LANKESTERIANA 7: 45-47. 2003.

PHYLOGENY OF THE *HETEROTAXIS* LINDLEY COMPLEX (MAXILLARIINAE): EVOLUTION OF THE VEGETATIVE ARCHITECTURE AND POLLINATION SYNDROMES

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Heterotaxis Lindl. comprises about 11 primarily epiphytic species ranging from the southeastern U.S.A. (Florida) and the Greater Antilles to Brazil, with most of the species occurring in Central and South America. This complex is characterized by a sympodial growth habit, with short rhizomes, laterally compressed oblong pseudobulbs (unifoliate), and subtended by various leaf-bearing sheaths. Exceptions are *Maxillaria equitans* (Schltr.) Garay and *Maxillaria valenzuelana* (Sw.) Nash, which exhibit a pseudomonopodial growth without pseudobulbs. The one-flowered inflorescence emerges from the leaf axils; the flowers are distinctly fleshy, a character shared with the *Ornithidium* complex, and colors varying from yellow to orange, with some species showing purple lips with calli varying in size and texture. The column exhibit an arcuate shape with the lip articulated to its base.

Lindley described *Heterotaxis* in 1826 based on a species known today as *Maxillaria crassifolia* (Lindl.) Rchb. f., and although in 1830 the same author described a new genus (*Dicrypta* Lindl.) based on the same species, this complex of species must be referred by priority under the first generic name, *Heterotaxis*.

The name *Heterotaxis* has been used to design a complex of species within *Maxillaria* Ruiz & Pav., and most authors considered it as a synonymous of this genus in their floristic treatments; however, some of them have pointed out that this complex represents a group of species at generic level.

Several studies based on morphology, anatomy, and DNA sequences have showed that *Maxillaria* represents a para or polyphyletic genus, and that some groups of species, commonly considered within *Maxillaria*, should be reevaluated and recognized at the generic level.

Heterotaxis represents one of these groups, and previous studies using DNA sequences (ITS 1 & 2) situated this complex of species in a basal position in the phylogeny of *Maxillaria s.l.*

Our major goals in the present work were: 1) to determinate if *Heterotaxis* represents a monophyletic group, 2) to establish the phylogenetic relationships among species considered within this complex, and 3) to study the evolution of the vegetative architecture and pollination syndromes.

We considered an in-group of 18 species, representing 12 described species in *Heterotaxis* and two new species plus four representative species of *Ornithidium* Salisb. complex. Outgroups species (*Lycaste cruenta*, *Xylobium zarumense*, *Cryptocentrum latifolium*, and *Maxillaria bicallosa*) were selected according to a previous approach to the phylogeny of *Maxillaria* and related genera based on DNA sequences of ITS 1 & 2.

A total of 58 morphological characters (morphology, and gross leaf anatomy) and DNA sequences of ITS 1 & 2 were used in the reconstruction of phylogenetic relationships.

We conducted separate analyses of morphology and DNA sequences, and a combined analysis using the Winclada and Nona programs.

In separate analyses of both data, morphology and DNA sequences, *Heterotaxis* represents a monophyletic group provided three species, *Maxillaria*

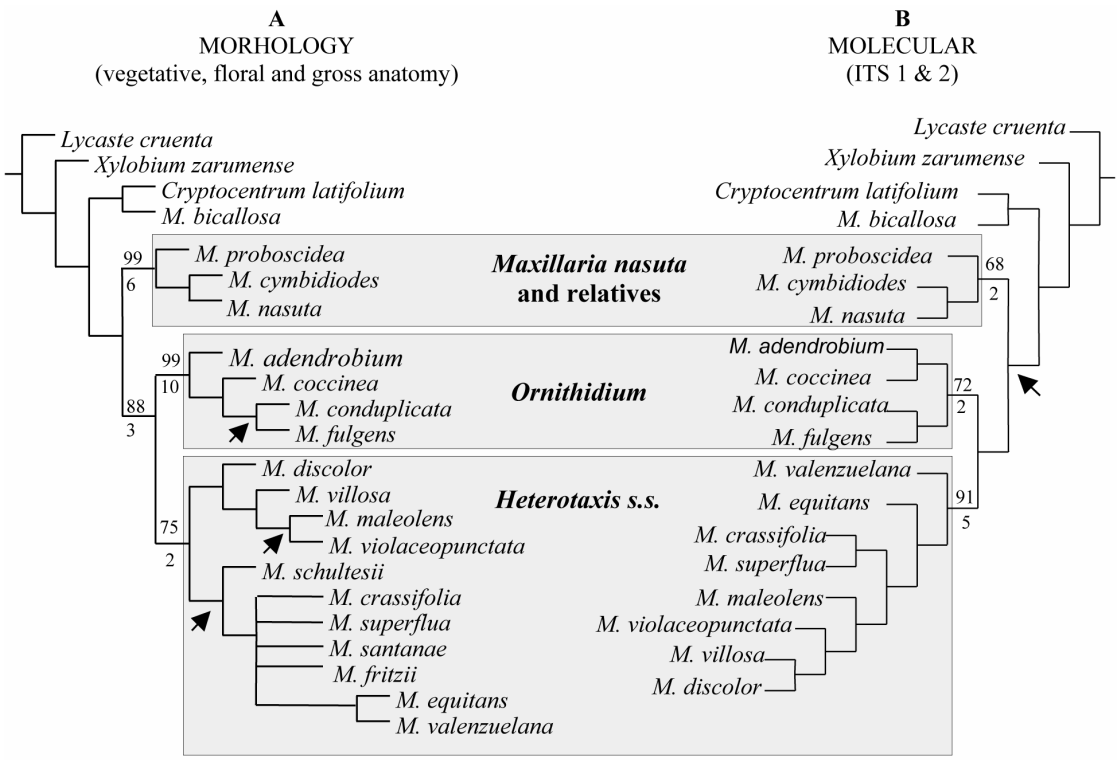

Figure 1. Consensus trees of the phylogenetic relationships of *Heterotaxis* complex, A - based on morphological characters (morphology and gross foliar anatomy), and B - DNA sequences of internal transcribed spacers (ITS 1 & 2). Numbers above branches represent jacknife values, and numbers below branches Bremer support values. Nodes with arrows represent collapsed clades in the jacknife tree.

nasuta, M. cymbidiodes, and *M. proboscidea* are excluded from this complex (Fig. 1).

A total of 20 most parsimonious tree (L = 106, CI = 0.85, RI = 0.92) were found in the analysis based on morphology; this evidence supports the position of *Heterotaxis s. s.* (excluding *M. nasuta, M. cymbidiodes*, and *M. proboscidea*) as a sister clade of *Ornithidium*.

Heterotaxis s.s. was supported by three synapomorphies, the pedicel of the flower is wider than the rest of the internodes of the peduncle, the column is articulated to the pedicel in an angle of 45°, and finally, the presence of a sub-apical mucron in sepals and petals. Two major clades were found within *Heterotaxis s.s.*; the *Violaceopunctata* clade contains only species with a sympodial growth habit and those species with larger size; this clade is supported by two synapomorphies, the labellum of these species is markedly 3-lobed in shape, and anatomically, these species share the presence of a pattern of 4-7 vascular bundles in the mesophyll repeated modularly, quite different from the rest of *Heterotaxis* species which present a modular pattern of three vascular bundles. The *Violaceopunctata* clade contains those species which are, due to similar size and growth habit, commonly confused with the species of *M. nasuta* and relatives.

The *Crassifolia* clade contains species with sympodial and the two species with a pseudomonopodial growth habit. This clade is supported by two sinapomorphies, blades of leaves are partially fused at the base (close to the articulation of the sheath), and a Y shape of sheaths in a transversal cross section. The position of *Maxillaria schultesii* is uncertain, and although in the consensus tree it is situated in *Crassifolia* clade, its position is not resolved in the jacknife tree (Fig. 1).

Maxillaria nasuta clade and relatives are supported by the next morphological synapomorphies: the shin-

ing surface (as varnished) and lacking of ridges of pseudobulb in dried material, this characteristic is quite different form the pseudobulb surface of *Heterotaxis s.s.*, which exhibit ridged and opaque surface. The size of the peduncle (of five internodes) of the inflorescence is longer (2 times) than size of the pseudobulb, and finally, the column shows a papillose surface in the dorsal portion.

A single most parsimonious tree was found in the analysis based on DNA sequences (L = 279, CI = 0.75, RI = 0.76), this data support the presence of three clades, *M. nasuta* and relatives, *Heterotaxis s.s*., and *Ornithidium*. However, the relationships among these clades are not resolved (Fig. 1). Sequences of ITS 1 & 2 also support the presence of the *Violaceopuntata* clade, and the pseudomonopodial plants are situated in a basal position within *Heterotaxis* clade, closely related to the species of the *Crassifolia* clade.

The total evidence analysis supports the position of *Heterotaxis s.s.* as a sister clade of *Ornithidium*, and the presence of the two previous clades, *Crassifolia* and *Violaceopunctata*, found with the morphological characters. According to this result, the sympodial growth habit observed in most of the species in *Heterotaxis s.s.*, and in the *M. nasuta* clade is plesiomorphic. The pseudomonopodial growth habit of *M. valenzuelana* and *M. equitans* is derived within *Heterotaxis*. All studied species of *Ornithidium* show a growth habit as the observed in *Heterotaxis*, and the most plesiomorphic growth habit found in this analysis is that observed in *M. coccinea*, which a production of repeated sympodiums with elongated rhizomes.

The floral characteristics of the *Heterotaxis* species suggest a pollination syndrome by wasps which collect pseudopollen or wax. This pollination syndrome has been reported in other groups of *Maxillaria*, and according to the present results, this pollination syndrome is plesiomorphic and has evolved several times within *Maxillaria*. The floral characteristics of *Ornithidium*, such as fused lip forming a cup, long peduncles of flower, nectar production, and bright red to yellow colors suggest a pollination syndrome by hummingbirds. According to the total evidence this pollination syndrome is derived in the *Heterotaxis – Ornithidium* clade, and this floral modification is associated with the great variation in vegetative architecture observed in this complex of species.

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