show a marginal callus; in some species (e.g., *M. chaetostoma*) a callus is missing (character 65). Both margins callous (character 66) and sulcate centrally (character 67), characterize subgenus *Masdevallia* section *Durae* (LUER, 2000). Both margins callous but not sulcate centrally are present in a few species of subgenus *Polyantha* and subgenus *Masdevallia* section *Coriaceae* (e.g. *M. echo*, *M. melanoxantha*, *M. civilis*). The callus from the labellar margin (characters 68-70) ending in an acute and retrose (uncinate) process near the base characterizes subgenus *Masdevallia* section *Masdevallia* (LUER, 1986-2001); the callus ending in an obtuse angle between the middle and the lower third characterizes subgenus *Masdevallia* section *Coriaceae* (LUER, 1986b-2000); and a callus ending in a broad and rounded process, some species of subgenus *Polyantha* sections *Alaticaules* and *Coaetanae* (Fig. 29).

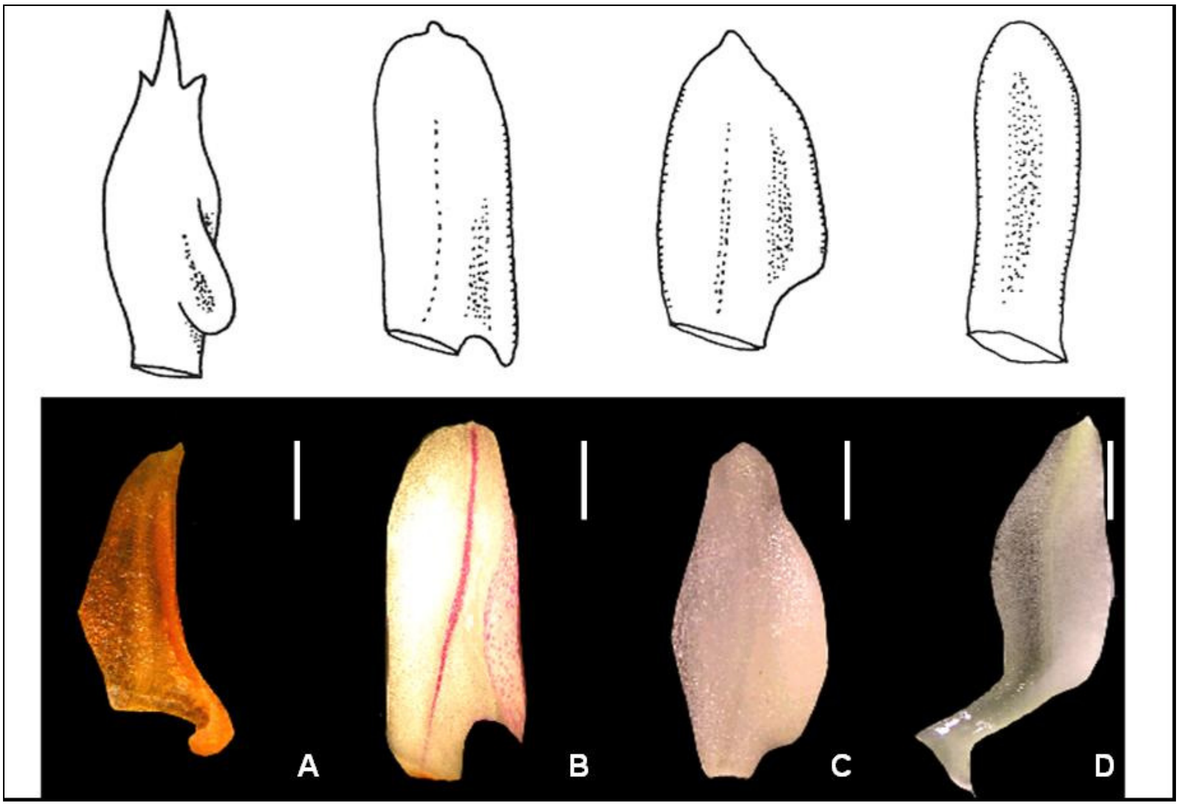

Fig. 29 The callus of petals: (A) ending in a broad rounded, thick process in *M. hirtzii* Luer & Andreetta, (B) ending in an acute, uncinate process in *M. deformis* Kraenzl., (C) ending in an obtuse angle in *M. reichenbachiana* Endres ex Rchb. f., (D) the callus not ending in a process or angle in *M. peristeria* Rchb. f. Scale bars: 5 mm (A, C); 2 mm (D); 1.5 mm (B).

71-90) Lip

The lip, which is usually not much larger than the petals, is more or less ligulate, from oblong to ovate or obovate (character 71), and entire or denticulate to crenate at the margin (character 72), with the apex recurved or not (character 73). The base is truncate or cordate and attached to a curved extension from the base of the column-foot. A base of the lip with elevated margins (character 75) is characteristic for some species of *Dracula*. Verrucose lips characterize species of subgenus *Polyanthae* and subgenus *Masdevallia* sections *Coriaceae* and *Durae* (LUER, 1986b-2000); smooth lips are present in most species, *M. ophioglossa* shows glandulose lips, and a few species such as *M. mezae* and *M. macrura* show lips that are papillose at the apex (character 76). A lip that is callous at the apex, characterizes most species of subgenus *Masdevallia section*s *Masdevallia* and *Durae* (character 77).

An oscillating lip (character 78) characterizes subgenus *Masdevallia* section *Masdevallia* subsection *Oscillantes*. The significant difference in subsection *Oscillantes* is the lip with wing-like, lateral margins often modified into lobes, and a base that is delicately hinged or balanced by a thin straplike extension from the column foot; the slightest motion or a breeze causes the lip to oscillate. In some species the flowers are nutant, or face downward, so that the lip dangles loosely from the column-foot. In some species of subsection *Caudatae* and *Alauticaules* (e.g., *M. pinocchio*) the lip may also oscillate.

A lip that is divided by marginal folds into an epichile an a hypochile (character 79) characterizes subgenera *Amanda*, *Cucullatia*, *Fissia*, *Nidificia*, *Polyantha*, and *Volvula*; species of subgenera *Masdevallia* and *Pygmaeia* are characterized by entire lips (not divided into an epichile and a hypochile) (LUER, 2000) (Fig. 30).

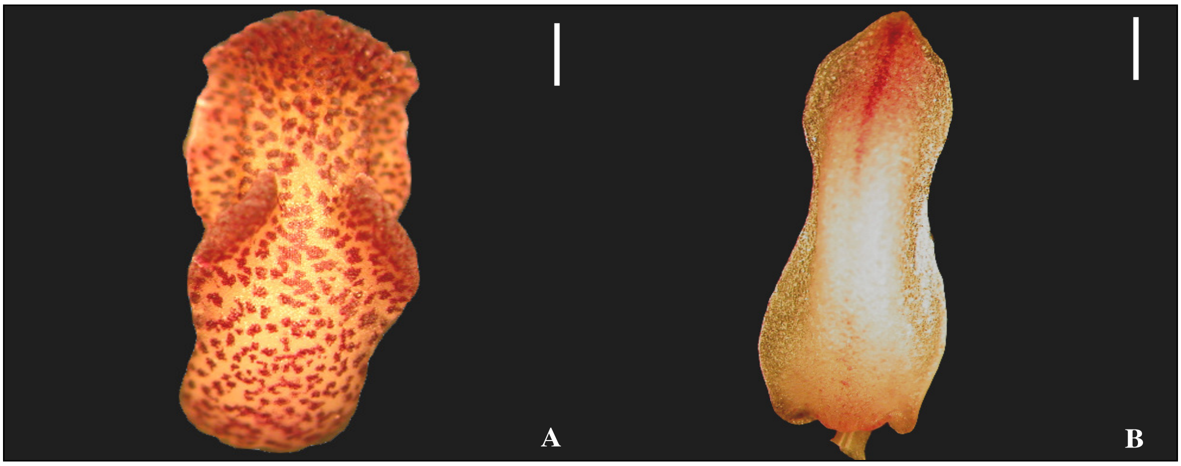

Fig. 30 Lip: (A) divided by marginal folds into an epichile and hypochile in *M. cardiantha* Königer, (B) simple in *M. fulvescens* Rolfe. Scale bars= 1mm (A, B).

The disc is usually sulcate to some degree between a pair of longitudinal calli (characters 80-81); the presence of a pair of longitudinal calli near the middle (Fig. 31) characterizes species of subgenus *Masdevallia* section *Reichenbachianae* as well as some species of subgenera *Masdevallia*, *Volvula*, *Polyanthae* and *Pygmaeia*. Four states were assigned: the disc with a central, flat callus below the middle [80(1)], the disc with a pair of calli near the middle [80(2)], the disc featureless [80(3)], the disc longitudinally thickened [80(4)], and the disc with three lamellae and several, radiating, elevated veins [80(5)]. The last character state [80(5)] refers to species of the genus *Dracula* characterized by lips with lamellae (Fig. 31D).

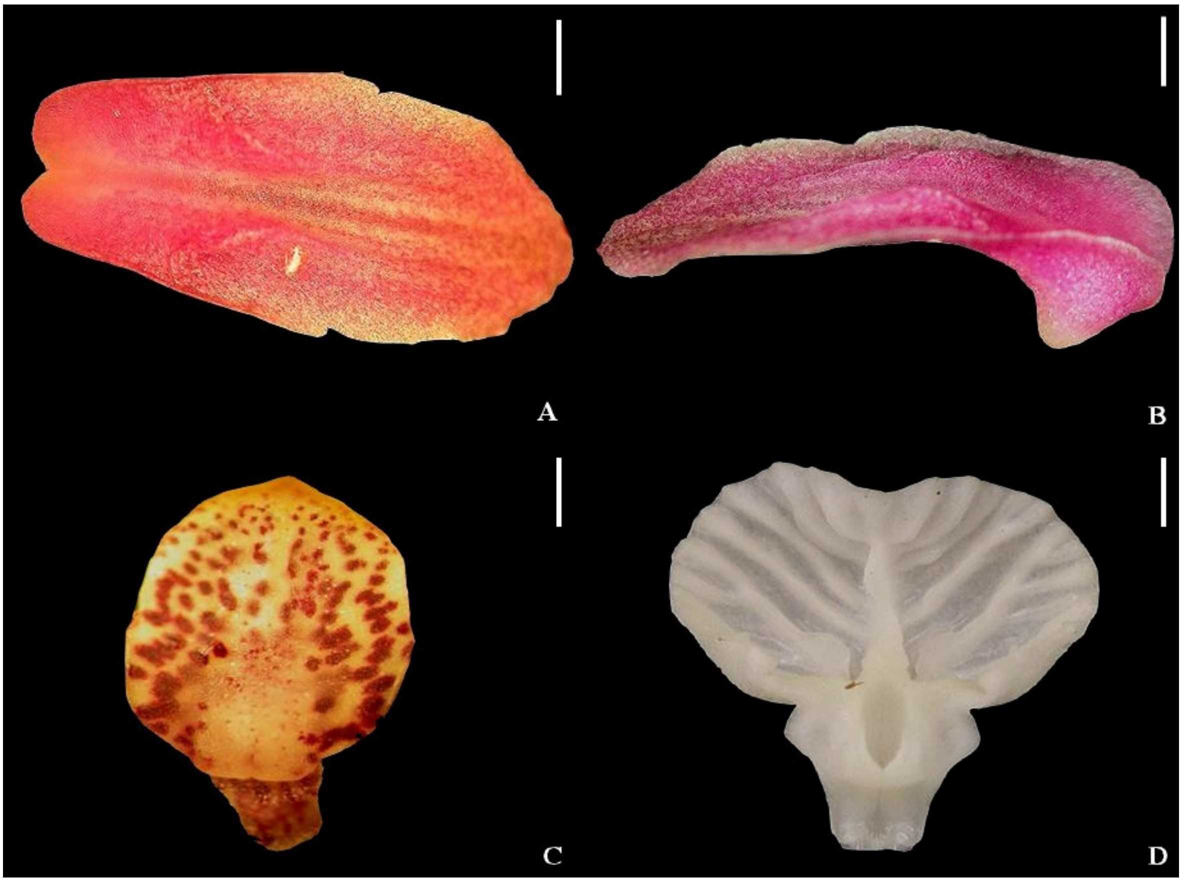

Fig. 31 (A-B) The lip of *M. patula* Luer & Malo with a pair of longitudinal calli near the middle, (C) the lip, featureless, in *M. decumana* Königer, (D) the lip of *Dracula bella* (Rchb. f.) Luer with lamellae and radiated veins. Scale bars: 1mm (A, B); 0.6 mm (C, D).

The lip, divided by marginal folds into an epichile and hypochile, characterizes many species of *Masdevallia*. The shape of the epichile (character 82) varies from elliptic to ovate and obovate, the same is shown for the shape of the hypochile (character 85). The margin of the epichile (character 83) is mostly entire, some species such as *M. echo* and *M. ophioglossa* show an epichile with microscopically dentate to serrate margins. Most species show a smooth epichile (character 84) but in a few species, the vestiture of the epichile varies from verrucose to papillose and cellular-glandulous. The margin of the hypochile is entire in most species, but in a few species the margin of the hypochile can be erose (e.g. *M. mezae*), serrate (e.g. *M. chaetostoma*) or crenate (e.g. *M. rubiginosa*). A hypochile with a pair of acute, uncinate processes (character 87), emerging from the lateral surface on the basal fourth is shown in *M. bicornis* of subgenus *Masdevallia* section *Racemosae* (Fig. 32).

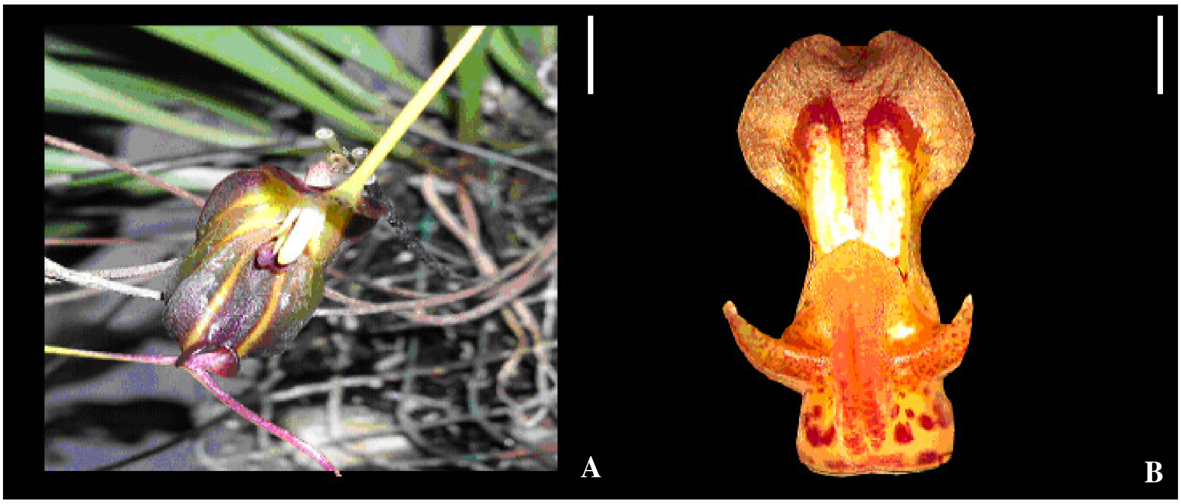

Fig. 32 *M. bicornis* Luer: (A) flower (B) labellum (note the pair of acute, uncinate processes). Scale bars= 5 mm (A); 0.7 mm (B).

A sensitive lip (character 88) is present in species of the genus *Porroglossum*. According to OLIVER (1888) "a tactile stimulus received by the callus of the lip in the `open´ or pollinator-receptive position causes a sudden loss of turgor in the outer layer of cells of the under surface of the claw in contact with the apex of the column-foot leaving the tension of the outer layer of cells of the under surface of the claw unopposed. This releasing of the pressure of the claw against the apex of the column-foot causes the lip to snap suddenly inwards to the `closed´ position, thereby thrusting the pollinator against the stigma and under surface of the column" (see Figs. 33a and 33b).

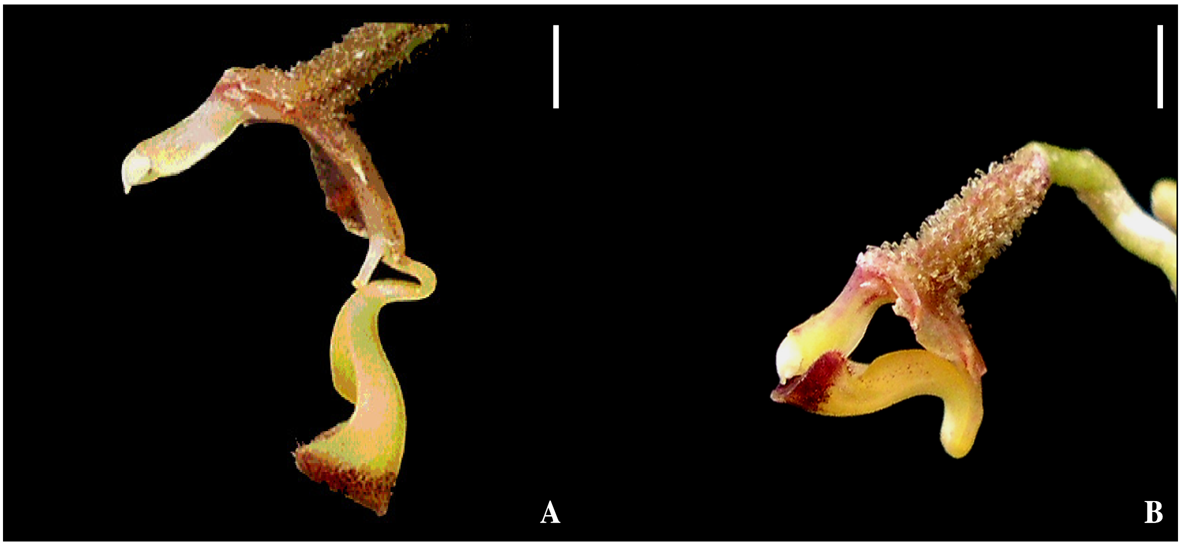

Fig. 33 *Porroglossum echidna* (Rchb. f.) Garay: (A) `open´ position, (B) `closed´ position. Scale bars= 1.4 mm.

The column, longer or similar in length to the labellum [89(1)] characterizes some species such as *M. decumana*, *M. schroederiana*, and *M. bicornis*; a column that is shorter than the labellum [89(2)], is present in most of the species. The column-foot shorter than the column [90(1)] characterizes most species; the column-foot longer than the column [90(2)] characterizes species of subgenus *Nidificia*; (Fig. 34).

Fig. 34 Column-foot: (A) column-foot similar in length to the column in *M. decumana* Königer, (B) column-foot longer than the column in *M. nidifica* Rchb. f., (C-D) column-foot shorter than the column in *M. melanoxantha* Linden & Rchb. f. and *M. fulvescens* Rolfe. Scale bars= 1mm (A, B, C, D).

The position of the rostellum (character 91) is in all species of *Masdevallia* retrorse; an apical rostellum characterizes species of the genus *Porroglossum* (Fig. 35).

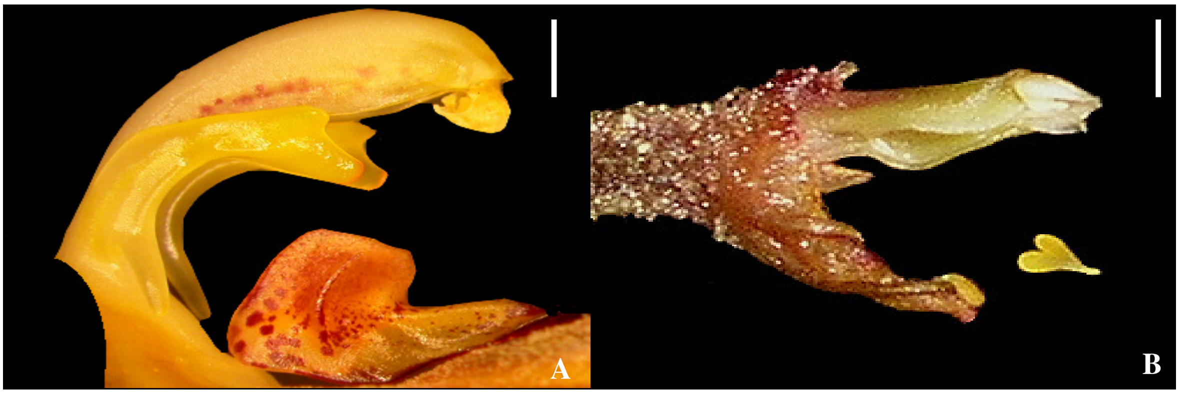

Fig. 35 Position of the column: (A) retrose column and rostellum in *M. bicornis* Luer, (B) apical column and rostellum in *P. echidna***.** Scale bars= 1mm (A, B).

94-99) Pollinia

Rather than focusing on details of the tectal structure, which has not been studied in a sufficient number of genera, in this work the external appearance of the pollen grains and their sculpture was studied. Three types of shape of pollinia are present in *Masdevallia*: drop-like [92(1)], lentiform [92(2)] and clavate [92(3)].

Four types of exine-sculpture are present on the pollinia surface: psilate [93(1)], fossulate [93(2)], verrucate to scabrate-gemmate [93(3)] and rugulate [93(4)] (Fig. 36).

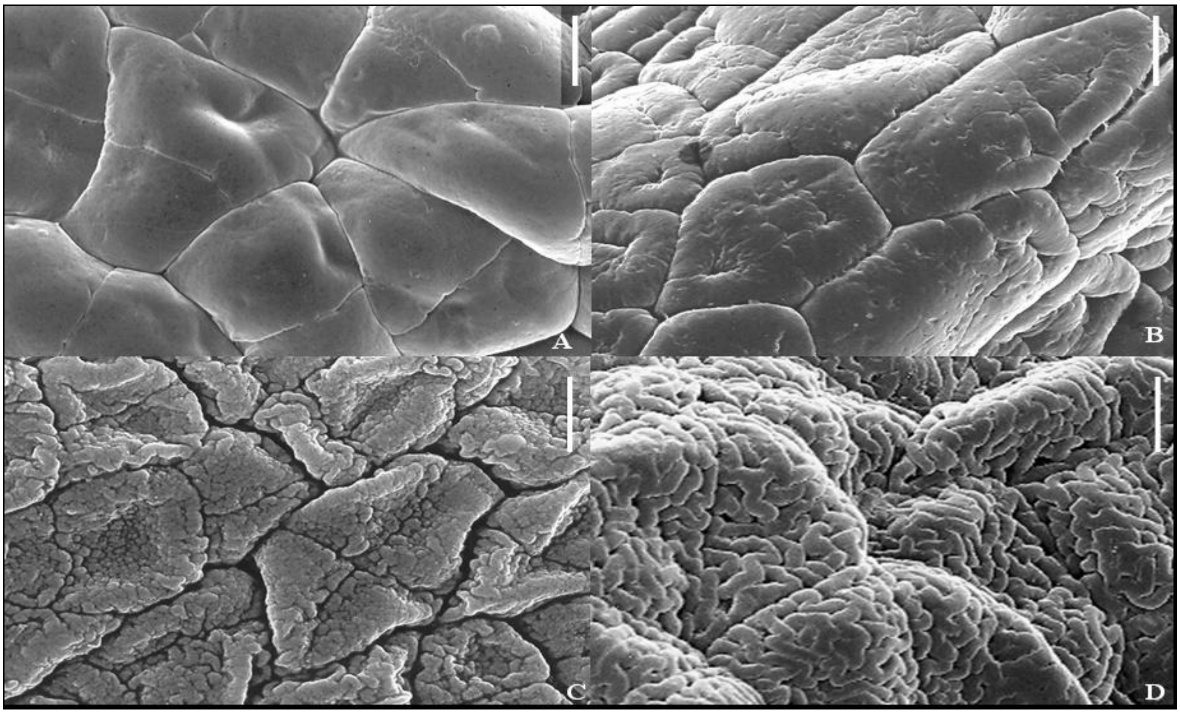

Fig. 36 Exine sculpture: (A) psilate in *M. civilis* Rchb. f. & Warsz., (B) fossulate in *M. caloptera* Rchb. f., (C) verrucate to scabrate-gemmate in *M. chaetostoma* Luer, (D) rugulate in *M. macrura* Rchb. f. Scale bars: 2 µm (A, B, C, D).

The margin of tetrads (character 94) is prominent in most species of subgenus *Masdevallia* section *Masdevallia* (Fig.38).

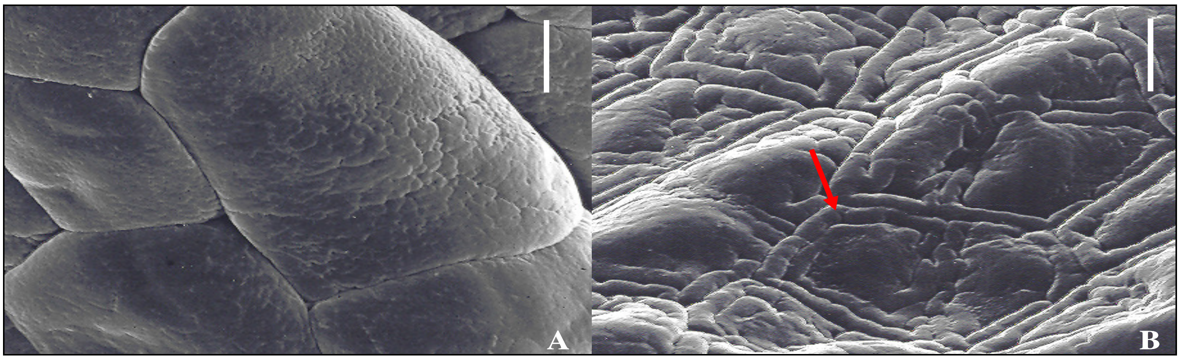

Fig. 37 Margin of tetrads: (A) normal in *M. coccinea* Linden ex Lindl., (B) prominent in *M. lamprotyria* Linden ex Lindl. Scale bars= 2 µm (A, B).

The size of the pollinia varies within species of *Masdevallia*; however, three character states are clearly distinguished in the length of the pollinia: pollinia shorter than 500 µm [95(1)], between 550 and 800 µm [95(2)], and more than 900 µm [95(3)]; the same is shown for the wide of the pollinia, of which three character states are clearly distinguished: <300 µm [96(1)], between 350 and 600 µm [96(2)], and >700 µm [96(3)]. In a few species of *Masdevallia* the caudicles (character 97) are very primitive and can be hardly distinguished. In most species the caudicles are very well developed and mostly elaborate.

3.1.2 Phylogenetic relationships

3.1.2.3 Data matrix characteristics

The final morphological data matrix included 94 characters (see appendix II). Three characters were excluded because they could not be unambiguously divided into discrete states as recommended by PIMENTEL & RIGGINS (1987) (see chapter 3.1.1). Of these 94 characters, 91 (96%) were found to be phylogenetically informative (Table 9).

Table 9 Characteristics and variation of the morphological data in *Masdevallia*.

	Vegetative characters	**Floral characters**	**Pollinia characters**	**All characters**
All	7	81	6	94
Constant	-	2	-	2
Variable, but parsimony uninformative= autapomorphies	-	1	-	1
Parsimony informative	7	78	6	91

3.1.2.4 Topology of the most parsimonious trees

The parsimony analysis of the morphological data set resulted in 6 718 most parsimonious trees with a length of 1 411 steps (CI = 0.29, RI = 0.47, RC = 0.108, HI = 0.860). A strict consensus tree is presented in Fig. 38.

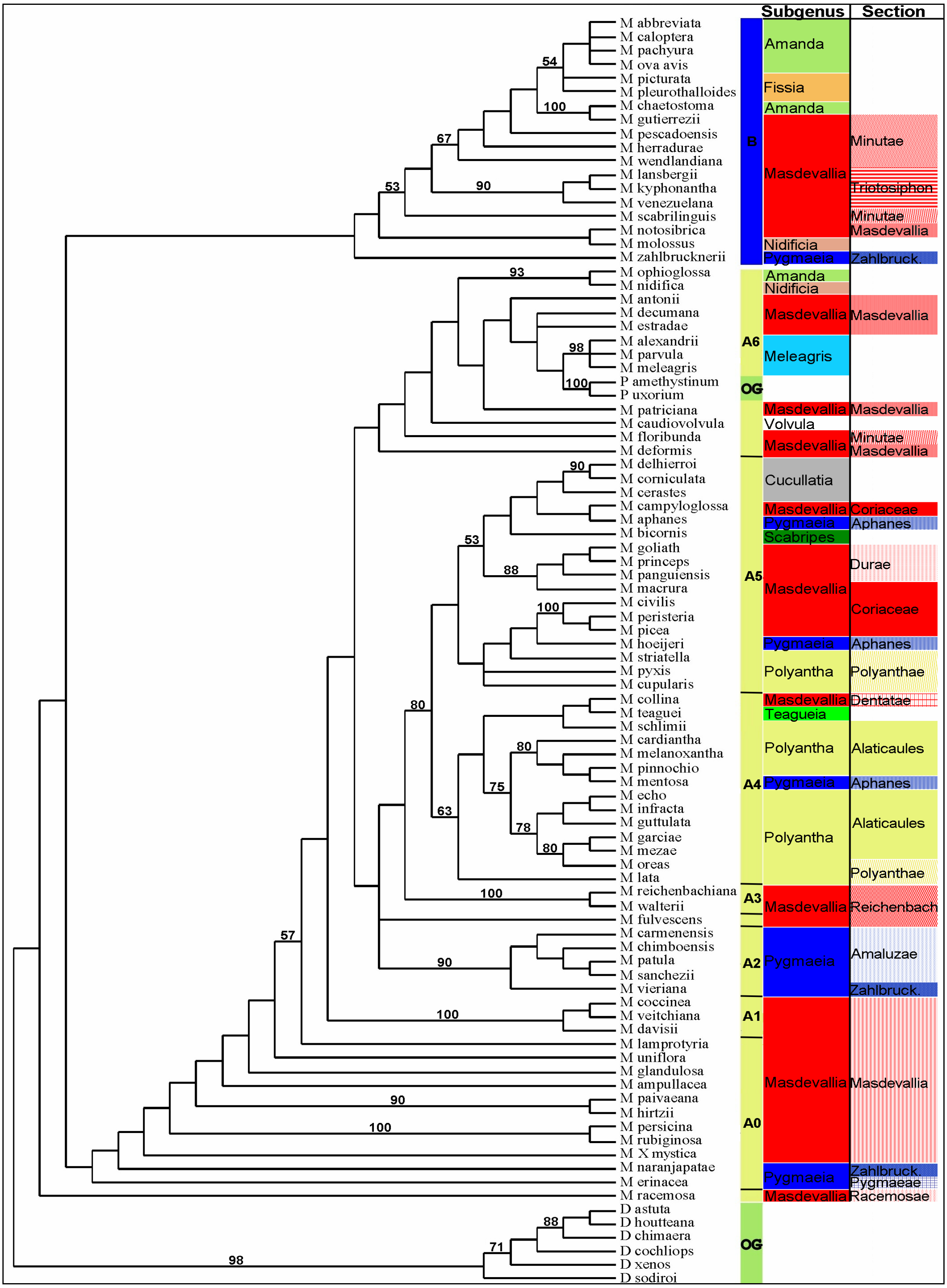

Fig. 38 Strict consensus tree of the analyzed species of *Masdevallia* and outgroups (OG) based on morphological data, computed from the 6 718 most parsimonious trees (tree length= 1 411, consistency index= 0.29, retention index= 0.47). The numbers above the branches are bootstrap percentages. Percentages ≥ 50% are not shown. A0 to A8, B= groups discussed in the text.

Analysis of the morphological data does not support the monophyly of the genus *Masdevallia*. Furthermore, one of the genera designated as outgroups, *Porroglossum*, was found nested within *Masdevallia*, albeit without significant bootstrap support. Within the most parsimonious tree, two larger clades, designated as A and B, were found (Fig. 38).

Subgenus *Masdevallia* section *Racemosae* occupies the most basal position in this study and appears as sister to the remaining *Masdevallia* species including *Porroglossum.*

The clade designated as A is composed of a basal grade designated as A0 and six subclades designed as A1 to A6 (Fig. 38). Of the six subclades founded within clade A, three received good bootstrap values: subclade A1 (100%), A2 (90%), and A3 (100%). Species grouped in clade A are members of subgenera *Cucullatia*, *Masdevallia*, *Meleagris*, *Nidificia*, *Pygmaeia*, and the monospecific *Scabripes*, *Teagueia*, and *Volvula*. *Porroglossum* taxa are nested within the subclade designated as A6.

Clade B (Fig. 38) constitutes a small clade without bootstrap support. It includes species of subgenera *Amanda*, *Fissia*, *Masdevallia* sections *Minutae* and *Triotosiphon*, as well as *M. notosibrica* (subgenus *Masdevallia* section *Masdevallia*), *M. molossus* (subgenus *Nidificia*) and *M. zahlbrucknerii* (subgenus *Pygmaeia* section *Zahlbrucknerae*).

3.2 Molecular analysis

3.2.1 Alignment and ITS characteristics

3.2.1.1 ITS Structure, Size, and Composition

Aligned DNA sequences of ITS1, the 5,8S subunit, and ITS2 from the studied species are presented in Appendix III. The length of the entire ITS region varied among *Masdevallia* DNAs from 624 to 634 bp. Length ranges of ITS1 - 5.8S - ITS2 sequences were 214 – 220, 166, and 244 – 249 bp, respectively. Boundaries of the ITS1, 5.8S gene, and ITS2 were taken from HERSHKOVITZ and LEWIS (1996). The ITS1 and ITS2 regions exhibited the following base composition: 19 – 23% A, 24 – 35% GC, and 18 - 22% T. The 5.8S region showed a lower T content (17%) and a higher G content (29%). The overall G + C content (58%) was rather low for *Masdevallia* in comparison to other angiosperms (reviewed in BALDWIN et al., 1995) (Table 10).

Table 10 Base composition of the ITS nrDNA region in *Masdevallia*

Mean length	**ITS1**	**5,8S**	**ITS2**	**Entire ITS Region**
Masdevallia length variation	**Ø ITS 1= 214,9 bp (214-220 bp)**	**Ø 5,8S= 166,0 bp (166 bp)**	**Ø ITS2= 246,0 bp (244-249 bp)**	**Ø ITS region= 626,9 bp (624-634 bp)**
A content	0,2361	0,2527	0,1923	0,2233
GC content	0,5846	0,5766	0,5911	0,591
T content	0,1791	0,1705	0,2164	0,1915

The final alignment matrix (see appendix III) has a length of 663 bp (233, 165, and 263 bp for ITS1, 5.8S, and ITS2, respectively), of which 98 (37, 11, and 50, respectively) were variable but parsimony-uninformative and 167 (80, 5, and 82, respectively) were phylogenetically informative (Table 11).

Table 11 Characteristics and variation of the ITS nrDNA region in *Masdevallia*.

	ITS 1 1-233 bp	**5,8S 234-399 bp**	**ITS 2 400-663 bp**	**ITS region 1-663 bp**
All	233	165	263	663
Constant	116	150	132	398
Variable, but variable and parsimony uninformative= autapomorphies	37	11	50	98
Parsimony informative	80	5	82	167

Length range of ITS1 - 5.8S - ITS2 sequences for outgroup taxa (species of *Dracula, Luerella*, *Porroglossum*, and *Trisetella*) were 213 – 219, 166, and 244 – 246 bp, respectively. The entire ITS region varied from 623 to 631 bp. The ITS1 and ITS2 regions exhibited the following base composition: 19 - 25% A, 24 - 35% GC, and 18 - 22% T. The 5.8S region shows a higher C content (28%) (Table 12). The A, T, and C content were similar to *Masdevallia*.

Table 12 Base composition of the ITS nrDNA region in outgroup taxa.

Mean length	**ITS1**	**5,8S**	**ITS2**	**Entire ITS Region**
Outgroups length variation	**Ø ITS 1= 214,8 bp (213-219 bp)**	**Ø 5,8S= 166,0 bp (166 bp)**	**Ø ITS2= 245,4 bp (244-246 bp)**	**Ø ITS region= 626,0 bp (623-631 bp)**
A content	0,2492	0,2530	0,1887	0,2266
GC content	0,5717	0,5782	0,5954	0,5827
T content	0,1790	0,1686	0,2158	0,1906

3.2.1.2 Divergence between ITS sequences

Within *Masdevallia*, the ITS1 sequence divergence between pairs of species ranged from 0% to 14%; highest values occur between *M. bicornis* and *M. mentosa* (14%) followed by *M. bicornis* and *M. civilis* (13%). The ITS1 sequence divergence between *Masdevallia* and outgroup species strongly overlapped with those from comparisons within *Masdevallia* and ranged from 0.9% between *Dracula xenos* and *M. abbreviata* to 19% between *Trisetella scobina* and *M. bicornis.*

Pairwise ITS2 sequence divergences of *Masdevallia* DNAs were generally lower (0% to 11%) than the values from the corresponding ITS1 sequences. The highest sequence divergence occurred between *M. corniculata* and *M. erinacea* (11%). In contrast, ITS2 sequence divergence between *Masdevallia* and outgroup species (3.2% between *M. picturata* and *D. xenos* to 16% between *T. scobina* and *M. cupularis*) were higher than values from corresponding ITS1 sequences.

Comparison of both ITS1 and ITS2 sequences within *Masdevallia* gave divergence values ranging from 0% to 7.2%; the latter is found between *M. erinacea* and *M. scabrilinguis*. Divergence values from ITS1 and ITS2 between *Masdevallia* and outgroup species spanned from 2% in *T. scobina* to 13% in *M. aphanes*.

3.2.1.3 ITS Length Mutations

Alignment of ITS1 sequences of all *Masdevallia* DNAs required one or more gaps at 5.1% of sites; the value increases to 7% with the addition of outgroup species. The aligned *Masdevallia* ITS 2 sequences necessitated one or more gaps at 6% of nucleotide positions; this value remained the same when outgroup species are added. No gaps were needed to align all 5,8S sequences.

There are eight phylogenetically informative gaps in ITS1: a one-base insertion (position 14) as synapomorphy for *M. picturata* and *M. pleurothalloides*, a two-base insertion (positions 47-48) as synapomorphy for subgenus *Pygmaeia* section *Zahlbrucknerae*; subgenus *Masdevallia* sections *Coriaceae*, *Dentatae*, *Minutae* and *Reichenbachianae* and subgenus *Polyantha*, sections *Polyanthae* and *Alaticaules*, a two-base insertion (positions 62-63) as synapomorphy for *M. caudivolvula*, *M. echo*, *M. infracta*, and *M. racemosa*, a one-base insertion (position 105), synapomorphic for species of the genus *Dracula*, and a two-base insertion (positions 171-172) as synapomorphy for *M. echo* and *M. infracta*. In ITS 2, eight gaps are phylogenetically informative: a one-base insertion (position 424) as synapomorphy for subgenus *Meleagris*, a two-base insertion (positions 449-450) as synapomorphy for *M. cardiantha* and *M. lamprotyria*, a two-base insertion as synapomorphy for *M. citrinella* and *M. persicina*; and a one-base deletion, occurs near the 5' end (position 645).

3.2.2 Phylogeny of *Masdevallia*

3.2.2.1 Topology of the most parsimonious trees

The >10 000 equally parsimonious trees obtained prior to the weighting procedure had 460 steps with a consistency index (CI) = 0.60, retention index (RI) = 0.75, and rescaled consistency index (RC) = 0.58. After successive weighting, the >10 000 equally parsimonious trees had 518 105 steps (2058 Fitch steps) before computer memory was exhausted. These trees are characterized by a CI of 0.54, a RI of 0.83, and a RC of 0.503. There were 488 characters with a weighting of 1, while 175 characters had a weighting other than 1. The strict consensus tree of >10 000 equally parsimonious trees resolved four major clades: clade A with a bootstrap support of 73, clade B with a bootstrap support of 91, clade C with a bootstrap support of <50, and clade D with a bootstrap support of 60 (Fig. 39).

The clade designated as A grouped *Masdevallia erinacea* (subgenus *Pygmaeia* section *Pygmaeae*), sister to *Luerella pelecaniceps,* and occupies the most basal position in this study, appearing as sister to the remaining *Masdevallia* species (Fig. 39).

The clade designated as B is composed of three subclades (Fig. 39). Subclade B1, with a bootstrap support of 92, is composed of species of subgenus *Masdevallia* sections *Minutae* and *Triotosiphon*. Subclade B2 with a bootstrap support of 66, grouped species of subgenus *Masdevallia* sections *Dentatae* and *Reichenbachianae*, *M. herradurae*, *M. floribunda*, and *M. scabrilinguis* (section *Minutae*); subgenus *Polyantha*; *M. mentosa* and *M. chimboensis* (subgenus *Pygmaeia* sections *Aphanes*, *Amaluzae*, and *Zahlbrucknerae*). Subclade B3, with a bootstrap support of 99, consists of species of subgenus *Masdevallia* section *Coriaceae*.

Clade C is divided into three subclades (Fig. 39): subclade C1, with a bootstrap support of 84, grouped *M. hoeijeri* (subgenus *Pygmaeia* section *Aphanes*) sister to *M. bicornis* (subgenus *Scabripes*); subclade C2, with a bootstrap support of 58, grouping species of subgenus *Volvula*, *Masdevallia* sections *Racemosae* and *Masdevallia*, and *M. macrura* (section *Coriaceae*); subclade C3, with a bootstrap support of 94, grouped species of subgenus *Masdevallia* section *Durae*, and subgenus *Pygmaeia* section *Amaluzae* (except *M. chimboensis*).

Clade D is divided into three subclades (Fig. 39). Subclade D1, with a bootstrap support of 93, included species of subgenera *Cucullatae* and *Teagueia.* Subclade D2, with a bootstrap support of 64, is composed of species of subgenus *Meleagris*. Subclade D3, with a bootstrap support of 95, grouping species of subgenus *Fissia* as well as *Dracula xenos*; and subclade D4, with a bootstrap support of 81, is composed of species of subgenus *Amanda* and *Nidificia*.

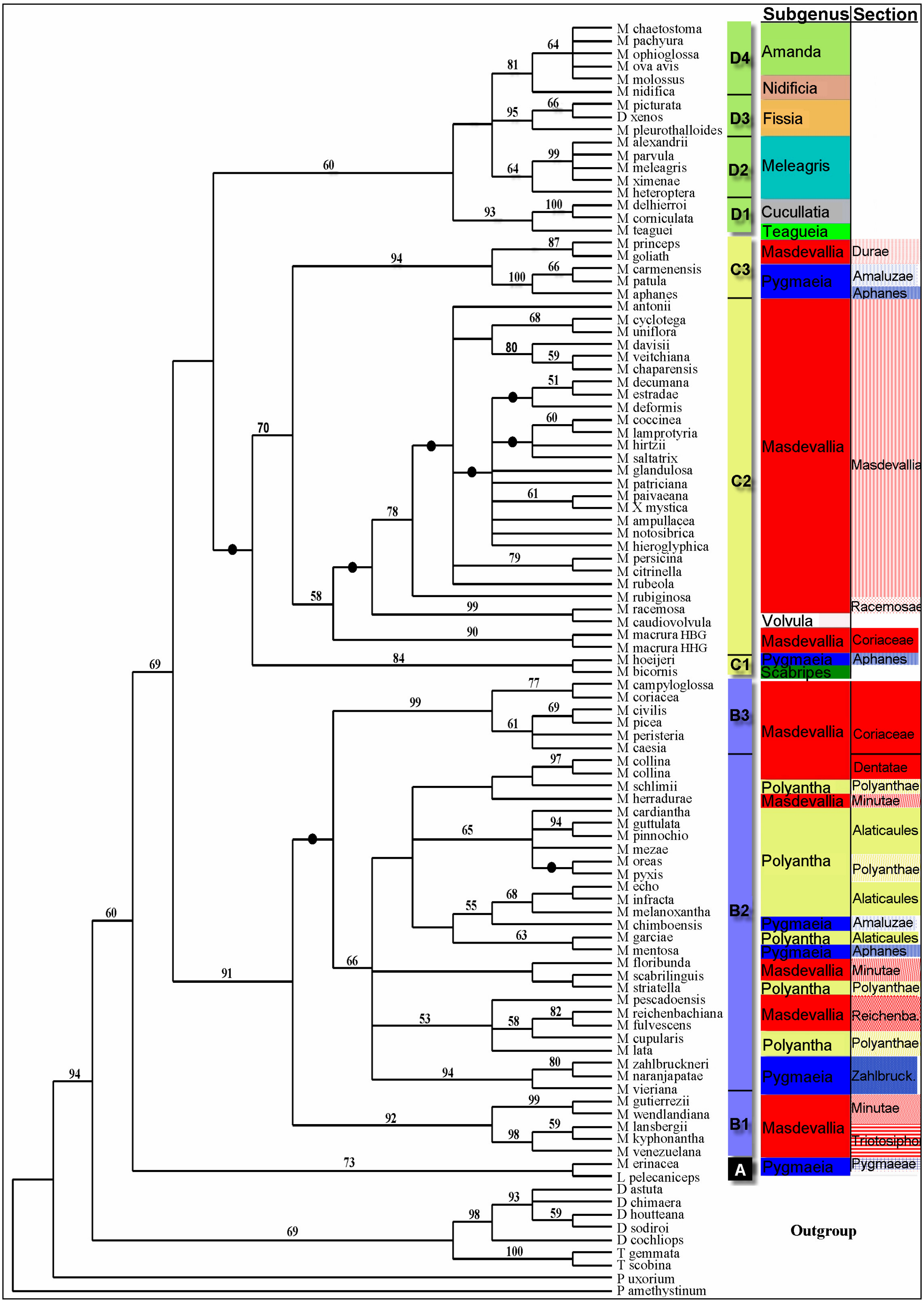

Fig 39 Strict consensus tree of the analyzed species of *Masdevallia* and outgroups based on ITS sequences data, computed from the >10 000 most parsimonious trees (tree length= 460, consistency index= 0.60, retention index= 0.75). The numbers above the branches are bootstrap percentages. Percentages ≥ 50% are not shown. Nodes not supported in the Bayesian analysis (Fig. 40) are indicated with a solid circle.

3.2.2.2 Bayesian analysis: comparison of two phylogenetic methods

The strict consensus tree obtained from the maximum parsimony analysis (Fig. 39) and the 50% majority rule consensus of the 3000 trees obtained from the Bayesian analysis (Fig. 40) recovered essentially the same topology. The Bayesian analysis data resolved a more structured tree (fewer polytomies). Furthermore, nodes with posterior clade probabilities of less than approximately 70% support were not supported in the maximum parsimony strict consensus tree (represented by solid dots in Fig. 39).

Five major clades were identified from the Bayesian analyses. *Masdevallia erinacea* (clade A) occupies the most basal position appearing as sister to the remaining *Masdevallia* species with 100% support. Clade B corresponds to clade C in the strict consensus, however with higher support (64% pp). Clade C (100% pp) corresponds to clade B in the strict consensus. Clade D1 in the strict consensus is resolved in the Bayesian analysis as a separate clade designed as clade D with 100% pp. Clade E (98% pp) is divided into three subclades: subclade E1 (76% pp), which corresponds to subclade D2 in the strict consensus; subclade E2 (100%), which corresponds to subclade D3 in the strict consensus; and subclade E3 (100%), which corresponds to subclade D4 in the strict consensus.

3.2.2.3 Bayesian posterior probabilities vs. bootstrap support

In general, posterior probabilities were higher than bootstrap values.The reverse was found for only a single node. Bootstrap support was 100% for 3 nodes and posterior probabilities was 100% for 28 nodes. Bootstrap values ranged from 51 to 100%, while the corresponding posterior probabilities ranged from 52 to 100%.

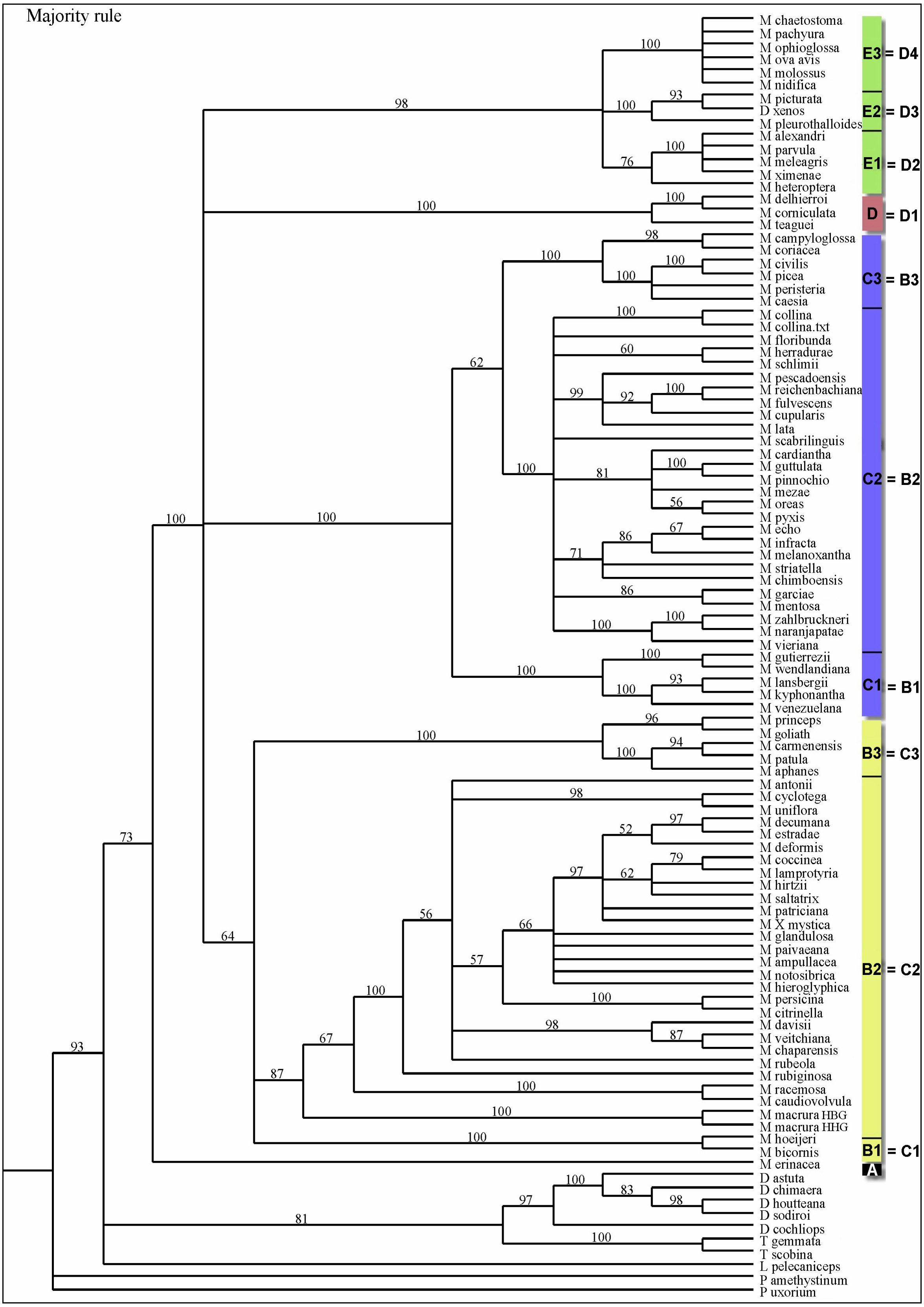

Fig. 40 Phylogenetic tree for 104 *Masdevallia* and outgroups species based on ITS sequences data using Bayesian analysis (majority rule consensus of 5 runs @ 10001 trees, excluding 3000 burn-in trees). The numbers above the branches are posterior probabilities.

3.2.3 Molecular synapomorphies of the major clades/subclades

Table 13 lists a summary of the specific indels/mutations supporting single in the maximum parsimony analysis clades in the genus *Masdevallia*. Twenty three indels were recognized in the ITS region. Twelve were found in the ITS1 and eleven in the ITS2 region.

Clade A: These two species forms the sister group to all other ingroup taxa, as well as of *Dracula xenos*. All *Masdevallia* species as well as *Dracula xenos* are united on the basis of an A or C to T change (char. 13, position 65) and a C or T to G change (char. 66, position 582), with a reversal in *M. infracta* and *M. erinacea* (Table 13, Fig. 42).

Clade B: Members of this clade share a GA insertion (char. 6, position 47 and 48), a T to C change (char. 8, position 56), a C to T change (char. 10, position 61), and a T to A change (char. 12a, position 64) in ITS1 (Table 13, Fig. 42). In ITS2 (Table 13, Fig. 59), they share a C to T change (char. 36, position 225), a G to A change (char. 60, position 501), and a T to C or G change (char. 68, position 601).

Clade C: Members of this clade share a C to A change (char. 19, position 82) in ITS1. A T to C change (char. 58, position 492), C to T change (char 59, position 499), and a C deletion (char 77, position 645) was present in ITS2 (this last deletion was not present in species of the subclade C1). Some synapomorphic features were encountered for species of section *Masdevallia*: in ITS1 a G to A change (char. 14, position 69); in ITS2 a G to A change (char. 56, position 476) and a T to A change (char. 61, position 508). Members of subclade D1 share some synapomorphic features: a G to A change (char. 7, position 49), a T to C change (char. 15, position 70), and a G to A change (char. 16, position 72) in ITS1. ITS2 showed a A to C change (char. 69, position 605) and a G to T change (char. 78a, position 646) (Table 13, Fig. 41).

Clade D: The following synapomorphic features are shared for the members of this clade: a G or T to A change in ITS1 (char. 7, position 49), a C to A change (char. 23, position 126) and a G to A change (char. 60, position 501) (Table 13, Fig. 41).

The distribution of the most unambiguous character transformations is summarized in Table 13 and on the strict consensus tree together with the infrageneric classification (Figs. 41 and 42).

Table 13 Distribution of 81 possibly informative unambiguous character transformations.

Char. #	From pos.	To Pos.	Most likely event, or sequence indel	Taxa (and remarks)
1	29	29	T→C	Subgenera *Polyantha*, *Masdevallia* sections *Reichenbachianae*, *Triotosiphon*, *Minutae* and *Dentatae*; *Pygmaeia* sections *Zahlbrucknerae, M. chimboensis* (section *Amaluzae*), and *M. mentosa* (section *Aphanes*); *L. pelecaniceps.*
2	33	33	G→T	Subgenera *Volvula* and *Masdevallia* sections *Coriaceae* and *Racemosae*.
3	37	37	C→T	Subgenus *Masdevallia* sections *Durae* and *Cucullatae.*
4	38	38	T→C	Subgenus *Masdevallia* section *Reichenbachianae*, *Minutae* (*except M. gutierrezii* and *M. wendlandiana*), *Dentatae*; *Polyantha* and *Pygmaeia* section *Zahlbrucknerae*, *M. chimboensis* (section *Amaluzae*), and *M. mentosa* (section *Aphanes*).
5	43	43	C→T	Subgenera *Amanda* and *Nidificia*, *M. bicornis*, *M. hoeijeri*, *M. cupularis*, *M. infracta*, *M. melanoxantha*, *M. echo*, *M. garciae*, *M. deformis*. Genera *Trisetella* and *Luerella*.
6	47	48	GA duplication	Subgenus *Polyantha*; *Masdevallia* sections *Coriaceae*, *Dentatae*, *Reichenbachianae*, *Triotosiphon* and *Minutae*; *Pygmaeia* sections *Aphanes*, *Amaluzae*, *Pygmaeae* and *Zahlbrucknerae*.
7	49	49	G or T →A	Subgenus *Amanda*, *Fissia*, *Meleagris*, *Nidificia*, *Cucullatae*, *Masdevallia* sections *Durae*, *M. antonii*, *M. cyclotega*, *M. uniflora*, *M. davisii*, *M. veitchiana*, and *M. chaparensis*.
8	56	56	T→C	Subgenus *Masdevallia* sections *Coriaceae*, *Dentatae*, *Reichenbachianae*, *Minutae*, and *Triotosiphon*; *Polyantha*; *Pygmaeia* section *Zahlbrucknerae*, *M. chimboensis* (section *Amaluzae*), and *M. mentosa* (section *Aphanes*), *M. deformis.*
9	60	60	A→G	Subgenus *Pygmaeia* section *Amaluzae* and *M. aphanes*; *M. pinocchio* and *M. guttulata.*
10	61	61	C→T	Subgenera *Masdevallia* sections *Coriaceae*, *Dentatae*, *Reichenbachianae*, *Minutae*, and *Triotosiphon*; *Polyantha*; *Pygmaeia* sections *Zahlbrucknerae*, *M. chimboensis* (section *Amaluzae*), and *M. mentosa* (section *Aphanes*).
11	62	63	T duplication	Subgenus *Masdevallia* section *Racemosae*; subgenus *Volvula*; *Masdevallia infracta*, *M. echo*.
12a	64	64	T→A	Subgenus *Masdevallia* sections *Dentatae*, *Reichenbachianae*, *Minutae*, and *Triotosiphon*; *Polyantha*; *Pygmaeia* section *Pygmaeae*, *Zahlbrucknerae*, *Amaluzae* and *Aphanes*.
12b	64	64	T→G	Subgenus *Volvula*; subgenus *Masdevallia* section *Racemosae*.
13	65	65	Aor C→T	Genus *Masdevallia*, *Dracula xenos*, *Luerella pelecaniceps*.
14	69	69	G→A	*Masdevallia pachyura*, section *Masdevallia*, section *Racemosae*; subgenus *Volvula*.
15	70	70	T→C	Subgenera *Scabripes*, *Masdevallia* section *Durae* and *Pygmaeia* section *Amaluzae* and *M. aphanes*.
16	72	72	G→A	Subgenera *Masdevallia* section *Durae* and *Pygmaeia* section *Amaluzae* and *M. aphanes*.
17a	74	74	G→C	Subgenus *Masdevallia* sections *Dentatae*, and *Minutae* (*except M. gutierrezii* and *M. wendlandiana*; subgenus *Polyantha*; subgenus *Pygmaeia* sections *Zahlbrucknerae*.
17b			G→T	Subgenus *Masdevallia* section *Triotosiphon*.
18	79	79	A→G	Subgenus *Masdevallia* section *Coriaceae*.
19	82	82	C→A	Subgenus *Masdevallia* sections *Durae*, *Masdevallia*, and *Racemosae; M. macrura* (section *Coriaceae);* subgenus *Pygmaeia* sections *Amaluzae* and *Aphanes;* subgenus *Scabripes.*
20	94	94	T→C	*Trisetella, Luerella pelecaniceps,* subgenera *Cucullatia* and *Masdevallia* section *Coriaceae, M. erinacea*, *M. mentosa*, *M. striatella*, *M. guttulata*, *M. scabrilinguis.*
21	106	106	G→A	*Dracula*, *Masdevallia* subgenera *Amanda* and *Nidificia*
22	113	113	C→T	Subgenus *Meleagris* (except *M. heteroptera*), *M. macrura*, *M. mystica*, *M. paivaeana*, and *Trisetella gemmata*.
23	126	126	C→A	Subgenera *Amanda*, *Nidificia*, *Fissia*, *Meleagris* and *Dracula xenos*.

Table 13 Cont. Distribution of 81 possibly informative unambiguous character transformations.

Char. #	**From pos.**	**To pos.**	**Most likely event, or sequence indel**	**Taxa (and remarks)**
24	127	127	A→G	Subgenus *Masdevallia* sections *Coriaceae*, *Dentatae*, *Minutae* (except *M. gutierrezii* and *M. wendlandiana*), and *Reichenbachianae*; subgenus *Polyantha*; subgenus *Pygmaeia* section *Zahlbrucknerae*, *M. chimboensis* (section *Amaluzae*), and *M. mentosa* (section *Aphanes*).
25	136	136	T→A	*Trisetella*, *Masdevallia* subgenus *Pygmaeia* section *Zahlbrucknerae*.
26	158	158	C→T	Subgenus *Masdevallia* section *Durae* and *M. erinacea*
27	164	164	G→T	Subgenus *Masdevallia* section *Masdevallia* (except *M. rubiginosa*), subgenus *Scabripes*, and *M. hoeijeri.*
28	168	168	A→G	Subgenus *Pygmaeia* section *Amaluzae* (except *M. chimboensis*), *M. aphanes*, *M. hoeijeri*, *M. infracta*, and *M. echo*.
29a 29b	169	169	C→A C→T	Subgenus *Meleagris* (except *M. meleagris*), *Luerella pelecaniceps*, and *Porroglossum amethystinum*. Subgenus *Masdevallia* section *Reichenbachianae*, *M. cupularis* and *M. floribunda.*
30	177	177	A→G	*L. pelecaniceps, Masdevallia* subgenus *Pygmaeia* section *Zahlbrucknerae*
31	188	188	G→T	Subgenus *Meleagris* (except *M. heteroptera*) and *M. ophioglossa.*
32	191	191	T→C	Subgenera *Cucullatia* and *Teagueia.*
33a 33b	192	192	A→C or T A→G	Genera *Luerella*, *Trisetella*, *Dracula*, and *Masdevallia*, except those below. Subgenus *Meleagris* (except *M. heteroptera*).
34	217	217	T→A or G	Genus *Masdevallia*
35	220	220	T→G	Genera *Luerella*, *Trisetella*, *Dracula*, and *Masdevallia.*
36	225	225	C→T	Subgenus *Masdevallia* sections *Coriaceae*, *Dentatae*, *Minutae*, and *Triotosiphon*; subgenus *Polyantha*, subgenus *Pygmaeia* section *Zahlbrucknerae*, *M. chimboensis* (section *Amaluzae*), and *M. mentosa* (section *Aphanes*). All this are members of clade C, species of section *Reichenbachianae* present a reversion at this position.
37	366	366	G→T	Subgenus *Pygmaeia* section *Zahlbrucknerae* and *Amaluzae* (except *M. chimboensis*), section *Triotosiphon*, *M. aphanes*, *M. saltatrix*, *M. X mystica*, *M. hirtzii*, *M. patriciana*, *M. lamprotyria*, *M. deformis*, *M. coccinea*, *M. estradae*, *M. decumana*, *M campyloglossa*, *M. picturata*, and *Dracula xenos*.
38	372	372	C→T	Subgenus *Pygmaeia* section *Amaluzae* (except *M. chimboensis*), *M. aphanes*, and *M. scabrilinguis.*
39	403	403	A→G	*Masdevallia* section *Coriaceae*; *M. caudivolvula*, *M. erinacea* and *M. racemosa.*
40	424	425	CA or CC duplication	Subgenus *Meleagris*, except *M. heteroptera*
41	429	429	T→A	Subgenus *Fissia*, *D. xenos.*
42	432	432	C→T	Subgenus *Cucullatia*
43	434	434	C→A	Subgenus *Masdevallia* section *Triotosiphon.*
44	435	435	A→G	Subgenus *Fissia* and *D. xenos*
45a 45b	438	438	C→T C→A	Subgenus *Amanda* and *M. molossus.* Subgenus *Pygmaeia* section *Amaluzae* (except *M. chimboensis*).
46	445	445	T→C	Subgenus *Fissia* and *D. xenos*
47	447	447	T→C	Subgenus *Cucullatia*, *M. schlimii*, *M. herradurae*, *M. collina* and *M. campyloglossa*
48	451	451	C→G	Subgenus *Pygmaeia* section *Amaluzae* (except *M. chimboensis*) and *M. aphanes*
49	452	452	A→G	Subgenus *Cucullatia* and *M. pleurothalloides.*
50	456	456	G→A	Subgenus *Cucullatia*
51	457	457	G→A	Subgenus *Fissia* and *D. xenos*
52	459	459	A→G	Subgenus *Masdevallia* section *Reichenbachianae* and *M. floribunda*
53	460	460	G→T	Subgenus *Cucullatia* and *Meleagris*.
54	470	470	T→C	Subgenus *Pygmaeia* section *Amaluzae*, *M. peristeria*, and *M. pyxis*.

Table 13 Cont. Distribution of 81 possibly informative unambiguous character transformations.

Char. #	**From pos.**	**To pos.**	**Most likely event, or sequence indel**	**Taxa (and remarks)**
55	472	472	T→C or G	Genera *Luerella* and *Trisetella*; *Dracula houtteana*, *D. sodiroi* and *D. chimera; Masdevallia* subgenus *Masdevallia* section *Coriaceae*; subgenus *Pygmaeia* section *Zahlbrucknerae*; *M. erinacea*, *M. oreas*, *M. pyxis*, *M. schlimii*, *M. melanoxantha*, *M. uniflora*, *M. estradae*, and *M. cyclotega*
56	476	476	G→A	Subgenus *Masdevallia* section *Masdevallia* and *D. xenos*
57	483	483	G→A or C	Subgenus *Meleagris*
58	492	492	T→C	Subgenera *Volvula* and *Masdevallia* sections *Masdevallia* (except *M. lamprotyria* and *M. hieroglyphica*), and *Racemosae*; *M. collina*, *M. hoeijeri* and *M. erinacea.*
58b			T→G	Genera *Luerella*, *Trisetella* and *Dracula* (except *D. xenos*)
59	499	499	C→T	Subgenera *Volvula* and *Masdevallia* sections *Masdevallia* and *Racemosae, Pygmaeia* section *Amaluzae*, *M. aphanes*, *M. macrura.*
60	501	501	G→A	Subgenera *Amanda*, *Nidificia*, *Fissia*, *Meleagris*, *Scabripes*, *Cucullatia*, *Teagueia*, *Masdevallia* sections *Coriaceae*, *Dentatae*, *Minutae*, *Reichenbachianae* and *Triotosiphon*; *Polyantha*; *Pygmaeia* section *Zahlbrucknerae*, *M. chimboensis* (section *Amaluzae*), *M. mentosa*; *M. hoeijeri* (section *Aphanes*), and *Dracula xenos*.
61	508	508	T→A T→C or G	Subgenus *Masdevallia* section *Masdevallia, D. astuta.* Subgenus *Pygmaeia* section *Zahlbrucknerae, M. campyloglossa*, *M. coriacea*, *M. heteroptera* and *Luerella pelecaniceps*
62	517	517	G→C	Subgenus *Masdevallia* section *Reichenbachianae*, *M. cupularis*, and *M. lata*.
63	531	531	T→C	Subgenus *Masdevallia* section *Reichenbachianae*, *M. erinacea* and *Luerella pelecaniceps*
64	532	532	G→T	Subgenera *Cucullatia, Teagueia*, and *Masdevallia veitchiana.*
65	575	575	C→T	Genera *Dracula*, *Trisetella*, and *Masdevallia*
66	582	582	C or T→G	Genus *Masdevallia* (except *M. erinacea*) and *D. xenos*
67	592	592	A→G	Subgenus *Pygmaeia* section *Zahlbruckneraeand M. erinacea.*
68	601	601	T→C or G	Subgenus *Masdevallia* sections *Coriaceae*, *Dentatae*, *Reichenbachianae, Minutae*, and *Triotosiphon*; *Polyantha*; *Pygmaeia* section *Zahlbrucknerae*, *M. chimboensis* and *M. mentosa.*
69	605	605	A→C	Subgenus *Masdevallia* section *Durae*; *Pygmaeia* section *Amaluzae* (except *M. chimboensis*) and *M. aphanes.*
70	606	606	T→C	Subgenera Cu*cullatia* and *Teagueia*, *M. mentosa*, and *M. scabrilinguis*
71	607	607	A→G	Subgenus *Masdevallia* section *Triotosiphon*, *M. garciae*, *M. wendlandiana* and *M. gutierrezii*
72	610	610	A→G	Subgenus *Pygmaeia* section *Zahlbrucknerae, M. mentosa*, *M. melanoxantha*, *M. guttulata.*
73	614	614	A→G	Subgenera *Polyantha*, *Masdevallia* sections *Dentatae* and *Reichenbachianae*; *Pygmaeia* section *Zahlbrucknerae*; *M. herradurae*, *M. chimboensis*, *M. floribunda*, *M. mentosa*, *M. scabrilinguis*, and *M. pescadoensis*.
74	629	629	C→G	Subgenus *Masdevallia* section *Reichenbachianae*, *M. cupularis*, *M. erinacea*, and *M. pescadoensis*
75	632	632	A→G	Subgenera *Amanda* and *Nidificia, M. naranjapatae*, *M. bicornis*, *M. zahlbruckneri, M. hoeijeri*, *M. lata*, and *M. striatella.*
76	638	638	C→T	Subgenus *Masdevallia* section *Masdevallia* subsections *Caudatae* (except *M. antonii* and *M. cyclotega*), *Coccinea*, *Masdevallia* (except *M. uniflora*), and *Saltatrices.* Genus *Dracula* except *D. cochliops* and *D. xenos.*
77	645	645	C deletion or C→A	Subgenera *Scabripes*, *Volvula*, *Masdevallia* sections *Masdevallia* and *Racemosae*, *M. macrura* and *M. hoeijeri*
78a 78b	646	646	G→T G→A	Subgenus *Masdevallia* section *Durae*, and *Pygmaeia* section *Amaluzae* Subgenera *Amanda* and *Nidificia*
79	648	648	A→T	Subgenus *Polyantha* (except *M. striatella*, *M. cupularis*, and *M. lata*), *M. herradurae*, and *M. mentosa*.

Table 13 Cont. Distribution of 81 possibly informative unambiguous character transformations.

Char. #	**From pos.**	**To pos.**	**Most likely event, or sequence indel**	**Taxa (and remarks)**
80	649	649	T→C	Subgenus *Masdevallia* section *Coriaceae*, *M. herradurae*, *M. cardiantha*, *M. naranjapatae*, and *Luerella pelecaniceps*
81	651	651	G→A	Subgenera *Meleagris* and *Masdevallia* section *Triotosiphon, M. gutierrezi,* and *M. wendlandiana*

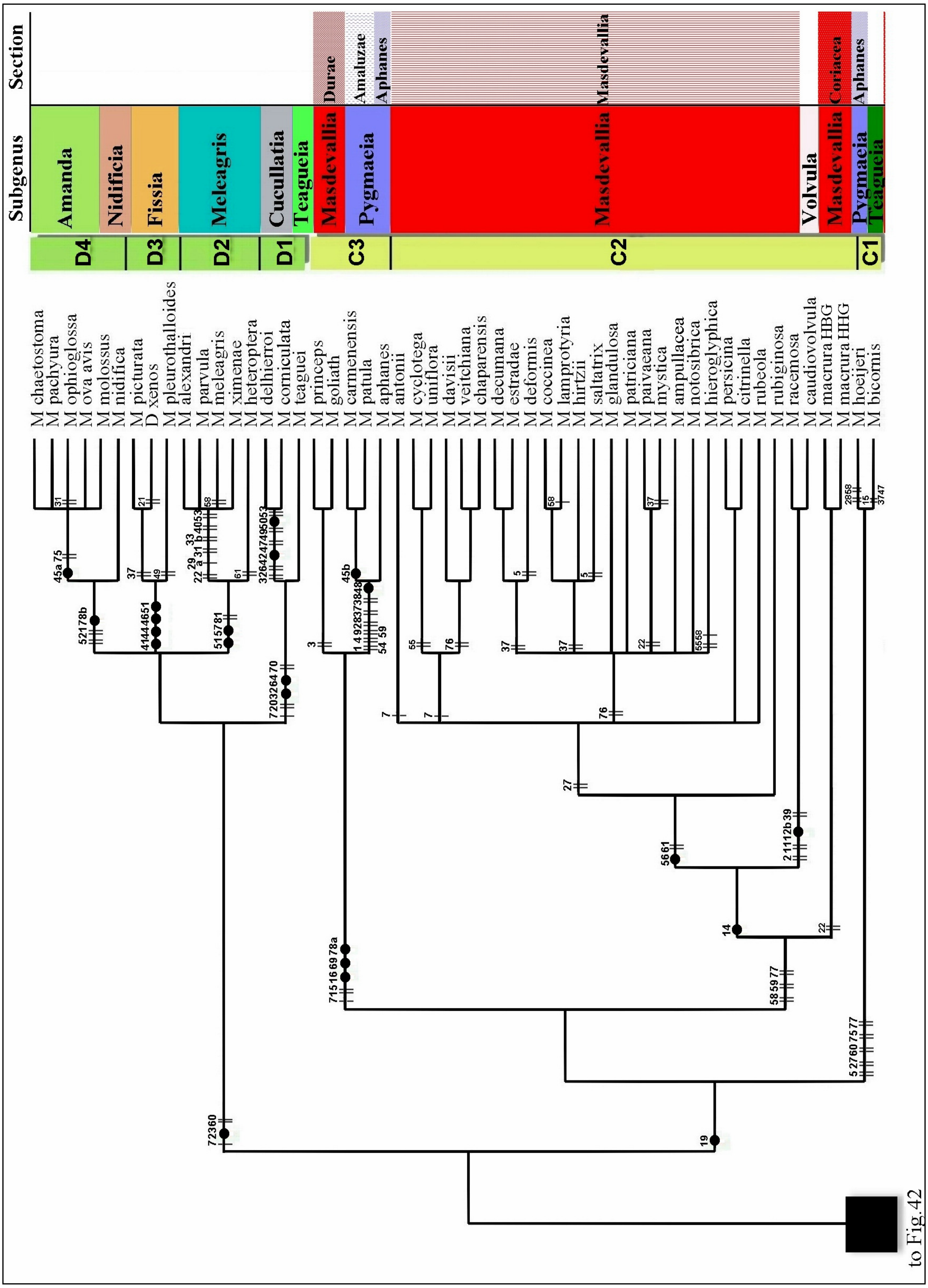

Fig. 41 Strict consensus tree of the analyzed species of *Masdevallia* and outgroups based on ITS sequences data and maximum parsimony analysis together with the infrageneric classification. The numbers above the branches are possibly informative unambiguous character transformations. A a solid circle indicate a possibly informative unambiguous character transformations with a single origin and one or two rows indicate a possibly informative unambiguous character transformations requiring parallel or reversal events

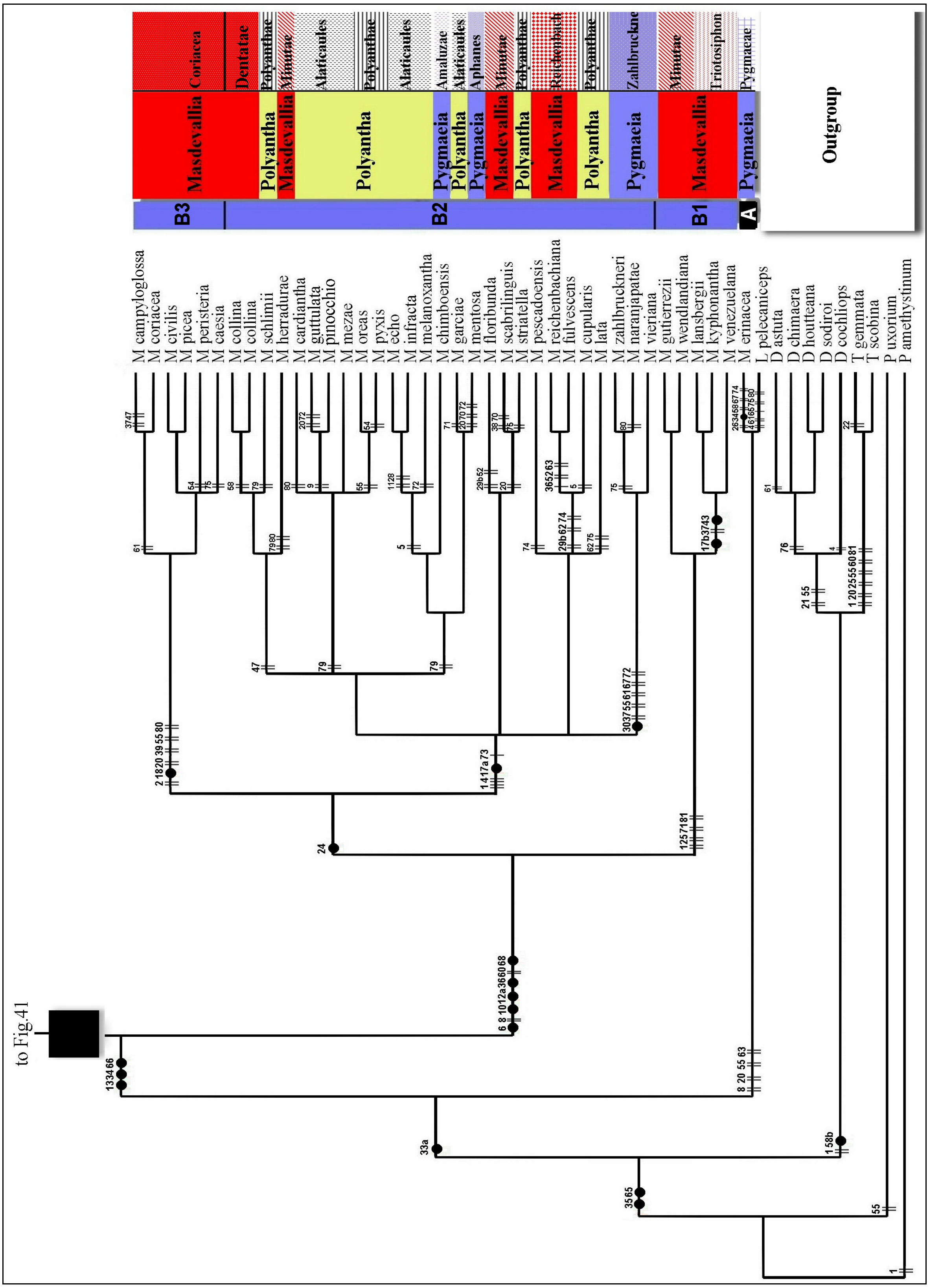
to Fig.41
M campyloglossa
M coriacea
M civilis
M picea
M peristeria
M caesia
M collina
M collina
M schlimii
M herradurae
M cardiantha
M guttulata
M pinocchio
M mezae
M oreas
M pyxis
M echo
M infracta
M melanoxantha
M chimboensis
M garciae
M mentosa
M floribunda
M scabrilinguis
M striatella
M pescadoensis
M reichenbachiana
M fulvescens
M cupularis
M lata
M zahlbruckneri
M naranjapatae
M vieriana
M gutierrezii
M wendlandiana
M lansbergii
M kyphonantha
M venezuelana
M erinacea
L pelecaniceps
D astuta
D chimaera
D houtteana
D sodiroi
D cochliops
T gemmata
T scobina
P uxorium
P amethystinum
B3
B2
B1
A
Masdevallia
Coriacea
Dentatae
Polyantha
Polyanthae
Masdevallia
Minutae
Polyantha
Alaticaules
Polyanthae
Alaticaules
Pygmaeia
Amaluzae
Polyantha
Alaticaules
Pygmaeia
Aphanes
Masdevallia
Minutae
Polyantha
Polyanthae
Masdevallia
Reichenbachia
Polyantha
Polyanthae
Pygmaeia
Zahlbruckne
Masdevallia
Minutae
Triotosiphon
Pygmaeia
Pygmaeae
Outgroup

Fig. 42 Cont.

3.2.2.4 Morphological synapomorphies of the major clades/subclades

All *Masdevallia* species as well as *Dracula xenos* share an oblong (to obovate lip) char. # [71(1,2,3,4,6)] (never spathulate), with a reversal in *M. aphanes* (Fig. 43), and callous petals, with a reversal in *M. chaetostoma* [65(1)] (Fig. 44).

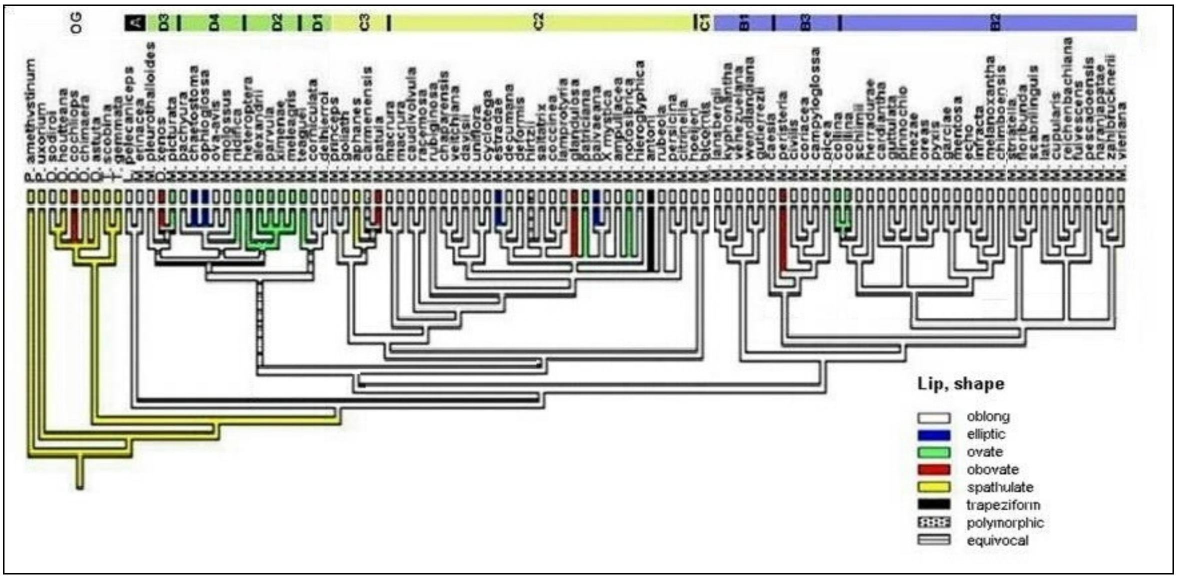

Fig. 43 Reconstruction of character state evolution of the shape of the lip optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

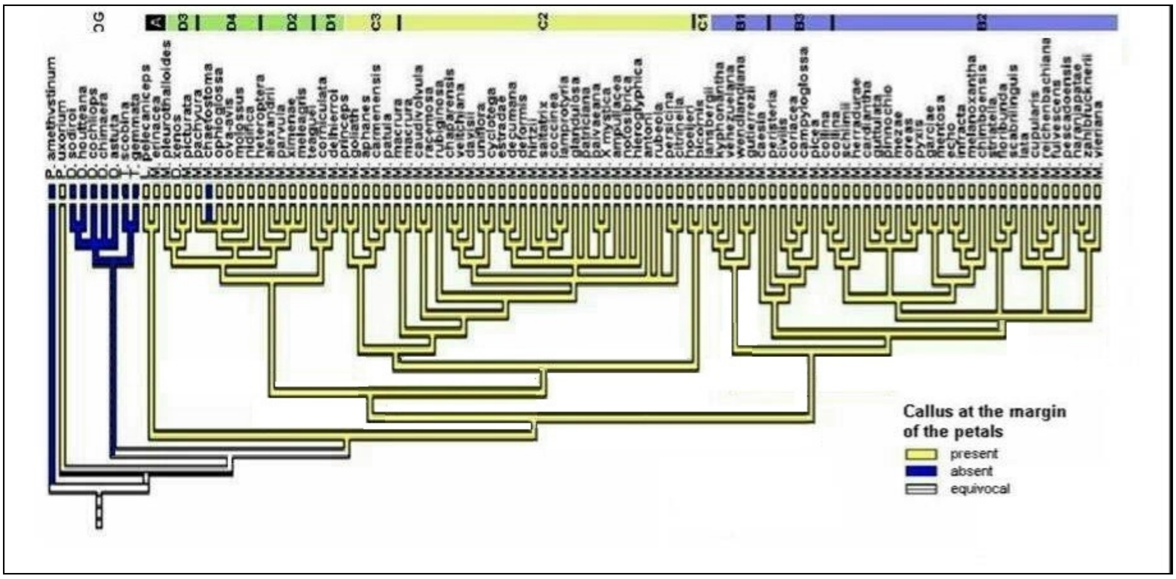

Fig. 44 Reconstruction of character state evolution of the shape of the prescence of a callus at the margin of the petals optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

Clade A: ***Masdevallia erinacea*** **(subgenus** ***Pygmaeia*** **section** ***Pygmaeae*****) and** ***Luerella pelecaniceps***

The first clade encountered grouped *M. erinacea* and *L. pelecaniceps*. Although these two species are united on the basis of many characters, none of them could be considered unambiguous.

Clade B: subgenus ***Pygmaeia*** **section** ***Zahlbrucknerae,*** **subgenus** ***Masdevallia*** **sections** ***Triotosiphon*****,** ***Reichenbachianae*****,** ***Minutae*****,** ***Coriaceae*** **and** ***Dentatae,*** **and subgenus** ***Polyantha*** **sections** ***Alaticaules*** **and** ***Polyanthae*****.**

Species grouped in this clade are characterized by a verrucose (to papillose) epichile [65(1)], despite the reversal in 2 clades, one comprising *M. pinnochio* and *M. guttulata*, the other comprising *M. herradurae*, *M. schlimii*, and *M. collina* (Fig. 45).

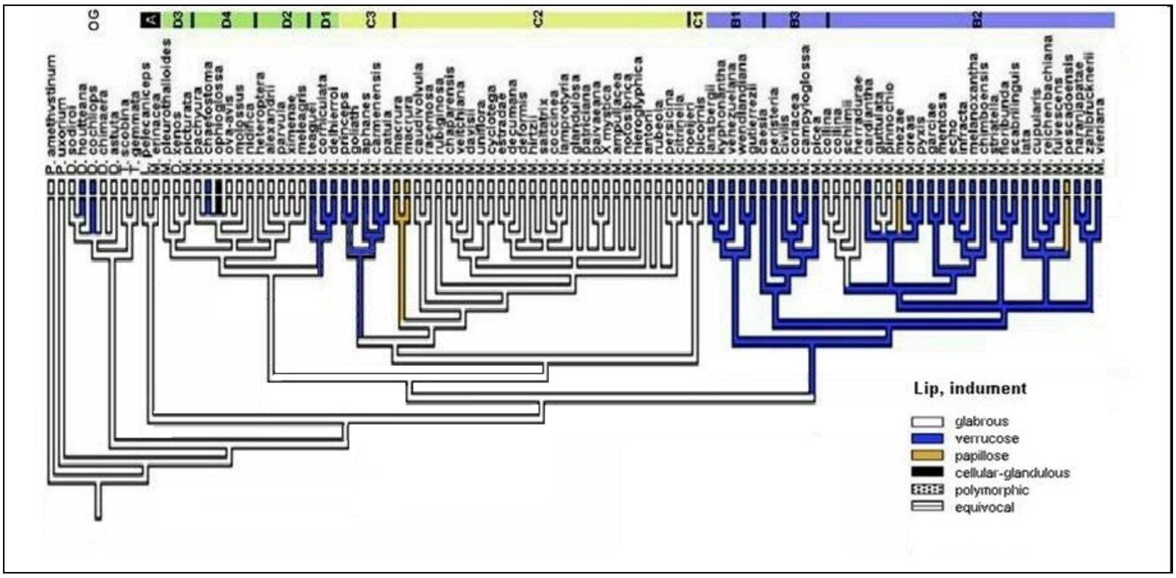

Fig. 45 Reconstruction of character state evolution of the indument of the lip optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

The first subclade within clade B, designed as B1, grouped species of subgenus *Masdevallia* section *Triotosiphon* as well as *M. wendlandiana* and *M. gutierrezii* (subgenus *Masdevallia* section *Minutae*). This group is characterized by a) dorsal and lateral sepals connate for similar lengths [28(1)] (Fig. 46), b) an oblong dorsal sepal [35(1)] (Fig. 47), c) oblong lateral sepals [45(1)], with a reversal in *M. lansbergii* (Fig. 48), and c) possibly by a not sulcate disc of the lip [81(1)] (Fig. 49).

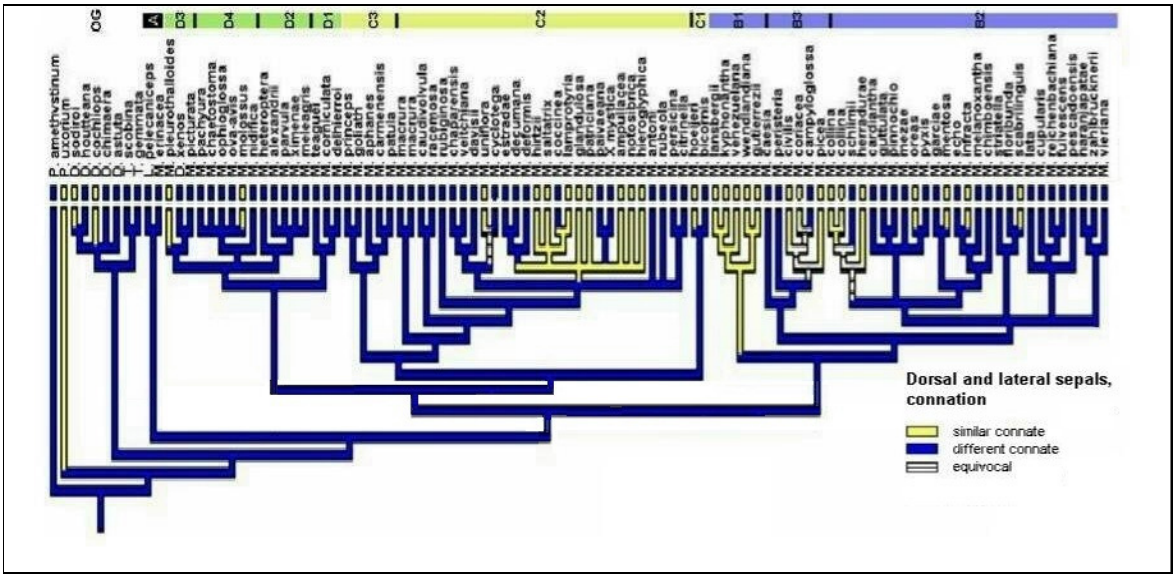

Fig. 46 Reconstruction of character state evolution of the indument of the grade of connation between dorsal and lateral sepals optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

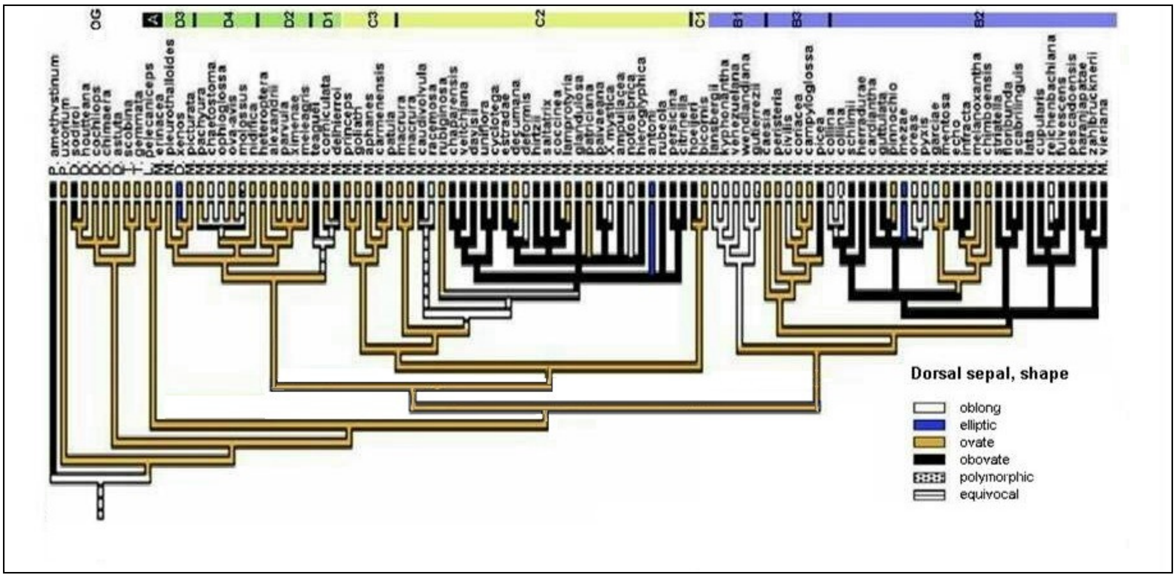

Fig. 47 Reconstruction of character state evolution of the indument of the shape of the dorsal sepal optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

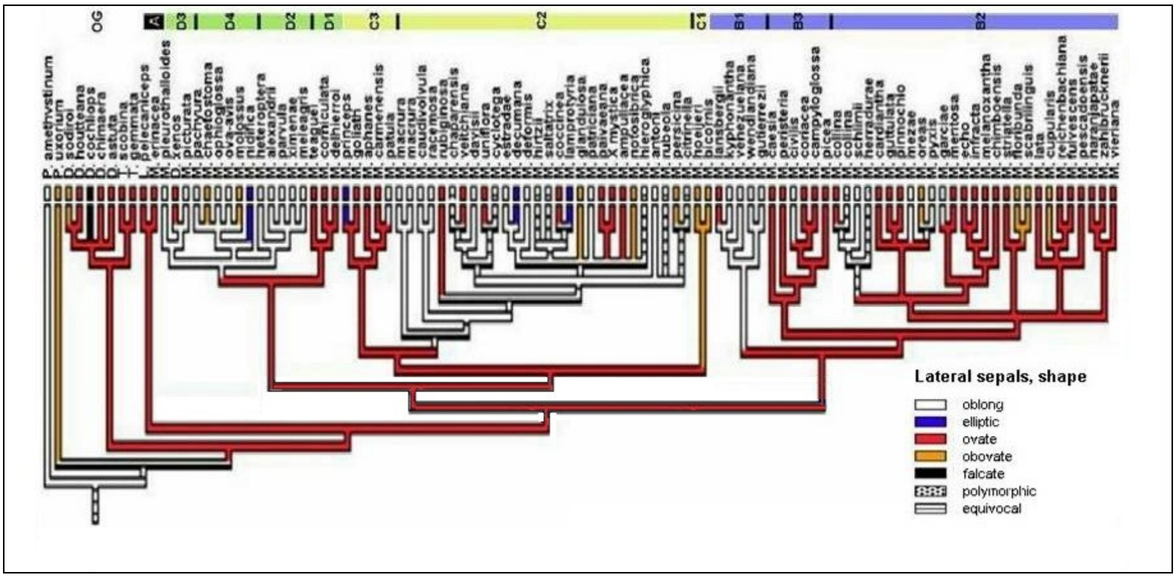

Fig. 48 Reconstruction of character state evolution of the indument of the shape of the lateral sepals optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

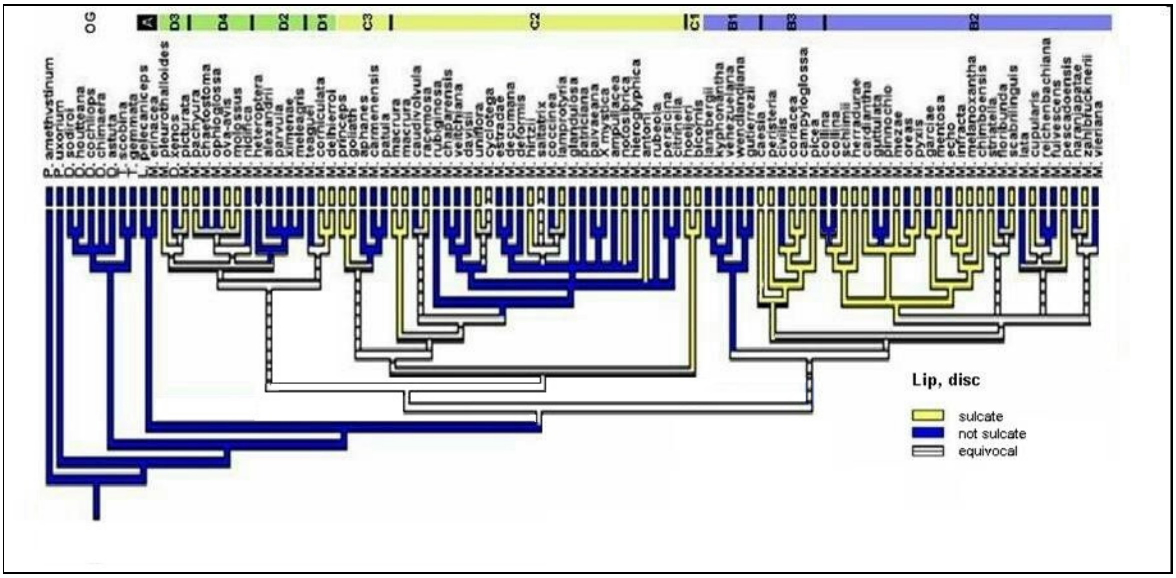

Fig. 49 Reconstruction of character state evolution of the disc of the lip (sulcate or not) optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

Subclade B2 grouped species of subgenera *Polyantha*, *Masdevallia* sections *Dentatae* and *Reichenbachianae*; *M. herradurae*, *M. floribunda*, *M. scabrilinguis*, and *M. pescadoensis* (section *Minutae*); *Pygmaeia* section *Zahlbrucknerae* and *M. mentosa* (section *Aphanes*). This grouping is supported by the following characters: a) the peduncle shorter than the leaves or as long as the leaves [18(2)] (synapomorphy with subclade B3) with a reversal in *M. lata*, and *M. reichenbachiana* and a large subclade within which there are 5 parallel origins of short peduncles (Fig. 50); b) obovate to oblong dorsal sepal [35(4)], with 2 reversal, one in a subclade comprising *M. chimboensis*, *M. melanoxantha*, and *M. mentosa* and one in *M. pinocchio* (see Fig. 47); c) approximate apices of the lateral sepals [50(2)] with a reversal in *M. vierana*, *M. fulvescens*, *M. cupularis*, *M. garciae*, *M. pyxis*, *M. mezae* and *M. herradurae* (Fig. 51); d) denticulate or apiculate apices of the petals (bilobed to entire in *M. naranjapatae*, *M. infracta*, *M. pyxis*, *M. pinocchio*, and *M. collina*) [61(4-5)], with a reversal in *M. vieriana*, a subclade comprising *M. fulvescens* and *M. reichenbachiana*, and once or twice in a subclade comprising *M. chimboensis* and *M. mentosa* (Fig. 52); e) and the lip divided into an epichile and a hypochile [79(1)], with 5 reversal, one in a subclade comprising *M. vieriana*, *M. zahlbrucknerii*, and *M. naranjapatae*, one in a subclade comprising *M. fulvescens*, and *M. reichenbachiana*, and in *M. scabrilinguis*, *M. chimboensis*, *M. mentosa*, and *M. collina* (Fig. 53).

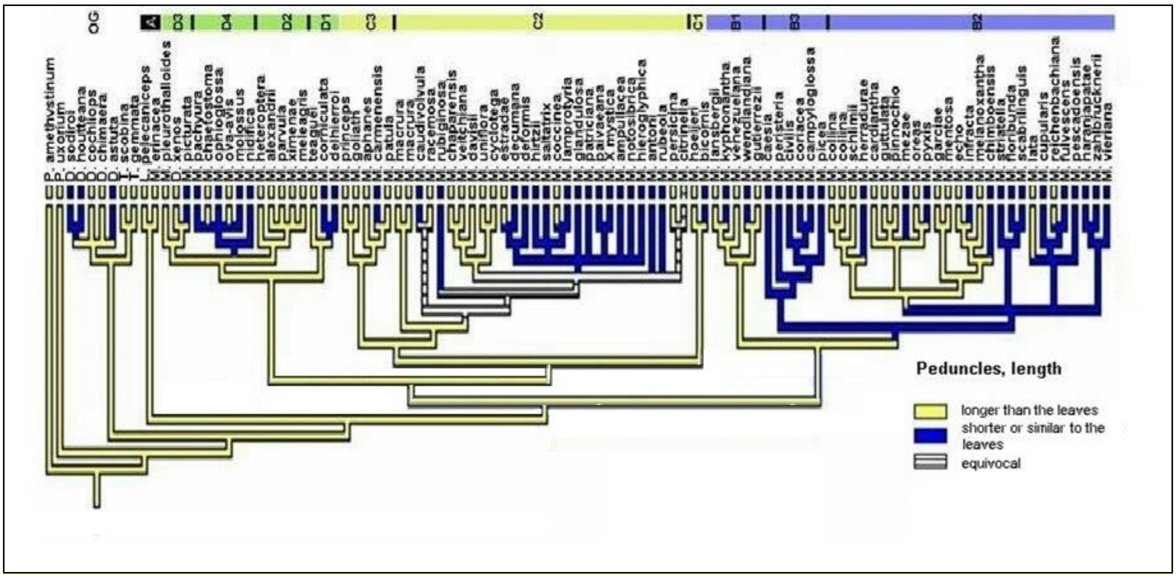

Fig. 50 Reconstruction of character state evolution of the margin of the the peduncles length optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

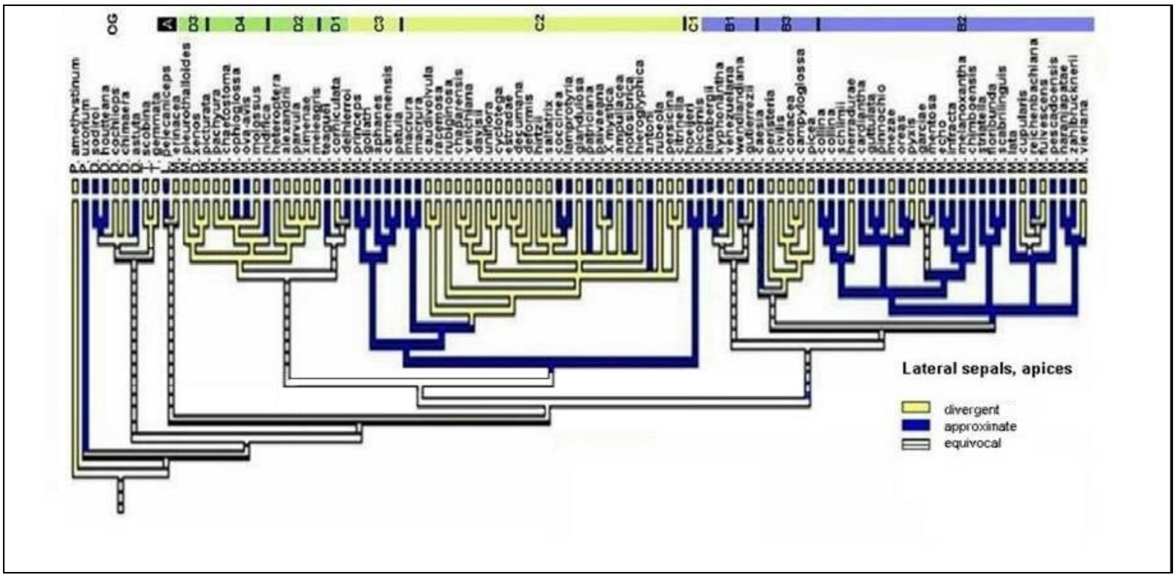

Fig. 51 Reconstruction of character state evolution of the apices of lateral sepals optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

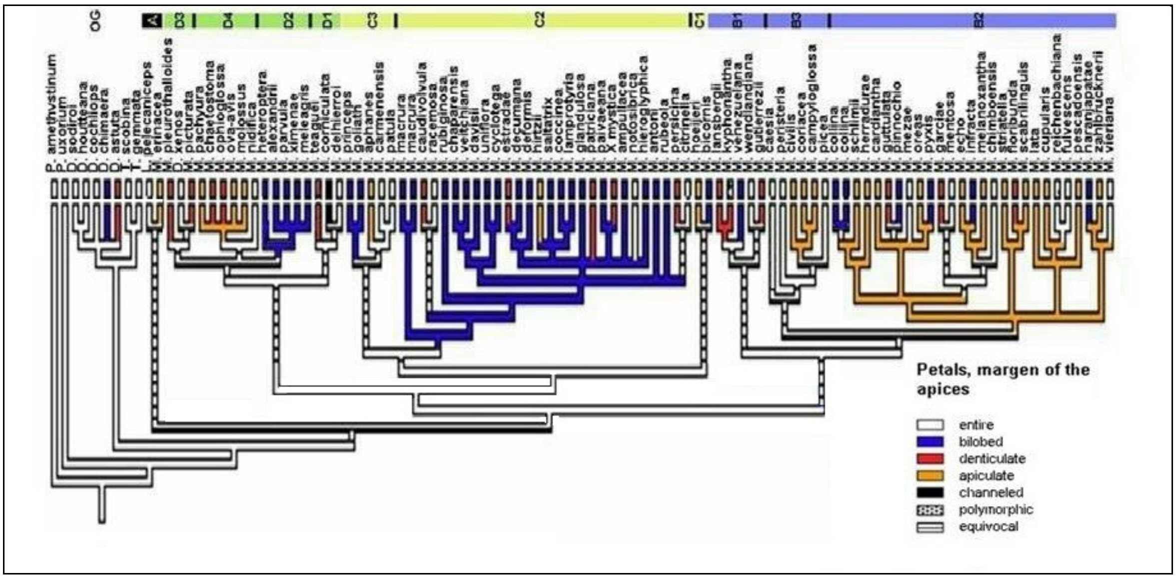

Fig. 52 Reconstruction of character state evolution of the margin of the apices of the dorsal sepal optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

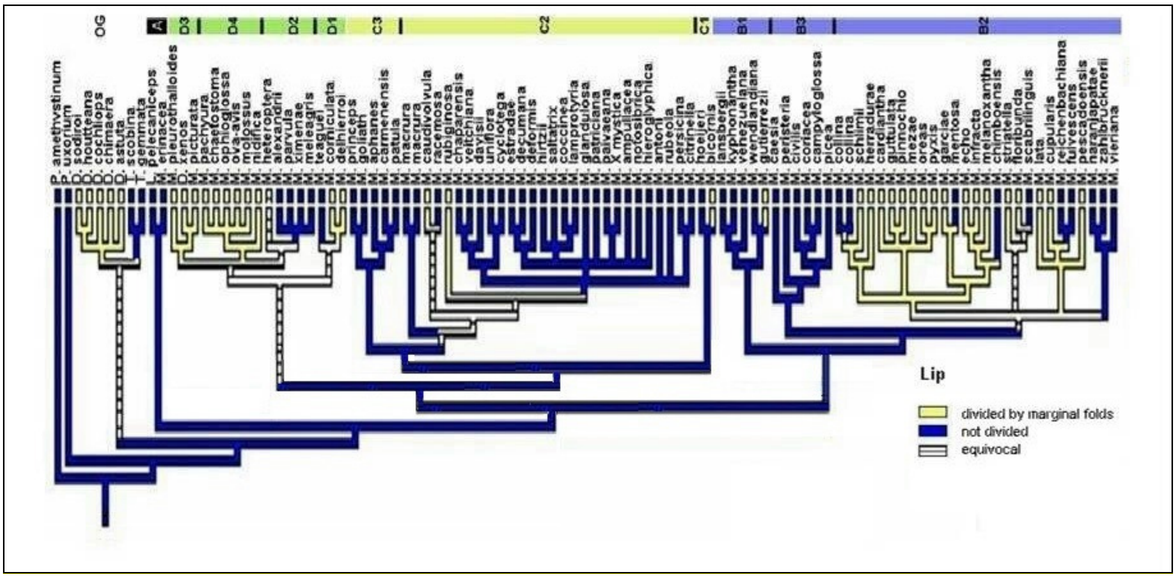

Fig. 53 Reconstruction of character state evolution of marginal folds dividing the lip optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

Subclade B3 comprised species of subgenera *Masdevallia* section *Coriaceae*, which are characterized by a peduncle that is shorter than the leaves or as long as the leaves [18(2)] (synapomorphy with subclade B3) (see Fig. 50), and by pedicels that are thicker and longer than their peduncle [23(1)], with a reversal in *M. campyloglossa* (Fig. 54).

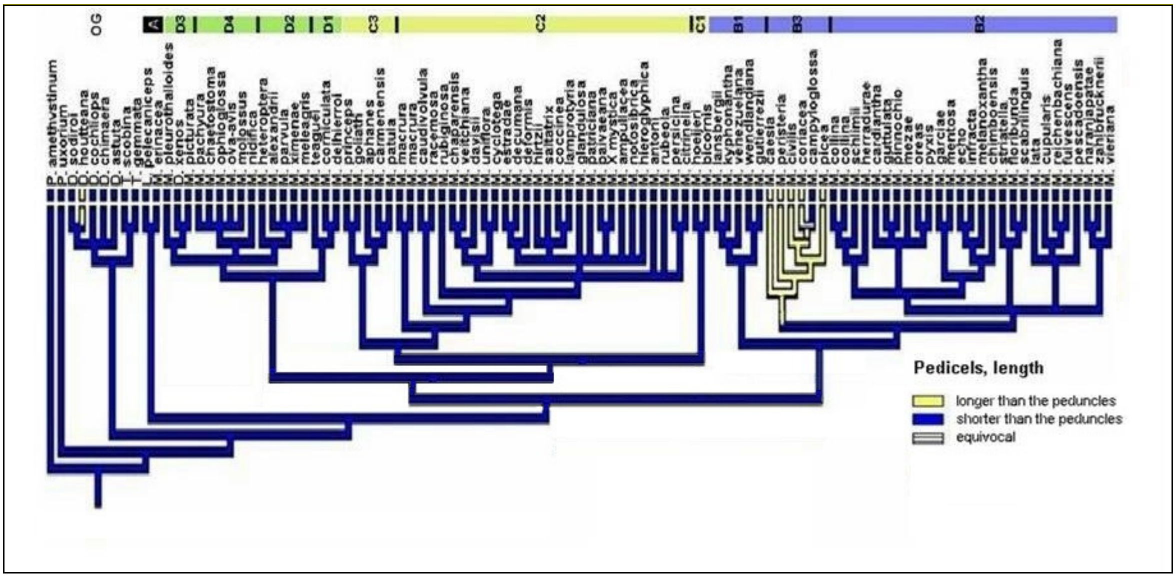

Fig. 54 Reconstruction of character state evolution of the margin of the length of pedicels optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

Clade C: subgenera *Pygmaeia* sections *Amaluzae* and *Aphanes, Masdevallia* sections *Durae*, *Racemosae* and *Masdevallia, Volvula*, *Scabripes*, *M*. *macrura* (subgenus *Masdevallia* section *Coriaceae*), and *M*. *hoeijeri* (subgenus *Pygmaeia* section *Aphanes*).

Lateral sepals connate without the formation of a broad mentum or a secondary mentum with the column-foot [34(1)] are present in most species of clade C, despite a reversal in *M*. *patriciana*, and (at least) two cases of parallelisms or reversals, one in *M. hoeijeri*, one, and the other in a subclade comprising *M*. *carmenensis* and *M*. *aphanes* (Fig. 55).

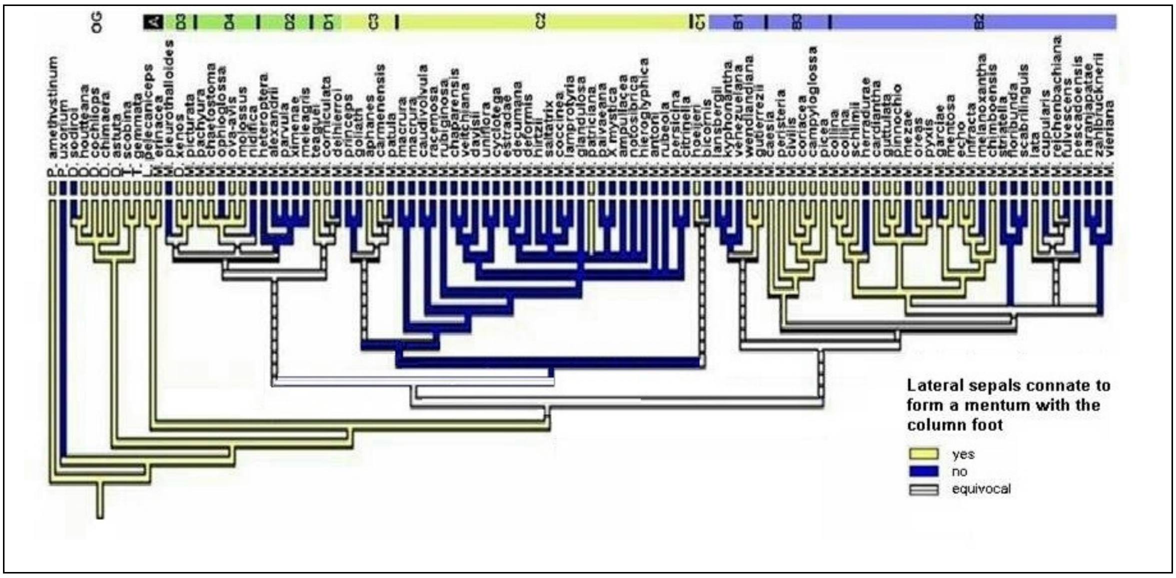

Fig. 55 Reconstruction of character state evolution of the lateral sepals connate to form a mentum optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

The first subclade encountered designated as C1 grouped *M. hoeijeri* and *M. bicornis.* Although these two species are united on the basis of many characters, none of them could be considered unambiguous.

The second subclade within clade C, designated as C2, is for the larger part characterized by the callus of the petals ending in a retrorse (or descending) process [69(1,2)] except a reversal in *M. notosibrica.* However, a few of the dorsal species of clade C2, *M. racemosa*, *M. caudivolvula*, and *M. macrura* retained the plesiomorphic state (Fig. 56).Character [74(1)], base of the lip truncate, shows a similar distribution (Fig. 57). It characterizes most of subclade C2, with reversals in *M. notosibrica*, *M.* X *mystica*, *M. coccinea*, *M. deformis* and *M. veitchiana. Masdevallia macrura* again retained the plesiomorphic state, while it is uncertain whether there is a reversal in *M. racemosa* or a parallelism in *M. caudivolvula*. Masdevallia macrura, M. caudivolvula and M. racemosa also retained the plesiomorphic state (not callous) in character 77 apex of the lip not callous. In most of the other species of subclade C2, the lip is callous at the apex [77(1)] except in *M. notosibrica*, *M. ampullacea*, *M.* X *mystica*, *M. hirtzii*, and *M. deformis* (Fig. 58). An even smaller subclade of subclade C2 is characterized by a prominent margin of the exine [94(2)]. Besides the afore mentioned species (*M. racemosa*, *M. caudivolvula*, and *M. macrura*), also *M. rubiginosa*, retained the plesiomorphic state (Fig. 59).

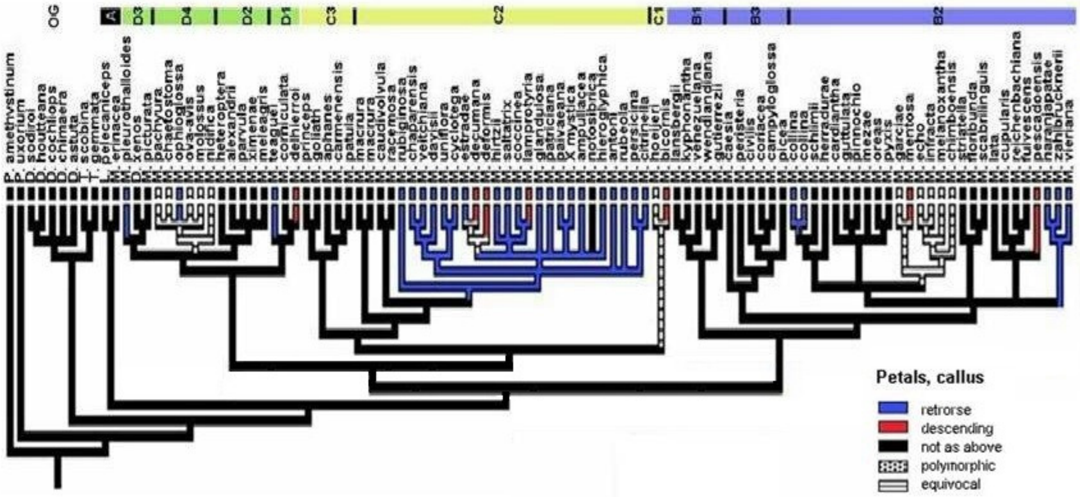

Fig. 56 Reconstruction of character state evolution of the of the ending of the callus of the petals optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

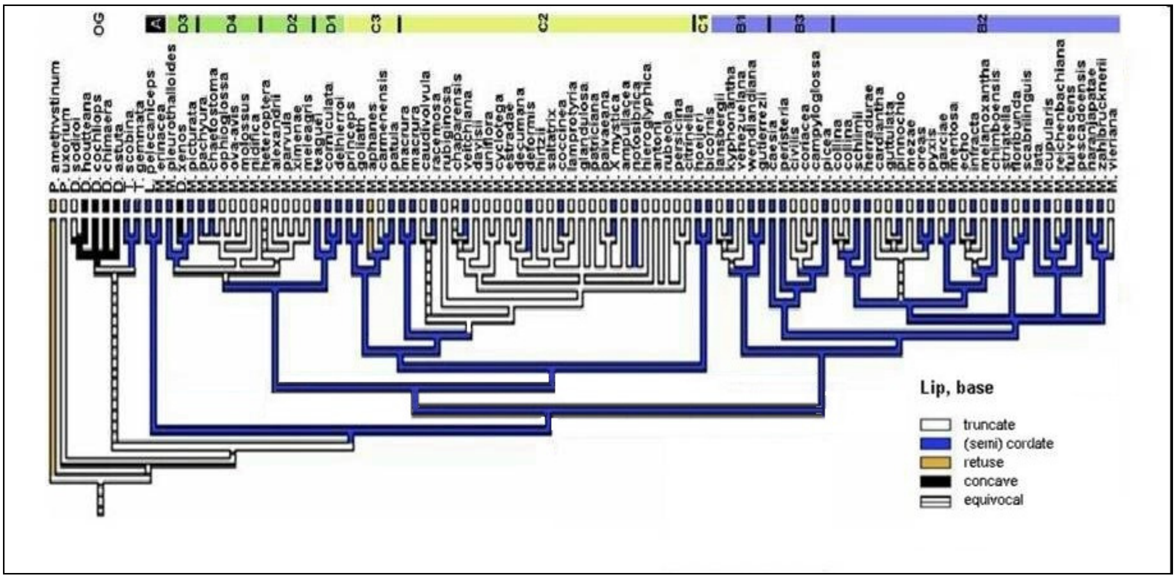

Fig. 57 Reconstruction of character state evolution of the base of the lip optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

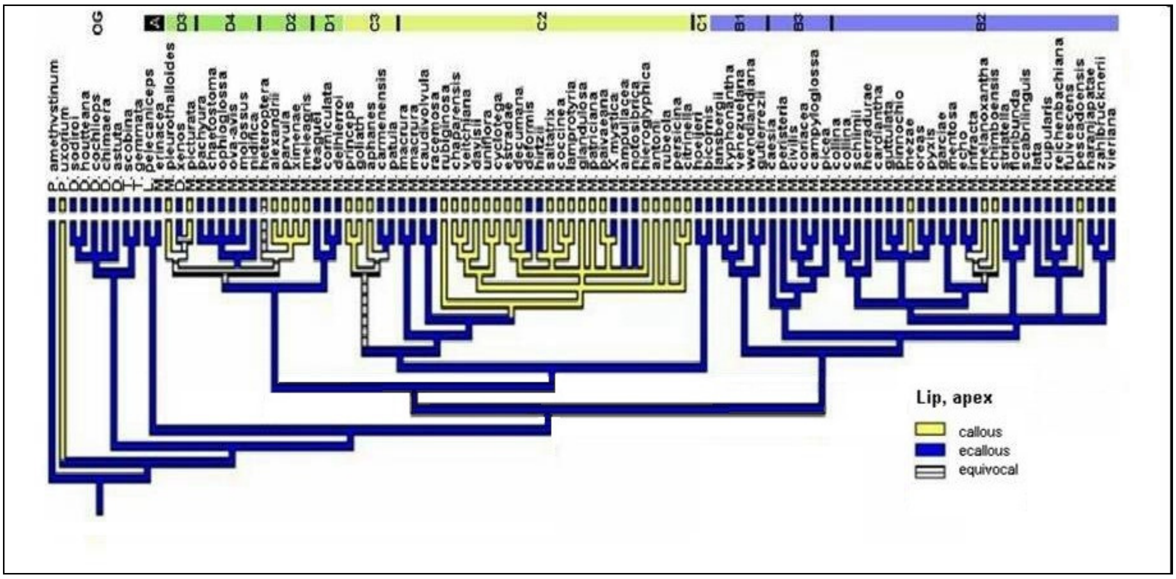

Fig. 58 Reconstruction of character state evolution of the prescence of a callus at the base of the lip optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

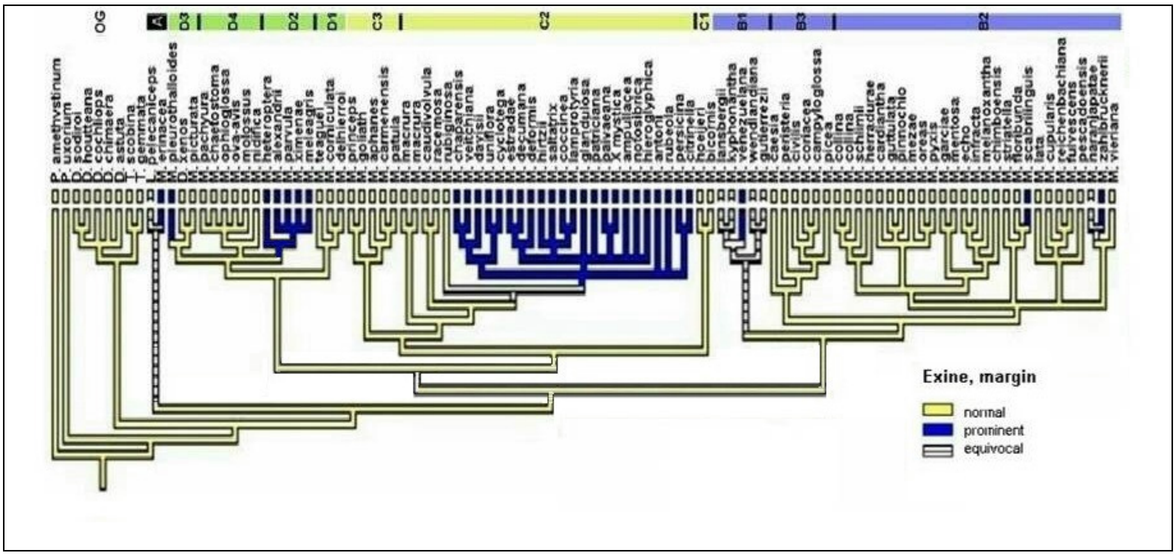

Fig. 59 Reconstruction of character state evolution of the margin of the exine optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

The species grouped in the subclade designated as C3 all share approximated tails of the lateral sepals [52(2)]. This, however, is plesiomorphic for clade C (see Fig. 51). A synapomorphy for this clade seems to be a verrucose lip [65(1)] (Fig. 45).

Clade D: subgenera *Teagueia*, *Cucullatia*, *Nidificia*, *Amanda*, *Fissia*, *Meleagris*, and *Dracula xenos*.

Synapomorphies of the species grouped in this clade are the arcuate sepaline tubes [31(1)] (Fig. 60), and the featureless disc of the lip [80(3)] (with three lamellae in *M. teaguei*), with two reversals, one in *M. molossus*, and the other in *M. chaetostoma* (Fig. 61).

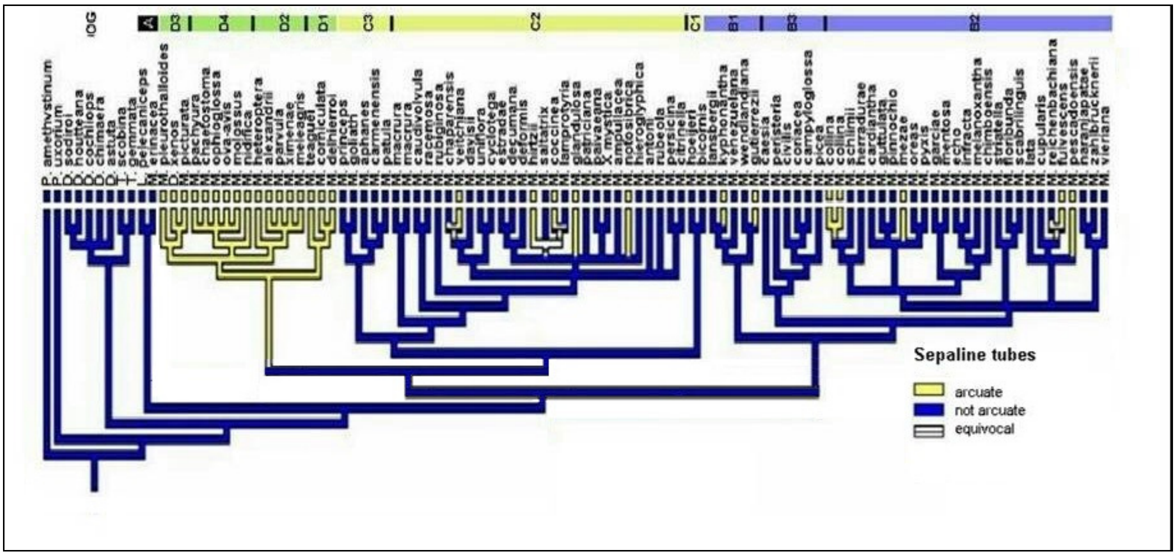

Fig. 60 Reconstruction of character state evolution of the shape of sepaline tubes optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

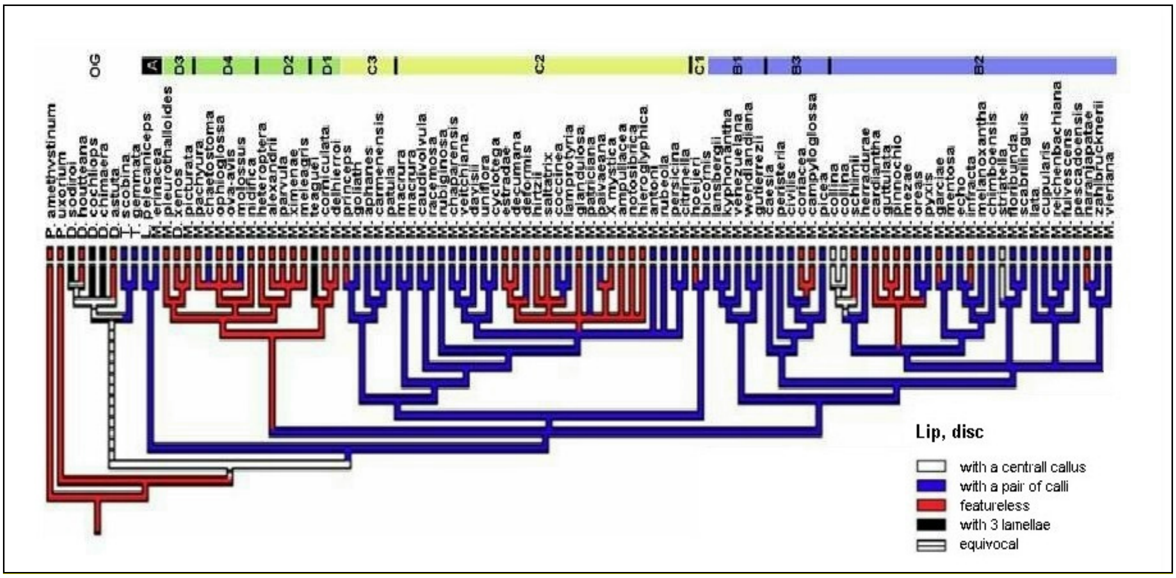

Fig. 61 Reconstruction of character state evolution of the surface of the disc of the lip optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

Two morphological synapomorphies characterize the species of subclade D1, the tail of the dorsal sepal longer than the tail of lateral sepals [44(3)] (Fig. 62), and a verrucose (to papillose) epichile [65(1)] (see Fig. 45).

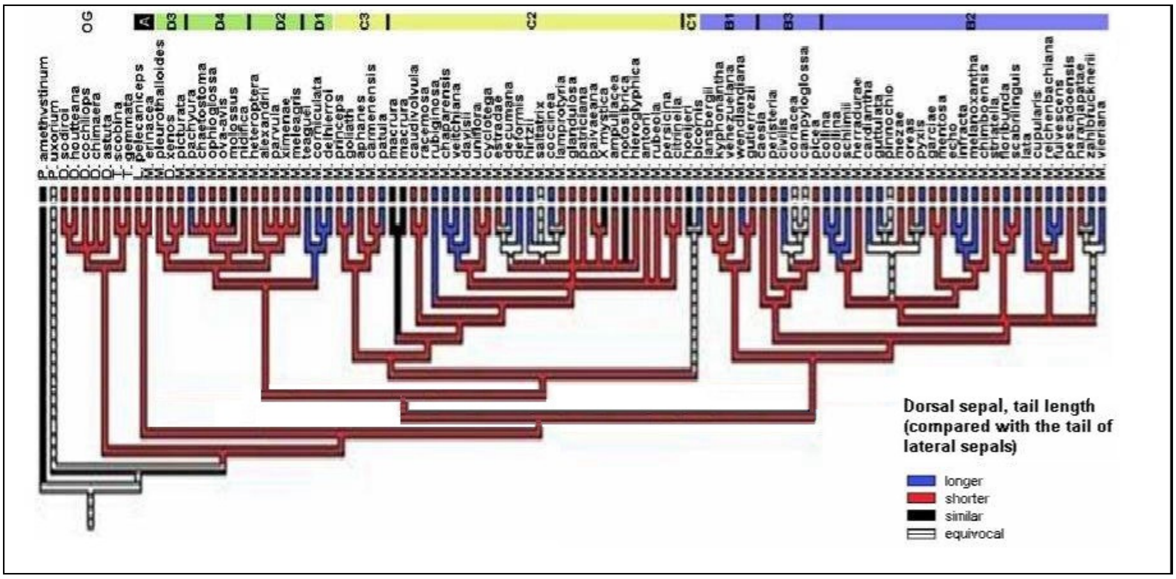

Fig. 62 Reconstruction of character state evolution of the tail length of the dorsal sepal optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

The next subclade, D2, is characterized by the following synapomorphies: a) papillose ovaries [25(2)] (Fig. 63), b) ovaries with undulating crests [24(2)] (synapomorphy with subclades D3 and D4) (Fig. 64), c) the dorsal sepal free from the lateral sepals (probable synapomorphy with subclade D3) [26(1)] (Fig. 65), d) the lateral sepals connate below the middle [33(3)] (synapomorphy with subclades D3 and D4) (Fig. 66), e) a ciliate margin of dorsal sepal [38(4)] and f) of the lateral sepals [48(4)]

(Fig. 67 and 68), g) tail of the dorsal sepal half as long to as long as its lamina [43(2)] (Fig. 69), h) pubescent lateral sepals [46(2)] (Fig. 70), i) tail of the lateral sepal half as long to as long as its lamina [54(2)] (Fig. 71), j) the petals and lip out of sight deep within the sepaline tube [55(1)] (Fig. 72), k) the longitudinal callus of the petals ending in an acute process [68(2)] (Fig. 73), and l) the prominent margin of the exine [94(2)] (see Fig. 59).

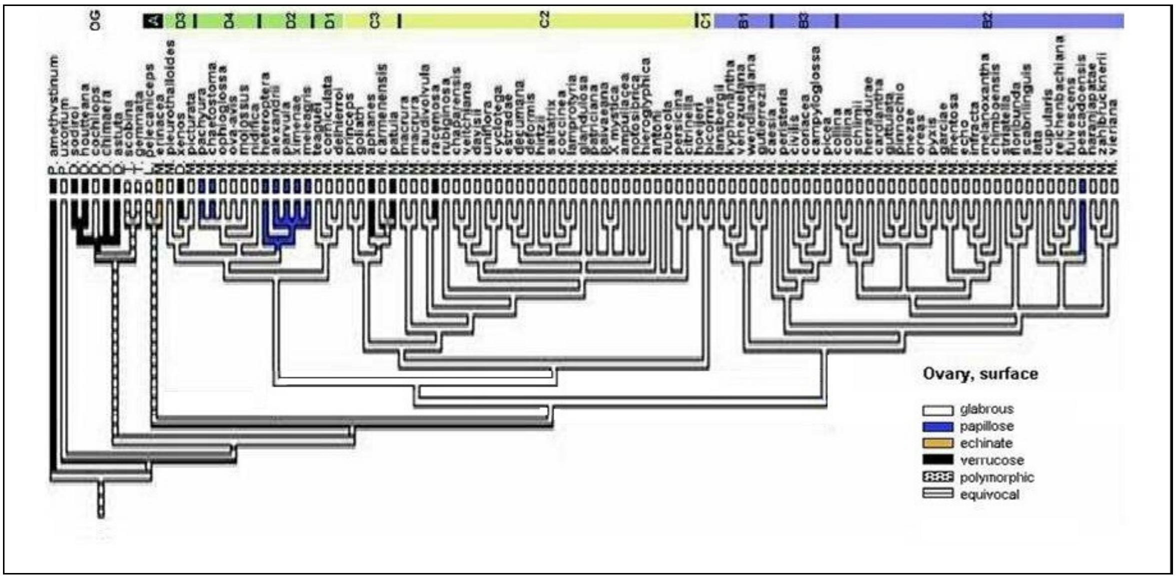

Fig. 63 Reconstruction of character state evolution of the surface of the ovary optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

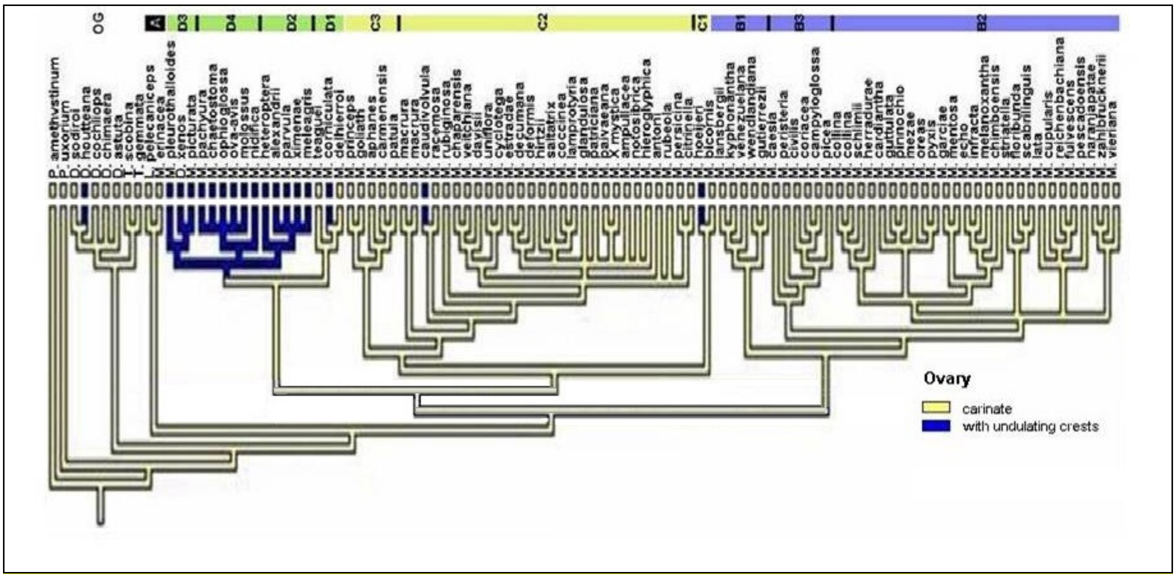

Fig. 64 Reconstruction of character state evolution of the surface of the ovary optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

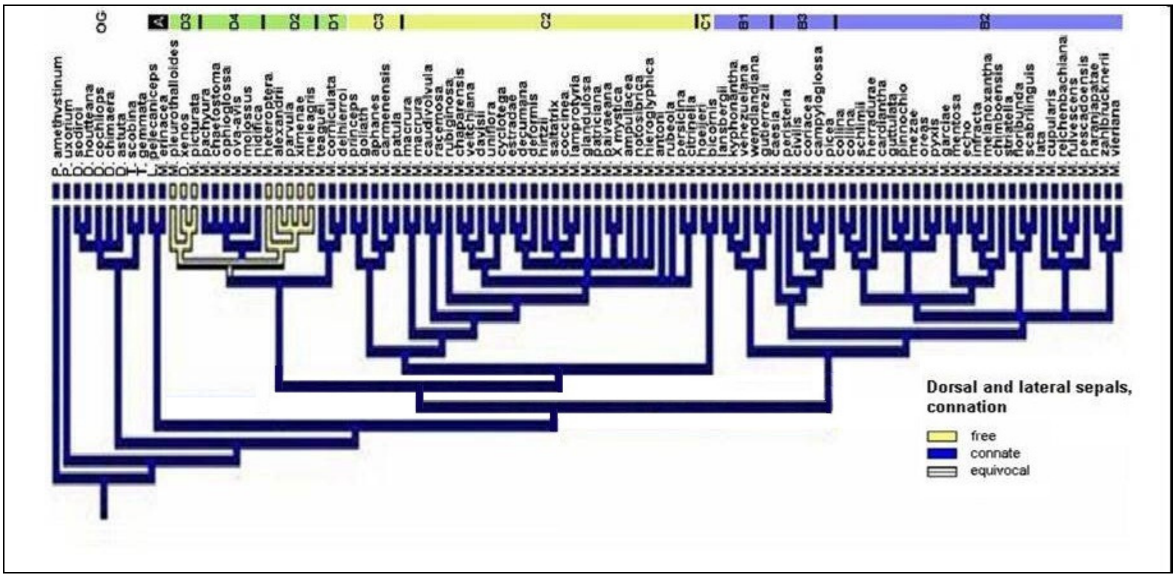

Fig. 65 Reconstruction of character state evolution of the dorsal and lateral sepals connation optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

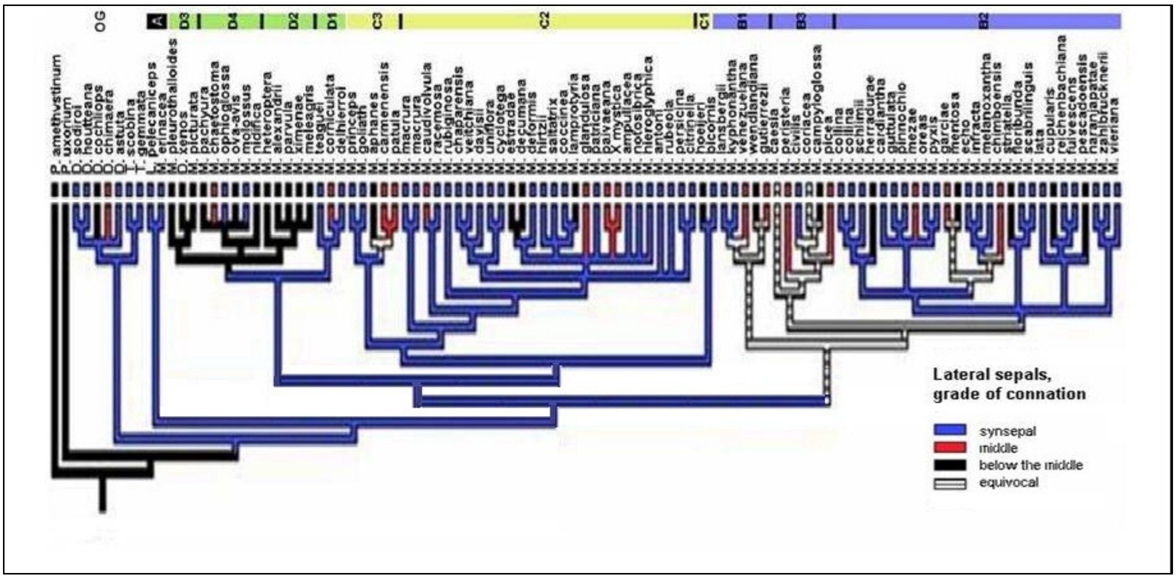

Fig. 66 Reconstruction of character state evolution of the grade of connation between the lateral sepals optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

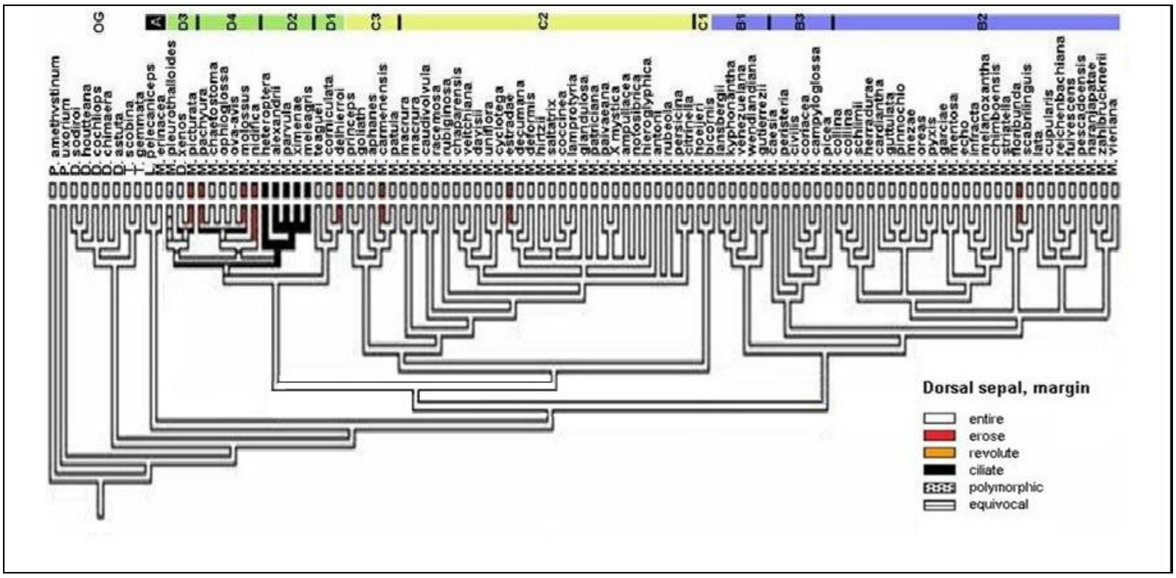

Fig. 67 Reconstruction of character state evolution of the margin of the dorsal sepal optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

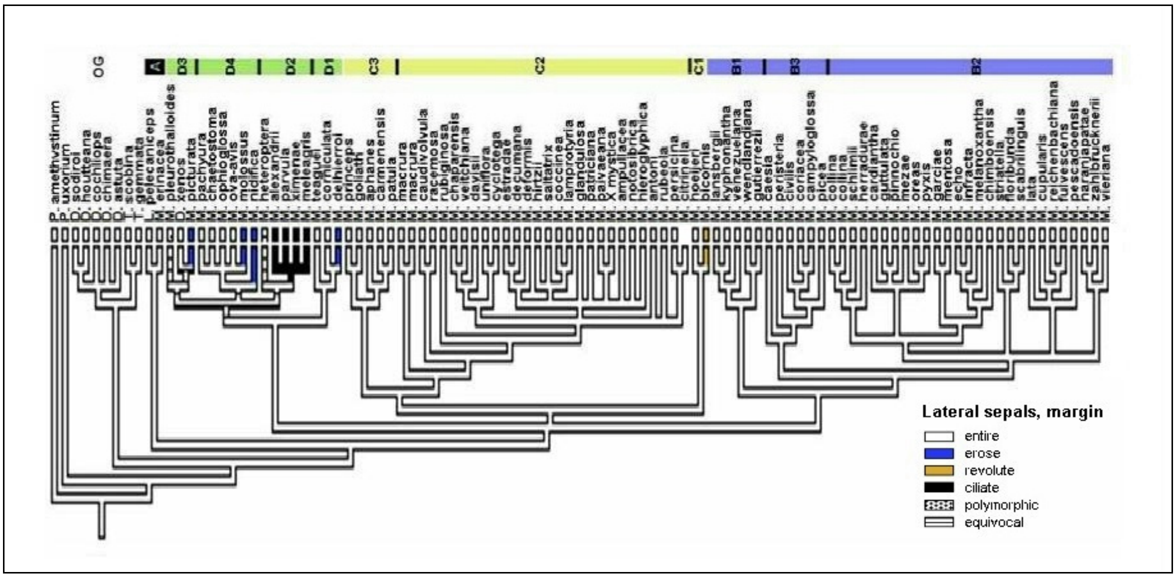

Fig. 68 Reconstruction of character state evolution of the margin of the lateral sepals optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

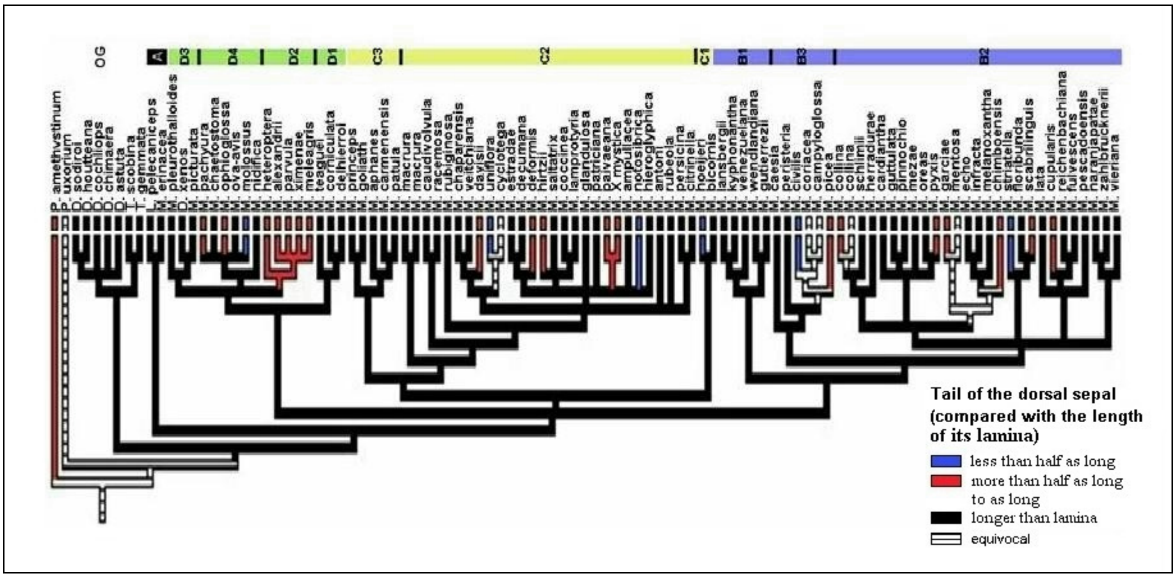

Fig. 69 Reconstruction of character state evolution of the tail of the dorsal sepal optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

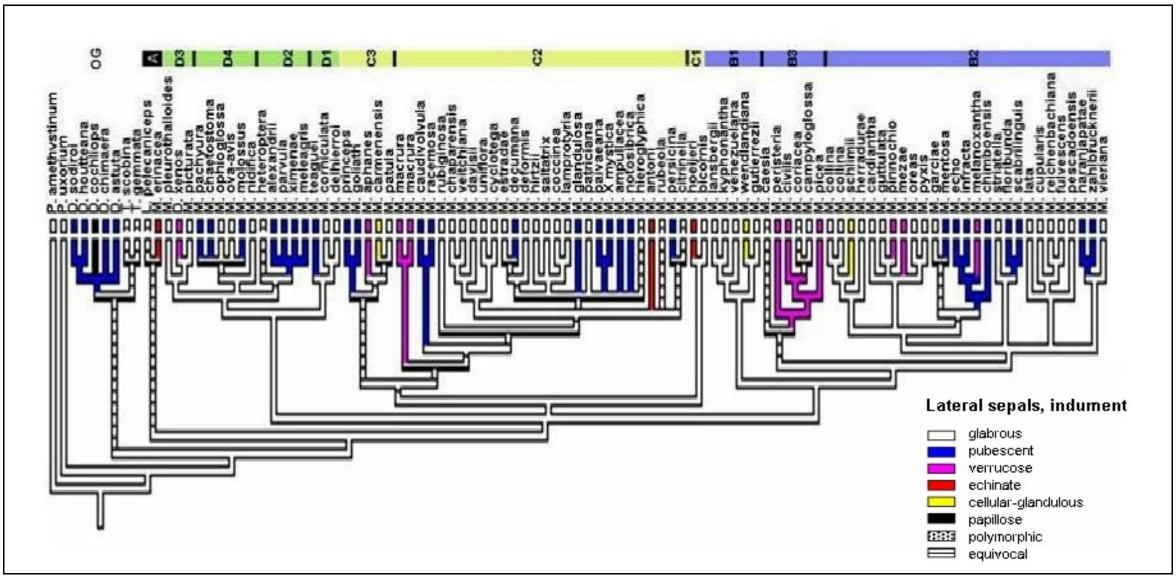

Fig. 70 Reconstruction of character state evolution of the indument of the lateral sepals optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

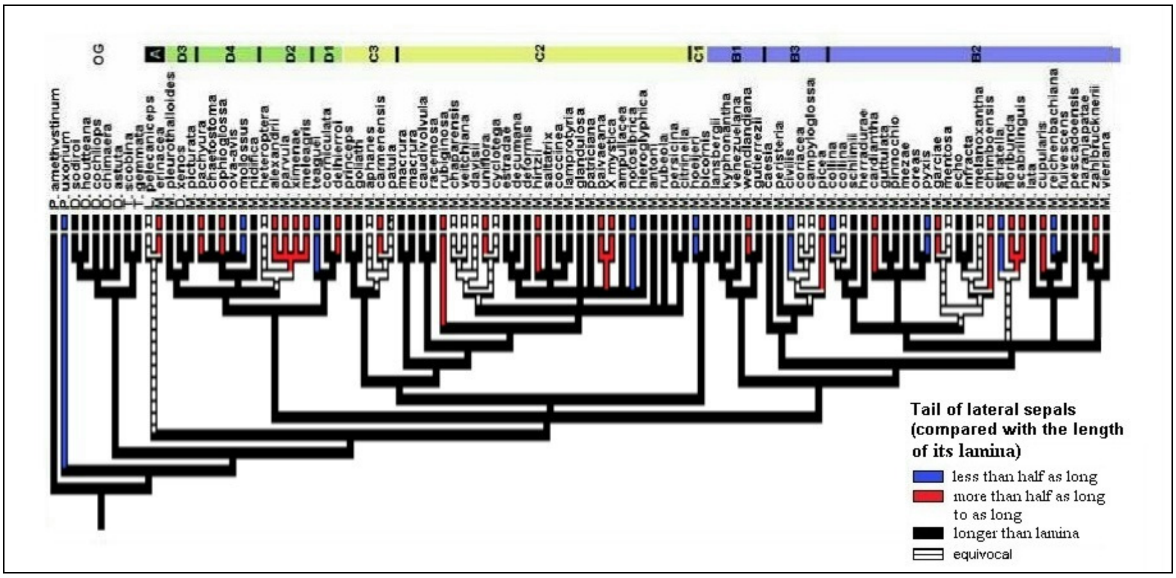

Fig. 71 Reconstruction of character state evolution of the tail of the lateral sepals optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

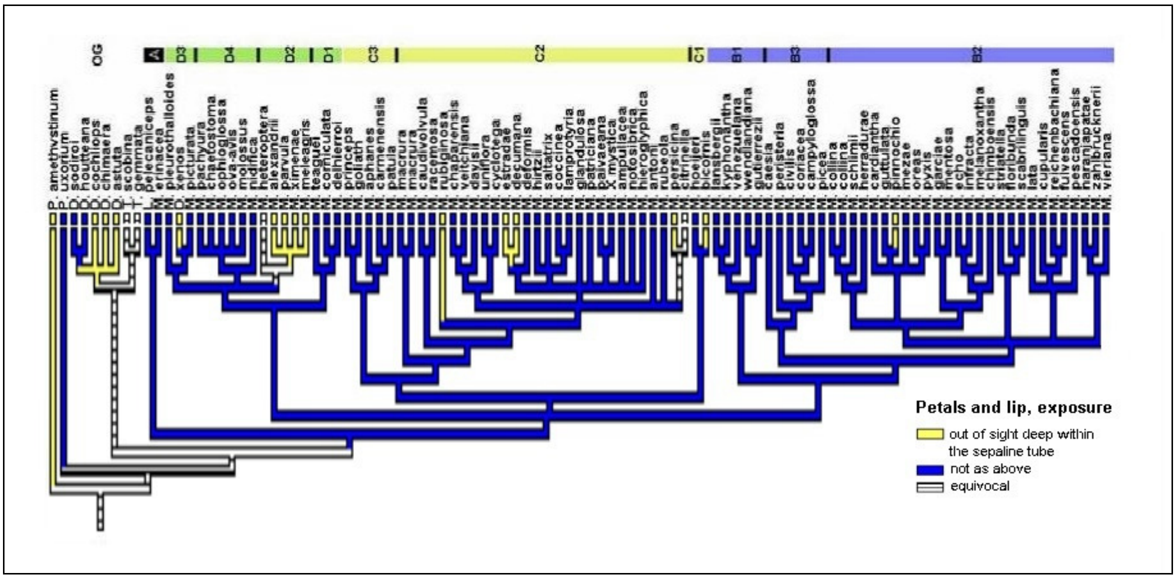

Fig. 72 Reconstruction of character state evolution of the exposure of petals and lip optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

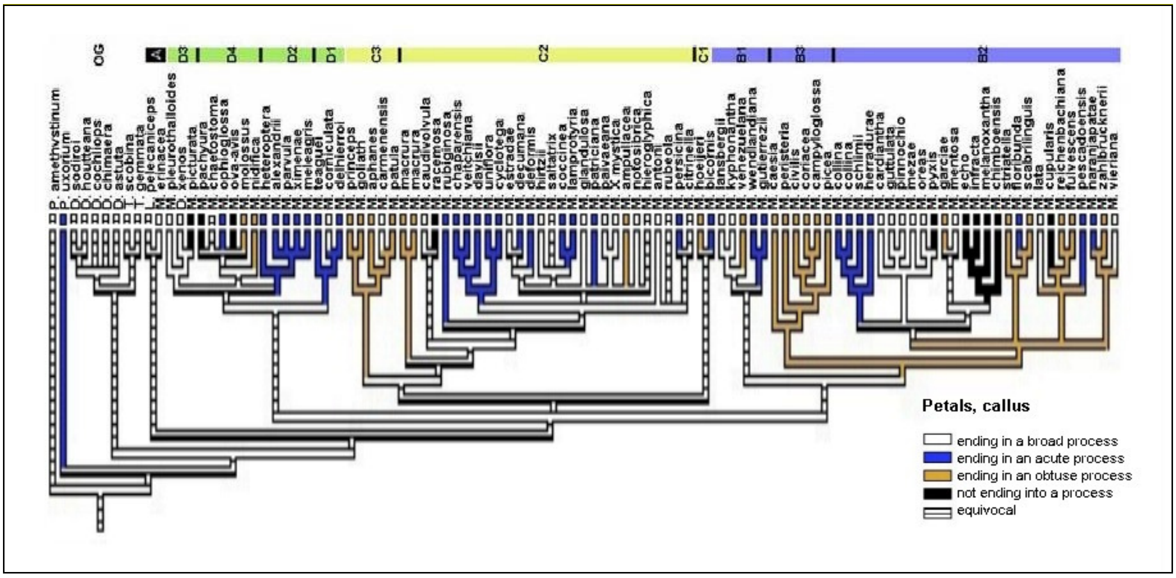

Fig. 73 Reconstruction of character state evolution of the callus of the petals optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

The next subclade D3 grouped species of subgenus *Fissia* and *Dracula xenos* and is characterized by a) ovaries with undulating crests [24(2)] (synapomorphy with subclades D2 and D4) (see Fig. 64), b) the lateral sepals connate below the middle [33(3)] (synapomorphy with subclades D2 and D4) (see Fig. 66), c) the dorsal sepal free from laterals [26(1)] (possible synapomorphy with subclade D2) (see Fig. 65), and d) a divided lip (possible synapomorphy with subclade D4) [79(1)] (see Fig. 53).

Subclade D4 grouped species of subgenera *Amanda* and *Nidificia*. Characteristic for the species grouped in this clade are a) the flowers mostly grouped into racemose inflorescences with the flowers opening in succession over a long periode of time [15(1)] (except in *M. nidifica*, which is single flowered) (Fig. 74), b) the inflated floral bract [21(2)] with a reversal in *M. molossus* and *M. ophioglossa* (Fig. 75), c) the ovary with undulating crests [24(2)] (synapomorphy with subclades D2 and D3) (see Fig. 64), d) the apiculate or denticulate apices of the petals [61(3-5)], with *M. nidifica* retaining the plesiomorphic state (Fig. 76), and e) a divided lip [79(1)] (possible synapomorphy with subclade D3, or possibly for the entire clade D) (see Fig. 53).

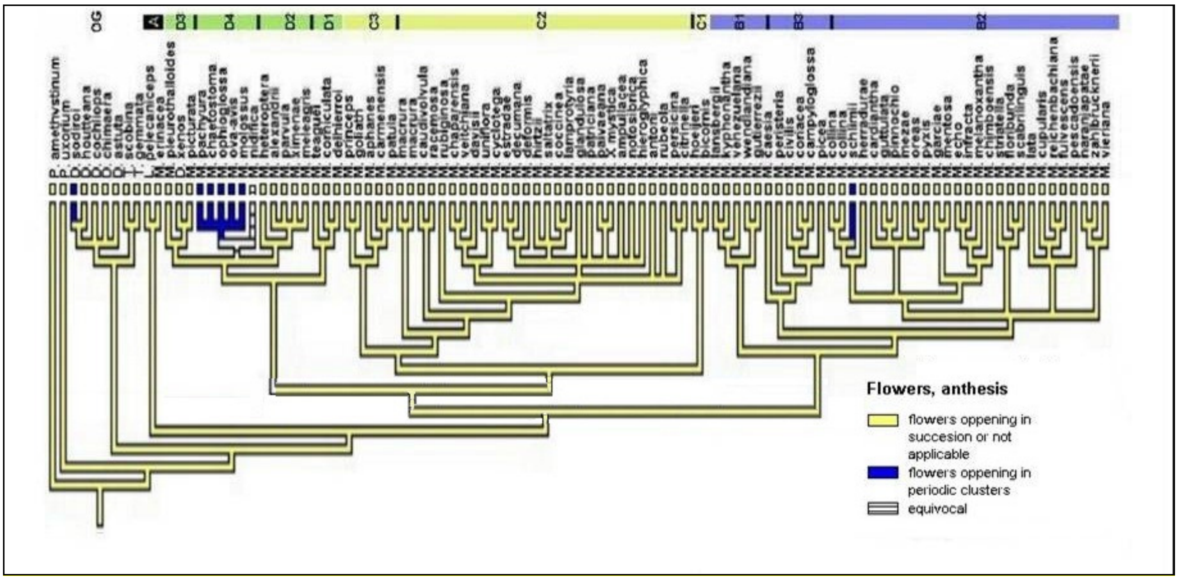

Fig. 74 Reconstruction of character state evolution of the anthesis optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

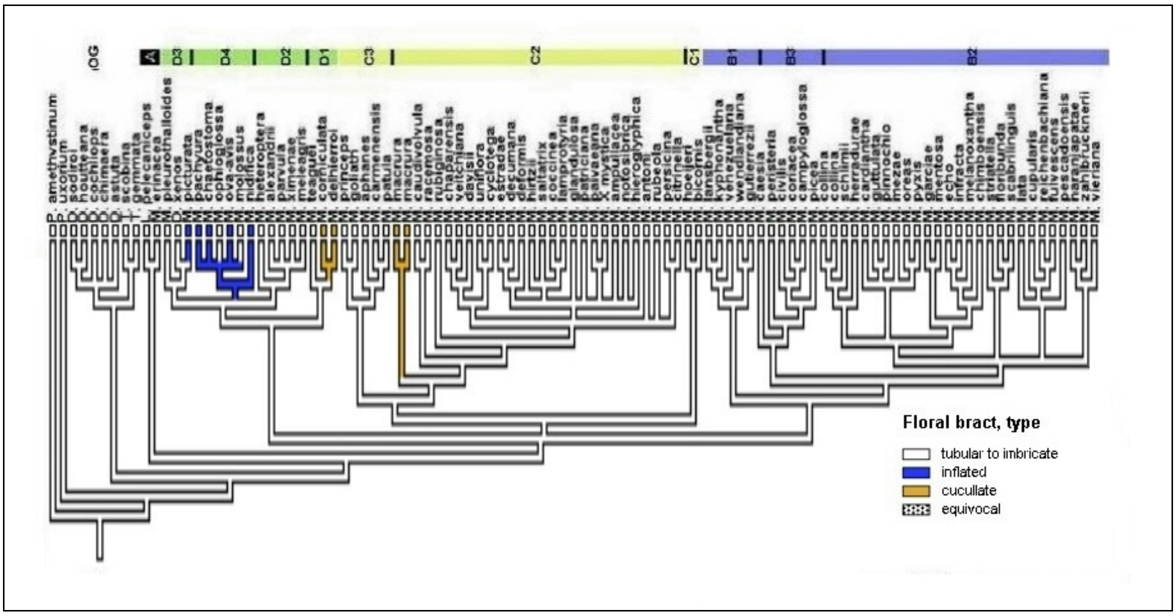

Fig. 75 Reconstruction of character state evolution of the type of floral bract optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

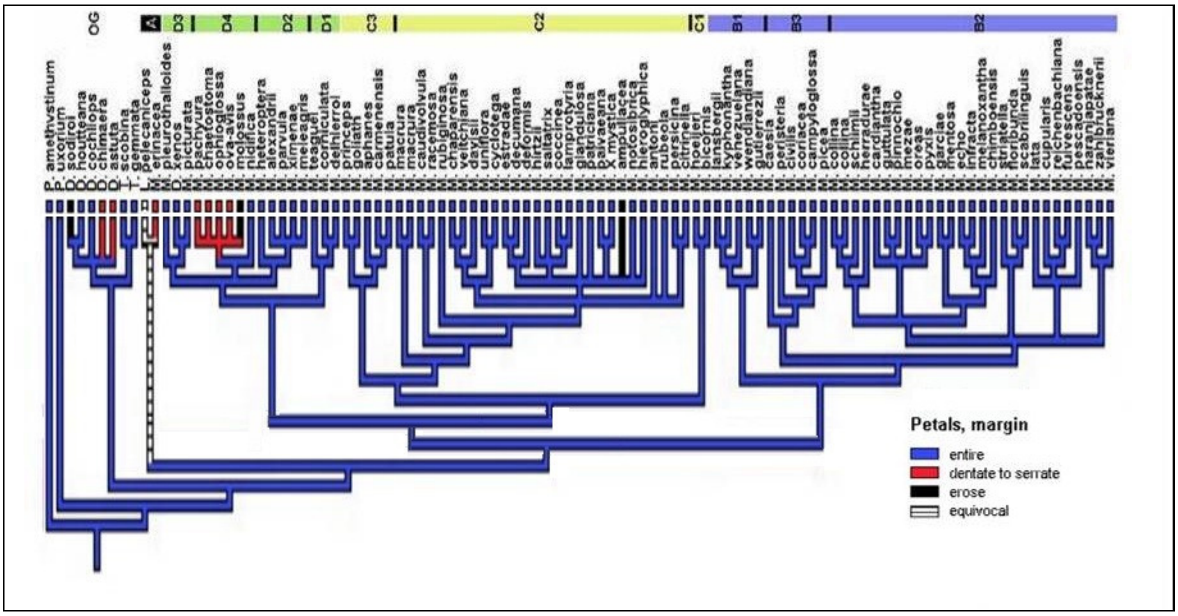

Fig. 76 Reconstruction of character state evolution of the margin of the petals optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

3.3 Combined analysis

3.3.1 Incongruence between the morphological and molecular data

3.3.1.1 Incongruence length difference test

An ILD test on the taxonomically equivalent ITS and morphological data sets detected a significant difference (P<0.01) between these partitions. Comparison of the poorly resolved morphological strict consensus with the ITS tree showed strongly supported topological incongruence. Although each data set showed strongly supported conflicting groups, ITS and morphological data sets were analyzed simultaneously.

3.3.2 Characteristics of the combined data matrix

The combined morphological and ITS matrix has a total length of 759 sites (663 and 96 sites for ITS sequences and morphological data, respectively), of which 327 (232 and 95, respectively) are variable and 224 (131 and 93, respectively) phylogenetically informative (Table 15).

Table 14 Characteristics and variation of the combined data in *Masdevallia*.

	Morphological characters	**Molecular Characters**	**Combined**
All	96	663	759
Constant	1	431	432
Variables **Parsimony uninformative= autapomorphies**	2	101	103
Parsimony informative	93	131	224

3.3.3 Phylogenetic relationships

3.3.3.1 Topology of the most parsimonious trees

Simultaneous analysis of ITS and morphological data resulted in 254 trees of 2134 steps, CI = 0.36, and RI = 0.54. The strict consensus of all 254 trees is shown in Fig. 95. The topology of the combined strict consensus tree was partly congruent with the ITS topology and relationships among species of *Masdevallia* and outgroups were very similar in each tree (see Fig. 39, and Fig. 77).

Six major clades were identified from the parsimony analyses of the combined data (Fig. 77): clade A, with a bootstrap support of 100%, including species of subgenus *Meleagris*; clade B, with a bootstrap

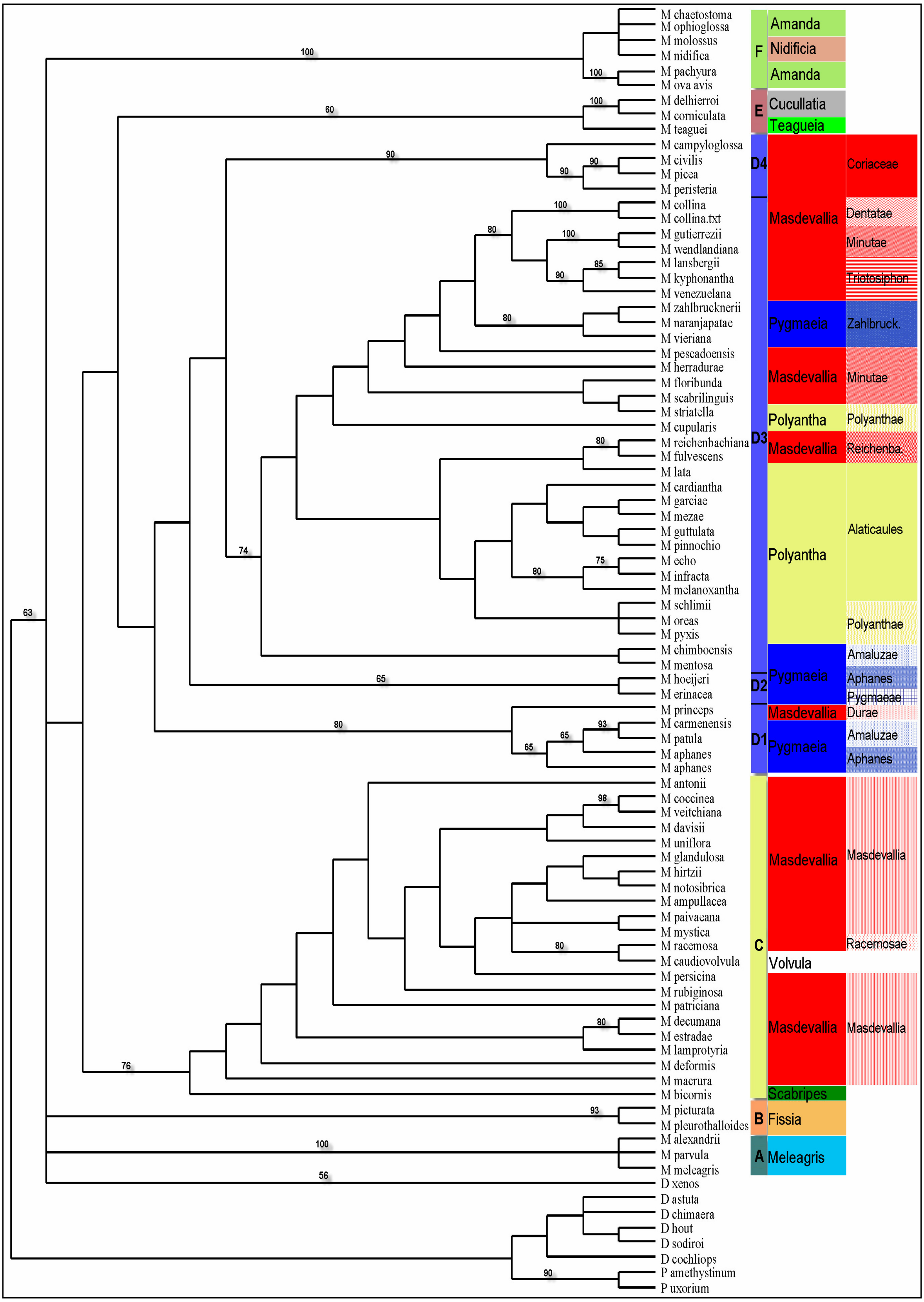

Fig. 77 Strict consensus tree of the analyzed species of *Masdevallia* and outgroups based on non molecular and ITS sequences data, computed from the 254 most parsimonious trees (tree length= 460, consistency index= 0.36, retention index= 0.54). The numbers above the branches are bootstrap percentages. Percentages < 50% are not shown.

support of 93%, composed of species of subgenus *Fissia*; clade C, with a bootstrap support of 76%, grouping species of subgenera *Scabripes*, *Masdevallia* and *Volvula*; clade D, without bootstrap support (but designed as a separate clade for comparison with the analysis of molecular data), including species of subgenera *Pygmaeia*, *Masdevallia*, and *Polyantha*; clade E, with a bootstrap support of 60%, grouping species of subgenus *Teagueia* and *Cucullatia*; and clade F, with a bootstrap support of 100%, grouping species of subgenera *Amanda* and *Nidificia*.

Clade D is composed of four subclades: subclade D1 (80% BS) grouping *M. princeps* (subgenus *Masdevallia* section *Durae*) and species of subgenus *Pygmaeia* sections *Amaluzae* and *Aphanes*; subclade D2 (65% BS) composed of *M. hoeijeri* (subgenus *Pygmaeia* section *Aphanes*) and *M. erinacea* (subgenus *Pygmaeia* section *Pygmaeae*); subclade D3 composed of species of subgenus *Masdevallia* sections *Dentatae*, *Minutae*, *Reichenbachianae*, and *Triotosiphon*; subgenus *Polyantha* sections *Alaticaules* and *Polyanthae*, and subgenus *Pygmaeia* section *Zahlbrucknerae*, *M. chimboensis* (section *Amaluzae*), and *M. mentosa* (section *Aphanes*).

3.4 Biogeography

3.4.1 General biogeographical patterns

Geographic distribution of the analyzed species indicates that there are six main geographic areas of diversification: the Andes, Central America, the Coastal Cordillera of Venezuela, the Guayana region, and the coastal Atlantic forest of southeastern Brazil (Fig. 78).

Of the 92 analyzed species of *Masdevallia*, only *M. wendlandiana* and *M. picturata* are found throughout the whole geographical range; four species are distributed in Central and South America from southern Mexico to Bolivia; nine species (10%) are restricted to Central America; 72 species (78%) are restricted to the northern Andes from Colombia to Ecuador (excluding Venezuela); three species are endemic to Venezuela; two species are distributed in Colombia and Venezuela; *M. lansbergii* is distributed in Venezuela and French Guiana; and *M. infracta* is distributed in Brazil and Bolivia (Figs. 81 to 84). The geographical distribution of the outgroup taxa ranges from Costa Rica to Bolivia (Fig. 80). About 35% of all species analyzed occur above 2 000 m above sea level, more than 50 % occur between 1 000 and 2 000 m above sea level and only 15% are found below 1 000 m above sea level (Fig. 79).

3.4.2 Biogeographical patterns of the major clades

Masdevallia erinacea (clade A) is one of the most widespread species of the genus, ranging from Panama to Ecuador. The second species within clade A, *Luerella pelecaniceps*, is endemic to Panama (Fig. 81).

Members of clade B are found throughout the whole geographical as well as altitudinal range, extending from southern Mexico and Belize to Bolivia, Venezuela to French Guiana and Brazil (Fig. 82); and from 2 to 3 900 m above sea level (Fig. 79).

The species in clade C are restricted to the southern part of the geographical range of the group, Colombia to Bolivia (Fig. 83). The altitudinal range varies from to 600 to 3 250 m above sea level (Fig. 79), but most species (at least in subclade C2) are from higher elevations (above 2 000 m above sea level).

Members of clade D have a wide range of geographical distribution, with the main center of radiation in Ecuador and Colombia. *Masdevallia nidifica* and *M. picturata* are the most widespread species of the clade (Fig. 84). The altitudinal range varies from 450 to 3 100 m above sea level (Fig.79).

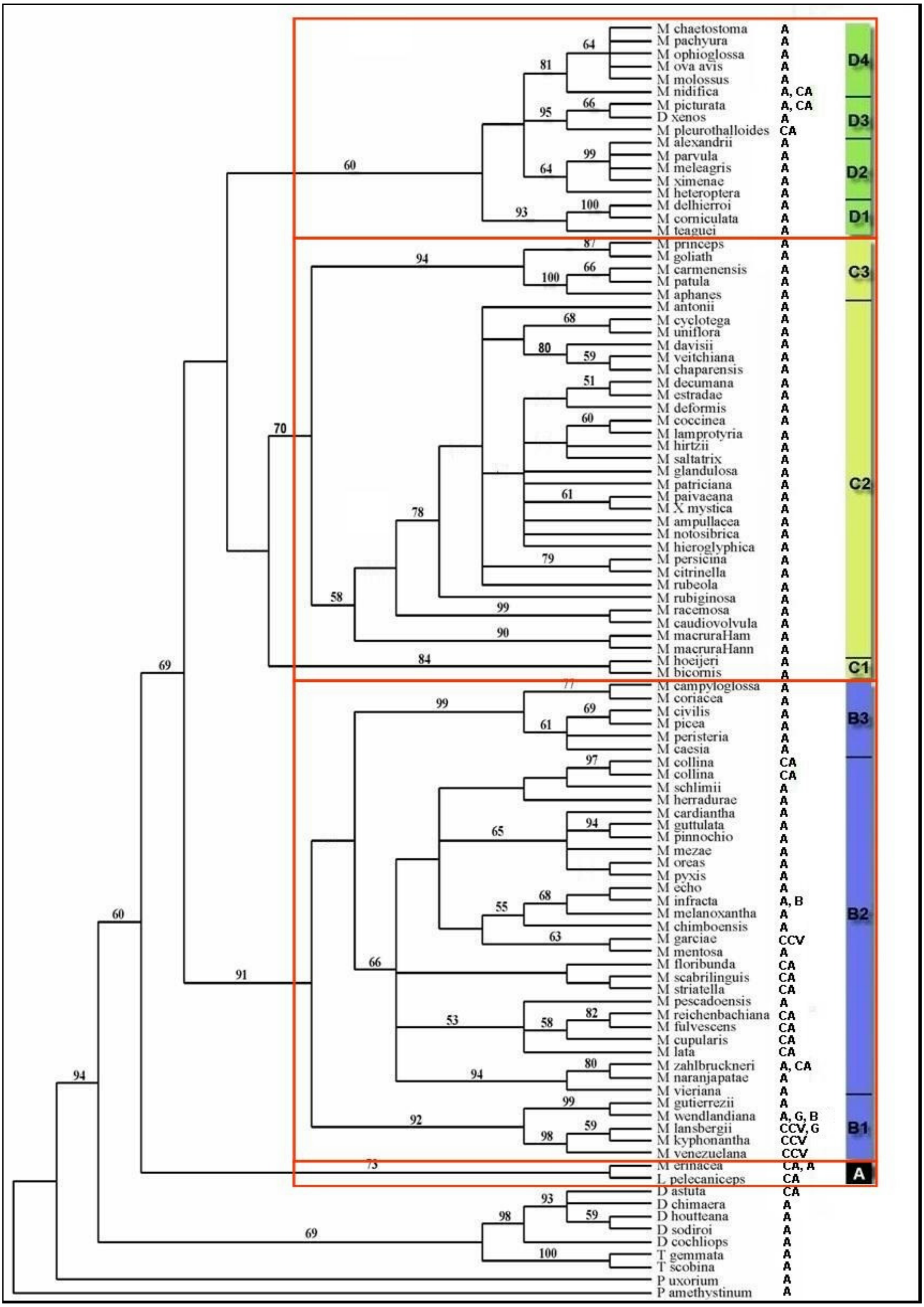

Fig. 78 Geographical areas of diversification of the genus *Masdevallia* based on phylogeny of ITS sequences data and maximum parsimony analysis. A= Andes, CA= Central America, B= coastal Atlantic forest of southeastern Brazil, CCV= Coastal Cordillera of Venezuela, G= Guayana.

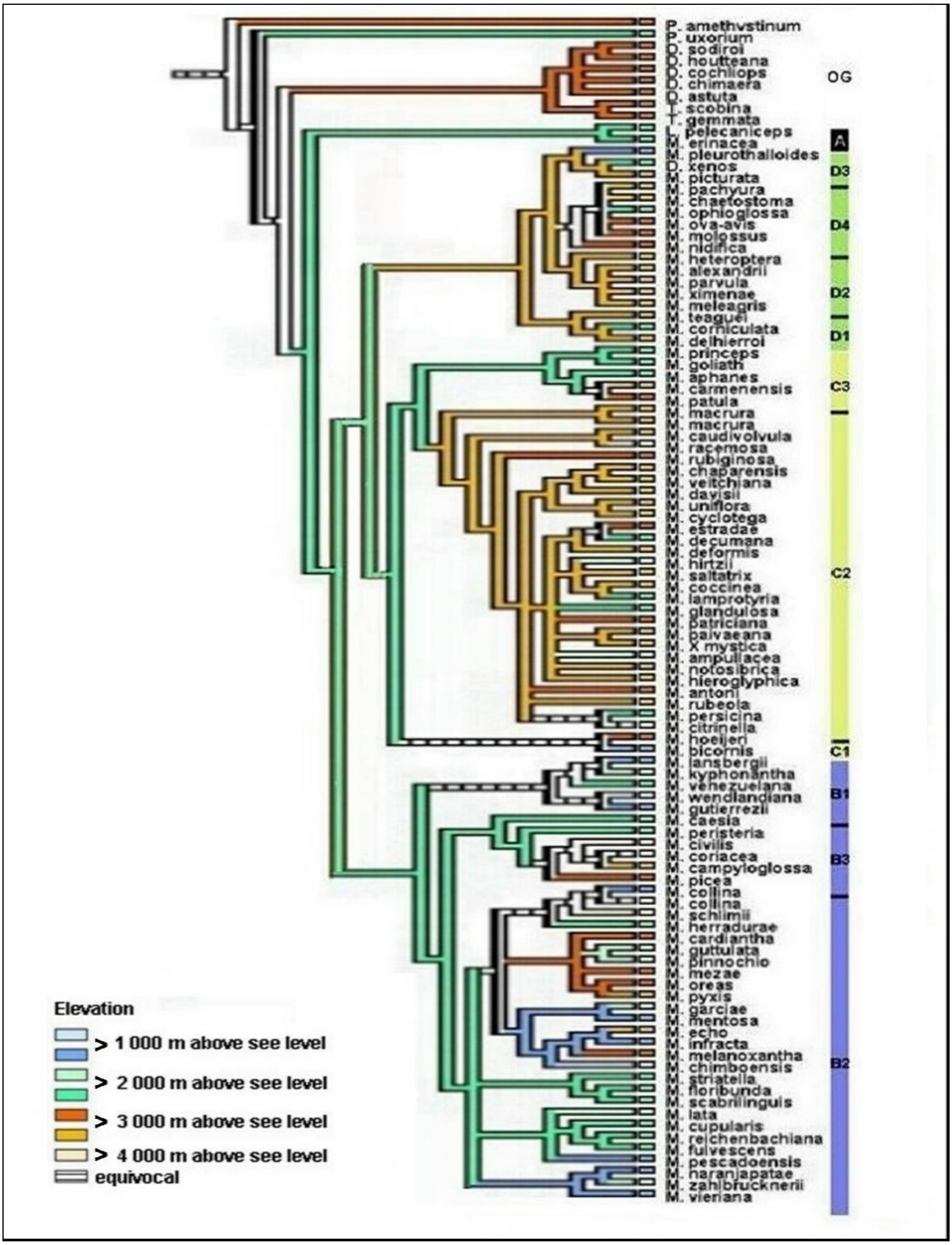

Fig. 79 Reconstruction of the altitudinal range optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

Fig. 80 Geographical distribution of outgroup taxa based on phylogeny of ITS sequences data.

Fig. 81 Geographical distribution of members of clade A based on phylogeny of ITS sequences data.

Fig. 82 Geographical distribution of members of clade B based on phylogeny of ITS sequences data.

Fig. 83 Geographical distribution of members of clade C based on phylogeny of ITS sequences data.

Fig. 84 Geographical distribution of members of clade D based on phylogeny of ITS sequences data.

4

DISCUSSION

4.1 Morphological analysis

The traditional classification systems of the genus *Masdevallia* are, as most of the classification systems of *Orchidaceae* and genera of *Orchidaceae*, based on relatively few characters, which have not been subjected to an explicit character analysis. Therefore, it is often not clear which characters really support the recognition of a particular group. The principal problem of all these classification systems, as suggested by FREUDENSTEIN and RASMUSSEN (1999), is that intuitive classifications usually focus on different key characters in different parts of the family or genera, meaning that it is often difficult to asses how characters are distributed over the family and genera as a whole.

The subtribe *Pleurothallidinae* is one of the best known orchidaceous groups compared to many other orchids. The morphological base of the subtribes was described by Luer in his comprehensive "Icones Pleurothallidinarum" (LUER 1986a). Cladistical analyses of the subtribes based on morphological and anatomical characters were performed first by PRIDGEON (1982), and complemented by NEYLAND et al. (1995). Finally, PRIDGEON et al. (2001) published a phylogenetic analysis based on a three-gene data set, with more than 500 transfers and nomina nova (PRIDGEON & CHASE 2001). Unfortunately, morphological issues were discussed almost exclusively if they were in concordance with molecular data. Direct morphological inconsistencies within DNA based clades were usually ignored.

Even if the anatomy and morphology of subtribe *Pleurothallidinae* are well studied, up to day there has not been any explicit phylogenetic analysis, neither morphological nor molecular, of allied genera in the subtribe. Although revisions of several sections of *Masdevallia* have been published during the last century, the delimitation of infrageneric taxa is still problematic, due to the lack of clear morphological synapomorphies.

In the phylogenetic analysis of the genus *Masdevallia* based on morphological data, most groups are not supported by many characters, as in many cladistic analyses of large groups based on morphological data (FREUDENSTEIN and RASMUSSEN, 1999; NEYLAND et al., 1995; PRIDGEON, 1982). In the cladistic analysis of the subtribe *Pleurothallidinae* based on morphological and anatomical data by NEYLAND et al. (1995), one of the most parsimonious trees obtained revealed nodes with one to six characters supporting them, with many of these being homoplastic changes. The examination of one of the most parsimonious trees obtained from the analysis of morphological data of the genus

Masdevallia reveals nodes with one to four characters supporting them, with many homoplastic changes. Hence there are few enough character changes per branch that they can be shown. Support indices such as bootstrapping (FELSENSTEIN, 1985) are less important for a morphological analysis than for most molecular analyses. However, they give a more quantitative assessment of relative branch support. The consistency index of 0.29 revealed a high level of homoplasy and may be a consequence of the rapid rates of evolution believed to have occurred in Orchidaceae (DRESSLER, 1993). However, the use of characters with polymorphic states used in this study, as well as some missing data, may also have contributed to this high level of homoplasy. The lack of resolution obtained in this study suggests that detailed classifications at the infrageneric level are not well supported by morphological evidence in most cases, and that, at this level, intuitive approaches may have reached conclusions beyond the ability of the data.

One of the purposes of this study was to test the current hypotheses of infrageneric classification of the genus *Masdevallia* based on the morphological data that have been recognized as diagnostic characters for infrageneric taxa within the genus *Masdevallia*, as well as some new characters produced for this study, such as pollinia micro-morphology. Comparison of the proposed infrageneric systems for *Masdevallia* and conclusions drawn from the cladistic analysis of the morphological data are presented below.

4.1.1 Outgroups relationships of *Masdevallia* based on morphological data

Analysis of the morphological data does not support the monophyly of the genus *Masdevallia*. Furthermore, one of the genera designated as outgroup, *Porroglossum*, was found nested within *Masdevallia*, albeit without significant bootstrap support (Fig. 38). Although the genus *Masdevallia* is now a well defined genus, it was not surprising that *Porroglossum* was found nested within *Masdevallia*. The genus *Porroglossum* was included within *Masdevallia* prior 1920. SCHLECHTER (1920) proposed to segregate *Masdevallia echidna* Rchb. f. into the new genus, *Porroglossum,* referring either to the position of the lip in relation to the column or elongated column-foot, or to the fact that the lip was far from the usual. The peculiar sensitive lip was noted by Oliver in 1888, who described the mechanism of movement and its influence on the pollination. LUER (1986a) stated that *Porroglossum* resembles *Masdevallia* by having short ramicauls and sepals with long tails; however, its sensitive labellum sufficiently distinguishes it from *Masdevallia.* In the phylogenetic analysis of the subtribe *Pleurothallidinae* based on morphological data by NEYLAND R. et al. (1995), *Masdevallia* and *Porroglossum* resulted sister taxa.

The results from the analysis of morphological data obtained in this study reveal a sister relationship between the *Masdevallia-Porroglossum* complex, and species of the genus *Dracula*, with considerable bootstrap support (98%).

In the analysis of molecular data (ITS nrDNA sequences), the genus *Masdevallia* appears to be more related to the genus *Dracula* (Fig. 39) than to genus *Porroglossum.* According to PATTERSON et al. (1993), incongruence between different data sets is the result mainly of procedural processes such as inadequate sampling either of taxa or data, different methods of analysis of the different data sets, etc. According to SYTSMA (1990) incongruence could be the result of a) unequal rates of morphological evolution, b) convergence of morphological characters, c) hybridization and/or introgression, and d) polyploidy. If substitution rates are concordant with changes in morphological characters, i.e. if molecular evolution reflects morphological evolution and vice versa is a frequently discussed question. Imbalances between the evolution of morphological, physiological and genetic characters seems to be a common trait in orchids (COX & al. 1997; BORBA & SEMIR 2001; BORBA & al. 2000, 2001a, 2001b, 2001c, 2002). There are most obvious in those instances, where at low taxonomic ranks doubtlessly similar morphology is contradicted by differences in sequences, and consecutively by topology. This can be observed in morphologically similar taxon pairs; however, it is most striking when comparing different samples from one and the same morphologically well defined species.

4.1.2 Infrageneric affinities based on morphological data

Analysis of the morphological data does not support the current infrageneric classification of the genus *Masdevallia* (LUER, 2000-2003) (Fig. 38). Of 11 subgenera proposed by LUER (2000-2003) only two appear to be monophyletic. These are subgenera *Meleagris*, represented by three out of twelve species here, and *Cucullatia*, represented by three out of six species here. Subgenera *Amanda*, *Fissia*, *Masdevallia*, *Nidificia*, *Polyantha*, and *Pygmaeia* are not monophyletic. Among eight sections proposed for subgenus *Masdevallia* five are monophyletic; these are sections *Triotosiphon*, *Durae*, *Reichenbachianae*, and the monospecific sections *Racemosae* and *Dentatae*. Sections *Masdevallia*, *Coriaceae*, and *Minutae* are not monophyletic. Both sections proposed for subgenus *Polyantha*, *Alaticaules* and *Polyanthae* (LUER, 2000), are not monophyletic. Of the four sections proposed for subgenus *Pygmaeia* (LUER, 2000), only two sections, *Amaluzae* and *Pygmaeae*, appear to be monophyletic. Sections *Zahlbrucknerae* and *Aphanes* are not monophyletic.

4.1.3 Phylogenetic implications based on morphological data

This study represents the first attempt to bring cladistic resolution to the genus *Masdevallia*. Despite the poorly resolved morphological strict consensus (Fig. 38), the discussions and conclusions drawn from the analysis of morphological data are presented below.

Two principal clades were obtained from the analysis of morphological data. *Masdevallia racemosa* occupies the most basal position in this study and appears as sister to the remaining *Masdevallia* species, with two *Porroglossum* species nested among them. The position of *Masdevallia racemosa* was not congruent with the molecular analysis. However, this controversial species shows some characters such as creeping rhizomes, which could not be compared with any other species.

Clade A - Ascending the cladogram, *M. erinacea* and *M. naranjapatae*, (subgenus *Pygmaeia* sections *Zahlbrucknerae* and *Pygmaeae*), occupied the most basal position in a basal grade (Fig. 38). The position of *Masdevallia erinacea* is congruent with the results obtained in the molecular analysis and will be discussed later. The next clade is formed by members of subgenus *Masdevallia* section *Masdevallia* subsections *Coccinea* (except *M. deformis*), *Masdevallia* (except *M. patriciana*), *Oscillantes*, and *Saltatrices* (except *M. notosibrica*). Species exhibiting a solitary flower and a retrorse callus along the labellar margin are grouped sensu LUER (1986b) into subgenus *Masdevallia* section *Masdevallia*. Except subsection *Caudatae*, all the subsections proposed by LUER for section *Masdevallia* resolved as sistergroup to each other. Subsection *Caudatae* appears more closely related to species of subgenus *Meleagris*, *Nidificia* and the two analyzed species of the genus *Porroglossum*; nevertheless, an explanation of a possible relationship between these taxa was not previously discussed. The unique synapomorphy that unites these taxa is a longitudinal callus along the labellar margin ending in an acute-uncinate process.

Species of subgenus *Pygmaeia* sections *Amaluzae*, *Aphanes*, and *M. vierana* (subgenus *Pygmaeia* section *Zahlbrucknerae*), subgenus *Masdevallia* sections *Reichenbachianae*, *Dentatae*, *Coriaceae*, and *Durae*, subgenus *Polyantha*, subgenus *Cucullatia*, and *M. teaguei* (subgenus *Teagueia*) are grouped into a large clade, which is in part congruent with the results obtained from the molecular analysis. Species of subgenus *Pygmaeia* section *Amaluzae* plus *M. vierana* form a strongly supported group, with several characters supporting them. Ascending the cladogram, species of subgenus *Masdevallia* section *Reichenbachianae* form a strongly supported group and are related to species of subgenus *Polyantha.* This grouping was also found in the analysis of molecular data. A relationship between species of subgenus *Masdevallia* sections *Reichenbachianae* and *Minutae*, as suggested by LUER (1986b), was not present in the analysis of morphological data, but it was obtained in the analysis of molecular data and will be discussed later.

Clade B - Subgenus *Amanda* has been a recognized group since REICHENBACH (1880). Of the six species analyzed, four grouped together in a subclade which is sister to the species of subgenus *Fissia*. A strong relationship between species of subgenus *Amanda* and *Fissia* was first suggested by LUER (1986b), who recognized *Fissia* as a section of subgenus *Amanda*. Section *Fissia* has been raised recently to a higher rank (LUER 2000), based, according to LUER (2003), on a combination of characters that is not present in any other subgenera of *Masdevallia*. Nevertheless, LUER (2003) suggested a not-too-distant relationship within *Amanda* and *Fissia* based on the similarities of the flowers of some species of subgenus *Fissia* (e. g. *Masdevallia dynastes*). Although subgenus *Amanda* has been a recognized group since Reichenbach, the synapomorphies of this group are not clearly defined. According to Luer (1986b), subgenus *Amanda* is characterized by racemes (loose or congested) that flower nearly simultaneously, peduncles that are round in cross section; more or less inflated floral bracts; carinate or crested ovaries; caudate sepals that are variously connate into a shallow cup or arcuate cylindrical tubes, the petals callous on the labellar half, the margins entire to denticulate; and the lip more or less divided by marginal folds into a hypochile and a smaller hypochile. The results obtained in this study indicate that most of the morphological characters that have been used to delimit subgenus *Amanda* occur in unrelated species. The unique character that appears as a synapomorphy for species of subgenus *Amanda* is simultaneously flowering racemes. A relationship between subgenera *Amanda*, *Fissia* and *Masdevallia* subsections *Minutae* and *Triotosiphon* was not previously discussed. Section *Minutae* was created to accommodate small species which cannot easily be placed in any other group; from the twelve species included by WOOLWARD in this section, seven are now dispersed in other sections. SCHLECHTER (1925) proposed to raise subgenus *Triotosiphon* to a higher rank. However, according to Luer (2003), this taxon meets the criteria for subgenus *Masdevallia*. An explanation of the incongruent position of these two sections, *Minutae* and *Triotosiphon*, could be the absence of reliable characters which define these groups, which have probably been grouped intuitively.

The results obtained from the morphological analysis showed that most of the current morphological characters that have been used to characterize the infrageneric groups are relatively homogenous, leaving the distinct impression that even a still more detailed study of nonmolecular characters is unlikely to reveal a vastly greater numbers of characters. These would be required for a more accurate assessment of infrageneric relationships. In addition, all previously sampled species would need to be sampled again for an accurate assessment of the distribution of any newly found potentially useful character. This is, of course, why we turned to DNA sequence analyses to identify additional characters for a better resolution of phylogenetic relationships.

4.2 Molecular analysis

4.2.1 Utility of ITS sequences in *Masdevallia*

ITS sequences provided insights into the relationship within *Masdevallia* due to moderate levels of interspecific sequence variation and low levels of intraspecific heterogeneity. Polymorphisms reported for ITS in some plant species (cf. WENDEL et al., 1995; CAMPBELL et al., 1997) were not detected in *Masdevallia*, although divergent ITS paralogues appear to be common in lineages having a history of hybridization and polyploidisation (BUCKLER et al., 1997). Especially natural hybridizations are common in *Orchidaceae* even between genera and have been observed in *Masdevallia* as well (LUER, 1986b-2003).

Although ITS sequences were phylogenetically informative, the ability to resolve relationships within some morphologically related taxa of *Masdevallia* was limited. Low levels of sequence variability among very closely related species also limited the utility of ITS sequences for resolving phylogenetic relationships within some sections. For example, nearly identical ITS sequences were obtained from closely related taxa, such as *M. caloptera* and *M. pachyura* (subgenus *Amanda*) or *M. princeps* and *M. goliath* (subgenus *Masdevallia* section *Durae*). Differences between the molecular (ITS) and morphological pace of evolution therefore should be a priori no surprise. Moreover, even within the ITS region mutations do not occur randomly. Pairs of species exhibiting little genetic distance have been reported from other orchidaceous groups, too (COX & al. 1997, BORBA & al. 2002). Despite their popularity at the species level, the ITS sequences failed to reflect putatively recent phenotypic differentiation. This has been observed also in other orchidaceous (BORBA & al. 2002, VAN DEN BERG & al. 2000) and other angiospermous taxa (PANERO & al. 1999). If we assume a clock-like rate in ITS evolution among lower taxonomic ranks at least, these results contradict the assumption (SOTO ARENAS 1996) that orchidaceous speciation processes are long-time events, although this may be the case in certain orchids (ACKERMAN & WARD 1999).

4.2.2 Outgroups relationships of *Masdevallia* based on molecular analysis

The phylogenetic relationship of the genus *Masdevallia* relative to outgroup taxa is well resolved using ITS sequences and parsimony analyses. The genus *Masdevallia* is a well-supported monophyletic group that is unambiguously part of *Pleurothallidinae*, as previously obtained by PRIDGEON et al. (2001) in a study of the subtribe *Pleurothallidinae* based on sequences of ITS, the plastid gene *matK* and the *trnL* intron with the *trnL*-F intergenic spacer (hereafter simply *trnL*-F). Species of *Masdevallia* appear sister to *Dracula* and *Trisetella*, but not to *Porroglossum*, as was previously obtained by PRIDGEON et al. (2001).

4.2.3 Monophyly of the infrageneric taxa of *Masdevallia* based on molecular analysis

Although PRIDGEON et al. (2001) did not propose further changes in the subgeneric classifications of *Masdevallia*, it was evident that the current subgeneric classification needed reconsideration. The results obtained in this study confirm this supposition (Fig. 39).

Of the 11 subgenera of *Masdevallia* considered in this study, six form strongly supported monophyletic groups in the analysis: these are the monospecific subgenera *Teagueia, Scabripes* and *Volvula* as well as the subgenera *Cucullatia*, *Meleagris* and *Fissia*. This is consistent with the morphological synapomorphies that characterize these subgenera. Subgenera *Masdevallia*, *Pygmaeia* and *Polyantha* are clearly polyphyletic, which is in accordance with the heterogeneity obvious in inflorescence type, flower size, and morphology of the petals and lip of these subgenera. Subgenera *Nidificia* and *Amanda* form a clade without any internal resolution.

Seven of the eight sections of subgenus *Masdevallia* are monophyletic: sections *Coriaceae*, *Durae*, *Masdevallia*, *Reichenbachianae*, *Triotosiphon*, and two monotypic sections, *Dentatae* and *Racemosae*. Section *Minutae* is not monophyletic. Its species are distributed among a clade which in addition contains species of subgenus *Polyantha*, subgenus *Masdevallia* sections *Dentatae*, *Reichenbachianae*, and *Triotosiphon*, subgenus *Pygmaeia* section *Zahlbrucknerae*, *M. chimboensis* (subgenus *Pygmaeia* section *Amaluzae*) and *M. mentosa* (subgenus *Pygmaeia* section *Aphanes*). According to LUER (2000-2003), section *Masdevallia* is divided into five subsections. None of these was retrieved in the present analyses of molecular as well as morphological data.

The two sections proposed for the subgenus *Polyantha*, *Alaticaules* and *Polyanthae* (LUER, 2000), are intermingled among species of subgenus *Masdevallia* sections *Dentatae*, *Minutae* and *Reichenbachianae*, *M. chimboensis* and *M. mentosa*. These sections can not be considered monophyletic.

Subgenus *Pygmaeia* was created to accommodate species of subgenera *Masdevallia* sections *Amaluzae* and *Aphanes*, and subgenus *Amanda* section *Pygmaeae* (LUER, 1986b), characterized by their small and caespitose habit. Luer (2000) suggested that treating these three sections in a single, loosely related, more easily recognized taxon, seemed preferable to maintaining several small subgenera (“Although all the species included in this proposed subgenus probably are not closely related”- LUER, 2000). At present subgenus *Pygmaeia* is divided into four sections: *Amaluzae*, *Aphanes*, *Pygmaeae*, and *Zahlbrucknerae* (LUER, 2000). Three of these sections resulted not monophyletic in the analysis of molecular and morphological data. Section *Zahlbrucknerae* appear to be monophyletic.

4.2.4 Phylogenetic implications

Despite poor resolution among some taxa, the analysis of molecular data yielded significant information about the phylogenetic position of several clades or individual taxa within the genus *Masdevallia*. Four principal clades were distinguished (Fig. 39):

- Clade A included *M. erinacea* and *Luerella pelecaniceps*.
- Clade B included subgenus *Pygmaeia* section *Zahlbrucknerae,* subgenus *Masdevallia* sections *Triotosiphon*, *Reichenbachianae*, *Minutae*, *Coriaceae,* and *Dentatae,* and subgenus *Polyantha* sections *Alaticaules* and *Polyanthae*, *M. chimboensis* (subgenus *Pygmaeia* section *Amaluzae*) and *M. mentosa* (subgenus *Pygmaeia* section *Aphanes*).
- Clade C grouped subgenus *Pygmaeia* sections *Amaluzae* and *Aphanes*, subgenus *Masdevallia* section *Masdevallia* with all subsections described by LUER (1986b-2002) for this section (*Caudatae*, *Coccinea*, *Masdevallia*, *Oscillantes* and *Saltatrices)*, section *Durae*, section *Racemosae*, *M. caudivolvula* (subgenus *Volvula*), *M. macrura* (subgenus *Masdevallia* section *Coriaceae*), *M. hoeijeri* (subgenus *Pygmaeia* section *Aphanes*), and *M. bicornis* (subgenus *Scabripes*).
- Clade D grouped subgenera *Teagueia*, *Cucullatia*, *Nidificia*, *Amanda*, *Fissia, Meleagris,* and *Dracula xenos*.

These groups and their phylogenetic implications will be discussed in the following.

Clade A – The most basal position is occupied by *Masdevallia erinacea* (subgenus *Pygmaeia* section *Pygmaeae*) and *Luerella pelecaniceps*. The position of *Masdevallia erinacea* was consistent with the results obtained in the morphological analysis. The results obtained in a first molecular systematic analysis of subtribe *Pleurothallidinae* (PRIDGEON et al., 2001) revealed that *M. erinacea* occupied a rather isolated position. For this reason this species and all species of subgenus *Pygmaeia* section *Pygmaeae* (LUER, 1986b) were placed in a new genus, *Diodonopsis* (PRIDGEON & CHASE, 2001). According to LUER (2002), this new genus should be invalidated, because it was not represented by their type taxon, *M. pygmaea*. *Masdevallia hoeijeri* (clade C1) was initially included within subgenus *Pygmaeia* section *Pygmaeae* and consequently segregated to *Diodonopsis.* However, the results obtained in this study indicated that there is no justification to segregate *M. hoeijeri* from the genus *Masdevallia* as member of the genus *Diodonopsis* as proposed by Pridgeon & Chase (2001). Even though the position of this species could be considered aberrant and cannot be defined by the morphological data which characterize species grouped in this clade (C1). In this analysis, *M. erinacea* as well as *M. hoeijeri*, appear to be part of *Masdevallia.*

A relationship between *M. erinacea* and *Luerella pelecaniceps* was not expected. In the first molecular systematic analysis of subtribe *Pleurothallidinae* (PRIDGEON et al., 2001), the *Luerella-Ophidion-Pleurothallis peperomiodes* group is sister to a clade comprising the genera *Trisetella*, *Masdevallia* and *Porroglossum,* as well as *Masdevallia erinacea*, albeit without bootstrap support (≤50%). Despite the lack of morphological evidence supporting them, the appearance of *Luerella pelecaniceps* as sister to *Masdevallia* could be explained. The monotypic genus *Luerella* was created to accommodate the atypical species *M. pelecaniceps*. Until 1979 this species was part of *Masdevallia*. Although LUER indicates that this species has no close relatives within *Masdevallia*, the morphological features indicated the contrary: The column is typical for *Masdevallia*, the excavate base between incurved marginal angles, as in many species of *Masdevallia* section *Coriaceae*, and the single-flowered peduncle borne from an annulus as in *M. macropus* and *M. macrura*. Some characters such as the boxlike, rigid and semiclosed flowers are also found in *M. navicularis*.

Clade B - Species of section *Triotosiphon* are grouped into a well supported clade that is sister to *M. gutierrezii* and *M. wendlandiana* (subgenus *Masdevallia* section *Minutae*). This taxon was suggested by SCHLECHTER (1925) as subgenus *Triotosiphon*. However, according to LUER (2003) and corroborated in this study, this taxon meets the criteria for subgenus *Masdevallia*. The remaining analyzed species of the non-monophyletic section *Minutae* are distributed among species of subgenera *Polyantha*, *Masdevallia* sections *Reichenbachianae* and *Dentatae*, *M. chimboensis* and *M. mentosa*. Possible morphological support for the sister relationship of species of section *Triotosiphon* and the two species of section *Minutae*, *M. gutierrezii* and *M. wendlandiana*, is provided by the fact that all species grouped in this subclade show dorsal and lateral sepals connate to a similar degree and a non sulcate disc of the lip. In the remaining species of section *Minutae* the dorsal and lateral sepals are connate to a different degree.

Species of subgenus *Pygmaeia* section *Zahlbrucknerae* are grouped into a well supported subclade (B2), which is sister to species of subgenus *Polyanthae,* and subgenus *Masdevallia* sections *Reichenbachianae*, *Minutae*, and *Dentatae*, *M. chimboensis* and *M. mentosa*. Species of section *Zahlbrucknerae* were previously included as members of section *Amaluzae*. However, according to LUER (2000), the section seems sufficiently distinct from section *Amaluzae* to be retained as a subsection. This suggestion is confirmed in this study. Of the four members included within section *Zahlbrucknerae* three were analyzed. The results indicate a close relationship among these species.

As previously discussed based on the analysis of morphological data, subgenus *Polyantha* is not correctly delimited. This is confirmed by the molecular data. Species of this subgenus appear distributed among species of subgenus *Masdevallia* sections *Reichenbachianae* and *Minutae* (excluding *M. wendlandiana* and *M. gutierrezii*), and two species of subgenus *Pygmaeia* sections *Amaluzae* and *Aphanes*. A sister relationship between species of subgenus *Masdevallia* sections *Minutae* and *Reichenbachianae* was previously discussed (LUER, 2000). These two Central American sections are separated only because of the absence of a protruding callus on the petals in species of section *Reichenbachianae*. Considering this weak differentiation, it is not surprising that some species of subgenus *Polyantha*, such as *M. striatella* and *M. garciae*, group among species of sections *Minutae* and *Reichenbachianae.* These two species were transferred from subgenus *Masdevallia* section *Reichenbachianae* to subgenus *Polyantha* by LUER (2000). The monotypic section *Dentatae* (*M. collina*) was initially recognized as a subsection of *Reichenbachianae*. The results obtained in this study show that a close relationship is present between species of section *Reichenbachianae* and species of section *Minutae*, subgenus *Polyantha, M. chimboensis* and *M. mentosa*. A relationship between *M. collina* and subgenus *Masdevallia* section *Durae*, as recently proposed by LUER (2000), on the basis of the cartilaginous petals with thick-descending processes below the middle and the disc shallowly channeled between callous margins can be discarded.

Sister to this large group is the monophyletic and well supported subclade containing the species of section *Coriaceae* (subclade B3). Species of this group are well characterized morphologically: single flowers, often malodorous and pollinated by carrion flies, sepals thick and fleshy, often verrucose on adaxial side, petals cartilaginous, without a process but with an angled labellar margin, lip undivided by marginal folds. Section *Coriaceae* was initially thought to be allied with section *Durae* (LUER, 1986b), which was considered as a subsection of *Coriaceae*. Although the morphological data corroborated this supposition (Fig. 38), the molecular data indicated that there is no close relationship among these taxa. Section *Coriaceae* was considered as Andean counterpart of the Central American section *Reichenbachianae* (LUER, 2000). A relationship between species of section *Coriaceae,* subgenus *Pygmaeia* section *Zahlbrucknerae*, subgenus *Masdevallia* sections *Triotosiphon*, *Reichenbachianae*, *Minutae*, and *Dentatae*, and subgenus *Polyantha* sections *Alaticaules* and *Polyanthae*, *M. chimboensis* and *M. mentosa* can be characterized molecular even as well as morphologically. *Masdevallia macrura*, member of the section *Coriaceae*, was the only species whose position (here in clade C) could not be explained. This species appears as member of a clade which grouped together subgenus *Masdevallia* sections *Durae, Masdevallia*, and *Racemosae*, subgenus *Pygmaeia* sections *Amaluzae* and *Aphanes*, and subgenera *Volvula* and *Scabripes*. Because of the incongruent position of *M. macrura*, two different specimens were analyzed, without any variation. This species was treated initially as member of section *Cucullatae* (RCHB. f., 1874), but its position in this analysis is inconsistent with a relationship with subgenus *Cucullatia*. *Masdevallia macrura* show morphological characters such as sepals fleshy and verrucose on adaxial side; petals cartilaginous with the labellar margin angled, and a lip undivided by marginal folds, which characterize section *Coriaceae*.

Clade C - A well supported relationship of *M. hoeijeri* and *M. bicornis* (subclade C1) was not expected and cannot be defined in morphological terms. The same is attributable to *M. racemosa* and *M. caudivolvula* (within C2). However a relationship between *M. racemosa* and species of section *Masdevallia* was suggested by LUER (1986b), on the basis of the similarities between their flowers. A relationship between *M. racemosa* and species of section *Coriaceae* was suggested as well (LUER, 1986), because of the callous petals without a tooth and thick ligulate lips. *Masdevallia caudivolvula* (subgenus *Volvula*) presents a combination of characters similar to species of subgenus *Masdevallia.* According to LUER (2003), the combination of characters present in this species is not present in any other taxa of *Masdevallia*: single flowers, lip divided by marginal folds, and thick sepals that are carinate internally with thick-twisted tails. The results obtained in this study show that *M. caudivolvula* cannot be separated as a subgenus based on sepals with thick-twisted tails alone.

Subgenus *Masdevallia* section *Masdevallia* (subclade C2) is reasonably supported by molecular data as well as by morphological analysis. Several morphological synapomorphies such as the single-flowered peduncles, the cartilaginous petals, usually with a well-developed retrorse process from the callus near the base on the labellar margin, and the undivided lip, characterize this section. However, there is no support for segregating the section *Masdevallia* into subsections *Caudatae*, *Coccinea*, *Masdevallia*, *Oscillantes* and *Saltatrices.* Once again, the low level of sequence divergence indicates that many of the current infrageneric concepts of *Masdevallia* are trivial, and all taxa in this subclade could be accommodated in the section *Masdevallia* (lectotype *Masdevallia uniflora*, included here).

Subgenus *Masdevallia* section *Durae*, two species from subgenus *Pygmaeia* section *Amaluzae*, and *M. aphanes* form a strongly supported subclade (C3). Species of section *Durae* show low levels of sequence variability. A relationship between species of section *Durae* and subgenus *Pygmaeia* sections *Amaluzae* and *Aphanes* was not previously discussed, however, these groups of species are morphologically well characterized by callous petals, with the callus ending in an obtuse process above the base, and by a lip divided into a hypochile and an epichile.

Clade D - All species of subgenus *Cucullatia* and the monospecific subgenus *Teagueia* (subclade D1) share a rachis with long internodes, the petals that are callous along the labellar margin producing a small uncinate process, and their lateral sepals are connate above the middle into a lamina (LUER, 1986b-2003). LUER (2003) maintained that on the basis of the actively mobile lip (with a pair of plates covering the disc), *Teagueia* should be maintained as a monospecific subgenus.

Sister to this small subclade are subgenera *Amanda*, *Nidificia*, *Fissia*, and *Meleagris*, grouped into a large subclade without significant support. In the first infrageneric classification by LUER (1986b), subgenera *Amanda*, *Fissia*, *Nidificia*, and *Meleagris* were treated as sections of subgenus *Amanda*, distinguished by single-flowered or simultaneously two- to many- flowered inflorescence, crested ovaries, more or less membranous relatively thin petals, and a lip more or less divided by marginal folds into a hypochile and an epichile. In the most recent classification by LUER (2003), these four sections were raised to the rank of subgenera. Subgenera *Amanda* and *Nidificia* are, however, not resolved in the data.

Subgenus *Meleagris* (subclade D2) contains 12 species distributed throughout Colombia, Ecuador, Peru and Bolivia, in wet forest at high or relatively high altitudes. BRAAS (1979) proposed the genus *Rodrigoa* for them. However, all the species meet critical criteria for the genus *Masdevallia*, including the most specific: callous petals and a lip hinged to a free extension of the column-foot (LUER, 2003) and the molecular results confirm their inclusion in *Masdevallia*.

Dracula xenos is found between the two species of subgenus *Fissia* examined here (subclade D3). There are three possible explanations for this position: 1) a hybrid origin of *D. xenos*, which is not unlikely, considering the many natural hybrids occurring in *Masdevallia* and between *Masdevallia* and *Dracula*. 2) Parallel development of a *Dracula*-type lip in *Masdevallia*. These two possibilities have already been discussed by PRIDGEON et al. (2001). 3) Introgression of nuclear genes of *M. picturata* or a related species into the genome of *D. xenos,* without formation of a stabilized hybrid. Gene flow is highly probable between closely related taxa that share a recent common ancestor (OLSEN & SCHAAL, 1999). The low levels of divergence in DNA sequences found in *Masdevallia* suggest a recent diversification, which is further supported by the interfertility between morphologically divergent species in artificial crosses and the relatively recent geological origin of their current distribution area. According to GREGORY-WODZICKI (2000) the uplifting of the Andean Cordillera took place in the late Miocene.

Subgenera *Amanda* and *Nidificia* (subclade D4) form a nearly unresolved branch in a polytomy. Floral similarities between species of these subgenera are taken as indications of a closer relationship to each other than to subgenera *Meleagris* and *Fissia*.

4.2.5 Bootstrap frequencies vs. Bayesian posterior probabilities

Although nonparametric bootstrap frequencies and posterior probabilities are not equivalent analyses, both analyses were performed and the results compared. One of the reasons, why both analyses were performed, is that the analysis of large data sets presents special problems for heuristic search strategies, especially when homoplasious characters form a large proportion of the variable sites. In most cases, the large number of most parsimonious trees exceeded the memory available to the computer used in the studies.

The strict consensus tree obtained from the maximum parsimony analysis (Fig. 39) and the 50% majority rule consensus of the 3000 trees obtained from the Bayesian analysis (Fig. 40) recovered essentially the same topology. Two major topological differences resulted from the two analyses: (i) a sister relationship between *M. erinacea* and *Luerella pelecaniceps*, which was not present in the parsimony analysis but in the Bayesian analysis, would support the exclusion of *M. erinacea* from the genus *Masdevallia*, as proposed by BRAAS (1979); (ii) a sister relationship of species of subgenera *Cucullatia* and *Teagueia* and species of subgenera *Amanda*, *Nidificia*, *Fissia* and *Meleagris*, which was not obtained in the Bayesian analysis. This relationship was neither expected, nor can it be explained.

Comparing the different levels of support for particular nodes of the Bayesian analysis and the parsimony analysis highlights differences between measures of support provided by bootstrap values (Fig. 39) and posterior clade probabilities (Fig. 40). Bayesian posterior probabilities for the clades in the phylogenetic tree were found to be considerably higher than corresponding nonparametric bootstrap frequencies. Discussion of these two measures of node support is a burning issue in the systematics literature (e.g., HUELSENBECK et al., 2002; SUZUKI et al., 2002; WILCOX et al., 2002; CUMMINGS et al., 2003; DOUADY et al., 2003; HOLDER and LEWIS, 2003). Simulation studies generally support the accuracy of posterior probabilities (WILCOX et al., 2002), although tendencies toward over-credibility of posterior clade probabilities have been identified (SUZUKI et al., 2002; CUMMINGS et al., 2003; DOUADY et al., 2003). It is important to recognize that bootstrap values and Bayesian posterior probabilities of node support measure two different processes. Bayesian posterior probabilities determine the strength of the data in supporting particular nodes, whereas bootstrap values indicate areas where additional data is needed to resolve relationships.

4.3 Combined analysis

Combining independent character matrices, whether both molecular or molecular and morphological, very often increases the resolution of the ingroup and the bootstrap support of the internal nodes of the phylogenetic trees (OLMSTEAD and SWEERE, 1994; CHASE et al., 1995; YUKAWA et al., 1996; RUDALL et al., 1998; SOLTIS et al., 1998; MEEROW et al., 1999). Important arguments against combining data in a total evidence approach are that gene trees can deviate from species trees because of paralogy, lineage sorting, ancestral polymorphisms, long branch attraction or lateral gene transfer (HUELSENBECK et al., 1996), and morphological data can be swamped by DNA sequence data because of the much lower number of characters (BULL et al., 1993). Nonetheless, there is controversy about whether different data sets should be analyzed separately or together (de QUEIROZ et al., 1995; HUELSENBECK, et al., 1996).

On of the principal problems combining different data sets is the incongruence obtained by the analysis of each data set separately. Numerous tree-based and character-based tests to identify incongruence have been developed, and each has strengths and weaknesses (CUNNINGHAM 1997*a*; JOHNSON and SOLTIS 1998). Currently, one of the most widely used methods for evaluating incongruence within a parsimony framework is the homogeneity test of FARRIS et al. (1995), usually termed the incongruence length difference (ILD) test (CUNNINGHAM 1997*a*; JOHNSON and SOLTIS 1998) or the partition homogeneity Test (SWOFFORD, 2002). The test has been argued to produce more accurate results than other tests (CUNNINGHAM, 1997*a*) and is also easy to implement using PAUP* (SWOFFORD, 2002). Congruence of the independent matrices has generally been demonstrated before they are combined, but it has also been argued that incongruence should not be a predetermined factor against doing so (SEELANAN et al., 1997; DUBUISSON et al., 1998). MIYAMOTO and FITCH (1995) argue that data sets should always be analyzed independently, as underlying assumptions, constraints, or weighting strategies will vary from data set to data set. KLUGE (1989) and NIXON and CARPENTER (1996) argue that simultaneous analysis of multiple data sets better maximizes parsimony and allows secondary signals to appear from the combined data. BULL et al. (1993), RODRIGO et al. (1993), and de QUEIROZ (1993) advocated combining data only after a statistical test of congruence, what HUELSENBECK et al. (1996) call ''conditional combination.''

An ILD test on the taxonomically equivalent ITS and morphological data sets performed in this study detected a significant difference ($P<0.01$) between these partitions, indicating substantial incongruence between the morphological and ITS matrices. Comparison of the poorly resolved morphological strict consensus with the ITS tree showed strongly supported topological incongruence.

Lack of resolution is interpreted by some authors to be lack of evidence for combining data (CUNNINGHAM, 1997); however, it may simply be evidence of insufficient information and signal (PENNINGTON, 1996). The latter may be the case in the morphological data set, in which there is an obvious deficit of discrete characters suitable for parsimony analysis. Much of the apparent incongruence can be attributed to the weak resolution of the morphologically based topologies, and we felt that it would still be informative to combine the two matrices in a single analysis. This seems especially useful given the degree of difficulty that has been encountered with cladistic analysis of purely morphological data in *Pleurothallidinae* (PRIDGEON, 1982; NEYLAND et al., 1995).

4.3.1 Monophyly of the infrageneric taxa of *Masdevallia* based on combined data

The strict consensus tree of the combined data was partly congruent with the ITS topology, and relationships among species of *Masdevallia* and outgroups were very similar in each tree. As in the analysis of molecular data alone, the genus *Masdevallia* appears monophyletic. The genus *Dracula* appears as sister to *Masdevallia*. *Dracula xenos* is not resolved in the strict consensus tree of the combined data. As in the analysis of molecular data alone, the subgenera *Cucullatia*, *Meleagris*, and *Fissia* (and the monospecific *Scabripes*, *Teagueia* and *Volvula*) form strongly supported monophyletic groups; subgenera *Masdevallia*, *Polyantha*, and *Pygmaeia* do not appear monophyletic; and subgenera *Amanda* and *Nidificia* are not resolved in the data (Fig. 77).

In disagreement with the analysis of the molecular data alone, section *Masdevallia* does not appear monophyletic. Section *Racemosae* and subgenus *Volvula* appear nested within section *Masdevallia*, albeit without bootstrap support. The two sections proposed for the subgenus *Polyantha*, *Polyanthae* and *Alaticaules* (LUER, 2000) do not form monophyletic groups, as in the molecular data alone. Of the four sections proposed for subgenus *Pygmaeia*, only section *Zahlbrucknerae* forms a monophyletic group, the remaining three sections, *Amaluzae*, *Aphanes* and *Pygmaeae*, do not appear monophyletic.

We interpret the topology of the strict consensus tree based on ITS sequences and parsimony analyses (Fig. 39) as representing our best estimate of phylogenetic relationships within *Masdevallia* and its outgroups. Most of the discussion in the next chapters will be focused on this topology. The lack of resolution obtained by the analysis of morphological data, and the substantial incongruence between the morphological and ITS matrices are taken here as arguments against using these analyses as the basis of further discussion.

4.4 Evolutionary significance of some morphological characters used as rapid identifiers

LUER (2000) used the following characters as rapid identifiers for diagnosing subgenera, sections and subsections within *Masdevallia* (Table 15): peduncle terete or triquetrous, anthesis of the flowers (whether the flowers are opening either successively or simultaneously), type of floral bract, the ovary smooth or with some external features such as crests or papillae, the grade of connation between the sepals, the free portion of the apex of the sepals produced into tails, the callus from the labellar margin ending in a process, and the lip divided into an epichile and a hypochile.

Table 15 Rapid identifier for subgenera and sections according to Luer (2000)

Subgenera/Section	**Peduncle**	**Raceme**	**Floral bract**	**Ovary**	**Connation of sepals**	**Sepaline tails**	**Process of petals**	**Lip divided**
Subgen. *Amanda*	Terete	Simul.	Infl.	+	+	+	0, mostly serrate	+
Subgen. *Cucullatia*	Terete	1-fl.	Infl.	+	+	+	0, tip verrucose	+
Subgen. *Fissia*	Terete	1-fl.	-	+	Free	+ 0	+	+
Subgen. *Masdevallia*								
Sect. *Amaluzae*	Terete	Succ.	-	+ 0	+	+	0	0
Sect. *Coriaceae*	Terete	1-fl.	-	-	+	+ 0	+	0
Sect. *Durae*	Terete	Succ.	-	-	+	+	0	0
Sect. *Dentatae*	Terete	Succ.	-	-	+	+	+	0
Sect. *Masdevallia*	Terete	1-fl.	-	-	+	+	+	0
Sect. *Minutae*	Terete	1, simul, Succ.	-	-	+	+	+ pointed	0
Sect. *Racemosae*	Terete	Simul.	-	-	+	0	0	0
Sect. *Reichenbachianae*	Terete	1, succ.	-	-	+	+	0	0
Sect. *Triotosiphon*	Terete	1-fl.	-	-	+	+	0	0
Subgen. *Meleagris*	Terete	Succ.	-	+	Free	+	0	0
Subgen. *Nidificia*	Terete	1-fl.	-	+	+	+	+	+
Subgen. *Polyantha*								
Sect. *Alaticaules*	Triquetrous	Succ.	-	-	+	+	+ 0	+
Sect. *Polyanthae*	Terete	1, simul, Succ.	-	-	+	+	0	+
Subgen. *Pygmaeia*								
Sect. *Aphanes*	Terete	1, succ.	-	+	+	+ 0	0	0
Sect. *Pygmaeae*	Terete	1, succ.	-	+	+	+	+	0
Subgen. *Scabripes*	Scabrous	Succ.	-	-	+	+	+	0
Subgen. *Volvula*	Terete	1-fl.	-	-	+	+	0	+

Key: terete = round in cross section; triquetrous= triangular in cross section; 1-fl. = peduncle single-flowered; simul. = raceme simultaneously flowered; succ. = raceme successively flowered; infl. = inflated; - = not remarkable; for ovaries, + = carinate, lamellate, or verrucose; for sepals and petals, + = tail or tooth present, 0 = absent; for lip, + = lip divided by marginal folds into an epichile and hypochile, 0 = lip not divided by marginal folds in two parts.

The polarity or probable direction of the evolution of the rapid identifier characters was not discussed. To evaluate their phylogenetic significance, we reconstructed their distribution on the strict consensus from the analysis of the molecular data.

Peduncle – Fig. 85 shows the most parsimonious derivation of the character 'peduncle triquetrous in cross section'. Peduncles triquetrous in cross section have been used as one of the most important characters for diagnosing all interrelated species of subgenus *Polyantha*. According to LUER (2000), four species of this large subgenus produce both, terete and triangular peduncles (*M. garciae* Luer, *M. infracta* Lindl., *M. richarsoniana* Luer, and *M. sprucei* Rchb. f.). The results of the molecular analysis suggest a non-monophyletic subgenus *Polyantha.* Its species are found in a clade mixed with species of subgenus *Masdevallia* sections *Minutae*, *Reichenbachianae*, and *Dentatae* and species of subgenus *Pygmaeia* sections *Amaluzae* and *Aphanes*. The reconstruction of the peduncle in cross section in one of the most parsimonious trees obtained from the analysis of molecular data shows a triquetrous peduncle in some members of subclade B2 derived from a terete peduncle. The data do not allow to decide with certainty whether this character had a single origin or not.

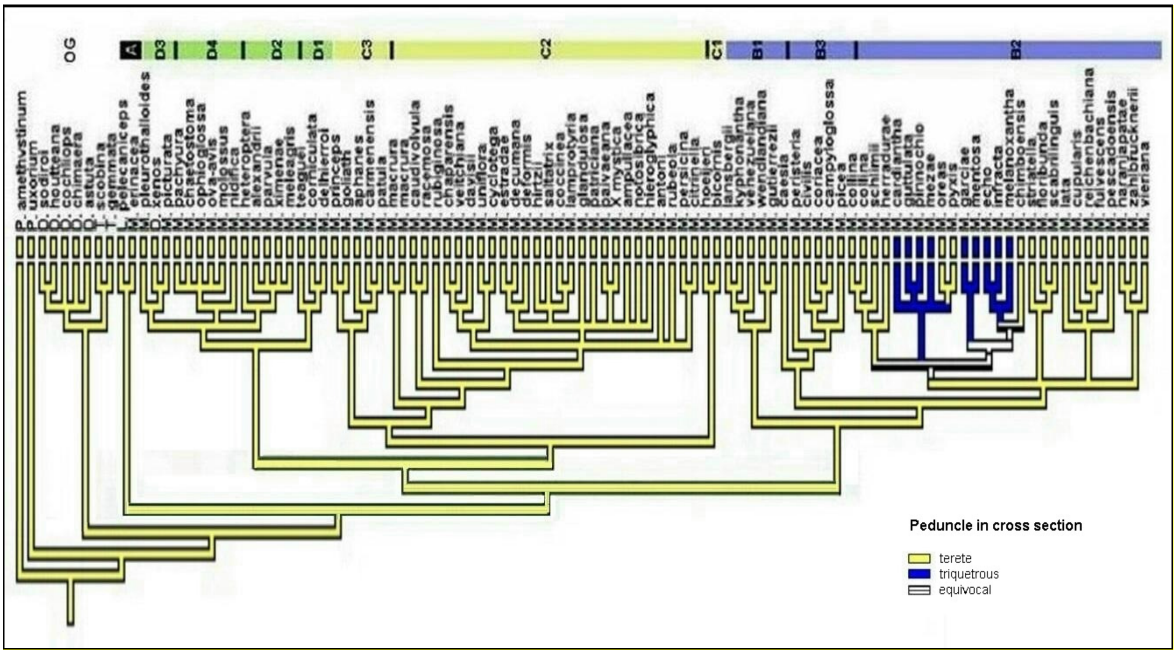

Fig. 85 Reconstruction of character state evolution of the peduncle in cross section optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

Raceme – Flowers opening either successively or simultaneously have been used to characterize some infrageneric taxa (Table 15). Flowers opening successively in periodic clusters has evolved 3-4 times within the genus (Fig. 86): once in subgenus *Amanda* and *M. nidifica* (clade D), once in *M. schlimii* (clade B), and once or twice in clade C3.

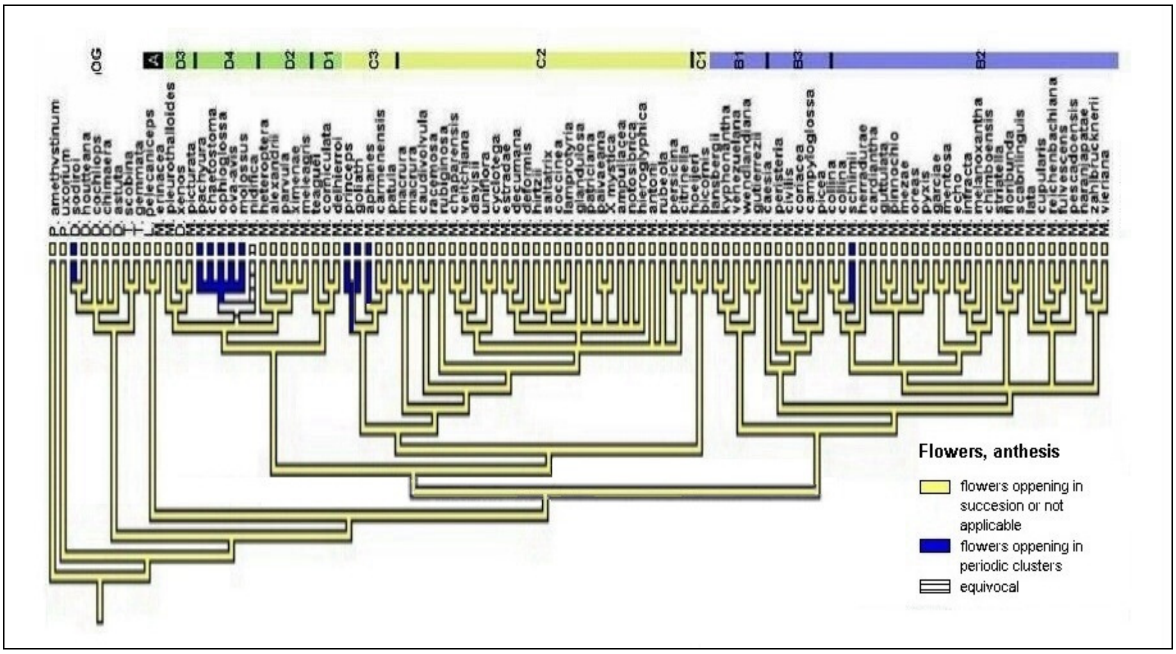

Fig. 86 Reconstruction of character state evolution of the peduncle in cross section optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

Floral bract – Fig. 75 shows the most parsimonious derivation of the type of floral bract. An inflated floral bract has evolved at least twice, once in subclade D4, with a reversal in *M. molossus* and *M. ophioglossa*, and once in *M. picturata* (subclade D3). A cucullate floral bract has evolved twice within the genus, once in subclade D1, with a reversal in *M. teaguei*, and once in *M. macrura*. This latter species was previously included within subgenus *Cucullatia* based on this character and later transferred to section *Coriaceae*. The molecular analysis does not support the inclusion of this species neither in subgenus *Cucullatia*, nor in section *Coriaceae*.

Ovary – Species with the ovaries with ribs manifested by crests or some other external features such as papillae or lamella are characteristic for subgenera *Amanda*, *Cucullatia*, *Fissia*, *Nidificia*, *Meleagris*, and *Pygmaeia* (Table 15). An ovary with undulating crests is reconstructed as having been derived four times within the genus *Masdevallia*, once in *M. hoeijeri*, once in *M. caudivolvula*, once in *M. corniculata,* and once in subclades D2, D3, and D4 (Fig. 64).

Connation of the sepals – According to LUER (2000) the subgenera *Fissia* and *Meleagris* can be characterized by a dorsal sepal that is free from the lateral (Table 15). This character has evolved at least once within the genus *Masdevallia*, in subgenus *Meleagris* (subclade D2) and subgenus *Fissia* (subclade D3) (Fig. 65). These subgenera form an unresolved trichotomy with subgenus *Meleagris*.

Sepaline tails – The free portion of the apex produced into tails has been used as rapid identifier for subgenera and sections of *Masdevallia* (Table 15). Tailless flowers characterize subgenus *Pygmaeia* section *Aphanes*. Some species of subgenus *Fissia* and subgenus *Masdevallia* section *Coriaceae* are characterized by tailless sepals. The sepaline tails apparently have been lost several times within Masdevallia (Fig. 87).

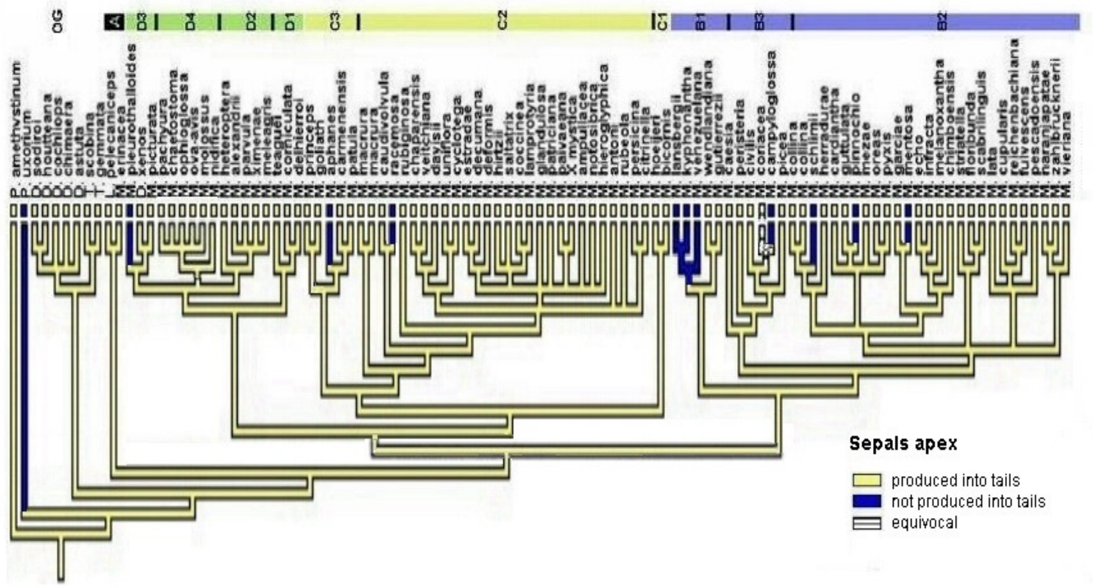

Fig. 87 Reconstruction of character state evolution of the apices of the sepals optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

Petal tails – According to LUER (2000) a callus from the labellar margin ending in a process is characteristic for the subgenera *Fissia*, and *Nidificia*, subgenus *Masdevallia* sections *Masdevallia* and *Dentatae*, subgenus *Polyantha* section *Alaticaules*, subgenus *Pygmaeia* section *Pygmaeae*, and subgenus *Scabripes*. A callus ending in an acute and retrorse (uncinate) process near the base characterizes subgenus *Masdevallia* section *Masdevallia* (LUER 2000). Figure 88 shows that this character originated repeatedly and revested at least occasionally. Therefore, it appears not to be phylogenetically useful at the infrageneric level. A callus ending in an obtuse angle between the middle and the lower third characterizes subgenus *Masdevallia* section *Coriaceae* (LUER, 2000). Figure 88 shows this character as synapomorphy for subclades B2 and B3. However it shows many reversals and cannot be considered phylogenetically useful and the infrageneric level. A callus ending in a broad and rounded process characterizes some species of subgenus *Polyantha* sections *Alaticaules* and *Coaetanae* (LUER 2000). Figure 88 shows that this character is very homoplasious and not useful at the infrageneric level.

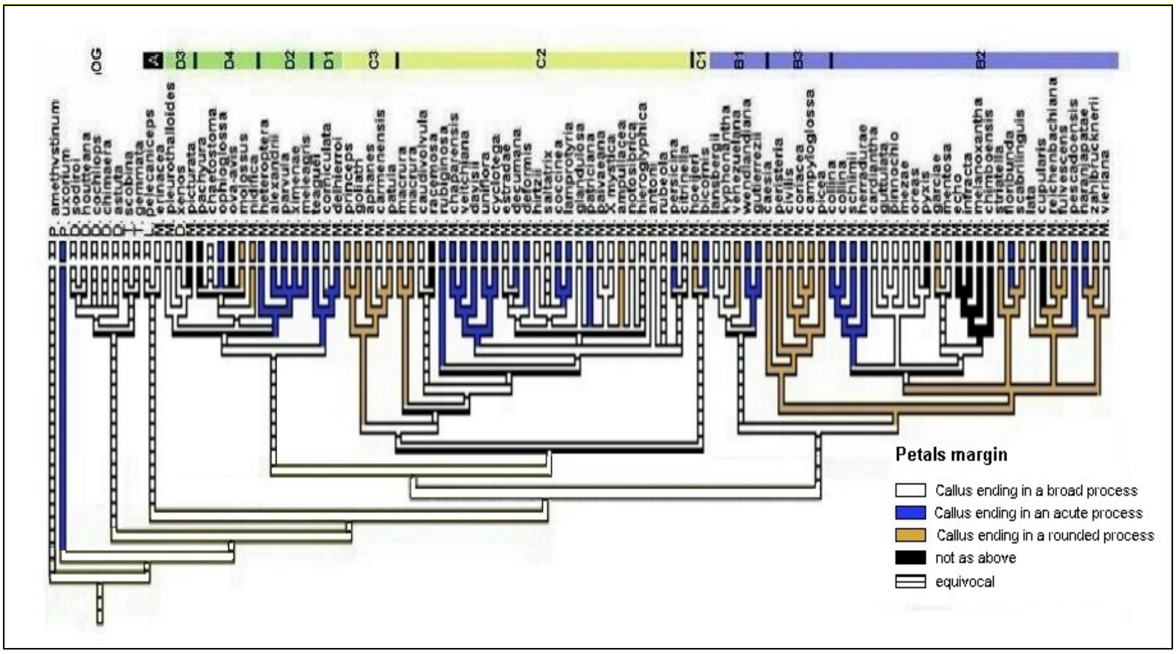

Fig. 88 Reconstruction of character state evolution of the callus of the petals optimized on one of the MPTs derived from the ITS sequences data analysis for *Masdevallia*.

Lip – Subgenera *Amanda*, *Cucullatia*, *Fissia*, *Nidificia*, *Polyantha*, and *Volvula* are characterized by a lip that is divided by marginal folds into an epichile and hypochile (LUER, 2000). Entire lips (not divided into an epichile and a hypochile) characterize species of subgenera *Masdevallia* and *Pygmaeia*. A lip that is divided by marginal folds into an epichile an a hypochile has evolved at least five times in the genus *Masdevallia*, once in subclade B2, with a reversal in a subclade comprising *M. vieirana*, *M. zahlbrucknerii*, and *M. naranjapatae*, in the subclade of *M. fulvescens* and *M. reichenbachiana*, as well as in *M. scabrilinguis*, *M. chimboensis*, *M. mentosa*, and *M. collina*. In addition, it originated in *M. gutierrezii* and *M. bicornis*, and (equivocally) in subclade C2 and clade D (Fig 53).

4.5 Biogeography and Radiation

4.5.1 Distribution patterns of *Masdevallia* species

The distribution patterns of *Masdevallia* species are not surprising, considering that this pattern represents the second major Neotropical phytogeographical pattern, according to GENTRY (1982), referred as Andean-centered. Genera with this pattern have their distributional centers in the northern Andes, where over a fourth of their species occur. Andean centered taxa are very well represented in Central America, especially in Costa Rica and Panama, where 22% of their species occur; well represented in the coastal Brazil region, and poorly represented in northern Venezuela and the West Indies. They are poorly represented in those regions where Amazonian centered taxa are well represented GENTRY (1982).

There are several factors that favored this phytogeographical pattern according to BENZING (1990):

1) **Topography**: the Andes is by far the most extensive mountain range at low latitudes and its recent orogeny has created an immense land archipelago, extending from Mexico to temperate South America, that has favored epiphytic speciation and dense packing of resulting taxa. The central Andes had a major uplift during the Oligocene (30 my BP) and emerged in their current form about 15 my BP between northern Chile and southern Peru, reaching their current structure within Pliocene and Pleistocene (JAMES, 1973; JORDAN et al., 1983). The northern Andes are the youngest, and most of their uplifting occurred in the last 5 million years (VAN DER HAMMEN, 1974; GENTRY, 1982), still enough time for orchids and several other lineages to generate an exuberant speciation which continues to this day. GENTRY and DODSON (1987) cite colliding offshore Pacific cold and warm currents at low latitudes as a major cause of the microclimatic variety that has helped to foster the unparalleled development of Andean epiphytism. The resulting niche partitioning supposedly favors high alpha diversity, whereas the dissected topography promotes evolution of ecologically similar allopatric species.
2) **Ethology**: *Pleurothallidinae* is perhaps the best Neotropical candidate for a taxon that supports the widely held view that specialized pollinators are the most important reason why there are so many species of Orchidaceae and, by extension, why epiphytes are so numerous. Fetid rather than pleasant odors characterize many species´ blossoms, and bizarre shapes are common. Most flowers are too small to attract strong fliers. However, there is no evidence that dipterans suspected of servicing pleurothallids are as constant or as effective, as male euglossines in producing either isolation among co-occurring populations or fruit set by widely dispersed conspecifics.

3) **Refuge theory**: The theory of refuges in the Pleistocene has been often used as a major explanation for the present day patterns of diversity and endemism of biota in the Neotropical region (HAFFER, 1969; VANZOLINI & WILIAMS, 1970; VANZOLINI, 1973; AB SABER, 1977; SIMPSON & HAFFER, 1978; DIXON, 1979; ABSY, 1982; GENTRY, 1982; PRANCE, 1973, 1982; VAN DER HAMMEN, 2000). Even though it has been shown that the theory has serious limitations at the theoretical level (AMORIN & PIRES, 1996; LYNCH, 1982; AMORIN, 2001), several authors still insist in a major role for the climatic changes in shaping actual patterns (i.e. HAFFER, 1974, 1977; PRANCE, 1982; VAN DER HAMMEN, 2000) and increasing speciation rates in the region. Disjunctions such as those observed between the Atlantic Forest and the Amazonian region are sometimes explained within the framework of the theory of Pleistocene refuges, but especially in orchids, long-distance dispersal appears to be a more likely option. However, according to BENZING (1990), refugia were less developed in premontane and low montane humid forests which are the characteristic epiphyte habits of most *Masdevallia* species. The continuity of forests throughout the Pleistocene must account in part for the unparalleled botanical variety of epiphytes and terrestrials in regions such as the currently pluvial Colombian Chocó.

4.5.2 Biogeographic patterns of the genus *Masdevallia* based on molecular analysis

Some species of the major clades in the molecular tree occur widespread across, overlapping regions in the Andes and Central America. Most of the species are distributed in Colombia and Ecuador, suggesting that the northern Andes may have been the most influential biogeographic arena for the diversification of lineages within the genus *Masdevallia*. The northern Andes are the youngest, and most of their uplifting occurred in the last 5 million years (VAN DER HAMMEN, 1974; GENTRY, 1982). The central Andes had a major uplift during the Oligocene (30 my BP) and emerged in their current form about 15 my BP between northern Chile and southern Peru, reaching their current structure by the Pliocene and Pleistocene (JAMES, 1973; JORDAN et al., 1983). Vicariance events and biogeographic patterns along the Andes are difficult to determine due to complex formation events and a long history. Two main areas of volcanic activities have been recognized: a northern zone in southern Colombia and northern Ecuador and a central zone in Peru, western Bolivia, and northern Chile and Argentina (WINDLEY, 1984).

Southern Central America is the second center of speciation for *Masdevallia*. In the Guyana Shield, *Masdevallia* species are very uncommon. It is likely that the extreme habitats often found in such areas, including rocky outcrops, dry forests, savannas, etc, are unsuitable for most species of

Masdevallia, which in general display a preference for humid and shady places. The Atlantic forest of Brazil, a belt of tropical rain forests along the coast of Brazil, exhibits a low species number of *Masdevallia*, comparable to that of the Antilles or the Guyana shield. This is somewhat surprising for the genus, if one considers the type of vegetation in that area. The tropical rainforests in this region are at present reduced to nearly 10% of their original cover (AMORIM, 2001), and the impact of deforestation should not be underestimated as a process distorting the values for species number in the area. Deforestation in the area dates back to about 1500 (HOEHNE, 1942) whereas the available herbarium records start about 1840. Some biogeographic studies stated that the history of the Atlantic Brazilian Forest was driven mainly by vicariance events that have produced a hierarchical pattern (MORITZ et al., 2000; RON, 2000; AMORIM, 2001; BATES, 2001; HALL & HARVEY, 2002).

Four well supported clades can be recognized within *Masdevallia*, the first two corresponding to the northern Andes and Central America (Clades A and B), and two roughly corresponding to the northern and central Andes (Clades C and D) with an approximate distribution break in the volcanic area of southern Colombia and northern Ecuador (Fig. 78).

Luerella pelecaniceps (Clade A) is endemic to Panama, being found at 800 to 1 000 m above the sea level. In contrast, *Masdevallia erinacea* is found throughout the whole geographical range. Their current distribution might be explained by long-distance dispersal.

Clade B has the highest level of ecological diversification within the *Masdevallia* lineages across all four clades. In terms of geographical distribution and diversity of microhabitats, this group represents the most successful clade. Most species analyzed are endemic to Venezuela, Colombia, and Ecuador. The species at the furthest geographical extremes of the genus (southeastern Brazil, Guayana, and the Coastal Cordillera of Venezuela) appear to be the most basal in this clade, and the Andean species appear to be derived. High dispersability appears to be characteristic of certain lineages in clade B. Within subclade B1, *M. venezuelana* and *M. kyphonantha* are restricted to the coastal cordillera of Venezuela. *Masdevallia lansbergi* is found in the coastal cordillera of Venezuela and in the Guayana region, growing at lower elevations, always associated with vegetation along bank roads or along forest edges. *Masdevallia wendlandiana* is one of the most widespread species, growing in exposed environments, at very low elevations. The current distribution of this species might be explained by long-distance dispersal events. Species in subclade B1, *M. gutierrezii*, is endemic to Bolivia, growing at low elevations

Subclade B2 corresponds to Central America and/or the northern Andes, and extends south into Bolivia. The current distribution of its species might be explained by long-distance dispersal. *Masdevallia lata*, *M. cupularis*, *M. fulvescens*, *M. reichenbachiana*, *M. striatella* and *M. scabrilinguis* are endemic to Costa Rica and Panama, growing at high elevations. *Masdevallia floribunda* has a wide and scattered geographical distribution from Belize and Mexico to Colombia over a broad elevational range from 75 to 1 500 m above sea level. Most of the remaining species of this subclade are from the central Andes, growing at high elevations. *Masdevallia infracta*, from Sierra do Itatiaia in Brazil, is nested within subclade B2, suggesting a long-distance dispersal event and supporting the pattern of shared flora between the Eastern Cordillera of Colombia and the Brazilian highlands (SAFFORD, 1999). Numerous other genera of plants and animals also share a disjunct distribution between the Andes and the coastal region of Brazil and/or the Brazilian highlands (RAMBO, 1951; LYNCH, 1979; BROWN, 1987; HAFFER, 1987; CLARK, 1992; SAFFORD, 1999). For example, about one-third of the plant genera found in the Sierra do Itatiaia in Brazil are shared with the Páramos of the Eastern Cordillera of Colombia (SAFFORD, 1999). *Masdevallia garciae* is endemic to the Coastal Cordillera of Venezuela and *M. collina* is endemic to Panama.

Subclade B3 corresponds to the central Andes with most species found in the Western and the Central Cordillera of Colombia, ranging southward through the department of Nariño and into northwestern Ecuador, with *M. civilis* and *M. picea* apparently endemic in Northern Peru. *Masdevallia coriacea* and *M. campyloglossa* are frequent in the Páramos of the Eastern Cordillera of Colombia, and both become infrequent in the other two Cordilleras of Colombia, as well as in Ecuador and Peru. Most species of this subclade grow terrestrically on semi-arid, rocky slopes, fully exposed to the extremes of heat in the midday tropical sun, and chilly nights at an altitude over 2 000 m above sea level.

All species grouped into Clade C are from the Andes, most of them growing epiphytically at very high altitudes. Within subclade C1, *Masdevallia bicornis* is endemic in lowland eastern Ecuador, and *M. hoeijeri* is distributed in southeastern Ecuador and in the Cordillera del Condor in Colombia. Species grouped in subclade C2 are widely distributed in the Andes. The basal species, *Masdevallia macrura*, *M. caudivolvula* and *M. racemosa*, are distributed in Colombia, at elevations of 2 000 to 3 400 m above sea level. Ascending the cladogram, *M. rubiginosa* occurs in southeastern Ecuador and neighboring Peru, and *M. rubeola* occurs uncommonly in the Andes of central Peru and northern Bolivia. The other species found within subclade C2 are principally distributed in the forests of Ecuador, with most of them being endemic. The extremely low genetic divergence between these taxa could be an indication that their speciation occurred rather recently. The remaining species within Clade C, treated as subclade C3, are restricted to the cloud forest of southeastern Ecuador and northern Peru, being found at high altitude from 2 000 to 3 400 m above the sea level.

Clade D is composed mainly of Andean species, with *M. pleurothalloides* apparently endemic in the wet forested hills east of Panama City, and *M. picturata* and *M. nidifica* widely distributed through Central America and the Andes of South America. Within subclade D1, *M. teaguei* is found infrequently in southern Ecuador, at high altitude from 2 000 to 3 400 m above sea level. *Masdevallia corniculata* occurs in all three cordilleras of Colombia and on the eastern slopes of the Andes of Ecuador, from 1 500 to 2 500 m above sea level. *Masdevallia delhierroi* is endemic to east-central Ecuador at 2 600 m above sea level. All species within subclade D2 grow epiphytically in wet forests at high or relatively high altitudes in the Andes of Colombia, Ecuador, Peru and Bolivia. *Masdevallia heteroptera* is endemic in the mountains around Medellín in the central and western cordilleras of Colombia, *M. alexandri* is endemic to the western declivity of central Ecuador, *M. meleagris* is endemic to the Western Cordillera of Colombia, and *M. ximenae* is endemic in southern Ecuador. The widely distributed *M. parvula* grows on mossy branches of stunted trees in cool, wet cloud forests from Colombia through Ecuador and Peru, into Bolivia, usually at altitudes about 3 000 m above sea level. In subclade D3, *M. pleurothalloides* is endemic to a small area east of Panama City, whereas *M. picturata* is one of the most common and widely distributed species of the genus, through Central America and the Andes of South America into Guayana, at an elevation of more than 1 500 m above sea level. Long-distance dispersal may have played a role in the current distribution of *M. picturata*. *Dracula xenos*, apparently endemic in the Valle del Cauca in Colombia, has not been recollected since its original discovery. *Masdevallia nidifica* (subclade D4), sister to the remaining members of subgenera *Amanda* and *Nidificia*, has a wide and scattered geographical distribution from Central America to the Eastern Cordillera of Colombia and to southwestern Ecuador, over a broad elevational range from 250 to 2 500 m above sea level. The remaining species included in this subclade are principally found in the Andes of Ecuador, and one species, *M. molossus*, is widely distributed in the western and central Cordilleras of Colombia.

4.5.3 Some factors promoting the radiation of the genus *Masdevallia*

The family *Orchidaceae* is one of the two largest families of flowering plants; the other one, *Asteraceae*, is sometimes stated to be larger. Within the family *Orchidaceae*, *Pleurothallidinae* is the largest subtribe, and within this subtribe, the genus *Masdevallia* is one of the largest genera in number of species, exceeded by *Lepanthes*, *Pleurothallis* and *Stelis*.

Several hypotheses for the enormous species richness of orchids, and especially of *Masdevallia* are described below:

1) Habit

The first hypothesis given by BENZING (1990) describes the highly fragmented nature of the epiphytic substratum, especially in mid-montane rainforest, as an ideal speciation condition since it should promote allopatric speciation. According to BENZING (1990), this would explain why not only orchids, but also epiphytic aroids and bromeliads are so species-rich despite their different morphological adaptations to the arboreal habitat. This argument is contradicted by IBISCH et al. (1996), who mentioned that, in plant families that have evolved epiphytism other than the Orchidaceae, the terrestrial species have higher rates of speciation.

Of the 25 000 orchid species so far described, ca. 18 000 are epiphytes (Royal Botanic Gardens, Kew 2003). The montane epiphyte flora is not only characterized by high species richness, but also by pronounced endemism. So the mid-elevation bulge in species richness of GENTRY and DODSON (1987) is in part a result of a strong presence of endemic (orchid) species, which cannot be comprehensively explained by favourable climate conditions. The epiphyte habitat is discontinous everywhere, even in primary forests, but not to the same degree. In montane regions, the forest and therefore of the epiphytes substratum, is fragmented, a condition conducive to speciation (TEMPLETON, 1981). Where climate, elevation, and type of vegetation are more monotonous (e.g., Amazonia), epiphyte species tend to be wide-ranging but not very numerous.

Epiphyte species richness in montane habitats is made possible by high air humidity. This is confirmed by numerous local studies (INGRAM et al., 1996, SCHMIT-NEUERBURG, 2002, KREFT et al., 2004). One main difference between lowland and montane forests is that regular dry periods but also periodically occurring events such as El Niño reduce the abundance and diversity of epiphytes in Amazonian lowland forests drastically, e.g. at the Surumoni site (SCHMIT-NEUERBURG, 2002). In contrast, in montane rain forests, the impact of dry periods is mitigated by the 'horizontal precipitation' (VOGELMANN, 1973), which in cloud forests frequently contributes 20% or more to the total water input (JUVIK & EKERN, 1978, STADTMÜLLER, 1987).

2) Niche partitioning

GENTRY & DODSON (1987) proposed that the high species diversity of orchids might be correlated with their exceptionally fine niche partitioning. Floristic inventories by PITTENDRIGH (1948), JOHANSSON (1974), TER STEEGE & CORNELISSEN (1989), EK et al. (1997), and WOLF & FLAMENCO (2003) indeed demonstrated microhabitat specialization in the tropical epiphytic environment and showed that the total bark and branch surface area available for occupation by epiphytic species greatly exceeds that of the ground area. These studies also show that many more orchid species and individuals are crowded in the tree crown and on the branches compared to a similar ground area. Four main epiphytic microhabitats exist. The first consists of the shaded and humid tree base, where species growing directly on the bark survive. The second microhabitat encompasses the upper trunk, where epiphytes grow only when suitable germination sites are present. The third microhabitat comprises the inner canopy, which is a heterogeneous assemblage of the environments of the upper tree trunk and the outer canopy. Here, shade-adapted species can survive in the inner forks and branches next to hemi-epiphytes growing in packages of moss and humus, and to species that can endure sites in direct sun. The largest diversity of epiphytic species and crown-foraging pollinators is usually found here. The fourth microhabitat is the outer canopy, with high levels of disturbance, prolonged periods of drought and large fluctuations in temperature, where largely xeromorphic species are present, rooting directly on the outer well-illuminated twigs. Speciation may be increased since specialized morphological adaptations allow a survival advantage in each of these four microhabitats. In addition, the high diversity in tropical tree species might stimulate further niche differentiation owing to host specificity.

3) Pollinators

A third hypothesis explaining the species richness of orchids is pollinator specialization. The orchids are well known for certain pollination strategies that often involve highly specialized relationships between plant and pollinator. For example, flowers of species of *Ophrys* in Europe and the Meditteranean as well as several Australian genera produce highly specific suites of olfactory and visual stimuli that attract a unique species of pollinator, usually a male bee or wasp (DAFNI & BERNHARDT 1990) to each species of orchid. The insect confuses these stimuli with the conspecific female and pollinates through repeated pseudo-copulations. High speciation rates within these genera are suggested to be due to the fact that because different species of bees use slightly different olfactory stimuli to attract mates.Therefore, even a slight mutation in the floral scent of the orchid may be sufficient to cause adaptation to a new species of pollinator and thus reproductive isolation (SCHIESTL & AYASSE 2002). Even in moderately specialized 'pollinator syndromes'- such as those associated with bumble-bee and hummingbird pollination, where a plant species is pollinated by a small number of bumblebee or hummingbird species - one major gene mutation may be all that is required to cause an adaptive switch between the two syndromes (BRADSHAW & SCHEMSKE 2003). Thus chance mutations within plant species that are only moderately specialized in their pollination could also potentially drive speciation. GENTRY & DODSON (1987) consider bee, fly, hummingbird, hawkmoth, bat and small mammal pollination syndromes all to be moderately specialized in terms of the number of pollinator species attracted.

Orchids generally are less pollinator specialized than is generally assumed - most species have more than one pollinator. Within subtribe *Pleurothallidinae*, the pollinator specialization was studied only in a few species. Within the genus *Masdevallia*, little is know about the pollination. Pollination in *Masdevallia* has been only rarely observed, and on the other side, the systematics of the tropical *Drosophilidae* and related families is poorly understood.

Some species are characterized by foul odors, a dark or dull color of the perianth, sepaline tails, and hinged lip. All these characters certainly indicate myophily or sapromyophily. Flies tend to be important pollinators in high-altitude and high-latitude systems, where they are numerous and other insect groups may be lacking (LARSON et al., 2001).

DODSON (1962) reported pollination of *M. fractiflexa* by blowflies (*Calliphoridae*). The osmophores of *M. caudata*, *M. nidifica*, and *M. calura* were described in detail by VOGEL (1962, 1990). Some species with brightly coloured, odourless flowers and sepaline tube such as *M. rosea*, and *M. coccinea* are reported to be pollinated by hummingbirds (DODSON 1962, VAN DER PJIL and DODSON, 1966), and it is probable that related species, such as *M. veitchiana*, *M. barleana*, and *M. davisii*, are also bird pollinated. However, in the absence of enough data, we can neither confirm nor rule out the hypothesis that pollinator specialization has been important for the speciation in *Masdevallia*.

4.6 Comparison with traditional classification and possible taxonomical solutions

4.6.1 Incongruence between cladograms and taxonomic systems

Incongruence between cladograms and taxonomic systems of the same group is widely discussed by many authors (ANDERBERG A. A. C. et al., 2002; CRONN R. C. et al., 2002; CRONQUIST A., 1981, 1987; DAY A. G., 1993b, DIGGS G. M. AND B. L. LIPSCOMB, 2002; FERGUSON C. J. AND R. K. JANSEN, 2002). As explained by GRANT (2002), incongruence is to be expected, especially in groups of large size. This is a result of the differences between cladistics and taxonomy in goals and methods.

The taxonomy of *Masdevallia* is mainly based on floral structures. REICHENBACH (1880) recognized 15 sections, PFITZER (1888) 5 sections, WOOLWARD (1896) 15 sections and KRAENZLIN (1925) 14 sections. LUER (1986b) grouped the species into 5 subgenera, 17 sections and 12 subsections.Later (LUER, 2000-2003) he recognized into 11 subgenera, 13 sections and 13 subsections, and recently (LUER 2006), he established 19 smaller genera from among the infrageneric taxa of *Masdevallia*.

The differences observed in the delimitation of infrageneric taxa results not only from the large species number. In addition, the identification of morphological and anatomical synapomorphies in the subtribe is complicated by the homoplasy rife in vegetative and floral features (PRIDGEON, 1982), as shown in the cladistic study by NEYLAND et al. (1995). Morphological features such as fleshy or terete leaves, variously connate sepals, and ornamented ovaries occur in clearly unrelated species (LUER, 1986b). The same is true for anatomical features such as thickenings in the foliar hypodermis, differentiation of foliar chlorenchyma, and spirally thickened idioblasts (PRIDGEON, 1982; NEYLAND et al. 1995). Most of these features are either xeromorphic adaptations or phenotypic responses to selection pressures imposed by pollinators with similar behaviors.

An overview of the most important classification systems of *Masdevallia* is briefly discussed below.

Reichenbach (1873-1878) – The earliest attempt to indicate subdivisions of the genus *Masdevallia* was made by Reichenbach. Usually he did not mention the rank of the subdivisions, but in a few instances he indicated groups or "sections". In the whole 14 groups/sections were recognized by Reichenbach.

Pfitzer (1888) – The second proposed infrageneric classification was that of Pfitzer. It included five sections, of which four (*Tubulosae*, *Polyanthae*, *Saccilabiatae*, and *Triaristellae*) had been previously recognized by Reichenbach (1873-1878). One new section was described, and section *Verrucosae* was raised to generic rank (genus *Scaphosepalum*).

H. J. Veitch (1889) – H. J. Veitch proposed for the genus *Masdevallia* an infrageneric classification based on Reichenbach´s classification. The infrageneric classification comprises 3 sections and 6 subsections, these last ones demoted from the rank of section in Reichenbach´s classification to subsections of *Eumasdevallia*.

Woolward (1889) – Woolward used the classification of Reichenbach with minor changes. The species were grouped into 15 sections, of which three (*Muscosae*, *Racemosae* and *Reichenbachianae*), were newly proposed by Woolward. The remaining sections were *Amandae*, *Coccineae*, *Coriaceae*, *Cucullatae*, *Fissae*, *Minutae*, *Polyanthae*, *Saccolabiatae*, *Saltatrices*, *Triangulares*, *Triaristellae*, and *Tubulosae*.

Schlechter (1920) – Schlechter proposed to segregate *Masdevallia echidna* Rchb. f. into a new genus, *Porroglossum*.

Kraenzlin (1925) – The infrageneric classification proposed by Kraenzlin included 14 sections, of which two (*Urceolares* and *Floribundae*), were new sections proposed by Kraenzlin. Five sections (*Polystictae*, *Leontoglossae*, *Alaticaules*, *Chimaeroideae*, and *Rhombopetalae*), were renamed, and two sections (*Racemosae* and *Minutae*) were merged into other sections. Some species were transferred to different sections.

Luer (1986b) – The first infrageneric classification for the genus *Masdevallia* proposed by Luer was in part based on Reichenbach's classification. It included 5 subgenera, 17 sections, and 12 subsections. Luer placed Reichenbach's sections *Amanda*, *Cucullatae*, *Fissae*, and *Polyantha* on a higher level. Four new subgenera and nine new sections were described.

Luer (2000-2003) – The second infrageneric classification for the genus *Masdevallia* proposed by Luer divided the genus into 11 subgenera, 13 sections and 13 subsections. Sections Fissae, Cucullatae, Nidificae, Polyanthae, and Pygmaeae were placed on a higher level. Two new subgenera were described.

Luer (2006) – From among the subgenera of *Masdevallia* and on the basis of "marked morphological differences among some of the subgenera" Luer established the new genera *Acinopetala*, *Alaticaulia*, *Buccella*, *Byrcella*, *Fissia*, *Luzana*, *Megema*, *Petalodon*, *Pteroon*, *Regalia*, *Reichantha*, *Spectaculum*, *Spilotantha*, *Streptoura*, *Triotosiphon*, and *Zahleria*. Recent DNA analyses are barely mentioned, and no cladogram is reproduced.

4.6.2 Comparison of Luer´s taxonomy and the results obtained from the molecular analysis – Possible taxonomical solutions

Possible taxonomic solutions based on the analysis of the molecular results obtained in this study (in which only monophyletic groups are recognized) are discussed below:

Subgenus *Amanda* – Subgenus *Amanda* was first recognized as section by REICHENBACH. KRAENZLIN (1925) renamed the section "Polystictae" because the most representative species of this section, according to KRAENZLIN, was *M. polysticta* Rchb. The new name is therefore illegimate. LUER (1986b) raised the section to the rank of subgenus and included four sections: *Amanda*, *Fissia*, *Nidificia*, *Ophioglossae* and *Pygmaeae*. LUER (2000) raised these sections, previously contained in subgenus *Amanda*, to the rank of subgenera. *Masdevallia ophioglossa* (previously section *Ophioglossae*) was included within subgenus *Amanda* (LUER 2000-2003). The results obtained in this study indicate that there is a strong relationship (in the Bayesian analysis) between subgenera *Amanda*, *Fissia*, *Nidificia*, and *Meleagris*. Subgenera *Fissia* and *Meleagris* are well delimited, whereas subgenera *Amanda* and *Nidificia* are not resolved in our data. A possible taxonomic solution for a new phylogenetic classification of this group would be to include all sampled species of subgenera *Amanda*, *Fissia*, *Nidificia*, and *Meleagris* within a single subgenus. According to the rules of priority, this subgenus should be called *Amanda*.

Subgenus *Cucullatia* – Subgenus *Cucullatia* has been a well delimited group since REICHENBACH. LUER (1986b) included it as section within subgenus *Masdevallia*, and in 2000 he raised the section to the rank of subgenus. The results obtained from the molecular analysis indicate that subgenus *Cucullatia* is a well delimited group and no further changes are proposed.

Subgenus *Masdevallia* – According to LUER, all species of subgenus *Masdevallia* seem to be related whereas the boundaries of some species are not well defined. 1986, Luer divided the subgenus into twelve sections and twelve subsections; and 2000 divided the subgenus into nine sections and seven subsections (Table 3). The subgenus grouped six of the sections proposed by REICHENBACH.

The results obtained in this study show a polyphyletic subgenus *Masdevallia*, with its representatives separated into two major groups designated clade B and clade C in Fig. 39. Clade B includes section *Minutae* (not monophyletic), *Reichenbachianae*, *Triotosiphon*, and *Coriaceae*, excluding one species, *M. macrura*, which was previously included within section *Durae*, and the monospecific section *Dentatae*, mixed with species of the subgenera *Pygmaeia* and *Polyantha*. Clade C includes a monophyletic section *Masdevallia*, a monophyletic section *Durae,* and the monospecific section *Racemosae*. In addition, clade C includes a few species of subgenera *Pygmaeia*, and the monospecific subgenera *Scabripes* and *Volvula*.

A possible taxonomic solution for a new phylogenetic classification of subgenus *Masdevallia* could be reached by the following steps. (i) Transfer of sections *Minutae*, *Reichenbachianae*, and *Dentatae* to subgenus *Polyantha.* (ii) Section *Triotosiphon* would be raised to a higher taxonomic rank, subgenus *Triotosiphon*. (iii) Section *Coriaceae* would be raised to a higher taxonomic rank, subgenus

Coriaceae. (iii) Section *Durae* would be raised to a higher taxonomic rank, subgenus *Durae.* (iii) Subgenus *Masdevallia* would include only members of section *Masdevallia* with all remaining subsections. The results obtained from the molecular analysis do not support the fine subsectional classification of section *Masdevallia.* Not one of the subsections included by Luer within section *Masdevallia* seems to be monophyletic – but of course the data are also insufficient to reject his classification completely. For the time being, a section *Masdevallia* without any further subdivision appear to be the best solution.

Subgenus *Polyantha* – The members of subgenus *Polyantha* are all found in one large clade (B2), but with all members of subgenus *Masdevallia* sections *Minutae*, *Reichenbachianae*, and *Dentatae* scattered among them. The results obtained in this study indicate that sections *Minutae*, *Reichenbachianae*, and *Dentatae* are more closely related to subgenus *Polyantha* than to subgenus *Masdevallia*, as previously suggested by LUER (1986b).

A possible taxonomic solution for a new phylogenetic classification of this group would be to re-include all representatives of sections *Minutae*, *Reichenbachianae*, and *Dentatae* within a large subgenus *Polyantha.* This group would also include species currently refered to subgenus *Pygmaeia*: *Masdevallia mentosa*, *M. chimboensis*, and section *Zahlbrucknerae*.

Masdevallia mentosa is a smal Ecuadorian species currently included within subgenus *Pygmaeia* section *Aphanes* and previously considered as a monospecific section of subgenus *Masdevallia.* According to Luer, this species is characterized by a slender, successively flowering peduncle, triquetrous in cross section, which would place it in *Masdevallia* section *Polyanthae* if it didn't have an entire and smooth lip. The results obtained in this study confirm that *M. mentosa* is more closely related to subgenus *Polyantha* than to subgenus *Pygmaeia*.

Section *Zahlbrucknerae* includes four species previously included within subgenus *Masdevallia* section *Amaluzae*. *Masdevallia schizopetala*, previously treated as member of section *Minutae*, is now included within section *Zahlbrucknerae.* This illustrates a considerable resemblance between section *Zahlbrucknerae* and section *Minutae.*

Subgenus *Pygmaeia* – Species currently attributed to subgenus *Pygmaeia* appear scattered all over the cladogram in the results obtained from the molecular analysis. Since 2003, Luer´s treatment of subgenus *Pygmaeia* includes four sections. Sections *Amaluzae* and *Aphanes* had been previously considered as section of subgenus *Masdevallia*, whereas the type section *Pygmaeae* had been previously considered as section of subgenus *Amanda*. Section *Zahlbrucknerae* has already been discussed above.

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Appendix I

Morphological Data Matrix

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
D. astuta	2	2	2	1	2	2	3	2	1	2	1	1	1	1	1	1	1	1	1	2	1	1
D. chimaera	1/2	1	2	1	2	2	3	2		2	1	2	1	1	2	1	1	1	1	2	1	4
D. cochliops	2	1	2	1/2	1	1	1	2	1	1	1	1	2	1	1	1	2	1/4	1	2		1
D. houtteana	2	1	2/3	1	2	2	3	2	1	2	2	1	2	1	2	1	1	1	1	2	1	4
D. sodiroi	2	1	2	1	1	1	1	2	1	1	1	1	1	2	1	2	1	1	1	2	1	1
D. xenos	2	1	2	1/2	1	1	1	1	1				1	1	2	1	1	1	1	2	1	1
M. abbreviata	2	1	2	2	1	1	1	1	1				1	1	1	1	1	3	1	2	1	1
M. alexandrii	2	1	3	1	2	2	1	1	1				1	1	2	1	1	1	1	2	1	1
M. ampullacea	2	1	2/3	2	1	1	1	1	1				1	1	2	1	1	1	1	2	1	1
M. antonii	2	1	2	1	1	1	3	2	1	2	1	1	2	1	1	1	1	1	1	2	1	4
M. aphanes	2	1	1/2	1	1	1	1	1	1				2	1	2	1	1	1	1	2	1	1
M. bangii	2	1	3	2	1	2	1	2	1	1	2	1	1	1	1	1	1	1/4	1	2	1	1
M. bicornis	2	1	2	2	2	1	1	1	1				1	1	2	1	1	3	1	2	1	1
M. caloptera	2	1	3	2	2	1	1	2	1	2	2	2	1	1	1	1	1	2	1	2	2	1
M. campyloglossa	2	1	2	1	1	1	1	2	1	1	2	1	1	2	1	2	1	1/4	1	2	1	1
M. cardiantha	2	1	2	1	1	1	1	2	1	1	2	1	1	2	1	2	1	1/4	1	2	1	1
M. carmenensis	2	1	2/3	1	1	1	1	1	1				1	1	2	1	1	1	1	2	1	1
M. caudivolvula	2	1	2/3	1/2	1	1	1	2	1	1	1	1	1	1	1	1	1	1/4	1	2	1	1
M. cerastes	2	1	2	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1/4	1	2	2	2
M. chaetostoma	2	1	3	2	1	2	1	2	1	1	1	1	1	1	1	1	1	1	1	2	1	1
M. chimboensis	2	1	3	1	2	2	1	1	1				1	1	1	1	1	1	1	2	2	1
M. civilis	2	1	1/2	2	1	2	1	1	1				1	2	2	1	1	1	1	1	1	1
M. coccinea	1	1	2/3	2	2	2	1	1	2				1	1	1	1	1	1	1	2	1	1
M. collina	2	1	2	1	1	1	1	2	1	1	1	1	1	2	1	1	1	1/4	1	2	1	1
M. corniculata	1/2	1	1/2	1	1	1	1	2	1	1	2	2	1	1	1	1	1	2	1	2	2	1
M. cupularis	2	1	3	2	2	2	1	2	1	1	2	1	1	1	2	1	1	1	1	2	1	1
M. davisii	2	1	2	1	1	1	1	1	2				1	1	2	1	1	1	1	2	1	1
M. decumana	2	1	2	2	1	1	1	1	2				1	1	2	1	1	1	1	2	1	1
M. deformis	2	1	2/3	2	1	1	1	1	2				1	1	1	1	1	1	1	2	1	1
M. delhierroi	1/2	1	3	1	2	1	1	2	1	1	1	1	1	1	1	1	1	1/4	1	2	1	4
M. echo	2	1	2	1	1	1	1	2	1	1	2	1	1	2	2	2	1	1/4	1	2	1	1
M. erinacea	2	1	2	2	1	1	1	1	2				1	1	2	1	1	3	1	2	2	1
M. estradae	2	1	2	2	1	1	1	1	2				1	1	2	1	1	2	1	2	2	1
M. floribunda	2	1	3	1	2	2	1	1	1				1	1	1	1	1	1	1	2	2	1
M. fulvescens	2	1	2	1	1	1	1	2	1	1	1	1	1	2	2	1	1	1	1	2	1	1
M. garciae	1/2	1	2	1	1	1	1	1	2				1	1	1	1	1	1	1	2	1	1
M. glandulosa	2	1	2	1	1	1	1	1	1				1/2	1	2	1	1	1	1	2	1	1
M. glomerosa	2	1	2	1	1	1	1	2	1	1	1	1	2	1	1	1	1	1	1	2	1	4
M. goliath	2	1	3	2	2	2	1	1	1				1	1	1	1	1	1	1	2	1	1
M. gutierezii	2	1	2	1	1	1	1	1	1				1	1	2	1	1	1	1	2	1	1
M. guttulata	2	1	2	1	2	2	1	2	1	1	2	1	1	2	2	2	1	1/4	1	2	1	1
M. herradurae	2	1	2/3	1	1	1	1	2	1	1	1	1	2	1	2	1	2	1	1	2	1	1/4
M. hirtzii	2	1	2	1	1	2	1	1	2				1	2	2	1	1	1	1	2	1	1
M. hoeijeri	2	1	2	1/2	2	1	1	1	1				1	1	2	1	1	1	1	2	2	1
M. infracta	1/2	1	1/2	2	2	2	1	1	1				1	1	2	1	1	1	1	1	1	1
M. lamprotyria	2	1	2	1	1	1	1	1	2				1	1	2	1	1	1	1	2	1	1
M. lata	2	1	2	2	1	1	1	1	1				1	2	2	1	1	1	1	2	1	1
M. macrura	2	1	2/3	2	2	1	1	2	1	1	1	1	1	2	2	1	1	1	1	2	1	1
M. melanoxantha	2	1	2	2	1	1	1	2	1	1	2	1	1	2	1	2	1	1/4	1	2	1	1
M. meleagris	1	2	2	1	1	2	1	2	1	2	1/2	1	1	1	1	1	1	1	1	2	1	4
M. mentosa	2	1	2	2	2	2	1	1	1				1	1	2	1	1	1	1	2	1	1
M. mezae	2	1	3	1	2	2	1	2	1	1	1	1	1	1	1	1	1	1/4	1	2	1	3
M. molossus	2	1	2	1	1	1	1	1	1				2	1	1	1	1	1	1	2	1	4
M. mystica	2	1	2	1	2	2	1	1	1				2	1	2	1	1	1	1	2	1	1
M. naranjapatae	2	1	2	1/2	1	1	1	2	1	2	1	1	1	1	2	1	1	1	1	2	1	1
M. nidifica	2	1	2	2	1	1	1	1	2				1	1	2	1	1	1	1	2	1	1
M. notosibrica	2	1	2	2	2	1	1	2	1	2	2	2	1	1	1	1	1	1/4	1	2	1	1
M. ophioglossa	2	1	3	2	2	2	1	1	1				1	1	2	1	1	1	1	2	1	2
M. oreas	2	1	2/3	2	2	1	1	1	1				2	2	2	1	1	1	1	2	1	1
M. ova-avis	2	1	2/3	2	1	1	1	1	1				2	1	2	1	1	1	1	2	1	1
M. pachyura	2	1	2	2	2	1	1	2	1	2	2	2	1	1	2	1	1	2	1	2	2	2

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
M. paivaeana	*2*	*1*	*2*	*1*	*2*	*1*	*1*	*1*	*2*				*1*	*2*	*2*	*1*	*1*	*1*	*1*	*2*	*1*	*1*
M. panguiensis	*2*	*1*	*1*	*2*	*1*	*1*	*1*	*1*	*1*				*1*	*1*	*2*	*1*	*1*	*1*	*1*	*2*	*2*	*1*
M. parvula	*2*	*1*	*2*	*2*	*1*	*1*	*1*	*1*	*1*				*1*	*1*	*1*	*1*	*1*	*1*	*1*	*2*	*1*	*4*
M. patriciana	*2*	*1*	*2*	*1*	*2*	*1*	*1*	*2*	*1*	*1*	*2*	*1*	*1*	*2*	*1*	*2*	*1*	*1/4*	*1*	*2*	*1*	*1*
M. patula	*2*	*1*	*2*	*1*	*1*	*1*	*1*	*1*	*1*				*1*	*2*	*1*	*1*	*1*	*1*	*1*	*2*	*1*	*1*
M. peristeria	*2*	*1*	*3*	*2*	*2*	*1*	*1*	*1*	*1*				*1*	*1*	*2*	*1*	*1*	*1*	*1*	*2*	*2*	*1*
M. perscicina	*1*	*1*	*2/3*	*1/2*	*2*	*1*	*1*	*2*	*1*	*1*	*1*	*1*	*1*	*2*	*2*	*1*	*1*	*1*	*1*	*2*	*1*	*1*
M. pescadoensis	*1*	*1*	*3*	*1*	*2*	*1*	*1*	*1*	*1*				*1*	*1*	*1*	*1*	*1*	*1*	*1*	*2*	*1*	*1*
M. picea	*2*	*1*	*3*	*2*	*1*	*1*	*1*	*2*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1/4*	*1*	*2*	*1*	*1*
M. picturata	*2*	*1*	*1/2*	*1*	*2*	*2*	*1*	*2*	*1*	*2*	*2*	*2*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*2*	*2*	*1*
M. pinocchio	*2*	*1*	*2/3*	*2*	*1*	*1*	*1*	*1*	*1*				*2*	*2*	*2*	*1*	*1*	*1*	*1*	*2*	*1*	*1*
M. pleurothalloides	*2*	*1*	*2*	*1*	*2*	*2*	*3*	*2*	*1*	*2*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*2*	*2*	*4*
M. princeps	*1*	*1*	*2*	*2*	*2*	*2*	*1*	*1*	*1*				*1*	*1*	*2*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
M. prodigiosa	*2*	*1*	*2*	*1*	*1*	*1*	*1*	*1*	*1*				*1*	*1*	*2*	*1*	*1*	*1*	*1*	*2*	*1*	*1*
M. pyxis	*2*	*1*	*3*	*2*	*2*	*2*	*1*	*2*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*2*	*1*	*1*
M. racemosa	*2*	*1*	*3*	*1*	*2*	*2*	*1*	*2*	*1*	*1*	*1*	*1*	*2*	*1*	*2*	*1*	*1*	*1*	*1*	*2*	*1*	*1*
M. reichenbachiana	*2*	*1*	*2/3*	*2*	*2*	*1*	*1*	*2*	*1*	*1*	*1*	*1*	*1*	*2*	*1*	*1*	*1*	*1*	*1*	*2*	*1*	*1*
M. rimarima-alba	*2*	*1*	*3*	*2*	*2*	*2*	*1*	*1*	*2*				*1*	*1*	*1*	*1*	*1*	*1*	*1*	*2*	*1*	*1*
M. rubiginosa	*2*	*1*	*2*	*2*	*1*	*1*	*1*	*1*	*1*				*1*	*1*	*2*	*1*	*1*	*1*	*1*	*2*	*1*	*1*
M. sanchezii	*2*	*1*	*2/3*	*2*	*2*	*2*	*1*	*1*	*1*				*1*	*1*	*2*	*1*	*1*	*1*	*1*	*2*	*1*	*1*
M. scabrilinguis	*1/2*	*1*	*3*	*2*	*1*	*2*	*1*	*2*	*1*	*2*	*2*	*2*	*1*	*1*	*1*	*1*	*1*	*2*	*1*	*2*	*2*	*2*
M. schlimii	*2*	*1*	*3*	*2*	*2*	*2*	*1*	*1*	*1*				*2*	*1*	*2*	*1*	*1*	*1*	*1*	*2*	*1*	*1*
M. schroederiana	*2*	*1*	*3*	*2*	*2*	*2*	*1*	*1*	*2*				*1*	*1*	*2*	*1*	*1*	*1*	*1*	*2*	*1*	*1*
M. striatella	*2*	*1*	*3*	*2*	*2*	*2*	*1*	*1*	*1*				*1*	*1*	*2*	*1*	*1*	*1*	*1*	*2*	*1*	*1*
M. teaguei	*2*	*1*	*3*	*2*	*2*	*2*	*1*	*1*	*1*				*1*	*1*	*1*	*1*	*1*	*1*	*1*	*2*	*1*	*1*
M. uniflora	*1/2*	*1*	*2/3*	*2*	*2*	*2*	*1*	*1*	*1*				*1*	*1*	*2*	*1*	*1*	*2*	*1*	*2*	*2*	*1*
M. veitchiana	*1*	*1*	*2/3*	*1*	*2*	*2*	*1*	*1*	*1*				*1*	*1*	*1*	*1*	*1*	*1*	*1*	*2*	*1*	*1*
M. venezuelana	*2*	*1*	*2*	*2*	*1*	*1*	*1*	*1*	*1*				*1*	*2*	*1*	*2*	*1*	*1*	*1*	*2*	*1*	*1*
M. verecunda	*2*	*1*	*2*	*1*	*1*	*1*	*1*	*2*	*1*	*2*	*1*	*1*	*2*	*1*	*2*	*1*	*1*	*1*	*1*	*2*	*1*	*1*
M. vieirana	*2*	*1*	*2*	*1*	*1*	*1*	*1*	*1*	*1*				*1*	*2*	*2*	*1*	*1*	*3*	*1*	*2*	*1*	*1*
M. weberbaueri	*2*	*1*	*1/2*	*2*	*2*	*2*	*1*	*2*	*1*	*1*	*2*	*1*	*1*	*2*	*1*	*2*	*1*	*1/4*	*1*	*2*	*1*	*1*
M. wendlandiana	*2*	*1*	*3*	*2*	*2*	*2*	*1*	*2*	*1*	*2*	*1*	*1*	*2*	*1*	*2*	*1*	*1*	*1*	*1*	*2*	*1*	*1*
M. zahlbrucknerii	*2*	*1*	*2*	*1*	*2*	*1*	*1*	*2*	*1*	*1*	*2*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*2*	*1*	*1*
P. amethystinum	*2*	*1*	*2/3*	*1*	*1*	*2*	*3*	*2*	*1*	*2*	*2*	*1*	*2*	*1*	*2*	*1*	*1*	*1*	*1*	*1*	*2*	*4*
P. uxorium	*2*	*1*	*2/3*	*1/2*	*1*	*1*	*1*	*2*	*1*	*1*	*2*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*2*	*1*	*1*

Species	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
D. astuta	*2*	*1*	*1*	*2*			*2*	*3*	*1*	*3*	*6*	*2*	*1*	*2*	*1*	*3*	*2*	*3*	*2*	*3*	*5*	*6*
D. chimaera	*2*	*1*	*1*	*1*	*2*	*2*	*1*	*1*	*2*	*4*	*2*	*2*	*1*	*5*	*1*	*3*	*2*	*3*	*2*	*3*	*4*	*2*
D. cochliops	*2*	*1*	*1*	*2*			*2*	*3*	*2*	*3*	*1*	*2*	*1*	*2*	*2*					*3*	*4*	*1*
D. houtteana	*2*	*1*	*2*	*7*			*2*	*1*	*1*	*3*	*2*	*2*	*1*	*2*	*1*	*3*	*2*	*3*		*3*	*3*	*2*
D. sodiroi	*2*	*1*	*1*	*1*	*2*	*2*	*2*	*3*	*1*	*3*	*2*	*1*	*1*	*1*	*2*					*3*	*3*	*2*
D. xenos	*2*	*1*	*2*	*2*			*2*	*1*	*2*	*2*	*4*	*2*	*1*	*4*	*1*	*3*	*2*	*3*	*2*	*1*	*1*	*4*
M. abbreviata	*2*	*1*	*2*	*2*			*2*	*1*	*2*	*3*	*3*	*1*	*1*	*1*	*1*	*3*	*2*	*3*	*3*	*3*	*1*	*3*
M. alexandrii	*2*	*1*	*1*	*1*	*2*	*2*	*1*	*3*	*2*	*1/4*	*1*	*2*	*1*	*1*	*1*	*3*	*2*	*3*	*2*	*3*	*1/4*	*1*
M. ampullacea	*2*	*1*	*1*	*2*			*1*	*1*	*1*	*3*	*1*	*2*	*1*	*2*	*1*	*3*	*2*	*3*	*2*	*1*	*1*	*1*
M. antonii	*2*	*1*	*2*	*7*			*2*	*2*	*1*	*3*	*2*	*2*	*1*	*1/2*	*1*	*3*	*2*	*3*	*2*	*3*	*3*	*2*
M. aphanes	*2*	*1*	*2*	*1*	*2*	*2*	*1*	*1*	*2*	*1/4*	*1*	*2*	*1*	*1*	*1*	*1*	*2*	*3*	*1*	*3*	*3*	*1*
M. bangii	*2*	*1*	*1*	*1*	*2*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*2*	*1*	*1*	*2*	*2*	*1*	*3*	*3*	*1*
M. bicornis	*2*	*1*	*1*	*2*			*2*	*1*	*2*	*2*	*3*	*1*	*1*	*2/4*	*1*	*1*	*2*	*2*	*1*	*1*	*3*	*3*
M. caloptera	*2*	*1*	*2*	*2*			*1*	*3*	*2*	*2*	*1*	*2*	*3*	*4*	*1*	*3*	*2*	*2*	*1*	*1*	*2*	*1*
M. campyloglossa	*2*	*1*	*2*	*2*			*2*	*1*	*1*	*3*	*3*	*1*	*1/4*	*1*	*2*					*3*	*3*	*3*
M. cardiantha	*2*	*1*	*2*	*1*	*2*	*2*	*2*	*1*	*1*	*4*	*1*	*1*	*1*	*1*	*1*	*3*	*2*	*3*	*1*	*3*	*3*	*1*
M. carmenensis	*2*	*1*	*2*	*1*	*1*	*2*	*1*	*2*	*2*	*1*	*2*	*1*	*1*	*4*	*1*	*1*	*2*	*2*	*3*	*3*	*3*	*2*
M. caudivolvula	*1*	*1*	*2*					*3*	*1*	*4*	*1*	*2*	*3*	*2/5*	*1*	*1*	*2*	*3*	*2*	*1*	*3*	*1*
M. cerastes	*1*	*1*	*2*					*3*	*2*	*3*	*1*	*2*	*5*	*1*	*1*	*3*	*2*	*2*	*2*	*1*	*1*	*2*
M. chaetostoma	*2*	*1*	*2*	*1*	*2*	*2*	*2*	*1*	*2*	*3*	*2*	*1*	*1*	*6*	*1*	*1*	*2*	*3*	*2*	*3*	*2*	*2*
M. chimboensis	*1*	*1*	*1*					*3*	*2*	*3*	*1*	*2*	*3/5*	*1*	*2*					*3*	*1*	*1*
M. civilis	*2*	*1*	*1*	*1*	*2*	*2*	*1*	*2*	*1*	*4*	*3*	*1*	*1*	*1*	*1*	*3*	*2*	*2*	*2*	*3*	*3*	*3*
M. coccinea	*2*	*1*	*2*	*1*	*2*	*1*	*1*	*1*	*2*	*4*	*1*	*2*	*1*	*1*	*1*	*1*	*2*	*3*	*1*	*3*	*3*	*1*
M. collina	*1*	*2*	*2*						*1*	*2*	*1*	*2*	*1*	*4*	*1*	*3*	*2*	*3*	*2*	*1*	*1/4*	*1*
M. corniculata	*2*	*1*	*2*	*2*			*2*	*3*	*1*	*3*	*1*	*2*	*1*	*4*	*1*	*1*	*2*	*3*	*2*	*1*	*1*	*1*
M. cupularis	*2*	*1*	*2*	*1*	*2*	*2*	*2*	*1*	*2*	*3*	*3*	*1*	*1*	*3*	*1*	*3*	*2*	*3*	*1*	*3*	*3*	*3*
M. davisii	*2*	*1*	*1*	*1*	*2*	*1*	*1*	*2*	*2*	*4*	*2*	*2*	*1*	*4*	*1*	*3*	*2*	*3*	*2*	*1/3*	*4*	*2*

Species	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
M. decumana	*2*	*1*	*2*	*1*	*2*	*2*	*1*	*2*	*2*	*4*	*2*	*2*	*1*	*4*	*1*	*1*	*2*	*2*	*2*	*3*	*3*	*2*
M. deformis	*2*	*1*	*2*	*2*			*2*	*3*	*2*	*4*	*1*	*2*	*3*	*4*	*1*	*3*	*2*	*3*	*2*	*1*	*1*	*1*
M. delhierroi	*2*	*1*	*2*	*2*			*1*	*3*	*1*	*4*	*1*	*2*	*1*	*3*	*1*	*1*	*1*	*2*	*3*	*3*	*1*	*1*
M. echo	*2*	*1*	*1*	*3*			*1*	*1*	*1*	*1/4*	*2*	*1*	*1*	*2*	*1*	*3*	*2*	*3*	*1*	*1*	*3*	*2*
M. erinacea	*2*	*1*	*2*	*5*	*2*	*1*	*1*	*2*	*1*	*3*	*1*	*1*	*1*	*2*	*1*	*3*	*2*	*3*	*1*	*2*	*3*	*1*
M. estradae	*2*	*1*	*2*	*4*	*1*	*1*	*1*	*3*	*2*	*3*	*1*	*2*	*3*	*2*	*1*	*3*	*2*	*3*	*2*	*1*	*2*	*1*
M. floribunda	*2*	*1*	*1*	*1*	*2*	*2*	*1*	*3*	*1*	*4*	*4*	*1*	*1*	*2*	*1*	*3*	*1*	*1*	*3*	*3*	*4*	*4*
M. fulvescens	*2*	*1*	*2*	*1*	*1*	*1*	*1*	*1*	*2*	*4*	*1*	*2*	*1*	*1*	*1*	*3*	*2*	*3*	*1*	*3*	*3*	*1*
M. garciae	*2*	*1*	*1*	*3*			*1*	*1*	*2*	*4*	*1*	*2*	*1*	*4*	*1*	*3*	*2*	*1*	*2*	*3*	*3*	*1*
M. glandulosa	*2*	*1*	*2*	*1*	*2*	*2*	*2*	*1*	*2*	*1*	*1*	*2*	*1*	*1*	*1*	*3*	*2*	*2*	*1*	*3*	*1*	*1*
M. glomerosa	*2*	*1*	*2*	*1*	*2*	*2*	*2*	*2*	*2*	*3*	*1*	*2*	*1*	*6*	*1*	*3*	*2*	*3*	*1*	*3*	*1*	*1*
M. goliath	*2*	*1*	*1*	*1*	*2*	*1*	*1*	*2*	*1*	*1/3*	*1*	*2*	*1*	*6*	*1*	*1*	*2*	*3*	*2*	*3*	*1*	*1*
M. gutierezii	*2*	*1*	*1*	*1*	*2*	*1*	*3*	*1*	*2*	*1*	*2*	*2*	*1*	*2*	*1*		*2*	*1*	*3*	*1*	*4*	*2*
M. guttulata	*2*	*1*	*2*	*1*	*2*	*1*	*1*	*2*	*2*	*2*	*3*	*1*	*1*	*1*	*1*	*3*	*2*	*3*	*2*	*1*	*1*	*3*
M. herradurae	*2*	*1*	*2*	*5*	*2*	*2*	*2*	*1*	*2*	*3*	*1*	*1*	*1*	*1*	*1*	*2*	*2*	*3*	*1*	*3*	*4*	*1*
M. hirtzii	*2*	*1*	*1*	*1*	*2*	*2*	*1*	*1*	*2*	*4*	*2*	*2*	*1*	*4*	*1*	*1*	*2*	*3*	*2*	*3*	*3*	*2*
M. hoeijeri	*2*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1/4*	*2*	*2*	*3*	*2*	*1*	*3*	*2*	*1*	*3*	*1*	*4*	*2*
M. infracta	*2*	*1*	*2*	*1*	*2*	*2*	*1*	*2*	*1*	*3*	*3*	*1*	*1*	*1/2*	*1*	*3*	*2*	*3*	*2*	*3*	*3*	*3*
M. lamprotyria	*2*	*1*	*1*	*1*	*2*	*1*	*1*	*1*	*2*	*1/4*	*1*	*2*	*1*	*2*	*1*	*1*	*2*	*2*	*1*	*1*	*1/4*	*1*
M. lata	*2*	*1*	*2*	*2*			*1*	*1*	*2*	*3*	*1*	*2*	*1*	*4*	*1*	*1*	*2*	*3*	*1*	*3*	*3*	*1*
M. macrura	*2*	*1*	*2*	*3*			*1*	*1*	*1*	*4*	*1*	*1*	*1*	*2*	*1*	*3*	*2*	*3*	*1*	*1*	*3*	*1*
M. melanoxantha	*2*	*1*	*2*	*1*	*2*	*2*	*2*	*1*	*2*	*3*	*1*	*1*	*1*	*1*	*1*	*3*	*2*	*3*	*1*	*3*	*1/3*	*3*
M. meleagris	*2*	*1*	*2*	*1*	*2*	*2*	*1*	*1*	*2*	*1*	*2*	*2*	*1*	*2/3*	*2*					*1*	*1*	*2*
M. mentosa	*2*	*1*	*1*	*1*	*2*	*1*	*1*	*1*	*2*	*1*	*1*	*2*	*1*	*3*	*2*					*1*	*1*	*1*
M. mezae	*2*	*1*	*2*	*2*			*3*	*1*	*1*	*3*	*4*	*2*	*1*	*4*	*1*	*3*	*1*	*3*	*2*	*3*	*3*	*4*
M. molossus	*2*	*1*	*2*	*1*	*2*	*2*	*2*	*3*	*1*	*3*	*1*	*2*	*1*	*1/6*	*1*	*2*	*2*	*3*	*2*	*3*	*3*	*1*
M. mystica	*2*	*1*	*2*	*5*	*2*	*2*	*2*	*3*	*1*	*3*	*1*	*1*	*1*	*1*	*2*					*3*	*3*	*1*
M. naranjapatae	*2*	*1*	*2*	*5*	*2*	*2*	*2*	*2*	*1*	*3*	*2*	*2*	*1*	*1*	*1*	*3*	*2*	*2*	*2*	*3*	*3*	*2*
M. nidifica	*2*	*1*	*2*	*2*			*2*	*3*	*2*	*3*	*2*	*2*	*1*	*4*	*1*	*3*	*2*	*3*	*1*	*1*	*2*	*2*
M. notosibrica	*2*	*1*	*2*	*1*	*2*	*2*	*1*	*1*	*1*	*4*	*5*	*1*	*1*	*1*	*1*	*1/3*	*2*	*3*	*1*	*3*	*1*	*5*
M. ophioglossa	*2*	*1*	*2*	*1*	*2*	*1*	*1*	*3*	*2*	*4*	*1*	*2*	*1*	*1*	*1*	*3*	*2*	*3*	*2*	*1*	*3*	*1*
M. oreas	*2*	*1*	*2*	*5*	*2*	*2*	*1*	*3*	*2*	*4*	*1*	*1*	*1*	*1*	*1*	*3*	*2*	*2*	*2*	*3*	*4*	*1*
M. ova-avis	*2*	*1*	*2*	*3*			*1*	*2*	*1*	*4*	*1*	*1*	*1*	*1*	*1*	*3*	*2*	*3*	*2*	*3*	*1*	*1*
M. pachyura	*2*	*1*	*2*	*2*			*2*	*3*	*1*	*3*	*1*	*2*	*3*	*2*	*1*	*3*	*1*	*2*	*1*	*1*	*1*	*2*
M. paivaeana	*2*	*1*	*1*	*1*	*2*	*2*	*2*	*3*	*2*	*3*	*1*	*2*	*1*	*1*	*1*	*1*	*2*	*3*	*2*	*3*	*2*	*1*
M. panguiensis	*2*	*1*	*2*	*5*	*2*	*2*	*1*	*2*	*2*	*4*	*1*	*1*	*1*	*4*	*1*	*3*	*2*	*3*	*2*	*1*	*1*	*2*
M. parvula	*2*	*1*	*2*	*5*	*2*	*2*	*2*	*3*	*1*	*3*	*3*	*1*	*1*	*2*	*2*					*3*	*3*	*3*
M. patriciana	*2*	*1*	*2*	*1*	*2*	*2*	*1*	*1*	*1*	*4*	*2*	*1*	*1*	*2*	*1*	*3*	*2*	*3*	*1*	*3*	*3*	*1*
M. patula	*2*	*1*	*2*	*1*	*2*	*2*	*1*	*1*	*2*	*4*	*2*	*2*	*1*	*4*	*1*	*1*	*2*	*3*	*2*	*3*	*4*	*2*
M. peristeria	*2*	*1*	*2*	*1*	*2*	*1*	*3*	*1*	*2*	*1*	*1*	*2*	*1*	*2*	*1*	*3*	*2*	*2*	*2*	*1*	*1*	*1*
M. perscicina	*2*	*1*	*2*	*1*	*2*	*2*	*1*	*1*	*2*	*1*	*1*	*1*	*1*	*3*	*1*	*3*	*2*	*2*	*1*	*3*	*1*	*1*
M. pescadoensis	*2*	*1*	*2*	*1*	*2*	*2*	*1*	*1*	*2*	*4*	*1*	*2*	*1*	*1*	*1*	*3*	*2*	*2*	*1*	*3*	*1*	*1*
M. picea	*2*	*1*	*2*	*1*	*2*	*2*	*2*	*1*	*1*	*4*	*1*	*1*	*1*	*1*	*1*	*2*	*2*	*3*	*1*	*3*	*3*	*1*
M. picturata	*2*	*1*	*2*	*5*	*2*	*1*	*1*	*3*	*1*	*4*	*1*	*2*	*2*	*4*	*1*	*3*	*2*	*2*	*2*	*1*	*1/3*	*1*
M. pinocchio	*2*	*1*	*2*	*2*			*2*	*1*	*2*	*3*	*1*	*2*	*1*	*4*	*1*	*1*	*2*	*3*	*1*	*1*	*2*	*1*
M. pleurothalloides	*1*	*1*	*2*					*3*	*1*	*2*	*3*	*2*	*1*	*2*	*1*	*3*	*2*	*3*	*2*	*3*	*3*	*3*
M. princeps	*2*	*1*	*1*	*1*	*1*	*2*	*1*	*1*	*1*	*1*	*2/3*	*1*	*1*	*1*	*1*	*3*	*2*	*1*	*1*	*3*	*1*	*2/3*
M. prodigiosa	*2*	*1*	*2*	*1*	*2*	*1*	*1*	*1*	*2*	*4*	*1*	*1*	*1*	*4*	*1*	*3*	*2*	*3*	*2*	*1*	*1*	*1*
M. pyxis	*2*	*1*	*2*	*6*	*2*	*2*	*2*	*1*	*2*	*3*	*2*	*1*	*1*	*6*	*1*	*3*	*2*	*3*	*1*	*3*	*3*	*2*
M. racemosa	*2*	*1*	*2*	*1*	*2*	*2*	*2*	*1*	*2*	*4*	*2*	*2*	*1*	*3*	*1*	*1*	*2*	*3*	*2*	*3*	*3*	*2*
M. reichenbachiana	*2*	*1*	*2*	*3*			*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*2*	*3*	*1*	*3*	*3*	*1*
M. rimarima-alba	*2*	*1*	*1*	*1*	*1*	*2*	*2*	*2*	*2*	*1*	*1*	*1*	*1*	*1*	*2*					*3*	*1*	*1*
M. rubiginosa	*2*	*1*	*2*	*1*	*2*	*2*	*1*	*1*	*2*	*4*	*2*	*2*	*3*	*2*	*1*	*1*	*2*	*3*	*1*	*3*	*4*	*2*
M. sanchezii	*2*	*1*	*2*	*1*	*2*	*2*	*1*	*3*	*2*	*4*	*1*	*1*	*1*	*1*	*1*	*3*	*2*	*1*	*2*	*3*	*3*	*1*
M. scabrilinguis	*2*	*1*	*2*	*1*	*2*	*1*	*1*	*2*	*1*	*1*	*2*	*2*	*1*	*2*	*1*	*1*	*2*	*3*	*2*	*1*	*4*	*2*
M. schlimii	*2*	*1*	*1*	*1*	*2*	*2*	*1*	*3*	*1*	*1*	*5*	*2*	*1*	*1*	*1*	*3*	*2*	*3*	*1*	*3*	*1*	*5*
M. schroederiana	*2*	*1*	*1*	*1*	*2*	*2*	*1*	*1*	*2*	*1/4*	*2*	*2*	*1*	*1*	*1*	*3*	*2*	*2*	*2*	*3*	*4*	*2*
M. striatella	*2*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*2*	*1/3*	*1*	*1*	*1*	*1*	*2*					*1*	*1*	*1*
M. teaguei	*2*	*1*	*1*	*1*	*2*	*2*	*1*	*1*	*2*	*1*	*1*	*2*	*1*	*3*	*2*					*1*	*3*	*1*
M. uniflora	*1*	*1*	*2*					*3*	*1*	*3*	*1*	*2*	*3*	*1*	*1*	*3*	*2*	*3*	*2*	*3*	*1*	*1*
M. veitchiana	*2*	*1*	*2*	*1*	*2*	*1*	*2*	*1*	*1*	*3*	*2*	*2*	*1*	*1*	*1*	*3*	*2*	*2*	*1*	*2*	*3*	*2*
M. venezuelana	*2*	*1*	*2*	*1*	*2*	*2*	*1*	*2*	*2*	*1*	*1*	*1*	*1*	*2*	*1*	*3*	*2*	*2*	*2*	*1*	*1*	*1*
M. verecunda	*2*	*1*	*2*	*1*	*2*	*2*	*1*	*2*	*1*	*4*	*1*	*2*	*3*	*1*	*1*	*2*	*2*	*3*	*2*	*3*	*3*	*5*
M. vieirana	*2*	*1*	*2*	*3*			*1*	*1*	*2*	*4*	*1*	*1*	*3*	*4*	*1*	*3*	*2*	*3*	*1*	*3*	*3*	*1*
M. weberbaueri	*2*	*1*	*2*	*4*	*2*	*2*	*3*	*1*	*1*	*4*	*2*	*1*	*1*	*2*	*1*	*3*	*2*	*3*	*1*	*1*	*3*	*2*
M. wendlandiana	*2*	*1*	*2*	*1*	*2*	*2*	*1*	*1*	*2*	*4*	*5*	*2*	*1*	*2*	*1*	*3*	*2*	*3*	*1*	*3*	*3*	*2*
M. zahlbrucknerii	*2*	*1*	*1*	*1*	*2*	*2*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*2*	*1*	*3*	*2*	*3*	*2*	*3*	*4*	*1*
P. amethystinum	*2*	*1*	*2*	*2*			*2*	*1*	*1*	*3*	*2*	*2*	*1*	*2*	*1*	*3*	*2*	*3*	*2*	*3*	*3*	*2*

Species	**45**	**46**	**47**	**48**	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**	**59**	**60**	**61**	**62**	**63**	**64**	**65**	**66**
P. uxorium	*2*	*1*	*2*	*3*			*2*	*1*	*1*	*4*	*2*		*1*	*2*	*1*	*1*	*2*	*3*	*1*	*3*	*3*	*2*
D. astuta	*2*	*1*	*2*	*1*	*3*	*1*	*2*	*3*	*1*	*6*	*1*	*1*	*2*	*6*	*1*	*1*	*3*	*2*	*2*			
D. chimaera	*2*	*1*	*6*	*1*	*3*	*2*	*2*	*3*	*2*	*4*	*3*	*2*	*1*	*2*	*1*	*1*	*2*	*1*	*2*			
D. cochliops	*2*	*1*	*2*	*1*	*3*	*2*	*1*	*1*	*2*	*1/3*	*1*	*2*	*2*	*3*	*1*	*1*	*1*	*2*	*1*	*2*		*2*
D. houtteana	*2*	*1*	*2*	*1*	*3*	*2*	*2*	*3*	*1*	*1*	*2*	*2*	*1*	*3*	*3*	*1*	*3*	*2*	*2*			
D. sodiroi	*1*	*1*	*1*	*2*					*2*	*1*	*1*	*2*	*2*	*1*	*1*	*1*	*1*	*2*	*1*	*2*		*1*
D. xenos	*2*	*1*	*2*	*1*	*1*	*2*	*2*	*3*	*2*	*1*	*1*	*2*	*2*	*4*	*2*	*1*	*1*	*2*	*1*	*2*		*1*
M. abbreviata	*1*	*1*	*1*	*1*	*3*	*2*	*2*	*3*	*2*	*1*	*1*	*2*	*2*	*4*	*2*	*1*	*1*	*2*	*1*	*1*	*2*	*3*
M. alexandrii	*2*	*1*	*1*	*1*	*3*	*1*	*2*	*3*	*2*	*1*	*1*	*2*	*2*	*2*	*4*	*1*	*1*	*2*	*1*	*2*		*2*
M. ampullacea	*2*	*1*	*2*	*1*	*3*	*2*	*2*	*3*	*2*	*1*	*1*	*1*	*2*	*4*	*3*	*1*	*1*	*2*	*1*	*2*		*2*
M. antonii	*2*	*1*	*1*	*1*	*3*	*1*	*2*	*3*	*1*	*1/2*	*2*	*2*	*1*	*3*	*2*	*1*	*3*	*2*	*2*			
M. aphanes	*2*	*1*	*1*	*1*	*3*	*1*	*2*	*3*	*2*	*1*	*1*	*2*	*2*	*1*	*1*	*1*	*1*	*2*	*1*	*2*		*1*
M. bangii	*1*	*1*	*2*	*1*	*3*	*2*	*2*	*1*	*2*	*1*	*1*	*2*	*2*	*4*	*2*	*1*	*1*	*2*	*1*	*1*	*2*	*2*
M. bicornis	*1*	*1*	*1*	*1*	*1*	*2*	*2*	*2*	*2*	*2*	*1*	*2*	*2*	*4*	*5*	*1*	*1*	*2*	*1*	*2*		*2*
M. caloptera	*2*	*2*	*2*	*1*	*3*	*1*	*2*	*2*	*2*	*1/2*	*2*	*2*	*2*	*4*	*4*	*1*	*1*	*2*	*1*	*2*		*3*
M. campyloglossa	*1*	*1*	*1*	*2*					*1*	*1/3*	*1*	*2*	*2*	*4*	*2*	*1*	*1*	*2*	*1*	*2*		*1*
M. cardiantha	*1*	*1*	*1*	*1*	*3*	*2*	*2*	*2*	*2*	*1/3*	*1*	*1*	*2*	*1*	*4*	*1*	*1*	*2*	*1*	*2*		*1*
M. carmenensis	*2*	*1*	*2*	*1*	*1*	*2*	*2*	*2*	*2*	*1*	*1*	*2*	*2*	*4*	*3*	*1*	*1*	*2*	*1*	*2*		*1*
M. caudivolvula	*2*	*2*	*1*	*1*	*1*	*1*	*2*	*3*	*1*	*1*	*1*	*2*	*2*	*1*	*1*	*1*	*1*	*2*	*1*	*2*		*2*
M. cerastes	*2*	*4*	*1*	*1*	*3*	*1*	*2*	*2*	*1*	*1/2*	*1*	*2*	*2*	*4*	*2*	*1*	*1*	*2*	*1*	*2*		*2*
M. chaetostoma	*1*	*1*	*2*	*1*	*1*	*2*	*2*	*3*	*2*	*1*	*1*	*2*	*2*	*4*	*2*	*1*	*2*	*2*	*1*	*1*	*1*	*3*
M. chimboensis	*2*	*2/4*	*1*	*2*					*2*	*1*	*1*	*2*	*2*	*4*	*3*	*1*	*1*	*2*	*1*	*2*		*1*
M. civilis	*1*	*1*	*1*	*1*	*3*	*1*	*2*	*2*	*2*	*1*	*1*	*2*	*2*	*2/3*	*1*	*1*	*1*	*2*	*1*	*1*	*2*	*3*
M. coccinea	*2*	*1/3*	*1*	*2*					*2*	*1*	*1*	*2*	*2*	*2*	*2*	*2*	*1*	*2*	*1*	*2*		*2*
M. collina	*2*	*1*	*2*	*1*	*3*	*1*	*2*	*3*	*1*	*1*	*1*	*2*	*2*	*2*	*4*	*1*	*1*	*2*	*1*	*2*		*1*
M. corniculata	*2*	*1*	*1*	*1*	*1*	*2*	*2*	*3*	*2*	*1/2*	*2*	*2*	*2*	*2*	*4*	*1*	*1*	*2*	*1*	*2*		*4*
M. decumana	*1*	*1*	*1*	*1*	*3*	*1*	*2*	*2*	*2*	*4*	*1*	*2*	*2*	*3*	*2*	*1*	*1*	*2*	*1*	*1*	*1*	*4*
M. deformis	*2*	*1*	*5*	*1*	*3*	*1*	*2*	*3*	*2*	*1*	*1*	*1*	*2*	*2*	*2*	*1*	*1*	*2*	*1*	*2*		*1*
M. delhierroi	*2*	*1*	*2*	*1*	*1*	*1*	*2*	*2*	*2*	*1*	*1*	*2*	*2*	*4*	*2*	*1*	*1*	*2*	*1*	*2*		*1*
M. echo	*1*	*1*	*5*	*1*	*3*	*1*	*2*	*3*	*1*	*1*	*1*	*2*	*2*	*4*	*3*	*1*	*1*	*2*	*1*	*2*		*1*
M. erinacea	*1*	*1*	*2*	*1*	*3*	*1*	*2*	*3*	*1*	*3*	*1*	*2*	*2*	*3*	*1*	*1*	*1*	*2*	*2*			
M. estradae	*2*	*2*	*1*	*1*	*3*	*2*	*2*	*3*	*2*	*1*	*1*	*2*	*2*	*4*	*2*	*1*	*1*	*2*	*1*	*1*	*2*	*4*
M. floribunda	*1*	*1*	*2*	*1*	*1*	*1*	*2*	*3*	*2*	*1/3*	*1*	*2*	*2*	*2*	*5*	*1*	*2*	*2*	*1*	*1*	*2*	*1*
M. fulvescens	*2*	*1*	*1*	*1*	*3*	*2*	*2*	*3*	*2*	*1*	*1*	*2*	*2*	*1*	*1*	*1*	*1*	*2*	*1*	*2*		*3*
M. garciae	*2*	*1*	*2*	*1*	*3*	*2*	*1*	*1*	*2*	*1*	*1*	*2*	*2*	*4*	*4*	*1*	*1*	*2*	*1*	*2*		*3*
M. glandulosa	*2*	*1*	*5*	*1*	*3*	*1*	*2*	*3*	*2*	*1*	*1*	*2*	*2*	*2*	*1*	*1*	*1*	*2*	*1*	*2*		*3*
M. glomerosa	*2*	*1*	*1*	*1*	*3*	*1*	*2*	*2*	*2*	*5*	*1*	*2*	*2*	*3*	*2*	*1*	*1*	*2*	*1*	*2*		*2*
M. goliath	*2*	*1*	*7*	*2*					*2*	*1*	*1*	*1*	*2*	*4*	*2*	*2*	*1*	*2*	*1*	*2*		*2*
M. gutierezii	*2*	*1*	*2*	*1*	*3*	*2*	*2*	*2/3*	*2*	*2*	*1*	*2*	*2*	*1*	*1*	*1*	*1*	*2*	*1*	*1*	*2*	*3*
M. guttulata	*1*	*1*	*1*	*1*	*1*	*1*	*2*	*3*	*2*	*1*	*1*	*2*	*2*	*4*	*3*	*1*	*1*	*2*	*1*	*2*		*2*
M. herradurae	*1*	*3*	*2*	*1*	*4*	*2*	*2*	*1*	*2*	*1*	*1*	*1*	*2*	*2*	*1*	*1*	*1*	*2*	*1*	*2*		*1*
M. hirtzii	*2*	*1*	*2*	*1*	*3*	*1*	*2*	*3*	*2*	*1*	*1*	*2*	*2*	*1*	*1*	*1*	*1*	*2*	*1*	*2*		*1*
M. hoeijeri	*2*	*2*	*2*	*1*	*3*	*2*	*2*	*3*	*1*	*1*	*1*	*1*	*2*	*2*	*2*	*1*	*1*	*2*	*1*	*2*		*2*
M. infracta	*1*	*1*	*1*	*1*	*3*	*1*	*2*	*3*	*2*	*1*	*3*	*2*	*2*	*2*	*2*	*1*	*1*	*2*	*1*	*2*		*3*
M. lamprotyria	*2*	*1*	*1*	*1*	*3*	*1*	*2*	*1*	*2*	*1*	*3*	*2*	*2*	*4*	*4*	*1*	*1*	*2*	*1*	*2*		*3*
M. lata	*2*	*1*	*6*	*1*	*3*	*1*	*2*	*3*	*2*	*1*	*1*	*2*	*2*	*2*	*1*	*1*	*1*	*2*	*1*	*2*		*3*
M. macrura	*1*	*1*	*1*	*1*	*3*	*1*	*2*	*2*	*2*	*1*	*1*	*2*	*2*	*4*	*4*	*1*	*1*	*2*	*1*	*2*		*1*
M. melanoxantha	*1*	*1*	*1*	*1*	*3*	*1*	*2*	*2*	*1*	*1*	*1*	*2*	*2*	*4*	*2*	*1*	*1*	*2*	*1*	*2*		*2*
M. meleagris	*2*	*1*	*4/5*	*1*	*3*	*2*	*2*	*3*	*2*	*2*	*1*	*1*	*2*	*2*	*1*	*1*	*1*	*2*	*1*	*2*		*3*
M. mentosa	*2*	*1*	*4*	*2*					*2*	*1*	*1*	*2*	*2*	*4*	*4*	*1*	*1*	*2*	*1*	*1*	*2*	*4*
M. mezae	*2*	*1*	*5*	*2*					*2*	*2*	*1*	*2*	*2*	*1*	*1*	*1*	*1*	*2*	*1*	*2*		*4*
M. molossus	*2*	*1*	*7*	*2*					*2*	*4*	*1*	*2*	*2*	*2*	*3/4*	*1*	*1*	*1*	*1*	*2*		*1*
M. mystica	*1*	*1*	*1*	*1*	*3*	*1*	*1*	*2*	*2*	*4*	*2*	*2*	*2*	*3*	*4*	*1*	*1*	*2*	*1*	*2*		*1*
M. naranjapatae	*1*	*1*	*1*	*1*	*3*	*2*	*2*	*3*	*2*	*3*	*3*	*2*	*2*	*1*	*1*	*1*	*1*	*2*	*1*	*2*		*4*
M. nidifica	*2*	*1*	*2*	*2*					*2*	*4*	*1*	*2*	*2*	*2/3*	*4*	*1*	*1*	*2*	*1*	*2*		*3*
M. notosibrica	*1*	*1*	*2*	*1*	*3*	*2*	*2*	*2*	*2*	*3*	*1*	*2*	*2*	*1*	*1*	*1*	*1*	*2*	*1*	*1*	*2*	*4*
M. ophioglossa	*2*	*1*	*1*	*1*	*3*	*1*	*2*	*3*	*1*	*1*	*1*	*2*	*2*	*2*	*2*	*1*	*1*	*2*	*1*	*2*		*2*
M. oreas	*1*	*1*	*1*	*1*	*1*	*2*	*2*	*3*	*2*	*1*	*1*	*2*	*2*	*4*	*4*	*1*	*1*	*2*	*1*	*2*		*2*
M. ova-avis	*2*	*1*	*1*	*1*	*3*	*2*	*2*	*3*	*2*	*1*	*1*	*2*	*2*	*4*	*4*	*1*	*1*	*2*	*1*	*2*		*2*
M. pachyura	*2*	*1*	*1*	*1*	*3*	*1*	*2*	*2*	*2*	*1/2*	*1*	*2*	*2*	*2*	*4*	*1*	*1*	*2*	*1*	*1*	*2*	*4*
M. paivaeana	*2*	*1*	*1*	*1*	*1*	*1*	*2*	*3*	*2*	*1*	*1*	*2*	*2*	*4*	*3*	*1*	*1*	*2*	*1*	*2*		*1*
M. panguiensis	*1*	*1*	*2*	*1*	*3*	*1*	*1*	*2*	*2*	*1*	*2*	*2*	*2*	*4*	*4*	*1*	*1*	*1*	*1*	*1*	*2*	*4*
M. parvula	*1*	*1*	*2*	*1*	*3*	*2*	*2*	*3*	*2*	*1*	*1*	*2*	*2*	*2*	*2*	*1*	*1*	*2*	*1*	*2*		*2*
M. patriciana	*1*	*1*	*1*	*1*	*4*	*1*	*2*	*3*	*2*	*1*	*1*	*2*	*2*	*4*	*3*	*1*	*1*	*2*	*1*	*2*		*1*
M. patula	*2*	*1*	*2*	*2*					*2*	*2*	*1*	*2*	*2*	*3*	*4*	*1*	*1*	*2*	*1*	*2*		*3*
M. peristeria	*2*	*1*	*1*	*2*					*2*	*1*	*1*	*2*	*2*	*4*	*3*	*1*	*1*	*2*	*1*	*2*		*1*
M. perscicina	*1*	*1*	*2*	*1*	*3*	*1*	*2*	*3*	*1*	*1*	*1*	*2*	*2*	*4*	*3*	*1*	*1*	*2*	*1*	*2*		*2*
M. pescadoensis	*2*	*1*	*1*	*1*	*3*	*2*	*2*	*2*	*2*	*5*	*2*	*2*	*2*	*1*	*3*	*2*	*1*	*2*	*1*	*2*		*2*
M. picea	*1*	*1*	*2*	*1*	*3*	*1*	*2*	*1*	*2*	*1*	*1*	*2*	*2*	*2*	*2*	*1*	*1*	*2*	*1*	*1*	*1*	*4*
M. picturata	*2*	*1*	*1*	*2*					*2*	*1*	*1*	*1*	*2*	*3*	*2*	*1*	*1*	*2*	*1*	*2*		*2*
M. pinocchio	*2*	*1*		*1*	*3*	*2*	*2*	*3*	*2*	*1*	*1*	*2*	*2*	*2*	*4*	*1*	*1*	*2*	*1*	*2*		*1*

Species	**45**	**46**	**47**	**48**	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**	**59**	**60**	**61**	**62**	**63**	**64**	**65**	**66**
M. pleurothalloides	*2*	*1*	*1*	*1*	*3*	*1*	*2*	*2*	*2*	*4*	*2*	*2*	*2*	*4*	*3*	*1*	*1*	*1*	*1*	*2*		*4*
M. princeps	*1*	*1*	*1*	*1*	*1*	*1*	*2*	*3*	*1*	*1*	*1*	*2*	*2*	*4*	*2*	*1*	*1*	*2*	*1*	*2*		*1*
M. prodigiosa	*2*	*1*	*5*	*1*	*3*	*1*	*2*	*3*	*1*	*1*	*1*	*2*	*2*	*1*	*1*	*1*	*2*	*2*	*1*	*2*		*1*
M. pyxis	*1*	*1*	*7*	*1*	*3*	*1*	*2*	*1*	*2*	*1/2*	*1*	*2*	*2*	*2*	*4*	*1*	*1*	*2*	*1*	*1*	*2*	*3*
M. racemosa	*2*	*1*	*7*	*1*	*3*	*2*	*2*	*3*	*2*	*2*	*1*	*2*	*2*	*4*	*3*	*1*	*1*	*2*	*1*	*2*		*1*
M. reichenbachiana	*1*	*1*	*1*	*1*	*3*	*2*	*2*	*3*	*2*	*1*	*1*	*2*	*2*	*4*	*2*	*1*	*2*	*2*	*1*	*1*	*1*	*3*
M. rimarima-alba	*1*	*1*	*1*	*1*	*1*	*2*	*2*	*3*	*2*	*1*	*1*	*2*	*2*	*1*	*2*	*1*	*1*	*2*	*1*	*2*		*2*
M. rubiginosa	*2*	*1*	*5*	*1*	*1*	*2*	*2*	*1*	*2*	*2*	*1*	*2*	*2*	*2*	*1/2*	*1*	*1*	*2*	*1*	*2*		*3*
M. sanchezii	*1*	*1*	*2*	*2*					*2*	*1*	*1*	*2*	*2*	*2*	*2*	*1*	*1*	*2*	*1*	*2*		*3*
M. scabrilinguis	*2*	*1*	*1*	*1*	*3*	*2*	*2*	*2*	*2*	*1/2*	*1*	*2*	*2*	*4*	*3*	*1*	*1*	*2*	*1*	*2*		*2*
M. schlimii	*2*	*1*	*1*	*1*	*3*	*2*	*2*	*1*	*2*	*1/2*	*1*	*2*	*2*	*2*	*4*	*1*	*1*	*2*	*1*	*1*	*2*	*3*
M. schroederiana	*2*	*1*	*2*	*1*	*1*	*1*	*2*	*3*	*2*	*1*	*2*	*2*	*2*	*4*	*3*	*1*	*1*	*2*	*2*			
M. striatella	*1*	*1*	*1*	*1*	*3*	*2*	*2*	*2*	*2*	*1*	*1*	*2*	*2*	*1*	*1*	*1*	*1*	*2*	*1*	*2*		*2*
M. teaguei	*2*	*1*	*4*	*1*	*3*	*2*	*2*	*2*	*2*	*1/3*	*1*	*2*	*2*	*1*	*4*	*1*	*1*	*2*	*1*	*2*		*3*
M. uniflora	*2*	*2*	*1*	*2*					*2*	*1*	*1*	*2*	*2*	*1/2/4*	*2*	*1*	*1*	*1*	*1*	*2*		*1*
M. veitchiana	*2*	*1*	*1*	*2*					*2*	*1*	*1*	*2*	*2*	*4*	*3*	*1*	*1*	*2*	*1*	*2*		*1*
M. venezuelana	*1*	*1*	*1*	*1*	*2*	*1*	*2*	*3*	*2*	*2*	*1*	*2*	*2*	*4*	*3*	*1*	*1*	*2*	*1*	*2*		*4*
M. verecunda	*2*	*1*	*1/4*	*1*	*3*	*2*	*2*	*1*	*2*	*1*	*1*	*2*	*2*	*1*	*3*	*1*	*2*	*2*	*1*	*2*		*3*
M. vieirana	*1*	*2*	*2*	*1*	*3*	*1*	*2*	*2*	*2*	*2*	*1*	*2*	*2*	*4*	*3*	*1*	*1*	*2*	*1*	*2*		*3*
M. weberbaueri	*1*	*1*	*2*	*1*	*1*	*2*	*2*	*2*	*2*	*1*	*1*	*2*	*2*	*1*	*1*	*1*	*1*	*2*	*1*	*2*		*1*
M. wendlandiana	*1*	*1*	*1*	*1*	*3*	*2*	*2*	*2*	*2*	*3*	*1*	*2*	*2*	*1*	*1*	*1*	*2*	*2*	*1*	*2*		*2*
M. zahlbrucknerii	*1*	*1*	*1*	*1*	*3*	*2*	*2*	*3*	*2*	*1*	*1*	*2*	*2*	*4*	*4*	*1*	*1*	*2*	*1*	*1*	*2*	*4*
P. amethystinum	*2*	*1*	*2*	*1*	*3*	*2*	*2*	*2*	*2*	*1/2*	*1*	*2*	*2*	*2*	*4*	*1*	*1*	*2*	*1*	*2*		*3*
P. uxorium		*1*	*2*	*1*	*3*	*2*	*2*	*3*	*2*	*1*	*1*	*2*	*2*	*1*	*4*	*1*	*1*	*2*	*1*	*2*		*1*

Species	**67**	**68**	**69**	**70**	**71**	**72**	**73**	**74**	**75**	**76**	**77**	**78**	**79**	**80**	**81**	**82**	**83**	**84**	**85**	**86**	**87**	**88**
D. astuta			*4*	*1*	*3*	*4*	*2*	*2*	*2*	*2*	*1*	*5*	*2*	*1*	*1*	*2*	*1*	*1*	*1*	*3*	*2*	*2*
D. chimaera			1	1	2	1	2	1	2	2	1	5			1	1	1	1	1	3	2	2
D. cochliops	*3*	*3*	*5*	*1*	*2*	*1*	*1*	*5*	*1*	*2*	*2*	*3*	*2*								*1*	*2*
D. houtteana			*5*	*2*	*3*	*4*	*1*	*1*	*2*	*2*	*1*	*3*	*2*	*1*	*1*	*1*	*1*	*1*	*1*	*3*	*2*	*2*
D. sodiroi	*2*	*3*	*1*	*1*	*1*	*2*	*2*	*1*	*2*	*2*	*2*	*2*	*1*								*2*	*2*
D. xenos	*1*	*1*	*6*	*1*	*1*	*1*	*1*	*1*	*1*	*2*	*2*	*2*	*1*							*2*	*2*	*2*
M. abbreviata		*2*	*1*	*1*	*1*	*2*	*1*	*3*	*2*	*2*	*1*	*2*	*1*	*2*	*1*	*3*	*3*	*1*	*1*	*2*	*2*	*2*
M. alexandrii	*3*	*3*	*1/4*	*1*	*1*	*2*	*2*	*1*	*2*	*2*	*1*	*2*	*1*	*3*	*1*	*1*	*3*	*1*	*1*	*2*	*2*	*2*
M. ampullacea	*1*	*2*	*3*	*1*	*1*	*1*	*2*	*1*	*1*	*2*	*2*	*2*	*2*							*2*	*2*	*2*
M. antonii			*5*	*2*	*3*	*4*	*2*	*1*	*2*	*2*	*1*	*5*	*2*	*1/3*	*2*	*1*	*1*	*1*	*1*	*3*	*2*	*2*
M. aphanes	*1*	*2*	*1*	*1*	*2*	*1*	*2*	*1*	*2*	*2*	*2*	*2*	*2*							*2*	*2*	*2*
M. bangii	*1*	*3*	*3*	*2*	*2*	*1*	*2*	*1*	*2*	*2*	*2*	*1*	*2*							*2*	*2*	*2*
M. bicornis	*1*	*1*	*1*	*1*	*1*	*2*	*2*	*2*	*2*	*2*	*1*	*2*	*2*	*3*	*2*	*2*	*3*	*2*	*1*	*2*	*2*	*2*
M. caloptera		*2*	*1*	*1*	*2*	*1*	*2*	*1*	*2*	*2*	*1*	*3*	*2*	*3*	*1*	*1*	*3*	*1*	*1*	*2*	*2*	*2*
M. campyloglossa	*3*	*2*	*1*	*5*	*1*	*2*	*1*	*1*	*2*	*1*	*1*	*3*	*2*	*1*	*1*	*1*	*3*	*1*	*1*	*2*	*2*	*2*
M. cardiantha	*3*	*3*	*1/4*	*1*	*1*	*1*	*2*	*2*	*2*	*2*	*1*	*3*	*1*	*3*	*1*	*2*	*3*	*1*	*1*	*2*	*2*	*2*
M. carmenensis	*1*	*2*	*1*	*1*	*1*	*2*	*2*	*1*	*2*	*2*	*2*	*3*	*2*							*2*	*2*	*2*
M. caudivolvula	*1*	*3*	*4*	*1*	*2*	*2*	*2*	*1*	*2*	*2*	*2*	*3*	*1*							*2*	*2*	*2*
M. cerastes	*3*	*3*	*3*	*1*	*1*	*1*	*2*	*1*	*1*	*2*	*2*	*3*	*2*							*2*	*2*	*2*
M. chaetostoma		*2*	*1*	*1*	*1*	*2*	*2*	*2*	*1*	*2*	*2*	*3*	*1*							*2*	*2*	*2*
M. chimboensis	*1*	*2*	*1*	*1*	*1*	*2*	*2*	*1*	*1*	*2*	*1*	*3*	*1*	*2*	*1*	*1*	*3*	*1*	*1*	*2*	*2*	*2*
M. civilis		*3*	*1*	*2*	*1*	*2*	*2*	*2*	*2*	*2*	*2*	*2*	*1*							*2*	*2*	*2*
M. coccinea	*1*	*2*	*1*	*1*	*1*	*2*	*2*	*1*	*1*	*2*	*2*	*2*	*2*							*2*	*2*	*2*
M. collina	*3*	*1*	*1*	*1*	*2*	*2*	*1*	*1*	*2*	*2*	*2*	*2*	*2*							*2*	*2*	*2*
M. corniculata		*2*	*1*	*1*	*2*	*1*	*2*	*1*	*2*	*2*	*1*	*3*	*1*	*1*	*1*	*1*	*3*	*2*	*1*	*2*	*2*	*2*
M. cupularis		*2*	*1*	*2*	*1*	*2*	*1*	*2*	*2*	*2*	*2*	*3*	*2*							*2*	*2*	*2*
M. davisii	*1/2*	*2*	*4*	*5*	*2*	*1*	*2*	*1*	*1*	*2*	*2*	*3*	*2*							*2*	*2*	*2*
M. decumana	*1/2*	*1*	*2*	*1*	*2*	*1*	*2*	*1*	*1*	*2*	*2*	*2*	*2*							*2*	*2*	*2*
M. deformis	*1*	*2*	*2*	*1*	*2*	*1*	*1*	*1*	*1*	*2*	*2*	*3*	*2*							*2*	*2*	*2*
M. delhierroi			*5*	*1*	*1*	*3*	*1*	*1*	*2*	*2*	*2*	*3*	*2*							*2*	*1*	*2*
M. echo		*1*	*1*	*5*	*1*	*2*	*2*	*2*	*2*	*2*	*1*	*3*	*1*	*3*	*1*	*2*	*3*	*1*	*1*	*2*	*2*	*2*
M. erinacea	*3*	*1*	*1*	*4*	*2*	*2*	*1*	*2*	*2*	*2*	*1*	*3*	*1*	*1*	*4*	*2*	*3*	*1*	*4*	*2*	*2*	*2*
M. estradae		*2*	*3*	*4*	*1*	*1*	*2*	*1*	*2*	*2*	*1*	*3*	*2*	*3*	*4*	*1*	*3*	*1*	*1*	*2*	*2*	*2*
M. floribunda		*3*	*1*	*2*	*1*	*2*	*2*	*2*	*2*	*2*	*2*	*3*	*1*							*2*	*2*	*2*
M. fulvescens		*2*	*1*	*1*	*1*	*2*	*2*	*1*	*2*	*2*	*2*	*2*	*2*							*2*	*2*	*2*
M. garciae	*1*	*2*	*1*	*3*	*1*	*1*	*2*	*2*	*1*	*2*	*2*	*2*	*1*							*2*	*2*	*2*
M. glandulosa	*2*	*2*	*1*	*2*	*2*	*2*	*1*	*5*	*2*	*2*	*2*	*2*	*2*							*2*	*2*	*2*
M. glomerosa		*3*	*4*	*4*	*2*	*2*	*1*	*1*	*2*	*2*	*2*	*2*	*2*							*2*	*2*	*2*
M. goliath	*3*	*3*	*1*	*1*	*1*	*2*	*2*	*2*	*2*	*2*	*1*	*2*	*2*	*1*	*1*	*2*	*3*	*1*	*1*	*2*	*2*	*2*
M. gutierezii	*3*	*1*	*3*	*5*	*1*	*2*	*2*	*1*	*2*	*2*	*2*	*3*	*1*							*2*	*2*	*2*

Species	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88
M. guttulata	*3*	*2*	*1*	*2*	*2*	*1*	*2*	*3*	*1*	*2*	*1*	*3*	*1*	*3*	*2*	*3*	*3*	*1*	*4*	*2*	*2*	*2*
M. herradurae	*2*	*2*	*1*	*1*	*2*	*2*	*2*	*1*	*2*	*2*	*1*	*2*	*1*	*1*	*1*	*1*	*3*	*2*	*1*	*1*	*2*	*1*
M. hirtzii		*1*	*1*	*5*	*2*	*1*	*2*	*1*	*2*	*2*	*2*	*3*	*2*							*2*	*2*	*2*
M. hoeijeri		*3*	*1*	*1*	*1*	*1*	*2*	*1*	*2*	*2*	*1*	*2*	*1*	*2*	*4/5*	*1*	*3*	*1*	*1*	*2*	*2*	*2*
M. infracta		*3*	*4*	*1*	*1*	*2*	*1*	*2*	*2*	*2*	*2*	*2*	*1*							*2*	*2*	*2*
M. lamprotyria	*1*	*2*	*2/3*	*1*	*2*	*1*	*2*	*1*	*2*	*2*	*2*	*3*	*1*							*2*	*2*	*2*
M. lata	*1*	*1*	*1*	*3*	*1*	*1*	*2*	*1*	*1*	*1*	*1*	*2*	*2*	*2*	*3*	*1*	*3*	*3*	*3*	*2*	*2*	*1*
M. macrura		*2*	*1*	*1*	*1*	*1*	*2*	*1*	*2*	*2*	*2*	*2*	*1*							*2*	*2*	*1*
M. melanoxantha		*2*	*1*	*1*	*1*	*1*	*2*	*2*	*1*	*2*	*1*	*2*	*1*	*1*	*1*	*2*	*3*	*3*	*1*	*2*	*2*	*2*
M. meleagris		*3*	*1*	*4*	*2*	*2*	*2*	*1*	*2*	*2*	*2*	*2*	*1*							*2*	*2*	*2*
M. mentosa	*3*	*3*	*1*	*1*	*1*	*2*	*2*	*4*	*2*	*2*	*2*	*2*	*2*							*2*	*2*	*2*
M. mezae	*3*	*2*	*1/2*	*5*	*1*	*2*	*2*	*2*	*2*	*2*	*2*	*2*	*2*							*2*	*2*	*2*
M. molossus		*3*	*2*	*1*	*2*	*2*	*2*	*1*	*2*	*2*	*2*	*2*	*2*							*2*	*2*	*2*
M. mystica		*2*	*1/3*	*4*	*1*	*1*	*2*	*2*	*2*	*2*	*2*	*3*	*1*							*2*	*2*	*2*
M. naranjapatae		*2*	*1*	*1*	*1*	*2*	*2*	*2*	*1*	*2*	*2*	*2*	*1*							*2*	*2*	*2*
M. nidifica	*2*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*2*	*2*	*3*	*2*							*2*	*2*	*1*
M. notosibrica	*3*	*2*	*1*	*1*	*1*	*2*	*2*	*1*	*2*	*2*	*1*	*3*	*1*	*3*	*1*	*1*	*3*	*1*	*1*	*2*	*2*	*2*
M. ophioglossa	*2*	*3*	*1*	*4*	*2*	*2*	*2*	*3*	*1*	*2*	*1*	*2*	*1*	*1*	*4*	*3*	*3*	*1*	*1*	*2*	*2*	*2*
M. oreas		*2*	*1*	*2*	*1*	*2*	*2*	*2/3*	*2*	*2*	*1*	*2*	*1*	*3*	*2*	*2/3*	*3*	*4*	*1*	*2*	*2*	*2*
M. ova-avis	*1*	*2*	*1*	*4*	*1*	*1*	*2*	*1*	*1*	*2*	*2*	*2*	*1*							*2*	*2*	*2*
M. pachyura		*1*	*1*	*1*	*2*	*2*	*2*	*1*	*2*	*2*	*1*	*3*	*1*	*2*	*1*	*1*	*3*	*1*	*1*	*2*	*2*	*2*
M. paivaeana	*2*	*2*	*1*	*5*	*1*	*1*	*2*	*1*	*1*	*2*	*2*	*2*	*1*							*2*	*2*	*2*
M. panguiensis	*3*	*2*	*1*	*1*	*1*	*1*	*2*	*1*	*2*	*2*	*1*	*2*	*2*	*2*	*2*	*1*	*3*	*2*	*1*	*2*	*2*	*2*
M. parvula		*3*	*5*	*4*	*1*	*3*	*2*	*2*	*1*	*2*	*2*	*2*	*2*							*2*	*2*	*2*
M. patriciana	*3*	*1*	*1*	*1*	*2*	*1*	*2*	*2*	*2*	*2*	*1*	*3*	*2*	*1*	*1*	*1*	*3*	*1*	*1*	*2*	*2*	*2*
M. patula	*1*	*2*	*1*	*1*	*2*	*1*	*2*	*1*	*1*	*1*	*2*	*2*	*2*							*2*	*2*	*2*
M. peristeria	*1*	*2*	*2*	*1*	*2*	*1*	*2*	*4*	*2*	*2*	*1*	*3*	*2*	*2*	*2*	*4*	*3*	*1*	*1*	*2*	*2*	*2*
M. perscicina		*2*	*1/4*	*1*	*2*	*2*	*2*	*2*	*2*	*2*	*1*	*2*	*1*	*2*	*1*	*2*	*3*	*1*	*1*	*2*	*2*	*2*
M. pescadoensis	*1*	*2*	*1*	*1*	*1*	*1*	*2*	*1*	*1*	*2*	*2*	*2*	*2*							*2*	*2*	*2*
M. picea	*3*	*2*	*1*	*5*	*2*	*2*	*2*	*2*	*2*	*2*	*1*	*2*	*2*	*3*	*1*	*2*	*3*	*1*	*1*	*2*	*2*	*2*
M. picturata		*1*	*1*	*1*	*1*	*1*	*2*	*1*	*1*	*2*	*1*	*2*	*1*	*1*	*1*	*1*	*3*	*1/2*	*1*	*2*	*2*	*2*
M. pinocchio	*1/2*	*2*	*3*	*4*	*1*	*1*	*2*	*1*	*1*	*2*	*2*	*3*	*2*							*2*	*2*	*2*
M. pleurothalloides	*3*	*3*	*4*	*1*	*2*	*4*	*1*	*1*	*2*	*2*	*1*	*3*	*2*	*2*	*1*	*1*	*1*	*3*	*1*	*3*	*2*	*2*
M. princeps		*3*	*1/4*	*2*	*2*	*1*	*1*	*2*	*2*	*2*	*2*	*2*	*2*							*2*	*2*	*2*
M. prodigiosa	*1*	*1*	*1*	*1*	*1*	*2*	*2*	*1*	*1*	*2*	*2*	*3*	*1*							*2*	*2*	*2*
M. pyxis		*3*	*1*	*5*	*1*	*2*	*1*	*2*	*1*	*2*	*1*	*2*	*1*	*2*	*4*	*2*	*3*	*2*	*1*	*2*	*2*	*2*
M. racemosa	*1*	*2*	*1*	*1*	*2*	*2*	*2*	*1*	*2*	*2*	*2*	*3*	*2*							*2*	*2*	*2*
M. reichenbachiana		*2*	*1*	*1*	*1*	*1*	*2*	*1*	*2*	*2*	*2*	*2*	*2*							*2*	*2*	*2*
M. rimarima-alba		*3*	*1*	*4*	*1*	*1*	*1*	*1*	*2*	*2*	*2*	*2*	*2*							*2*	*2*	*2*
M. rubiginosa	*3*	*3*	*1*	*1*	*1*	*1*	*2*	*2*	*2*	*2*	*1*	*2*	*2*	*2*	*1*	*2*	*3*	*1*	*1*	*2*	*2*	*2*
M. sanchezii		*3*	*1*	*1*	*2*	*2*	*1*	*2*	*2*	*2*	*1*	*1*	*1*	*2*	*1*	*2*	*3*	*1*	*1*	*2*	*2*	*2*
M. scabrilinguis			*2*	*1*	*2*	*2*	*2*	*2*	*2*	*2*	*1*	*2*	*2*	*1*	*2*	*2*	*3*	*2*	*2*	*2*	*2*	*2*
M. schlimii	*3*	*3*	*1*	*1*	*2*	*2*	*2*	*2*	*2*	*2*	*2*	*2*	*2*							*2*	*2*	*2*
M. schroederiana		*3*	*1*	*2*	*2*	*2*	*2*	*2*	*2*	*2*	*2*	*2*	*1*							*2*	*2*	*2*
M. striatella	*3*	*3*	*1*	*1/4*	*2*	*2*	*2*	*1*	*2*	*2*	*2*	*2*	*2*							*2*	*2*	*2*
M. teaguei	*3*	*3*	*1*	*1*	*2*	*1*	*2*	*4*	*2*	*2*	*2*	*2*	*2*							*2*	*2*	*2*
M. uniflora		*3*	*3*	*1*	*2*	*2*	*1*	*1*	*1*	*2*	*1*	*3*	*1*	*1*	*1*	*1*	*3*	*1*	*1*	*2*	*2*	*2*
M. veitchiana		*2*	*1*	*5*	*1*	*2*	*2*	*2*	*1*	*2*	*2*	*3*	*2*							*2*	*2*	*2*
M. venezuelana		*3*	*1*	*1*	*1*	*1*	*2*	*2*	*2*	*2*	*1*	*3*	*2*	*3*	*2*	*2*	*3*	*1*	*1*	*2*	*2*	*2*
M. verecunda	*3*	*1*	*1/4*	*1*	*1*	*1*	*1*	*1*	*2*	*2*	*2*	*2*	*2*							*2*	*2*	*2*
M. vieirana	*2*	*2*	*1*	*1*	*1*	*2*	*2*	*2*	*2*	*2*	*1*	*3*	*1*	*1*	*1*	*2*	*3*	*1*	*1*	*2*	*2*	*2*
M. weberbaueri		*2*	*1*	*2*	*1*	*1*	*2*	*2*	*2*	*2*	*1*	*2*	*2*	*4*	*2*	*2*	*3*	*1*	*1*	*2*	*2*	*2*
M. wendlandiana		*2*	*1*	*1*	*2*	*2*	*2*	*1*	*2*	*2*	*2*	*2*	*1*							*2*	*2*	*2*
M. zahlbrucknerii	*3*	*1*	*1*	*1*	*1*	*2*	*2*	*2*	*2*	*2*	*1*	*2*	*2*	*3*	*1*	*2*	*3*	*1*	*1*	*2*	*2*	*2*
P. amethystinum			*5*	*2*	*2*	*4*	*1*	*2*	*2*	*2*	*1*	*3*	*2*	*3*	*2*	*2*	*2*	*1*	*1*	*3*	*2*	*2*
P. uxorium	*1*	*2*	*3*	*1*	*1*	*2*	*1*	*6*	*2*	*2*	*2*	*5*	*2*								*2*	*2*

Species	89	90	91	92	93	94	95	96	97
D. astuta	*1*	*2*							*1*
D. chimaera	*2*	*2*							*1*
D. cochliops	*1*	*1*							*1*
D. houtteana	*1*	*2*							*1*
D. sodiroi	*2*	*2*							*2*
D. xenos	*2*	*2*							*1*
M. abbreviata	*2*	*2*	*1*	*4*	*1*	*3*	*2*	*1*	*1*
M. alexandrii	*2*	*2*	*1*	*4*	*1*	*1*	*1*	*1*	*1*

Species	**89**	**90**	**91**	**92**	**93**	**94**	**95**	**96**	**97**
M. ampullacea	*2*	*2*	*1*	*3*	*2*	*1*	*2*	*1*	*1*
M. antonii	*1*	*2*							*1*
M. aphanes	*2*	*2*	*1*	*4*	*1*	*2*	*1*	*1*	*1*
M. bangii	*2*	*2*							*1*
M. bicornis	*2*	*2*	*2*	*4*	*1*	*2*	*2*	*2*	*1*
M. caloptera	*2*	*2*	*1*	*2*	*1*	*2*	*2*	*1*	*1*
M. campyloglossa	*2*	*2*	*1*	*3*	*1*	*3*	*2*	*1*	*2*
M. cardiantha	*2*	*2*	*1*	*3*	*1*	*2*	*2*	*2*	*1*
M. carmenensis	*2*	*2*	*1*	*1*	*2*	*2*	*2*	*1*	*1*
M. caudivolvula	*2*	*2*							*1*
M. cerastes	*2*	*2*	*1*	*2*	*2*	*2*	*2*	*1*	*1*
M. chaetostoma	*2*	*2*	*1*	*3*	*1*	*3*	*2*	*1*	*1*
M. chimboensis	*2*	*2*	*1*	*1*	*2*	*3*	*2*	*1*	*2*
M. civilis	*2*	*2*	*2*	*2*	*1*	*3*	*3*	*1*	*1*
M. coccinea	*2*	*2*	*3*	*3*	*1*	*2*	*2*	*1*	*2*
M. collina	*2*	*2*							*1*
M. corniculata	*2*	*2*	*1*	*4*	*1*	*2*	*2*	*1*	*1*
M. cupularis	*2*	*2*							*1*
M. davisii	*2*	*2*	*1*	*3*	*2*	*2*	*2*	*1*	*1*
M. decumana	*2*	*2*	*1*	*2*	*1*	*2*	*2*	*1*	*1*
M. deformis	*2*	*2*	*1*	*2*	*1*	*2*	*1*	*1*	*1*
M. delhierroi	*1*	*2*	*1*	*2*	*1*	*1/2*	*1*	*1*	*1*
M. echo	*2*	*2*	*1*	*4*	*1*	*2*	*2*	*1*	*1*
M. erinacea	*2*	*2*	*1*	*4*	*1*	*2*	*2*	*1*	*1*
M. estradae	*1*	*2*	*2*	*3*	*1*	*3*	*1*	*1*	*1*
M. floribunda	*2*	*2*	*3*	*1*	*1*	*3*	*2*	*1*	*1*
M. fulvescens	*2*	*2*	*1*	*3*	*1*	*2*	*2*	*1*	*1*
M. garciae	*2*	*2*	*1*	*3*	*1*	*2*	*2*	*1*	*1*
M. glandulosa	*2*	*2*	*1*	*1*	*1*	*2*	*2*	*1*	*2*
M. glomerosa	*2*	*2*	*2*	*3*	*1*	*1*	*2*	*2*	*1*
M. goliath	*2*	*2*							*1*
M. gutierezii	*2*	*2*							*1*
M. guttulata	*2*	*2*	*1*	*3*	*1*	*1*	*2*	*1*	*1*
M. herradurae	*2*	*2*	*2*	*4*	*1*	*3*	*3*	*1*	*1*
M. hirtzii	*2*	*2*	*1*	*2*	*1*	*3*	*2*	*1*	*1*
M. hoeijeri	*1*	*2*							*1*
M. infracta	*2*	*2*	*1*	*2*	*1*	*3*	*3*	*1*	*1*
M. lamprotyria	*2*	*2*	*1*	*2*	*1*	*2*	*2*	*1*	*1*
M. lata	*2*	*2*	*1*	*1*	*2*	*2*	*1*	*1*	*1*
M. macrura	*1*	*2*	*3*	*3*	*2*	*2*	*2*	*1*	*1*
M. melanoxantha	*2*	*2*	*1*	*4*	*1*	*3*	*2*	*1*	*2*
M. meleagris	*2*	*2*							*2*
M. mentosa	*2*	*2*							*2*
M. mezae	*2*	*2*	*1*	*1/4*	*2*	*1*	*2*	*1*	*1*
M. molossus	*2*	*2*	*2*	*3*	*2*	*1*	*1*	*2*	*1*
M. mystica	*2*	*2*	*2*	*1*	*1*	*2*	*2*	*2*	*2*
M. naranjapatae	*2*	*2*	*3*	*3*	*1*	*2*	*1*	*1*	*1*
M. nidifica	*2*	*2*	*1*	*4*	*1*	*2*	*2*	*1*	*1*
M. notosibrica	*2*	*2*							*1*
M. ophioglossa	*2*	*2*	*1*	*3*	*1*	*2*	*1*	*1*	*1*
M. oreas	*2*	*2*							*1*
M. ova-avis	*2*	*2*	*1*	*1*	*2*	*2*	*2*	*1*	*1*
M. pachyura	*2*	*2*	*1*	*2*	*1*	*2*	*2*	*1*	*1*
M. paivaeana	*2*	*2*	*1*	*1*	*2*	*2*	*2*	*1*	*1*
M. panguiensis	*2*	*2*							*1*
M. parvula	*2*	*2*							*2*
M. patriciana	*2*	*2*	*1*	*4*	*1*	*2*	*2*	*1*	*2*
M. patula	*2*	*2*	*1*	*1*	*2*	*2*	*2*	*1*	*1*
M. peristeria	*2*	*2*	*1*	*3*	*1*	*1*	*1*	*1*	*1*
M. perscicina	*2*	*2*	*2*	*3*	*1*	*3*	*2*	*2*	*1*
M. pescadoensis	*2*	*2*	*1*	*3*	*2*	*2*	*2*	*1*	*2*
M. picea	*2*	*2*	*1*	*3*	*1*	*2*	*2*	*1*	*1*
M. picturata	*2*	*2*	*1*	*2*	*1*	*1*	*1*	*1*	*1*
M. pinocchio	*2*	*2*	*1*	*2*	*1*	*2*	*2*	*1*	*1*
M. pleurothalloides	*2*	*2*							*1*
M. princeps	*2*	*2*	*1*	*1*	*1*	*3*	*2*	*1*	*1*
M. prodigiosa	*2*	*2*	*1*	*1*	*2*	*2*	*2*	*1*	*1*
M. pyxis	*2*	*2*							*1*

Species	**89**	**90**	**91**	**92**	**93**	**94**	**95**	**96**	**97**
M. racemosa	*2*	*2*							*1*
M. reichenbachiana	*2*	*2*	*1*	*3*	*1*	*2*	*2*	*1*	*1*
M. rimarima-alba	*1*	*2*	*1*	*1*	*2*	*2*	*1*	*1*	*2*
M. rubiginosa	*2*	*2*	*1*	*4*	*1*	*2*	*2*	*1*	*1*
M. sanchezii	*2*	*2*	*1*	*1*	*1*	*3*	*2*	*1*	*1*
M. scabrilinguis	*2*	*2*	*2*	*3*	*1*	*1*	*1*	*2*	*1*
M. schlimii	*2*	*2*							*1*
M. schroederiana	*2*	*2*	*1*	*3*	*2*	*2*	*2*	*1*	*1*
M. striatella	*2*	*2*	*1*	*3*	*1*	*1*	*1*	*1*	*2*
M. teaguei	*2*	*2*							*2*
M. uniflora	*2*	*2*	*1*	*2*	*1*	*2*	*2*	*1*	*1*
M. veitchiana	*2*	*2*	*3*	*3*	*1*	*3*	*2*	*1*	*1*
M. venezuelana	*2*	*2*	*1*	*2*	*1*	*2*	*2*	*1*	*1*
M. verecunda	*1*	*2*							*1*
M. vieirana	*2*	*2*	*2*	*4*	*1*	*2*	*2*	*2*	*1*
M. weberbaueri	*2*	*2*	*1*	*4*	*1*	*2*	*2*	*1*	*1*
M. wendlandiana	*2*	*2*	*1*	*1*	*2*	*2*	*2*	*1*	*1*
M. zahlbrucknerii	*2*	*2*	*2*	*3*	*1*	*1*	*2*	*2*	*1*
P. amethystinum	*2*	*2*							*1*
P. uxorium	*2*	*2*							*1*

Appendix II

Alignment of ITS sequences of *Masdevallia* and outgroups species

Comprising the 3' end of the 18S rDNA, the ITS1, the 5.8S rDNA, the ITS2, and the 5' end of the 26S rDNA

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        ITS 1 TCGAG
....              |....|.....| ...|.....|....|.....|....|.....|....|.....|.....|
                  5          15         25         35         45         55
D. astuta     TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GACA::::AA GCGA:TGGCA
D. chimaera   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GACT::::AA GCGA:TGGCA
D. cochliops  TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCCGT GACT::::AA GCGA:TGGCA
D. houtteana  TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GACT::::AA GCGA:TGGCA
D. sodiroi.   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GACT::::AA GCGA:TGGCA
D. xenos      TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GACT::::AA GCGG:TGGCA
L. pelecani   TCGAG:ACCG AAA:TATATC GAGCGATTCG GAGAACCCGT GAAA::::TA GCGG:CGGCA
M. abbrevia   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GATT::::AA GCGG:TGGCA
M. alexandr   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GACT::::AA GCGG:TGGCA
M. amaluzae   TCGAG:ACCA AAA:TATATC GAGCGATTCG GAGAACCCGT GACT::::AA GCGG:TGGCG
M. ampullac   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GACT::::GA GCGG:TGGCA
M. antonii    TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GACT::::AA GCGG:TGGCA
M. aphanes    TCGAG:ACCA AAA:TATATC GAGCGATTCG GAGAACCCGT GACT::::AA GCGG:AGGCG
M. aphanes.   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACTTGT GACT::::AA GCGG:TGGCA
M. bangii     TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GACT::::GA GCGG:TGGCA
M. bicornis   NNNNNNACCA AAA:TATATC GAACGATTTG GAGAACATGT GATTTT::GA GCGG:TGGCA
M. caesia     TCGAG:ACCA AAA:::TATC GAGCGATTTG GATAACCTGT GACT::GAGA GCGG:CGGCA
M. caloptera  TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GATT::::AA GCGG:TGGCA
M. campylog   TCGAG:ACCA AAA:TATATC GAGCGATTTG GATAACCTGT TACT::GAGA GCGG:CGGCA
M. cardiant   TCGAG:ACCA AAA:TATATC GAGCGATTCG GAGAACCCGT GACT::GAGA GCGG:CGGCA
M. carmenen   TCGAG:ACCA AAA:TATATC GAGCGATTCG GAGAACCCGT GACT::::AA GCGG:TGGCG
M. caudiovo   TCGAG:ACCA AAA:TATATC GAGCGATTTG GATAACCTGT GACT::::GA GCGG:TGGCA
M. cerastes   TCGAGGACCA AAA:TATATC GAGCGATTTG GAGAACTTGT GACT::::AA GCGG:TGGCA
M. chaetost   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GATT::::AA GCGG:TGGCA
M. chaparen   TCGAG:ACCA AAA:TATATC GAGCGATTTT GAGAACCTGT GACT::::AA GCGG:TGGCA
M. chimboen   TCGAG:ACCA AAA:TATATC GAGCGATTCG GAGAACCCGT GACT::AAGA GCGG:CGGCA
M. citrinel   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAAAACCTGT GACT::::GA GCGG:TGGCA
M. civilis    TCGAG:ACCA AAA:TATATC GAGCGATTTG GATAACCTGT GACT::GAGA GCGG:CGGCA
M. coccinea   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GACT::::GA GCGG:TGGCA
M. collina    TCGAG:ACCA AAA:TTTATC GAGCGATTCG GAGAACCCGT GACT::GAGA GCGG:CGGCA
M. collina.   TCGAG:ACCA AAA:TTTATC GAGCGATTCG GAGAACCCGT GACT::GAGA GCGG:CGGCA
M. coriacea   TCGAG:ACCA AAA:TATATC GAGCGATTTG GATAACCTGT GACT::GAGA GCGG:CGGCA
M. corniHam   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACTTGT GACT::::AA GCGG:TGGCA
M. corniHan   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACTTGT GACT::::AA GCGG:TGGCA
M. cupulari   TCGAG:ACCA AAA:TATATC GAGCGATTCG GAGAACCCGT GATT::GAGA GCGG:CGGCA
M. cycloteg   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GACT::::AA GCGG:TGGCA
M. davisii    TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GACT::::AA GCGG:TGGCA
M. decumana   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GACT::::GA GCGG:TGGCA
M. deformis   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GATT::::GA GCGG:CGGCA
M. delhierr   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACTTGT GACT::::AA GCGG:TGGCA
M. echo       TCGAG:ACCA AAA:TATATC GAGCGATTCG GAGAACCCGT GATT::GAGA GCGG:CGGCA
M. erinacea   TCGAG:ACCA AAA:TATATC GAGCGATTCG GAGAACCTGT GACT::::GA GCGG:CGGCA
M. estradae   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GACT::::GA GCGG:TGGCA
M. floribun   TCGAG:ACCA AAA:TATATC GAGCGATTCG GAGAACCCGT GACT::GAGA GCGG:CGGCA
M. fulvesce   TCGAG:ACCA AAA:TATATC GAGCGATTCG GAGAACCCGT GACT::GAGA GCGG:CGGCA
M. garciae    TCGAG:ACCG AAA:CATATC GAGCGATTCG GAGAACCCGT GATT::GAGA GCGG:CGGCA
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        ITS 1 TCGAG
                  |....|.....| ...|.....|....|.....|....|.....|....|.....|.....|
                  5          15         25         35         45         55
M. glandulo   TCGAG:ACCA AAA:TATATC GAGCGATTTA GAGAACCTGT TACT::::GA GCGG:TGGCA
M. goliath    TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACTTGT GACT::::AA GCGG:TGGCA
M. gutierre   TCGAG:ACCA AAA:CATATC GAGCGATTCG GAGAACCTGT TACT::GATG GCGG:CGGCA
M. guttulat   TCGAG:ACCA AAA:TATATC GAGCGATTCG GAGAACCCGT GACT::GAGA GCGG:CGGCG
M. herradur   TCGAG:ACCA AAA:TATATC GAGCGATTCG GAGAACCCGT GACT::GAGA GCGG:CGGCA
M. heteropt   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GACT::::AA GCGG:TGGCA
M. hierogly   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GACT::::GA GCGG:TGGCA
M. hirtzii    TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GACT::::GA GCGG:TGGCA
M. hoeijeri   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GATT::::GA GCGG:TGGCA
M. infracta   TCGAG:ACCA AAA:TATATC GAGCGATTCG GAGAACCCGT GATT::GAGA GCGG:CGGCA
M. kyphonan   TCGAG:ACCA AAA:TATATC GAGCGATTCG GAGAACCTGT GACT::GATA GCGG:CGGCA
M. lamproty   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GACT::::GA GCGG:TGGCA
M. lansberg   TCGAG:ACCA AAA:TATATC GAGCGATTCG GAGAACCTGT GACT::GATA GCGG:CGGCA
M. lata       TCGAG:ACCA AAA:TATATC GAGCGATTCG GAGAACCCGT GACT::GCGA GCGG:CGGCA
M. limax      TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GACT::::GA GCGG:TGGCA
M. macruraH   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GACT::::GA GCGG:TGGCA
M. macruraH   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GACT::::GA GCGG:TGGCA
M. melanoxa   TCGAG:ACCA AAA:CATATC GAGCGATTCG GAGAACCCGT GATT::GAGA GCGG:CGGCA
M. meleagri   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GACT::::AA GCGG:TGGCA
M. mentosa.   TCGAG:ACCG AAA:TATATC GAGCGATTCG GAGAACCCGT GACT::GAGA GCGG:CGGCA
M. mezae      TCGAG:ACCA AAA:TATATC GAGCGATTCG GAGAACCCGT GACT::GAGA GCGG:CGGCA
M. molossus   TCGAG:ACCA AAA:TATATC GAGAGATTTG GAGAACCTGT GATT::::AA GCGG:TGGCA
M. mystica    TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GACT::::GA GCGG:TGGCA
M. naranjap   TCGAG:ACCA AAA:TATATC GAGCGATTCG GAGAACCCGT GACT::GAGA GCGG:CGGCA
M. nidifica   TCGAG:ACCA AAA:TATATC GAGCGATTTA GAGAACCTGT GATT::::AA GCGG:TGGCA
M. notosibr   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GACT::::GA GCGG:TGGCA
M. ophioglo   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GATT::::AA CCGG:TGGCA
M. oreas      TCGAG:ACCA AAA:TATATC GAGCGATTCG GAGAACCCGT GACT::GAGA GCGG:CGGCA
M. oreas      TCGAG:ACCA AAA:TATATC GAGCGATTCG GAGAACCCGT GACT::GAGA GCGG:CGGCA
M. ova avis   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GATT::::AA GCGG:TGGCA
M. pachyura   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GATT::::AA GCGG:TGGCA
M. paivaean   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GACT::::GA GCGG:TGGCA
M. panguien   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACTTGT GACT::::AA GCGGGTGGCA
M. parvula    TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACTTGT GACT::::AA GCGG:TGGCA
M. patricia   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GACT::::GA GCGG:TGGCA
M. patula     TCGAG:ACCA AAA:TATATC GAGCGATTCG GAGAACCCGT GACT::::AA GCGG:TGGCG
M. perister   TCGAG:ACCA AAA:::TATC GAGCGATTTG GATAACCTGT GACT::GAGA GCGG:CGGCA
M. persicin   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GACT::::GA GCGG:TGGCA
M. pescadoe   TCGAG:ACCA AAA:TATATC GAGCGATTCG GAGAACCCGT GACT::GAGA GCGG:CGGCA
M. picea      TCGAG:ACCA AAA:TATATC GAGCGATTTG GATAACCTGT GACT::GAGA GCGG:CGGCA
M. picturat   TCGAG:ACCA AAAATATATC GAGCGATTTG GAGAACCTGT GACT::::AA GCGG:TGGCA
M. pinocchi   TCGAG:ACCA AAA:TATATC GAGCGATTCG GAGAACCCGT GACT::GAGA GCGG:CGGCG
M. pleuroth   TCGAG:ACCA AAAATATATC GAGCGATTTG GAGAACCTGT GACT::::AA GCGG:TGGCA
M. princeps   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACTTGT GACT::::AA GCGG:TGGCA
M. pyxis      TCGAG:ACCA AAA:CATATC GAGCGATTCG GAGAACCCGT GACT::GAGA GCGG:CGGCA
M. racemosa   TCGAG:ACCA AAA:TATATC GAGCGATTTG GATAACCTGT GACT::::GA GCGG:TGGCA
M. reichenb   TCGAG:ACCA AAA:TATATC GAGCGATTCG GAGAACCCGT GACT::GAGA GCGG:CGGCA
M. rubeola.   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GACT::::AA GCGG:TGGCA
M. rubigino   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GACT::::AA GCGG:TGGCA
M. saltatri   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GATT::::GA GCGG:TGGCA
M. sanchezi   TCGAG:ACCA AAA:TATATC GAGCGATTCG GAGAACCCGT GACT::::AA GCGG:TGGCG
M. scabrili   TCGAG:ACCA AAA:TATATC GAGCGATTCG GAGAACCCGT GACT::GAGG GCGG:AGGCA
M. schlimii   TCGAG:ACCA AAA:TATATC GAGCGATTCG GAGAACCCGT GACT::GAGA GCGG:CGGCA
M. striatel   TCGAG:ACCA AAA:TATATC GAGCGATTCG GAGAACCCGT GACT::GAGG GCGG:CGGCA
M. teaguei.   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GACT::::AA GCGG:TGGCA
M. titan      TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACTTGT GACT::::AA GCGG:TGGCA
M. uniflora   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GACT::::AA GCGG:TGGCA
M. veitchia   TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GACT::::AA GCGG:TGGCA
M. venezuel   TCGAG:ACCA AAA:TATATC GAGCGATTCG GAGAACCTGT GACT::GATA GCGG:CGGCA
M. vieriana   TCGAG:ACCA AAA:TATATC GAGCGATTCG GAGAACCCGT GACT::GAGA GCGG:CGGCA
M. walteri    TCGAG:ACCA AAA:TATATC GAGCGATTCG GAGAACCCGT GACT::GAGA GCGG:CGGCA
M. wendland   TCGAG:ACCA AAA:CATATC GAGCGATTCG GAGAACCTGT TACT::GATG GCGG:CGGCA
M. ximenae.   TCGAG:ACCA AAA:TATATC GAGCAATTTG GAGAACCTGT GACT::::AA GCGG:TGGCA
M. zahlbruc   TCGAG:ACCA AAA:TATATC GAGCGATTCG GAGAACCCGT GACT::GAGA GCGG:CGGCA
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       ITS 1 TCGAG
                 |....|.....| ...|.....|....|.....|....|.....|....|.....|.....|
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P. amethyst  TCGAG:ACCA AAA:TATATC GAGCGATTCG GAGAACCTGT GACT::::AA GCGG:TGGCA
P. uxorium.  TCGAG:ACCA AAA:TATATC GAGCGATTTG GAGAACCTGT GACT::::AA GCGG:TGGCA
T. gemmata.  TCGAG:ACCG AAA:TATATC GAGCGATTCG GAGAACATGT GAAT::::AA GTGA:TGGCA
T. scobina.  TCGAG:ACCG AAA:CATATC GAGCGATTCA GAGAACATGT GAAC::::AA GCGA:TGGCA

                 |....| ....|....| ....|....| ....|....| ....|....| ....|....|
                 65         75         85         95         105        115
D. astuta    C::TAGCCAT CGCGTGACAG CCATCC:::T GGTTG:TTGG CCTCCTTTCA GGCCGCAATG
D. chimaera  C::TAGCCAT CGCGTGACAG CCATCC:::T GGTTG:TTGG CCTCCTTTCA GGCCGCGATG
D. cochliops C::TAGCCAT CGCGTGACAG CCATCC:::T GGTTG:TTGG CCTCTTTTGA GGCCGCGATG
D. houtteana C::TAGCCAT CGCGTGACAG CCATCC:::T GGTTG:TTGG CCTCCTTTCA GGCCGCGATG
D. sodiroi.  C::TAGCCAT CGCGTGACAG CCATCC:::T GGTTG:TTGG CCTCCTTTCA GGCCGCGATG
D. xenos     C::TTGCCGT CGCGTGACAG CCATCC:::T GGTTG:TTGG CCTC:TTTGA GGCCGCGATG
L. pelecani  C::CAGCCGT CGCGTGACAG CCGTCCCGAT CGTCGGTTGG CCTC:GTCG: GGCCACGATG
M. abbrevia  C::TTGCCGT CGCGTGACAG CCATCC:::T GGTTG:TTGG CCTC:TTTGA GGCCGCGATG
M. alexandr  C::TTGCCGT CGCGTGACAG CCATCC:::T GGTTG:TTGG CCTC:GTTGA GGTCGCGATG
M. amaluzae  C::TTGCCGC CACGTGACAG CAATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCAATG
M. ampullac  C::TTGCCAT CGCGTGACAG CAATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. antonii   C::TTGCCAT CGCGTGACAG CAATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. aphanes   C::TTGCCGC CACGTGACAG CAATCC:::T GGTTG:TCGG CCTC:GTTGA GGCCGCAATG
M. aphanes.  C::TTGCCGC CACGTGACAG CAATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. bangii    C::TTGCCGT CGCGTGACAG CAATCC:::T GGTTG:TTGG CCTC:GTTGG GGCCGCAATG
M. bicornis  C::TTGCCGC CGCGCAACAG CAATCC:::T CGTTG:TTGG CCTC:GTTGG GGCCGCGATG
M. caesia    T::ATGCCGT CGCGTGACGG CCATCC:::C GGTCG:TTGG CCTC:GTTGA GGCCGCGATG
M. caloptera C::TTGCCGT CGCGTGACAG CCATCC:::T GGTTG:TTGG CCTC:TTTGA GGCCGCGATG
M. campylog  T::ATGCCGT CGCGTGACGG CCATCC:::T GGTCG:TTGG CCTC:GTTGA GGCCGCGATG
M. cardiant  T::ATGCCGT CGCCCGACAG CCATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. carmenen  C::TTGCCGC CACGTGACAG CAATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCAATG
M. caudiovo  CTTGTGCCAT CGCGTGACAG CAATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCAATG
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M. chimboen  T::ATGCCGT CGCCTGACAG CCATCC:::C GGTTG:TTGG CCTC:GTTGA GGCCGCAATG
M. citrinel  C::TTGCCAT CGCGTGACAG CAATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCACAATT
M. civilis   T::ACGCCGT CGCGTGACGG CCATCC:::C GGTCG:TTGG CCTC:GTTGG GGCCGCGATG
M. coccinea  C::TTGCCAT CGCGTGACAG CAATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. collina   T::ATGCCGT CGCCTGACAG CCATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. collina.  T::ATGCCGT CGCCTGACAG CCATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. coriacea  T::ACGCCGT CGCGCGACGG CCATCC:::T GGTCG:TTGG CCTC:GTTGA GGCCGCGATG
M. corniHam  C::TTGCCGT CGCGTGACAG CCATCC:::T GGTCG:TTGG CCTT:GTTGA GGCCGCGATG
M. corniHan  C::TTGCCGT CGCGTGACAG CCATCC:::T GGTCG:TTGG CCTT:GTTGA GGCCGCGATG
M. cupulari  T::ATGCCGT CGCCTGACAG CCATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. cycloteg  C::TTGCCAT CGCGCGACAG CAATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. davisii   C::TTGCCAT CGCGCGACAG CAATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. decumana  C::TTGCCAT CGCGTGACAG CAATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. deformis  C::TTGCCGT CGCGTGACAG CAATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCAATC
M. delhierr  C::TTGCCGT CGCGTGACAG CCATCC:::T GGTCG:TTGG CCTT:GTTGA GGCCGCGATG
M. echo      TTTATGCCGT CGCCTGACAG CCATCC:::C GGTTG:TTGG CCTC:GTCGA GGCCGCGATG
M. erinacea  C::TTGCCGT CGCGTGACAG CCGTCC:::C GATCG:TTGG CCTC:GCCGA GGCCGCGATG
M. estradae  C::TTGCCAT CGCGTGACAG CAATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. floribun  T::ATGCCGT CGCCTGACAG CTATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. fulvesce  T::ATGCCGT CGCCTGACAG CCATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. garciae   T::ATGCCGT CGCCTGACAG CCGTCC:::C GGTTG:TTGG CCTC:GTCGA GGCGGCGATG
M. glandulo  C::TTGCCAT CGCATGACAG CAATCC:::T CGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. goliath   C::TTGCCGC CACGTGACAG CAATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. gutierre  T::ATGCCGT CGCGTGACAG CCATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. guttulat  T::ATGCCGT CGCCCGACAG CCATCC:::T GGTCG:TCGG CCTC:GTTGA GGCCGCGATG
M. herradur  T::ATGCCGT CGCCAGACAG CCATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCAATG
M. heteropt  G::TTGCCGT CGCGTGACAG CCATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. hierogly  C::TTGCCAT CGCGTGACAG CAATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. hirtzii   C::TTGCCAT CGCGTGACAG CAATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. hoeijeri  C::TTGCCGT CGCGTAACAG CGATCC:::T TGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. infracta  TTTATGCCGT CGCCTGACAG CCATCC:::C GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. kyphonan  T::ATGCCGT CGCTTGACAG CCATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCAATG
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                  |....| ....|....| ....|....| ....|....| ....|....| ....|....|
                  65         75         85         95         105        115
M. lamproty   C::TTGCCAT CGCGTGACAG CAATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. lansberg   T::ATGCCGT CGCTTGACAG CCATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCAATG
M. lata       T::ATGCCGT CGCCTGACAG CCATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. limax      C::TTGCCAT CGCGTGACAG CAATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. macruraH   C::TCGCCGT CGCGTGACAG CAATCC:::T GGTTG:TTGG CCTC:GTTGA GGTCACGATG
M. macruraH   C::TTGCCGT CGCGTGACAG CAATCC:::T GGTTG:TTGG CCTC:GTTGA GGTCACGATG
M. melanoxa   T::ATGCCGT CGCCTGACAG CCATCC:::C GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. meleagri   C::TTGCCGT CGCGTGACAG CCATCC:::T GGTTG:TTGG CCTC:GTTGA GGTCGCGATG
M. mentosa.   T::ATGCCGT CGCCTGACAG CCGTCC:::C GGTCG:TTGG CCTC:GTCGA GGCCGCGATG
M. mezae      T::ATGCCGT CGCCCGACAG CCATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. molossus   C::TTGCCGT CGCGTGACAG CCATCC:::T GGTTG:TTGG CCTC:TTTGA AGCCGCGATG
M. mystica    C::TTGCCAT CGCGTGACAG CAATCC:::T GGTTG:TTGG CCTC:GTTGA GGTCGCGATG
M. naranjap   T::ATGCCGT CGCCTGACAG CCATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. nidifica   C::ATGCCGT CGCGTGACAG CCATCC:::T TGTTG:TTGG CCTC:TTTGA GGCCGCGATG
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M. oreas      T::ATGCCGT CGCCCGACAG CCATCC:::T GGTTG:TTGG CCTC:GTAGA GGCCGCGATG
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M. pachyura   C::TTGCCAT CGCGTGACAG CCATCC:::T GGTTG:TTGG CCTC:TTTGA GGCCGCGATG
M. paivaean   C::TTGCCAT CGCGTGACAG CAATCC:::T GGTTG:TTGG CCTC:GTTGA GGTCGCGATG
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M. parvula    C::TTGCCGT CGCGTGACAG CCATCC:::T GGTTG:TTGG CCTC:GTTGA GGTCGCGATG
M. patricia   C::TTGCCAT CGCGTGACAG CAATCC:::T GGTTG:TTGG CCTC:ATTGA GGCCGCAATG
M. patula     C::TTGCCGC CACGTGACAG CAATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCAATG
M. perister   T::ATGCCGT CGCGTGACGG CCATCC:::C GGTCG:TCGG CCTC:GTTGA GGCCGCGATG
M. persicin   C::TTGCCAT CGCGTGACAG CAATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCACGATT
M. pescadoe   T::ATGCCGT CGCCTAACAG CCATCC:::T GGTTG:TTGG CCTC:GTT:A GGCCGCGATG
M. picea      T::ACGCCGT CGCGTGACGG CCATCC:::C GGTCG:TTGG CCTC:GTTGG GGCCGCGATG
M. picturat   C::TTGCCGT CGCGTGACAG CCATCC:::T GGTTG:TTGG CCTC:GTAGA GGCCGCGATG
M. pinocchi   T::ATGCCGT CGCCCGACAG CCATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. pleuroth   C::TTGCCGT CGCGTGACAG CCATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. princeps   C::TTGCCGC CACGTGACAG CAATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. pyxis      T::ATGCCGT CGCCCGACAG CCATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. racemosa   CTTGTGCCAT CGCGTGACAG CAATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCAATG
M. reichenb   T::ATGCCGT CGCCTGACAG CCATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. rubeola.   C::TTGCCAT CGCGTGACAG CAATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. rubigino   C::TTGCCAT CGCGTGACAG CAACCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. saltatri   C::TTGCCAT CGCGTGACAG CAATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCAATG
M. sanchezi   C::TTGCCGC CACGTGACAG CAATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCAATG
M. scabrili   T::ATGCCGT CGCCTGACAG CCATCC:::T GGTCG:TTGG CCTC:GTTGA GGCCGCGATG
M. schlimii   T::ATGCCGT CGCCTGACAG CCATCC:::T GGTTG:TTGG CCTC:CTTGA GGCCGCGATG
M. striatel   T::ATGCCGT CGCCTGACGG CCATCC:::C GGTCG:TTGG CCTC:GTTGA GGCCGCGATG
M. teaguei.   C::TTGCCGT CGCGTGACAG CCATCC:::T TGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. titan      C::TTGCCGC CACGTGACAG CAATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. uniflora   C::TTGCCAT CGCGCGACAG CAATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. veitchia   C::TTGCCAT CGCACGACAG CAATCC:::T GGTTG:TTGG CTTC:GTTGA GGCCGCGATG
M. venezuel   T::ATGCCGT CGCTTGACAG CCATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCAATG
M. vieriana   T::ATGCCGT CGCCTGACAG CCATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. walteri    T::ATGCCGT CGCCTGACAG CCATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. wendland   T::ATGCCGT CGCGTGACAG CCATCC:::T GGTTG:TTGG CCTC:GTTGA GGCCGCGATG
M. ximenae.   C::TTGCCGT CGCGTGACAG CCATCC:::T GGTTG:TTGG CCTC:GTTGA GGTCGCAATG
M. zahlbruc   T::ATGCCGT CGCCTGACAG CCATCC:::C GGT:G:TTGG CCTC:GTTGA GGCCGCGATG
P. amethyst   C::TAGCCGT CGCGTGACAG TCATCC:::T TGTTG:TTGG CCTC:GTTGA GGCCGCAATG
P. uxorium.   C::CAGCCAT CGCGTGACAG CCATCC:::T TGTTG:TTGG CCTC:GTTGA GGCCGCAATG
T. gemmata.   C::TAGCCAT TGCATGACAG GCGTCC:::T GGTCG:TTGG CCTC:GTTGA GGTCGCGATG
T. scobina.   C::TAGCCAT TGCATGACGG GCGTCC:::T GGTCG:TTGG CCTC:ATTGA GGCCGCGAAG

              ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                 125        135        145        155        165        175
D. astuta     AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
D. chimaera   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
D. cochliops  AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
D. houtteana  AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
D. sodiroi.   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
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              ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                 125        135        145        155        165        175
D. xenos      AGGGGAAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
L. pelecani   CGGGGCGGAT GAAACTCAAA CCGGCGCAGC TAC:GCGCCA AGGGAATAAG GAAAGAGACA
M. abbrevia   AGGGGAAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. alexandr   AGGGGAAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATAAA AAATGAAACA
M. amaluzae   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATGCA ::ATGAAACA
M. ampullac   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGTAATACA ::ATGAAACA
M. antonii    AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGTAATACA ::ATGAAACA
M. aphanes    AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATGCA ::ATGAAACA
M. aphanes.   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGTCA AGGGAATACA ::ATGAAACA
M. bangii     AGGGGTAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. bicornis   AGGGGCAGCT GAAACTCAAA TCGGCGCAGT TAC:GCGCCA AGGTAATACA ::ATGAAACA
M. caesia     AGGGGCGGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::AAGAAACA
M. caloptera  AGGGGAAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. campylog   AGGGGCGGCC GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. cardiant   AGGGGCGGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. carmenen   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATGCA ::ATGAAACA
M. caudiovo   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TACCGCGCCA AGGGAATACA ::ATGAAACA
M. cerastes   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. chaetost   AGGGGAAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. chaparen   AGGGGTAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGTAATACA ::ATGAAACA
M. chimboen   AGGGGCGGCT CGAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. citrinel   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGTAATACA ::ATGAAACA
M. civilis    AGGGGCGGCC GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ACGAAACA
M. coccinea   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGTAATACA ::ATGAAACA
M. collina    AGGGGCGGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. collina.   AGGGGCGGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. coriacea   AGGGGCGGCC GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. corniHam   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. corniHan   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. cupulari   AGGGGCGGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATATA ::ATGAAACA
M. cycloteg   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGTAATACA ::ATGAAACA
M. davisii    AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGTAATACA ::ATGAAACA
M. decumana   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGTAATACA ::ATGAAACA
M. deformis   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGTAATACA ::ATGAAACA
M. delhierr   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. echo       AGGGGCGGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATGCA CGATGAAACA
M. erinacea   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGTCA AGGGAATACA ::ATGAAACA
M. estradae   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGTAATACA ::ATGAAACA
M. floribun   AGGGGCGGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATATA ::ATGAAACA
M. fulvesce   AGGGGCGGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATATA ::ATGAAACA
M. garciae    AGGGGCGGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. glandulo   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGTAATACA ::ATGAAACA
M. goliath    AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGTCA AGGGAATACA ::ATGAAACA
M. gutierre   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ACGAAACA
M. guttulat   AGGGGCGGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ACGAAACA
M. herradur   AGGGGCGGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. heteropt   AGGGGAAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. hierogly   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGTAATACA ::ATGAAACA
M. hirtzii    AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGTAATACA ::ATGAAACA
M. hoeijeri   AGGGGCAGCT GAAACTAAAA TCGGCGCAGC TAC:GCGCCA AGGTAATGCA ::ATGAAACA
M. infracta   AGGGGCGGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATGCA CGATGAAACA
M. kyphonan   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAT:GCGCCA AGGGAATACA ::ATGAAACA
M. lamproty   AGGGGCCGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGTAATACA ::ATGAAACA
M. lansberg   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAT:GCGCCA AGGGAATACA ::ATGAAACA
M. lata       AGGGGCGGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. limax      AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGTAATACA ::ATGAAACA
M. macruraH   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. macruraH   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. melanoxa   AGGGGCGGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACG ::ATGAAACA
M. meleagri   AGGGGAAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATAAA ::ATGAAACA
M. mentosa.   AGGGGCGGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ACGAAACA
M. mezae      AGGGGCGGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. molossus   AGGGGAAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. mystica    AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGTAATACA ::ATGAAACA
M. naranjap   AGGGGCGGCT GAAACACAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAGACA
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              ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                 125        135        145        155        165        175
M. nidifica   AGGGGAAGTT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. notosibr   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGTAATACA ::ATGAAACA
M. ophioglo   AGGGGAAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. oreas      AGGGTCGGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ACGAAACA
M. oreas      AGGGTCGGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ACGAAACA
M. ova avis   AGGGGAAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. pachyura   AGGGGAAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. paivaean   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGTAATACA ::ATGAAACA
M. panguien   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGTCA AGGGAATACA ::ATGAAACA
M. parvula    AGGGGAAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATAAA ::ATGAAACA
M. patricia   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGTAATACA ::ATGAAACA
M. patula     AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATGCA ::ATGAAACA
M. perister   AGGGGCGGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. persicin   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGTAATACA ::ATGAAACA
M. pescadoe   AGGGGTGGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. picea      AGGGGCGGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ACGAAACA
M. picturat   AGGAGAAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. pinocchi   AGGGGCGGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. pleuroth   AGGGGAAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. princeps   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGTCA AGGGAATACA ::ATGAAACA
M. pyxis      AGGGGCGGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ACGAAACA
M. racemosa   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. reichenb   AGGGGCGGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATATA ::ATGAAACA
M. rubeola.   AGGGGCAGCT GAAACTCAAA TCGGCGCAGA TAC:GCGCCA AGGTAATACA ::ATGAAACA
M. rubigino   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. saltatri   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGTAATACA ::ATGAAACA
M. sanchezi   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATGCA ::ATGAAACA
M. scabrili   AGGGGCGGCT GAAACTCAAA TCGGCGCAGT TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. schlimii   AGGGGCGGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. striatel   AGGGGCGGCT GAAACTCAAA CCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. teaguei.   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. titan      AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGTCA AGGGAATACA ::ATGAAACA
M. uniflora   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGTAATACA ::ATGAAACA
M. veitchia   AGGGGTAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGTAATACA ::ATGAAACA
M. venezuel   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAAACA
M. vieriana   AGGGGCGGCT GAAACACAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAGACA
M. walteri    AGGGGCGGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATATA ::ATGAAACA
M. wendland   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ACGAAACA
M. ximenae.   AGGGGAAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATAAA ::ATGAAACA
M. zahlbruc   AGGGGCGGCT GAAACACAAA CCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ATGAGACA
P. amethyst   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATAAA ::ATGAAACA
P. uxorium.   AGGGGCAGCT GAAACTCAAA TCGGCGCAGC TAC:GCGCCA AGGGAATACA ::ACGAAACA
T. gemmata.   AGGGGCGACT GAAACACAAA CCGGCGCAGC TAC:GCGCCA AGGGAATACA ::TTGAAACA
T. scobina.   AGGGGCGACT GAAACACAAA ACGGCGCAGC TAT:GCGCCA AGGGAATACA ::TTGAAACA

                                                                    5,8S  ATCAAAA
              ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                 185        195        205        215        225        235
D. astuta     CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATT::G CGCCCCACAC GGATCAAAAT
D. chimaera   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATT::G CGCCCCACAC GGATCAAAAT
D. cochliops  CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATT::G CGCCCCACAC GGATCAAAAT
D. houtteana  CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATT::G CGCCCCGCAC GGATCAAAAT
D. sodiroi.   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATT::G CGCCCCGCAC GGATCAAAAT
D. xenos      CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATT::G CGCCCCGCAC GGATCAAAAT
L. pelecani   CGAGCCCGCA ACGGGTTCGG TGGCGTGGGG CGCTGTT::G CGCACCGCAC GGATCAAAAC
M. abbrevia   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. alexandr   CGAGCCCTCA TGGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. amaluzae   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCCATA::G CGCCCCGCAC GGATCAAAAT
M. ampullac   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. antonii    CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCTC TGATCAAAAT
M. aphanes    CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. aphanes.   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. bangii     CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTGTA::G CGCCCCGCAT GGATCAAAAT
M. bicornis   CGAGCCCGCA TTGGGTTCGA TGGCGTGGGG TGCTATATAG TGCCCCGCAC GGATCAAAAT
M. caesia     CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG CGCAATG::G CGCCTCGCAC GGATCAAAAT
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                                                                5,8S   ATCAAAA
              ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                  185        195        205        215        225        235
M. caloptera  CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. campylog   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCAGTA::G CGCCTCGCAC GGATCAAAAT
M. cardiant   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCTCGCAC GGATCAAAAT
M. carmenen   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCCATA::G CGCCCCGCAC GGATCAAAAT
M. caudiovo   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. cerastes   CGAGCCCGCA CCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. chaetost   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. chaparen   CGAGCCCGCA TTGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. chimboen   CGAGCCCGCA TCGGGTTCGA TGGCGCGGGG CGCTATG::G CGCCTCGCAC GGATCAAAAT
M. citrinel   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. civilis    CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG CGCAACA::G CGCCTCGCAC GGATCAAAAT
M. coccinea   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. collina    CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG CGCTATA::G CGCCTCGCAC GGATCAAAAT
M. collina.   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG CGCTATA::G CGCCTCACAC GGATCAAAAT
M. coriacea   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTACA::G CGCCTCGCAC GGATCAAAAT
M. corniHam   CGAGCCCGCA CCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. corniHan   CGAGCCCGCA CCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. cupulari   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCTCGCAC GGATCAAAAT
M. cycloteg   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. davisii    CGAGCCCGCA TTGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. decumana   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. deformis   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. delhierr   CGAGCCCGCA CCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. echo       CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTACG::G CGCCTCGCAC GGATCAAAAT
M. erinacea   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTACG::G CGCCCCGCAC GGATCAAAAT
M. estradae   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. floribun   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCTCGCAT GGATCAAAAT
M. fulvesce   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCNCGCAC GGATCAAAAT
M. garciae    CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCTCGCAC GGATCAAAAT
M. glandulo   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CACCTTGCAC GGATCAAAAT
M. goliath    CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. gutierre   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCTCGCAC GGACCAAAAT
M. guttulat   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCTCGCAC GGATCAAAAT
M. herradur   CGAGCCCGTA TCGGGTTCGA TGGCGTGGGG TGCTGTA::G CGCCTCGCAC GGATCAAAAT
M. heteropt   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. hierogly   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. hirtzii    CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. hoeijeri   CGAGCCCGCA TCGGGTTCGA TGGCGCGGGG TGCTATA::G CGGCCCGCAC GGATCAAAAT
M. infracta   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATG::G CGCCTCGCAC GGATCAAAAT
M. kyphonan   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCTCGCAC GGATCAAAAT
M. lamproty   CGAGCCCACA TCGGGTTCGA TGGCGTGGGG TGCTGTA::G CGCCCTGCAC GGATCAAAAT
M. lansberg   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCTCGCAC GGATCAAAAT
M. lata       CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCTCGCAC GGATCAAAAT
M. limax      CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. macruraH   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. macruraH   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. melanoxa   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATG::G CGCCTCGCAC GGATCAAAAT
M. meleagri   CGAGCCCTCA TGGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGAACAAAAT
M. mentosa.   CGAGCCCGCG TCGGGTTCGA TGGCGTGGGG TGCTGTA::G CGCCTCGCAC GGATCAAAAT
M. mezae      CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCTCGCAC GGATCAAAAT
M. molossus   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. mystica    CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. naranjap   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTGTA::G CGCCTCGCAC GGATCAAAAT
M. nidifica   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. notosibr   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. ophioglo   CGAGCCCTCA TCGGGTTCGA TGGCGTGGGG TGCTACA::G CGCCCCGCAC GGATCAAAAT
M. oreas      CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATG::G CGCCTCGCAC GGATCAAAAT
M. oreas      CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATG::G CGCCTCGCAC GGATCAAAAT
M. ova avis   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. pachyura   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GTATCAAAAT
M. paivaean   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. panguien   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. parvula    CGAGCCCTCA TGGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. patricia   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
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                                                                 5,8S  ATCAAAA
              ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                 185        195        205        215        225        235
M. patula     CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTACA::G CGCCCCGCAC GGATCAAAAT
M. perister   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG CGCAATA::G CGCCTCGCAC GGATCAAAAT
M. persicin   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. pescadoe   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCTCGCAC GGATCAAAAT
M. picea      CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG CGCAACA::G CGCCTCGCAC GGATCAAAAT
M. picturat   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. pinocchi   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCTCGCAC GGATCAAAAT
M. pleuroth   CGAGCCCCCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCACAC GGATCAAAAT
M. princeps   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. pyxis      CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCTCGCAC GGATCAAAAT
M. racemosa   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. reichenb   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTGTA::G CGCCCCGCAC GGATCAAAAT
M. rubeola.   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. rubigino   CGAGCCCGCA TTGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. saltatri   CGAGCCCGCA TTGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCCCAC GGATCAAAAT
M. sanchezi   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTACA::G CGCCCCGCAC GGATCAAAAT
M. scabrili   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG CGCTGTA::G CGCCTCGCAC GGATCAAAAT
M. schlimii   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG CGCTGTA::G CGCCTCGCAC GGATCAAAAT
M. striatel   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATG::G CGCCTCGCAC GGATCAAAAT
M. teaguei.   CGAGCCCGCA CTGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. titan      CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. uniflora   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. veitchia   CGAGCCCGCA TTGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GAATCAAAAT
M. venezuel   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCTCGCAC GGATCAAAAT
M. vieriana   CGAGCCCGCA TCGGGTTCGA TGGCGCGGGG TGCTATA::G CGCCTCGCAC GGATCAAAAT
M. walteri    CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTGTA::G CGCCCCGCAC GGATCAAAAT
M. wendland   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCTCGCAC GGACCAAAAT
M. ximenae.   CGAGCCCTCA TGGGGTTCGA TGGCGTGGGG TGCTATA::G CGCCCCGCAC GGATCAAAAT
M. zahlbruc   CGAGCCCGCA TCGGGTTCGA TGGCGTGGGG TGCTGTA::G CGCCTCGCAC GGATCAAAAT
P. amethyst   CGAGCCTGCA TAGGGTTCGA TGGCGTGGGG TGATATT::T CGCCCCACAC GGATCAAAAT
P. uxorium.   CGAGCC:GCA TAGGGTTCGA TGGCGTGGGG TGCTATT::T CGCCCCACAC GGATCAAAAT
T. gemmata.   CGAGCCCGCA ACGGGTTCGA TGGCGTGGGG TGCTATT::G CGCGCCACAA ATATCAAAAT
T. scobina.   CGAGCCCGCA TCGGGCTCGA TGGCGTGGCG TGCTATT::G CGCGCCACAC AGATCAAAAT

              ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                 245        255        265        275        285        295
D. astuta     GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
D. chimaera   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
D. cochliops  GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
D. houtteana  GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
D. sodiroi.   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
D. xenos      GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
L. pelecani   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. abbrevia   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. alexandr   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. amaluzae   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. ampullac   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. antonii    GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. aphanes    GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. aphanes.   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. bangii     GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. bicornis   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. caesia     GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. caloptera  GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. campylog   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. cardiant   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. carmenen   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. caudiovo   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. cerastes   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. chaetost   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. chaparen   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. chimboen   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. citrinel   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. civilis    GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
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              ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                 245        255        265        275        285        295
M. coccinea   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. collina    GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. collina.   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. coriacea   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. corniHam   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. corniHan   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. cupulari   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. cycloteg   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. davisii    GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. decumana   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. deformis   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. delhierr   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. echo       GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. erinacea   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. estradae   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. floribun   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. fulvesce   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. garciae    GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. glandulo   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. goliath    GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. gutierre   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. guttulat   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. herradur   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. heteropt   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. hierogly   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. hirtzii    GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. hoeijeri   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. infracta   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. kyphonan   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. lamproty   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. lansberg   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. lata       GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. limax      GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. macruraH   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. macruraH   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. melanoxa   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. meleagri   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. mentosa.   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. mezae      GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. molossus   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. mystica    GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. naranjap   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. nidifica   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. notosibr   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. ophioglo   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. oreas      GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. oreas      GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. ova avis   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. pachyura   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. paivaean   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. panguien   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. parvula    GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. patricia   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. patula     GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. perister   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. persicin   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. pescadoe   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. picea      GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. picturat   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. pinocchi   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. pleuroth   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. princeps   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. pyxis      GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. racemosa   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. reichenb   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
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              ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                 245        255        265        275        285        295
M. rubeola.   GACTCTCGGC AATGGATATC TCGGCTCTCG CCTCGATGAA GAGCGCAGCG AAATGCGATA
M. rubigino   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. saltatri   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. sanchezi   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. scabrili   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATAAA GAGCGCAGCG AAATGCGATA
M. schlimii   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. striatel   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. teaguei.   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. titan      GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. uniflora   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. veitchia   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. venezuel   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. vieriana   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. walteri    GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. wendland   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. ximenae.   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
M. zahlbruc   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
P. amethyst   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
P. uxorium.   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA AAGCGCAGCG AAATGCGATA
T. gemmata.   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA
T. scobina.   GACTCTCGGC AATGGATATC TCGGCTCTCG CATCGATGAA GAGCGCAGCG AAATGCGATA

              ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                 305        315        325        335        345        355
D. astuta     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
D. chimaera   CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
D. cochliops  CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
D. houtteana  CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
D. sodiroi.   CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
D. xenos      CGTGGTGCGA ATTGCAGAAT CCCGGGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
L. pelecani   CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. abbrevia   CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. alexandr   CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. amaluzae   CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. ampullac   CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. antonii    CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. aphanes    CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. aphanes.   CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. bangii     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. bicornis   CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. caesia     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. caloptera  CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. campylog   CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. cardiant   CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. carmenen   CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. caudiovo   CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. cerastes   CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. chaetost   CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. chaparen   CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. chimboen   CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. citrinel   CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. civilis    CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. coccinea   CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. collina    CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. collina.   CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. coriacea   CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. corniHam   CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. corniHan   CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. cupulari   CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. cycloteg   CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. davisii    CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. decumana   CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. deformis   CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. delhierr   CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. echo       CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
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                ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                     305        315        325        335        345        355
M. erinacea     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. estradae     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. floribun     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. fulvesce     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. garciae      CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. glandulo     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. goliath      CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. gutierre     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. guttulat     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. herradur     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. heteropt     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAAAATT TGAACGCAAG TTGCGCCCGA
M. hierogly     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. hirtzii      CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. hoeijeri     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. infracta     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. kyphonan     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. lamproty     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. lansberg     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. lata         CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. limax        CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. macruraH     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. macruraH     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. melanoxa     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. meleagri     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. mentosa.     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. mezae        CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. molossus     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. mystica      CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. naranjap     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. nidifica     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. notosibr     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. ophioglo     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. oreas        CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. oreas        CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. ova avis     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. pachyura     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. paivaean     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. panguien     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. parvula      CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. patricia     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. patula       CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. perister     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. persicin     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. pescadoe     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. picea        CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. picturat     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. pinocchi     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. pleuroth     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. princeps     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. pyxis        CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. racemosa     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. reichenb     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. rubeola.     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. rubigino     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. saltatri     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. sanchezi     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. scabrili     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. schlimii     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. striatel     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. teaguei.     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. titan        CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. uniflora     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. veitchia     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. venezuel     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. vieriana     CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
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                    ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                      305        315        325        335        345        355
M. walteri          CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. wendland         CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
M. ximenae.         CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAA TTGCGCCCGA
M. zahlbruc         CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
P. amethyst         CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
P. uxorium.         CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
T. gemmata.         CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA
T. scobina.         CGTGGTGCGA ATTGCAGAAT CCCGCGAACC ATCGAGAATT TGAACGCAAG TTGCGCCCGA

                                                    ITS 2 G TTGC
                    ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                      365        375        385        395        405        415
D. astuta           GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTGCGTTGCT TCGTGCCAGC
D. chimaera         GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTGCGTTGCT TCGTGCCAGC
D. cochliops        GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTGCGTTGCT TCGTGCCAGC
D. houtteana        GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTGCGTTGCT TCGTGCCAGC
D. sodiroi.         GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTGCGTTGCT TCGTGCCAGC
D. xenos            GGCCATCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
L. pelecani         GGCCAGCCGG CCGAGGGCAC GTCCGCCTGG GCGTCAAGCG TTGCGTCGCT CTGTACCCTC
M. abbrevia         GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. alexandr         GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. amaluzae         GGCCATCCGG CTAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. ampullac         GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. antonii          GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. aphanes          GGCCATCCGG CTAAGGGCAC GCCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. aphanes.         GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. bangii           GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. bicornis         GGCCAGCCGG CCGAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. caesia           GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTGCGTTGCT CCGTGCCATC
M. caloptera        GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. campylog         GGCCATCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTGCGTTGCT CCGTGCCATC
M. cardiant         GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. carmenen         GGCCATCCGG CTAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. caudiovo         GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTGCGTTGCT CCGTGCCATC
M. cerastes         GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. chaetost         GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. chaparen         GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. chimboen         GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. citrinel         GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. civilis          GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTGCGTTGCT CCGTGCCATC
M. coccinea         GGCCATCCGG TCGAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. collina          GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGCGCCATC
M. collina.         GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGCGCCATC
M. coriacea         GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTGCGTCGCT CCGTGCCATC
M. corniHam         GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. corniHan         GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. cupulari         GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTACCATC
M. cycloteg         GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. davisii          GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. decumana         GGCCATCCGG CCGAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. deformis         GGCCATCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. delhierr         GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. echo             GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTCGCT CCGTGCCATC
M. erinacea         GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTGCGTCGCT CCGTGCCATC
M. estradae         GGCCATCCGG CCGAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. floribun         GGCCAGCCGG CCGAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. fulvesce         GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. garciae          GGCCAGCCGG CCGAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTCGCT CCGTGCCATC
M. glandulo         GGCCAGCAGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. goliath          GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. gutierre         GGCCAGCCGG CCGAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. guttulat         GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTTCCATC
M. herradur         GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. heteropt         GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. hierogly         GGCCAGCCGG CCAAGGGCAC GTCCGCTTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
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                                                  ITS 2 G TTGC
              ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                 365        375        385        395        405        415
M. hirtzii    GGCCATCCGG TCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. hoeijeri   GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. infracta   GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTCGCT CCGTGCCATC
M. kyphonan   GGCCATCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. lamproty   GGCCATCCGG TCGAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. lansberg   GGCCATCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. lata       GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. limax      GGCCATCCGG TCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. macruraH   GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. macruraH   GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. melanoxa   GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTCGCT CCGTGCCATC
M. meleagri   GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. mentosa.   GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. mezae      GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. molossus   GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. mystica    GGCCATCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. naranjap   GGCCATCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCCTC
M. nidifica   GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. notosibr   GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. ophioglo   GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. oreas      GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. oreas      GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. ova avis   GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. pachyura   GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. paivaean   GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. panguien   GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. parvula    GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. patricia   GGCCATCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. patula     GGCCATCCGG CTAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. perister   GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTGCGTTGCT CCGTGCCATC
M. persicin   GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. pescadoe   GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. picea      GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTGCGTTGCT CCGTGCCATC
M. picturat   GGCCATCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. pinocchi   GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTTCCATC
M. pleuroth   GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. princeps   GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. pyxis      GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. racemosa   GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTGCGTTGCT CCGTGCCATC
M. reichenb   GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. rubeola.   GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTACCATC
M. rubigino   GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. saltatri   GGCCATCCGG TCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. sanchezi   GGCCATCCGG CTAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. scabrili   GGCCAGCCGG CTAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. schlimii   GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. striatel   GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. teaguei.   GGCCAGCCGG CTAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. titan      GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. uniflora   GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. veitchia   GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. venezuel   GGCCATCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. vieriana   GGCCATCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. walteri    GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. wendland   GGCCAGCCGG CCGAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. ximenae.   GGCCAGCCGG CCAAGGGCAC ATCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCATC
M. zahlbruc   GGCCATCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTACGTTGCT CCGTGCCGTC
P. amethyst   GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTGCGTTGCT CCGTGCCATC
P. uxorium.   GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTGCGTTGCT CCGTGCCATC
T. gemmata.   GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTGCGTCGCT CCGTGCCAGC
T. scobina.   GGCCAGCCGG CCAAGGGCAC GTCCGCCTGG GCGTCAAGCG TTGCGTCGCT CCGTGCCAGC
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               ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                     425        435        445        455        465        475
D. astuta      T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGCCGGATGT GTAGAGTGGC
D. chimaera    T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGCCGGATGT GCAGAGTGGC
D. cochliops   T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGCCGGATGT GTAGAGTGGC
D. houtteana   T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGCCGGATGT GCAGAGTGGC
D. sodiroi.    T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGCCGGATGT GCAGAGTGGC
D. xenos       T:C:::CAA: :CCCGCCCGA AGGGCGTG:: CATGCGAGAA GGTCGGATGT GTAAAATGGC
L. pelecani    C:C:::CAT: :CCCACCCGG CGGGTGTG:: CATGGGGAAG GGTCGGATGC GGAGAGTGGC
M. abbrevia    T:C:::CAT: CCCCACCTGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAGTGGC
M. alexandr    T:CCC:CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAT GGTCGGATGT GTAGAGTGGC
M. amaluzae    T:C:::CAT: :CCCACCAGA AGGGTGTG:: GATGCGGGAG GGTCGGATGC GTAGAGTGGC
M. ampullac    T:C:::CAT: :CCCACCCGA AGGGTGTG:: TATGCGGGAG GGTCGGATGT GTAGAATGGC
M. antonii     T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAATGGC
M. aphanes     T:C:::CAT: :CCCACCCGA AGGGCGTG:: GATGCGGGAG GGTCGGATGC GTAGAGTGGC
M. aphanes.    T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGAAG GGTCGGATGT GTAGAGTGGC
M. bangii      T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGCCGGATGT GTAGAGTGGC
M. bicornis    T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAGTGGC
M. caesia      T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GCAGAGTGGC
M. caloptera   T:C:::CAT: TCCCACCTGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAGTGGC
M. campylog    T:C:::CAT: :CCCGCCCGA AGGGTGCG:: CATGCGGGAG GGCCGGATGT GCAGAGTGGC
M. cardiant    T:C:::CAT: :CCCACCCGA AGGGTGTGTG CATGCGGGAG GGTCGGATGT GTAGAGTGGC
M. carmenen    T:C:::CAT: :CCCACCAGA AGGGTGTG:: GATGCGGGAG GGTCGGATGC GTAGAGTGGC
M. caudiovo    T:C:::CAT: :CCCACCCAA AGGGTGTG:: CATGCGGGAG GGTCGTATGT GTAGAGTGGC
M. cerastes    T:C:::CAT: :TCCACCCGA AGGGTGCG:: CGTGCAGGAT GGCCGGATGT GTAGAGTGGC
M. chaetost    T:C:::CAT: CCCCACCTGA AGGGTGTG:: AATGCGGGAG GGTCGGATGT GTAGAGTGGC
M. chaparen    T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAATGGC
M. chimboen    T:C:::CAG: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAGTGGC
M. citrinel    T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAATGGC
M. civilis     T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGCCGGATGT GCAGAGTGGC
M. coccinea    T:C:::CAT: :CTCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAATGGC
M. collina     T:C:::CAT: :CCCACCCGA AGGGTGCG:: GATGCGGGAG GGTCGGATGT GTAGAGTGGC
M. collina.    T:C:::CAT: :CCCACCCGA AGGGTGCG:: GATGCGGGAG GGTCGGATGT GTAGAGTGGC
M. coriacea    T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGCCGGATGT GCAGAGTGGC
M. corniHam    T:C:::CAT: :TCCACCCGA AGGGTGCG:: CGTGCAGGAT GGCCGGATGT GTAGAGTGGC
M. corniHan    T:C:::CAT: :TCCACCCGA AGGGTGCG:: CGTGCAGGAT GGCCGGATGT GTAGAGTGGC
M. cupulari    T:C:::CAT: :CCCACCCGA AGGGTGTG:G CATGCGGGAG GGCCGGATGT GTAGAGTGGC
M. cycloteg    T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GCAGAATGGC
M. davisii     T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAATGGC
M. decumana    T:C:::CAT: :CCCACCCAA AGGGTGTG:: CATGCGGGAG G:TCGGATGT GTAGAATGGC
M. deformis    T:C:::CAT: :CCCACCCAA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAATGGC
M. delhierr    T:C:::CAT: :TCCACCCGA AGGGTGCG:: CGTGCAGGAT GGCCGGATGT GTAGAGTGGC
M. echo        T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAGTGGC
M. erinacea    C:CCGTCTT: :CCCACCCGA AGGGTGTG:: CACGCGGGAG GGTCGGACGT GCAGGGTGGC
M. estradae    T:C:::CAT: :CCCACCCAA AGGGTGTG:: CATGCGGGAG G:TCGGATGT GCAGAATGGC
M. floribun    T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGGG GGTCGGATGT GTAGAGTGGC
M. fulvesce    T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGGG GGTCGGATGT GTAGAGTGGC
M. garciae     C:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAGTGGC
M. glandulo    T:C:::CAT: :CCCACCGGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAATGGC
M. goliath     T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAGTGGC
M. gutierre    T:C:::CAT: :CCCACCCGA CGGGTGTG:: CATGCGGGAG GGCCGGATGT GTAGAGTGGC
M. guttulat    T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAGTGGC
M. herradur    T:C:::CAT: :CCCACCCGA AGGGTGCG:: CATGCGGGAG GGTCGGATGT GTAGAGTGGC
M. heteropt    T:C:::CAT: :CCCACCCAA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAGTGGC
M. hierogly    T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GCAGAATGGC
M. hirtzii     T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAATGGC
M. hoeijeri    T:C:::CAT: :CCCACC:GA AGGGTGTG:: CATGCGGGAG GGACGGATGT GTAGAGTGGC
M. infracta    T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGCCGGATGT GTAGAGTGGC
M. kyphonan    T:C:::CAT: :CCAACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAGTGGC
M. lamproty    T:C:::CAT: :CCCACCCGA AGGGTGTGTG CATGCGGGAG GGTCGGATGT GTAGAATGGC
M. lansberg    T:C:::CAT: :CCAACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAGTGGC
M. lata        T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAGTGGC
M. limax       T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAATGGC
M. macruraH    T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAGTGGC
M. macruraH    T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAGTGGC
M. melanoxa    T:C:::CAT: :CCCACCCGA AGGGTGTG:: CGTGCGGGAG GGCCGGATGT GCAGAGTGGC
M. meleagri    T:CCC:CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAT GGTCGGATGT GTAGAGTGGC
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                 425        435        445        455        465        475
M. mentosa.   T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAGTGGC
M. mezae      T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAGTGGC
M. molossus   T:C:::CAT: :CCCACCTGA AAGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAGTGGC
M. mystica    T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAATGGC
M. naranjap   T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GCAGAGTGGC
M. nidifica   T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGTGAG GGTCGGATGT GTAGAGTGGC
M. notosibr   T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAATGGC
M. ophioglo   C:C:::CATC CCCCACCTGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAGTGGC
M. oreas      T:C:::CAT: :CCCGCCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GCAGAGTGGC
M. oreas      T:C:::CAT: :CCCGCCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GCAGAGTGGC
M. ova avis   T:C:::CAT: CCCCACCTGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAGTGGC
M. pachyura   T:C:::CAT: CCCCACCTGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAGTGGC
M. paivaean   T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAATGGC
M. panguien   T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAGTGGC
M. parvula    T:CCC:CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAT GGTCGGATGT GTAGAGTGGC
M. patricia   T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAATGGC
M. patula     T:C:::CAT: :CCCACCAGA AGGGTGTG:: GATGCGGGAG GGTCGGATGC GTAGAGTGGC
M. perister   T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGCCGGATGC GCAGAGTGGC
M. persicin   T:C:::CAT: :CCCACCCAA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAATGGC
M. pescadoe   T:C:::CAT: :CCCACTCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAGTGGC
M. picea      T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GCAGAGTGGC
M. picturat   T:C:::CAA: :CCCGCCCGA AGGGCGTG:: CATGCGAGAG GGTCGGATGT GTAGAGTGGC
M. pinocchi   T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAGTGGC
M. pleuroth   T:C:::CAA: :CCCGCCCGA AGGGCGTG:: CGTGCGAGAG GGTCGGATGT GTAGAGTGGC
M. princeps   T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAGTGGC
M. pyxis      T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGG:AG GGCCGGATGC GCAGAGTGGC
M. racemosa   T:C:::CAT: :CCCACCCAA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAGTGGC
M. reichenb   T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGGG GGTCGGATGT GTAGAGTGGC
M. rubeola.   T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAATGGC
M. rubigino   T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAATGGC
M. saltatri   T:C:::CAT: :TCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAATGGC
M. sanchezi   T:C:::CAT: :CCCACCAGA AGGGTGTG:: GATGCGGGAG GGTCGGATGC GTAGAGTGGC
M. scabrili   TTC:::CAT: :CCCACCCGT AGGGTGAG:: CATGCGGGAG GGTCGGATGT GTAGAGTGGC
M. schlimii   T:C:::CAT: :CCCACCCGA AGGGTGCG:: CATGCGGGAG GGTCGGATGT GCAGAGTGGC
M. striatel   T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAGTGGC
M. teaguei.   T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAGTGGC
M. titan      T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGAAG GGTCGGATGT GTAGAGTGGC
M. uniflora   T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GCAGAATGGC
M. veitchia   T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAATGGC
M. venezuel   T:C:::CAT: :CCAACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAGTGGC
M. vieriana   T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GCAGAGTGGC
M. walteri    T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGGG GGTCGGATGT GTAGAGTGGC
M. wendland   T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGCCGGATGT GTAGAGTGGC
M. ximenae.   T:CCA:CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAT GGTCGGATGT GTAGAGTGGC
M. zahlbruc   T:C:::CAT: :CCCACCCGA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GCAGAGTGGC
P. amethyst   T:C:::CAT: :CCCACC:GA AGGGTGTG:: CATGCGGGAG GGTCGGATGT GTAGAGTGGC
P. uxorium.   T:C:::CAT: :CCCACC:GA AGGGTGTG:: AATGCGGGAG GGTCGGATGT GCAGAGTGGC
T. gemmata.   T:C:::CAT: :CCCACCC:A ACGGTGTG:: CATGCGGGAT GGTCGGATGT GCAGATTGGC
T. scobina.   T:C:::CAT: :CCCACCCGA ACGGTGTG:: CATGGGGGAT GGTCGGATGT GCAGAGTGGC

               ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                  485        495        505        515        525        535
D. astuta     TCGTCGTGCC TGCGGGCGCG GCGGGCTAAA GAGTTGGTGA TCGTGTCGT: TGGCCACGAG
D. chimaera   TCGTCGTGCC TGCGGGCGCG GCGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
D. cochliops  TCGTCGTGCT CGCGGGCGCG GCGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
D. houtteana  TCGTCGTGCC TGCGGGCGCG GCGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
D. sodiroi.   TCGTCGTGCC TGCGGGCGCG GCGGGCTTAA GAGTTGGTGA TCGTTTCGT: TGGCCACGAG
D. xenos      TTGTTGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TTGTCTCGT: TGGCCAAGAG
L. pelecani   TCGTCGTGCC CGCGGGCGCG GCGGGCTGAA GAGCGGGTGA TCGTCTCGT: CGGCCACGGG
M. abbrevia   TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. alexandr   TCATCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. amaluzae   TCGTCGTGCC CTCGGGCGTG GCGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. ampullac   TCGTCGTGCC CCCGGGCGTG GCGGGCTAAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. antonii    TCGTCGTGCC CCCGGGCGTG GCGGGCTAAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. aphanes    TCGTCGTGCC CTCGGGCGTG GCGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
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                  485        495        505        515        525        535
M. aphanes.   TCGTCGTGCC CTCGGGCGCG GCGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. bangii     TCATCGTGCC CCCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. bicornis   TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. caesia     TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAAATGGTGA TCGTCTCGT: TGGCCACGAG
M. caloptera  TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. campylog   TCGTCGTGCC CTCGGGCGCG ACGGGCTCAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. cardiant   TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. carmenen   TCGTCGTGCC CTCGGGCGTG GCGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. caudiovo   TCGTCGTGCC CCCGGGCGTG GCGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. cerastes   TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TTGCCACGAG
M. chaetost   TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. chaparen   TCGTCGTGCC CCCGGGCGTG GCGGGCTAAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. chimboen   TCGACGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. citrinel   TCGTCGTGCC CCCGGGCGTG GCGGGCTAAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. civilis    TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. coccinea   TCGTCGTGCC CCCGGGCGTG GCGGGCTAAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. collina    TCGTCGTGCC CCCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. collina.   TCGTCGTGCC CCCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. coriacea   TCGTCGTGCC CTCGGGCGCG ACGGGCTCAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. corniHam   TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TTGCCACGAG
M. corniHan   TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGGTGGTGA TCGTCTCGT: TTGCCACGAG
M. cupulari   TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGCTGCTGA TCGTCTCGT: TGGCCACGAG
M. cycloteg   TCGTCGTGCC CCCGGGCGTG GCGGGCTAAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. davisii    TCGTCGTGCC CCCGGGCGTG GCGGGCTAAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. decumana   TCGTCGTGCC CCCGGGCGTG GCGGGCTAAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. deformis   TCGTCGTGCC CCCGGGCGTG GCGGGCTAAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. delhierr   TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TTGCCACGAG
M. echo       TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. erinacea   TCGCCGTGCC CCCGGGCGCG GCGGGCTTAA GAGTTGGTGA TCGTCTCGT: CGGCCACGAG
M. estradae   TCGTCGTGCC CCCGGGCGTG GCGGGCTAAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. floribun   TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. fulvesce   TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGCTGA TCGTCTCGT: CGGCCACGAG
M. garciae    TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGCGA TCGTCTCGT: TGGCCACGAG
M. glandulo   TCGTCGTGCC CCCGGGCGTG GCGGGCTAAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. goliath    TCGTCGTGCC CTCGGGCGCG GCGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. gutierre   TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. guttulat   TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGCTGGTGA TCGTCTCGT: TGGCCACGAG
M. herradur   TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. heteropt   TCCTCGTGCC TTCGGGCGCG ACGGGCTGAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. hierogly   TCGTCGTGCC CTCGGGCGTG GCGGGCTGAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. hirtzii    TCGTCGTGCC CCCGGGCGTG GCGGGCTAAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. hoeijeri   TCGTCGTGCC CCCGGGCGCG ACGGGCTTAA GAGCTGGTGA TCGTCTCGT: TGGCCACGAG
M. infracta   TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. kyphonan   TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. lamproty   TCGTCGTGCC CTCGGGCGTG GCGGGCTAAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. lansberg   TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. lata       TCGTGGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGCTGA TCGTCTCGT: TGGCCACGAG
M. limax      TCGTCGTGCC CCCGGGCGTG GCGGGCTAAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. macruraH   TCGTCGTGCC CCCGGGCGTG GCGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. macruraH   TCGTCGTGCC CCCGGGCGTG GCGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. melanoxa   TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. meleagri   TCATCGTGCC CCCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. mentosa.   TCGCCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. mezae      TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. molossus   TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. mystica    TCGTCGTGCC CCCGGGCGTG GCGGGCTAAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. naranjap   TCGTCGTGCC CTCGGGCGCG ACGGGCTGAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. nidifica   TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTTTCGT: AGGCCACGAG
M. notosibr   TCGTCGTGCC CCCGGGCGTG GCGGGCTAAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. ophioglo   TCGTCGTGTC CTCGGGCGCG ATGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. oreas      TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. oreas      TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. ova avis   TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. pachyura   TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. paivaean   TCGTCGTGCC CCCGGGCGTG GCGGGCTAAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
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               ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                  485        495        505        515        525        535
M. panguien    TCGTCGTGCC CTCGGGCGCG GCGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. parvula     TCATCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. patricia    TCGTCGTGCC CCCGGGCGTG GCGGGCTAAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. patula      TCGTCGTGCC CTCGGGCGTG GCGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. perister    TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. persicin    TCGTCGTGCC CCCGGGCGTG GCGGGCTAAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. pescadoe    TCGTGGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. picea       TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. picturat    TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. pinocchi    TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. pleuroth    TCGTCGTGCC CTCGGGCGCC ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. princeps    TCGTCGTGCC CTCGGGCGCG GCGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. pyxis       TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. racemosa    TCGTCGTGCC CCCGGGCGTG GCGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. reichenb    TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGCTGA TCGTCTCGT: CGGCCACGAG
M. rubeola.    TCGTCGTGCC CCCGGGCGTG GCGGGCTAAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. rubigino    TCGTCGTGCC CCCGGGCGTG GCGGGCTAAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. saltatri    TCGTCGTGCC CCCGGGCGTG GCGGGCTAAA GCGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. sanchezi    TCGTCGTGCC CTCGGGCGTG GCGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. scabrili    TCGTCGTGCC CTCGGGTGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. schlimii    TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. striatel    TCGTCGTGCC ATCGTGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. teaguei.    TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TTGCCACGAG
M. titan       TCGTCGTGCC CTCGGGCGCG GCGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. uniflora    TCGTCGTGCC CCCGGGCGTG GCGGGCTAAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. veitchia    TCGTCGTGCC CCCGGGCGTG GCGGGCTAAA GAGTTGGTGA TCGTCTCGT: TTGCCACGAG
M. venezuel    TCGTCGTGCC CTCGGGTGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. vieriana    TCGTCGTGCC CTCGGGCGCG ACGGGCTCAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. walteri     TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGCTGA TCGTCTCGT: CGGCCACGAG
M. wendland    TCGTCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGCGA TCGTCTCGT: TGGCCACGAG
M. ximenae.    TCATCGTGCC CTCGGGCGCG ACGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
M. zahlbruc    TCGTCGTGCC CTCGGGCGCG ACGGGCTGAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
P. amethyst    TCGTCGTGCC CTCGGGCGCG GCGGGCTTAA GAGTTGGTGA TCGTCTCGTA TGGCCACGAG
P. uxorium.    TCGTCGTGCC CTCGG:CGCG GCGGGCTTAA GAGTTGGTGA TCGTCTCGT: TGGCCACGAG
T. gemmata.    TCGCCGTGCC CGTGGGCGCG ACGGGCTTAA GAGTGGGTGA TCGTCTCGT: TGGCCACGAC
T. scobina.    CCTTCGTGCT CGTGGGCGCG ACGGGTTTAA GAGTGGGTGA TCGTCTCGT: TGGCCACGAC

               ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                  545        555        5 5        575        585        595
D. astuta      CAGCAAGGG: TGGATGAAAA TTGTGCCTGT GATGTATCGT GCCGGCCAGA GAAG:AGA:T
D. chimaera    CAGCAAGGG: TGGATGAAAA TTGTGCCTGT GATGTATCGT GCCGGCCAGA GAAG:AGA:T
D. cochliops   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GCCGGCCAGA GAAG:AGA:T
D. houtteana   CAGCAAGGG: TGGATGAAAA TTGTGCCTGT GATGTATCGT GCCGGCCAGA GAAG:AGA:T
D. sodiroi.    CAGCAAGGG: TGGATGAAAA TTGTGCCTGT GATGTATCGT GCCGGCCAGA GAAG:AGA:T
D. xenos       CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
L. pelecani    CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GTTGCATCGT GCAGTCCCGA GAAG:AGA:T
M. abbrevia    CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. alexandr    CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. amaluzae    CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. ampullac    CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. antonii     CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. aphanes     CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. aphanes.    CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. bangii      CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. bicornis    CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:CGA:T
M. caesia      CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. caloptera   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. campylog    CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. cardiant    CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. carmenen    CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. caudiovo    CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. cerastes    CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. chaetost    CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. chaparen    CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. chimboen    CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
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              ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                 545        555        5 5        575        585        595
M. citrinel   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. civilis    CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. coccinea   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. collina    CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. collina.   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. coriacea   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. corniHam   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. corniHan   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. cupulari   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. cycloteg   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. davisii    CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. decumana   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. deformis   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. delhierr   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. echo       CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. erinacea   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GCCGGCCAGA GGAG:AGA:T
M. estradae   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. floribun   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. fulvesce   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. garciae    CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. glandulo   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. goliath    CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. gutierre   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. guttulat   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GATG:AGA:T
M. herradur   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCTGCCAGA GAAG:AGA:T
M. heteropt   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCCGCCTGA GAAG:AGA:T
M. hierogly   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. hirtzii    CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. hoeijeri   CAGCAAGGGG TGGATGAAAA ATGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. infracta   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. kyphonan   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GCCGGCCAGA GAAG:AGA:T
M. lamproty   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. lansberg   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. lata       CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGACT
M. limax      CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. macruraH   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. macruraH   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. melanoxa   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. meleagri   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. mentosa.   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. mezae      CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. molossus   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. mystica    CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. naranjap   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GGAG:AGA:T
M. nidifica   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. notosibr   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. ophioglo   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. oreas      CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GGAGAAGA:T
M. oreas      CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA G:AGAAGA:T
M. ova avis   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. pachyura   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. paivaean   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. panguien   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. parvula    CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. patricia   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. patula     CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. perister   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAT:AGA:T
M. persicin   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. pescadoe   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. picea      CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. picturat   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. pinocchi   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GATG:CGA:T
M. pleuroth   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:CGA:T
M. princeps   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. pyxis      CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:TGA:T
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              ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                545        555        5 5        575        585        595
M. racemosa   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. reichenb   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. rubeola.   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. rubigino   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. saltatri   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAT:AGA:T
M. sanchezi   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. scabrili   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. schlimii   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. striatel   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. teaguei.   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. titan      CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. uniflora   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. veitchia   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. venezuel   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. vieriana   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GGAG:AGA:T
M. walteri    CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. wendland   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. ximenae.   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GAAG:AGA:T
M. zahlbruc   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGTATCGT GGCGGCCAGA GGAG:AGA:T
P. amethyst   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGCGTCGT GCCTGCCAGA GAAG:AGA:T
P. uxorium.   CAGCAAGGGG TGGATGAAAA TTGTGCCTGT GATGCATCGT GTCGGCCAGA GAAG:AGA:T
T. gemmata.   CAGCAAGAGG TGGATGAAAA ATGTGCCTGT GCTGTATCGT GTCGACCAGA GTAG:AGA:T
T. scobina.   CAGCAAGAGG TGGATGAAAA ATGTGCCTGT GCTGTATCGT GCCGACCAGA GTAG:AGA:T

              ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                605        615        625        635        645        655
D. astuta     T:::ATACCA TGCG:::GAT GATCCCAGCC CAAGCGTTGA TCCACGGATG GCGGCTTGG:
D. chimaera   T:::ATACCA TGCG:::GAT GATCCCAGCC CAAGCGTTGA TCCACGGATG GCGGCTTGG:
D. cochliops  T:::ATACCA TGCG:::GAT GATCCCAGCC CAAGCGTCGA TCCACGGATG CCGGCTTGG:
D. houtteana  T:::ATACCA TGCG:::GAT GATCCCAGCC CAAGCGTTGA TCCACGGATG GCGGCTTGG:
D. sodiroi.   T:::ATACCA TGCG:::GAT GATCCCAGCC CAAGCGTTGA TCCACGGATG GCGGCTTGG:
D. xenos      T:::ATACCA TGCG:::GAT GATCCCAGCC CAAGCGTCGA TCCACGGATG GCGGCTTGG:
L. pelecani   T:::ATACCC TGCG:::GAT GATCCCGGCC CGAGCGTCGG TCCACGGACG GCGGCTTGG:
M. abbrevia   T:::ATACCA TGCA:::GAT GATCCCAGCC CGAGCGTCGA TCCACAGATG GCGGCTTGG:
M. alexandr   T:::ATACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCACGGATG ACGGCTTGG:
M. amaluzae   T:::CTACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCACTGATG GCGGCTTGG:
M. ampullac   T:::ATACCA TGCA:::GAT GATCCCAGCC CAAGCGTTGA TCCA:GGATG GCGGCTTGG:
M. antonii    T:::ATACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCA:GGATG GCGGCTTGG:
M. aphanes    T:::CTACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCACTGATG GCGGCTTGG:
M. aphanes.   T:::CTACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCACTGATG GCGGCTTGGG
M. bangii     T:::ATACCA CGCA:::GAT GATCCCGGCC CAAGCGTCGA TCGA:TGACG GCGGCTTGG:
M. bicornis   T:::ATACCA TGCA:::GAT GATCCCAGCC CGAGCGTCGA TCCA:GGATG GCGGCTTGG:
M. caesia     C:::GTACCA TGCA:::GAT GATCCCAGCC CGAGCGTCGA TCCACGGACG CCGGCTTGG:
M. caloptera  T:::ATACCA TGCA:::GAT GATCCCAGCC CGAGCGTCGA TCCACAGATG GCGGCTTGG:
M. campylog   C:::ATACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCGCGGACG GCGGCTTGG:
M. cardiant   CC::ATACCA TGCG:::GAT GATCCCGGCC CAAGCGTCGA TCCACGGTCG GCGGCTTGG:
M. carmenen   T:::CTACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCACTGATG GCGGCTTGG:
M. caudiovo   T:::ATACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCA:GGATG GCGGCTTGG:
M. cerastes   T:::ACACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCACGGATG GCGGCTTGG:
M. chaetost   T:::ATACCA TGCAA::GAT GATCCCAGCC CGAGCGTCGA TCCACAGATG GCGGCTTGG:
M. chaparen   T:::ATACCA TGCA:::GAT GATCCCAGCC CAAGCGTTGA TCCCAGGATG GCGGCTTGG:
M. chimboen   C:::GTACCA TGCG:::GAT GATCCCAGCC CAAGCGTCGA TCCACGGTTG GCGGCTTGG:
M. citrinel   T:ATATACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCA:GGATG GCGGCTTGG:
M. civilis    C:::GTACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCACGGACG GCGGCTTGG:
M. coccinea   T:::ATACCA TGCA:::GAT GATCCCAGCC CAAGCGTTGA TCCA:GGATG GCGGCTTGG:
M. collina    C:::ATACCA TGCG:::GAT GATCCCAGCC CAAGCGTCGA TCCACGGATG GCGGCTTGG:
M. collina.   C:::ATACCA TGCG:::GAT GATCCCAGCC CAAGCGTCGA TCCACGGATG GCGGCTTGG:
M. coriacea   C:::ATACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCGCGGACG GCGGCTTGG:
M. corniHam   T:::ACACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCACGGATG GCGGCTTGG:
M. corniHan   T:::ACACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCACGGATG GCGGCTTGG:
M. cupulari   G:::ATACCT AGCG:::GAT GATCCCAGGC CAAGCGCCGA TCCACGGATG GCGGCTTGG:
M. cycloteg   T:::ATACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGT TCCA:GGATG GCGGCTTGG:
M. davisii    T:::ATACCA TGCA:::GAT GATCCCAGCC CAAGCGTTGA TCCA:GGATG GCGGCTTGG:
M. decumana   T:::ATACCA TGCA:::GAT GATCCCAGCC CAAGCGTTGA TCCA:GGATG GCGGCTTGG:
M. deformis   T:::ATACCA TGCA:::GAT GATCCCAGCC CAAGCGTTGA TCCA:GGATG GCGGCTTGG:
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                ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                   605        615        625        635        645        655
M. delhierr     T:::ACACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCACGGATG GCGGCTTGG:
M. echo         C:::GTACCA TGCG:CGGAT GATCCCAGCC CAAGCGTCGA TCCACGGTTG GCGGCTTGG:
M. erinacea     T:::ATACCA TGCG:::GAT GATCCCGAGC CAGGCGTCGA TCCACGGATG GCGGCTTGG:
M. estradae     T:::ATACCA TGCA:::GAT GATCCCAGCC CAAGCGTTGA TCCA:GGATG GCGGCTTGG:
M. floribun     C:::GTACCA TGCG:::GAT GATCCCAGCC CAAGCGTCGA TCCACGGATG GCGGCTTGG:
M. fulvesce     G:::ATACCA TGCG:::GAT GATCCCAGGC CAAGCGTCGA TCCACGGATG GCGGCTTGG:
M. garciae      C:::ATGCCA TGCG:::GAT GATCCCAGCC CAAGCGTCGA TCCACGGTTG GCGGCTTGG:
M. glandulo     T:::ATACCA TGCA:::GAT GATCCCAGCC CAAGCGTTGA TCCA:GGATG GCGGCTTGG:
M. goliath      T:::CTACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCACTGATG GCGGCTTGG:
M. gutierre     C:::ATGCCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCAC:GATG ACGGCTTGG:
M. guttulat     C:::ATACCG TGCG:::GAT GATCCCGGCC CAAGCGTCGA TCCACGGTTG GCGGCTTGG:
M. herradur     C:::ATACGA TGCG:::GAT GATCCCAGCC CAAGCGTCGA TCCACGGTCG GCGGCTTGG:
M. heteropt     T:::ATACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCAGGGATG ACGGCTTGG:
M. hierogly     T:::ATACCA TGCA:::GAT GATCCCAGCC CAAGCGTTGA TCCA:GGATG GCGGCTTNNN
M. hirtzii      T:::ATACCA TGCA:::GAT GATCCCAGCC CAAGCGTTNN NNNNNNNNNN NNNNNNNNN:
M. hoeijeri     T:::ATACCA TGCA:::GAT GATCCCAGCC CGAGCGTCGA TCCA:GGATG GCGGCTTGG:
M. infracta     C:::GTACCA TGCG:CGGAT GATCCCAGCC CAAGCGTCGA TCCACGGTTG GCGGCTTGG:
M. kyphonan     C:::ATGCCA TGCA:::GAT GATCCCAGCG CAAGCGTCGA TCCACGGATG ACGGCTTGG:
M. lamproty     T:::ATACCA TGCA:::GAT GATCCCAGCC CAAGCGTTGA TCCA:GGATG GCGGCTTGG:
M. lansberg     C:::ATGCCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCACGGATG ACGGCTTGG:
M. lata         G:::ATACCA TGCG:::GAT GATCCCAGCC CGAGCGTCGA TCCACGGATG GCGGCTTGG:
M. limax        T:::ATACCA TGCA:::GAT GATCCCAGCC CAAGCGTTGA TCCA:GGATG GCGGCTTGG:
M. macruraH     T:::ATACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCA:GGATG GCGGCTTGG:
M. macruraH     T:::ATACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCA:GGATG GCGGCTTGG:
M. melanoxa     C:::ATACCG TGCG:::GAT GATCCCAGCC CAAGCGTCGA TCCACGGTTG GCGGCTTGG:
M. meleagri     T:::ATACC: TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCACGGATG ACGGCTTGG:
M. mentosa.     C:::ACACCG TGCG:::GAT GATCCCAGCC CAAGCGTCGA TCCACGGTTG GCGGCTTGG:
M. mezae        C:::ATACCA TGCG:::GAT GATCCCGGCC CAAGCGTCGA TCCACGGTTG GCGGCTTGG:
M. molossus     T:::ATACCA TGCG:::GAT GATCCCAGCC CGAGCGTCGA TCCACAGATG GCGGCTTGG:
M. mystica      T:::ATACCA TGCA:::GAT GATCCCAGCC CAAGCGTTGA TCCA:GGATG GCGGCTTGG:
M. naranjap     G:::ATACCG TGCG:::GAT GATCCCAGCC CGAGCGTCGA TCCACGGACG GCGGCTTGG:
M. nidifica     T:::ATACCA TACA:::GAT GATCCCAGCC CGAGCGTCGA TCCATAGATG GCGGCTTGG:
M. notosibr     T:::ATACCA TGCA:::GAT GATCCCAGCC CAAGCGTTGA TCCA:GGATG GCGGCTTGG:
M. ophioglo     T:::ATACCA TGGA:::GAT GATCCCAGCC CGAGCGTCGA TCAATAGATG GCGGCTTGG:
M. oreas        C:::ATACCA TGCG:::GAT GATCCCAGCC CAAGCGTCGA TCCACGGTTG GCGGCTTGG:
M. oreas        C:::ATACCA TGCG:::GAT GATCCCAGCC CAAGCGTCGA TCCANNNNNN NNNNNNNNNN
M. ova avis     T:::ATACCA TGCA:::GAT GATCCCAGCC CGAGCGTCGA TCCACAGATG GCGGCTTGG:
M. pachyura     T:::ATACCA TGCA:::GAT GATCCCAGCC CGAGCGTCGA TCCACAGATG GCGGCTTGG:
M. paivaean     T:::ATACCA TGCA:::GAT GATCCCAGCC CAAGCGTTGA TCCA:GGATG GCGGCTTGG:
M. panguien     T:::CTACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCACTGATG GCGGCTTGG:
M. parvula      T:::ATACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCACGGATG ACGGCTTGG:
M. patricia     T:::ATACCA TGCA:::GAT GATCCCAGCC CAAGCGTTGA TCCA:GGATG GCGGCTTGG:
M. patula       T:::CTACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCACTGATG GCGGCTTGG:
M. perister     C:::GTACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCACGGACG GCGGCTTGG:
M. persicin     T:ATATACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCCAGGATG GCGGCTTGG:
M. pescadoe     G:::ATACCA CGCG:::GAT GATCCCAGGC CAAGCGTCGA TCCACGGATG GCGGCTTGG:
M. picea        C:::GTACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCACGGACG GCGGCTTGG:
M. picturat     T:::ATACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCACGGATG GCGGCTTGG:
M. pinocchi     C:::AAACCA TGCG:::GAT GATCCCGGCC CAAGCGTCGA TCCACGGTTG GCGGCTTGG:
M. pleuroth     T:::ATACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCACGGATG GCGGCTTGG:
M. princeps     T:::CTACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCACTGATG GCGGCTTGG:
M. pyxis        C:::GTACCA TGCG:::GAT GATCCCGGCC CAAGCGTCGA TCCACGGTTG GCGGCTTGG:
M. racemosa     T:::ATACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCA:GGATG GCGGCTTGG:
M. reichenb     G:::ATACCA TGCG:::GAT GATCCCAGGC CAAGCGTCGA TCCACGGATG GCGGCTTGG:
M. rubeola.     T:::ATACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCA:GGATG GCGGCTTGG:
M. rubigino     T:::ATACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCA:GGATG NNNNNNNNNN
M. saltatri     T:::ATACCA TGCA:::GAT GATCCCAGCC CAAGCGTTGA TCCA:GGATG GCGGCTTGG:
M. sanchezi     T:::CTACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCACTGATG GCGGCTTGG:
M. scabrili     C:::GCACCA TGCG:::GAT GATCCCAGCC CAAGCGTCGA TCCACGGATG GCGGCTTGG:
M. schlimii     C:::GTACCA TGCG:::GAT GATCCCAGCC CAAGCGTCGA TCCACGGTTG GCGGCTTGG:
M. striatel     C:::GTACCA CGCG:::GAT GATCCCAGCC CGAGCGTCGA TCCACGGATG GCGGCTTGG:
M. teaguei.     T:::ACACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCACGGATG GCGGCTTGG:
M. titan        T:::CTACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCACTGATG GCGGCTTGGG
M. uniflora     T:::ATACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCA:GGATG GCGGCTTGG:
M. veitchia     T:::ATACCA TGCA:::GAT GATCCCAGCC CAAGCGTTGA TCCA:GGATG GCGGCTTGG:
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              ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                 605        615        625        635        645        655
M. venezuel   C:::ATGCCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCACGGATG ACGGCTTGG:
M. vieriana   C:::ATACCG TGCG:::GAA GATCCGAGCC CAAGCGTCGA TCCACGGATG GCGGCTTGG:
M. walteri    G:::ATACCA TGCG:::GAT GATCCCAGGC CAAGCGTCGA TCCACGGATG GCGGCTTGG:
M. wendland   C:::ATGCCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCAC:GATG ACGGCTTGG:
M. ximenae.   T:::ATACCA TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCACGGATG ACGGCTTGG:
M. zahlbruc   C:::ATACCG TGCG:::GAT GATCCCAGCC CGAGCGTCGA TCCACGGATG GCGGCTTGG:
P. amethyst   T:::ATACCA TGCG:::GAT GATCCCAGCC CAAGCGTCGA TCCACGGATG GCGGCTTGG:
P. uxorium.   T:::ATACCC TGCA:::GAT GATCCCAGCC CAAGCGTCGA TCCACGGATG GCGGCTTGG:
T. gemmata.   T:::ATACCA TGCG:::GAT GATCCCAACC CAAGCGTCAA TCTACGGATG ACAGCTTGG:
T. scobina.   T:::ATACCA TCGG::::AT GATCCCAACC CAAGCGTCAA TCTACGGATG AAAGCTTGT:


              ....|
D. astuta     TAT
D. chimaera   AAT
D. cochliops  AAT
D. houtteana  AAT
D. sodiroi.   AAT
D. xenos      AAN
L. pelecani   AAT
M. abbrevia   AAT
M. alexandr   AAT
M. amaluzae   AAT
M. ampullac   AAT
M. antonii    AAT
M. aphanes    AAT
M. aphanes.   AAT
M. bangii     AAT
M. bicornis   AAT
M. caesia     AAT
M. caloptera  AAT
M. campylog   AAT
M. cardiant   AAT
M. carmenen   AAT
M. caudiovo   AAT
M. cerastes   AAT
M. chaetost   AAT
M. chaparen   AAT
M. chimboen   AAT
M. citrinel   AAT
M. civilis    AAT
M. coccinea   AAT
M. collina    AAT
M. collina.   AAT
M. coriacea   AAT
M. corniHam   AAT
M. corniHan   AAT
M. cupulari   AAT
M. cycloteg   AAT
M. davisii    AAT
M. decumana   AAT
M. deformis   AAT
M. delhierr   AAT
M. echo       AAT
M. erinacea   AAT
M. estradae   AAT
M. floribun   AAT
M. fulvesce   AAT
M. garciae    AAT
M. glandulo   AAT
M. goliath    AAT
M. gutierre   AAT
M. guttulat   AAT
M. herradur   AAT
M. heteropt   AAT
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M. hierogly   NNN
M. hirtzii    NNN
M. hoeijeri   AAT
M. infracta   AAT
M. kyphonan   AAT
M. lamproty   AAT
M. lansberg   AAT
M. lata       AAT
M. limax      AAT
M. macruraH   AAT
M. macruraH   AAT
M. melanoxa   AAT
M. meleagri   AAT
M. mentosa.   AAT
M. mezae      AAT
M. molossus   AAT
M. mystica    AAT
M. naranjap   AAT
M. nidifica   AAT
M. notosibr   AAT
M. ophioglo   AAT
M. oreas      AAT
M. oreas      NNN
M. ova avis   AAT
M. pachyura   AAT
M. paivaean   AAT
M. panguien   AAT
M. parvula    AAT
M. patricia   AAT
M. patula     AAT
M. perister   AAT
M. persicin   AAT
M. pescadoe   AAT
M. picea      AAT
M. picturat   AAT
M. pinocchi   AAT
M. pleuroth   AAT
M. princeps   AAT
M. pyxis      AAT
M. racemosa   AAT
M. reichenb   AAT
M. rubeola.   AAT
M. rubigino   NNN
M. saltatri   AAT
M. sanchezi   AAT
M. scabrili   AAT
M. schlimii   AAT
M. striatel   AAT
M. teaguei.   AAT
M. titan      AAT
M. uniflora   AAT
M. veitchia   AAT
M. venezuel   AAT
M. vieriana   AAT
M. walteri    AAT
M. wendland   AAT
M. ximenae.   AAT
M. zahlbruc   AAT
P. amethyst   AAT
P. uxorium.   AAT
T. gemmata.   AAT
T. scobina.   AAT
```

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Eidesstattliche Versicherung

Hiermit versichere ich an Eides statt, daß ich die vorliegende Dissertation selbständig verfaßt und nicht schon als Diplomarbeit oder ähnliche Prüfungsarbeit verwendet habe.

Die verwendeten Hilfsmittel sowie die zur Hilfeleistung herangezogenen Institutionen sind vollständig angegeben.

Hamburg, im Oktober 2007

Analisa Daniela Abele, Dipl. Biol.