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A reappraisal of *Maxillaria* (Orchidaceae)

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Abstract

It is argued that a broad and expanded circumscription of *Maxillaria* is to be preferred over a narrower one that necessitates the recognition of many segregate genera. These more narrowly circumscribed genera are often difficult to diagnose, increasing the risk of misidentifications, especially when material is only identified to genus level. The genera of the *Maxillaria* alliance as recognised in *Genera orchidacearum* are treated as sections of an expanded genus *Maxillaria*. *Cryptocentrum*, *Cyrtidiorchis*, *Mormolyca*, *Pityphyllum*, and *Trigonidium* are here included in *Maxillaria*. Criteria for generic delimitation are discussed, the necessary combinations are made, and a key to the sections as well as a provisional checklist of the 634 species of *Maxillaria* arranged according to section are provided. *Maxillaria prolifera* is shown to be the correct name for *M. pendens*. *Maxillaria humilis* is a new combination for *M. gracilis*.

Key words: Generic circumscription, lumping, Maxillariinae, Neotropical flora, splitting

Introduction

Until recently, *Maxillaria* Ruiz & Pav. (Ruiz & Pavón 1794) was perhaps the prime example of an unduly neglected orchid genus. With some 570 species in its traditional circumscription (Christenson 2013), it is in the top ten largest orchid genera (Cribb & Govaerts 2005). In suitable habitats *Maxillaria* is a common component of the Neotropical orchid flora. The species occur mainly as epiphytes, from sea level up to well over 3,000 m. Few orchid genera display such diversity in vegetative architecture: plants can be caespitose or strongly rhizomatous, monopodial or sympodial, or even sympodial when young and monopodial when mature; pseudobulbs can be present or absent; stems can be much abbreviated or tall and cane-like; leaves can be dorsoventrally flattened, bilaterally flattened or terete, thick or thin-textured etc. The single-flowered inflorescences and non-plicate leaves are among the few constant, taxonomically relevant character states of *Maxillaria* s.l., their combination distinguishing these species from the other genera of Maxillariinae.

Many species of *Maxillaria* were described in genera that were later merged with it or split off, such as *Camaridium* Lindl. and *Ornithidium* Salisb. ex R.Br. in W.T. Aiton. Over the years, a number of infrageneric groups were haphazardly proposed in *Maxillaria* (summarised and added to by Christenson 2002). There have been a few valuable flora treatments, e.g. for Guatemala (Ames & Correll 1953), Panama (Allen 1949), Peru (Schweinfurth 1960), and Costa Rica (Atwood & Retana 1999), but it is accurate to say that by the early twenty-first century the phylogeny and classification of *Maxillaria* were no more clear than a hundred years before, as exemplified by the treatment of Maxillariinae by Senghas (1993–1994). With the hindsight of molecular evidence, it is apparent that for example Senghas's concepts of *Ornithidium* and *Marsupiarina* Hoehne are grossly polyphyletic, as is that of *Maxillaria* itself, including most of the groups he distinguished within *Maxillaria*.

The molecular evidence just mentioned is due in particular to the phylogenetic studies by Whitten *et al.* (2007), who analyzed four DNA markers in a combined analysis of c. 354 species of *Maxillaria* and allied genera. A slightly earlier study based on a far smaller sample of 27 species by Dathe & Dietrich (2006), using ITS, produced results that were similar in general conclusions; a study by Sitko *et al.* (2006) based on a sample of 34 species, also using ITS, suffered from sampling that was biased towards a limited number of clades. Systematic studies informed by molecular data of some individual genera, sections or species complexes in the *Maxillaria* alliance have also appeared since 2000 (Arévalo & Cameron 2013, Carnevali 2001, Carnevali *et al.* 2001, Whitten *et al.* 2006, Singer *et al.* 2007, Koehler *et al.* 2002, 2008 & 2012). Much of this work formed the foundation for the treatment of Maxillariinae by several authors in Pridgeon *et al.* (2009).

At the alpha-taxonomic level, the sadly unfinished "monograph" of *Maxillaria* by Christenson (2013) is, in spite of its fragmentary state and uneven quality, a valuable resource for the student of *Maxillaria*. A popular book by Sauvêtre (2009) serves as an attractive introduction to the genus. In the UK, a National Collection of *Maxillaria* is being maintained by Michael McIlmurray near London. Christenson as well as the authors of this paper have benefited considerably from this impressive, well-documented and well-maintained living collection.