

Floral convergence in Oncidiinae (Cymbidieae; Orchidaceae): an expanded concept of *Gomesa* and a new genus *Nohawilliamsia*

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- **Background** Floral morphology, particularly the angle of lip attachment to the column, has historically been the fundamental character used in establishing generic limits in subtribe Oncidiinae (Orchidaceae), but it has also been long recognized that reliance on this character alone has produced a highly artificial set of genera. In essence, lip/column relationships reflect syndromes associated with pollinator preferences; most genera of Oncidiinae as previously defined have consisted of a single floral type. Here, the degree to which this has influenced generic delimitation in Brazilian members of the largest genus of Oncidiinae, *Oncidium*, which previous molecular (DNA) studies have demonstrated to be polyphyletic, is evaluated.
- **Methods** Phylogenetic analyses of the following multiple DNA regions were used: the plastid *psbA-trnH* intergenic spacer, *matK* exon and two regions of *ycf1* exon and nuclear ribosomal DNA, comprised of the two internal transcribed spacers, ITS1 and ITS2, and the 5-8S gene. Results from all regions analysed separately indicated highly similar relationships, so a combined matrix was analysed.
- **Key Results** Nearly all species groups of Brazilian *Oncidium* are only distantly related to the type species of the genus, *O. altissimum*, from the Caribbean. There are two exceptions to this geographical rule: *O. baueri* is related to the type group and *O. orthostates*, an isolated species that lacks the defining tabula infrastigmata of *Oncidium*, is not exclusively related to any previously described genus in the subtribe. Several well-supported subclades can be observed in these results, but they do not correspond well to sections of *Oncidium* as previously circumscribed or to segregate genera as defined by several recent authors. In spite of their floral differences, these groups of *Oncidium*, formerly treated as *O.* sections *Barbata*, *Concoloria pro parte*, *Crispa*, *Ranifera*, *Rhinocerotes*, *Rostrata* (only *O. venustum*), *Synsepala*, *Verrucituberculata pro parte* and *Waluewa*, form a well-supported clade with *Gomesa* (including *Rodrigueziella* and *Rodrigueziopsis*) embedded in it. Two often recognized segregate genera, *Baptistonia* and *Ornithophora*, and the recently described *Carriella* are also embedded within the Brazilian clade. The level of variation within major subclades of the *Gomesa* clade is low and similar to that observed within other genera of Oncidiinae.
- **Conclusions** Convergence on a stereotypical syndrome of floral traits associated with pollination by oil-collecting bees has resulted in these characters not being reliable for producing monophyletic taxa, and the genus *Oncidium*, defined by these characters, is grossly polyphyletic. Vegetative and a few floral/inflorescence characters link these taxa with a mainly Brazilian distribution, and they were all transferred to *Gomesa* on this basis rather than separated from *Gomesa* based on their floral differences, which we hypothesize to be simple shifts in pollination strategies. Other authors have described a large number of new genera for these former members of *Oncidium*, but most of these are not supported by the results presented here (i.e. they are not monophyletic). A new genus, *Nohawilliamsia*, is described for *O. orthostates* because it does not fit in any currently recognized genus and is only distantly related to any other member of Oncidiinae.

Key words: *Baptistonia*, Brazilian orchids, *Carriella*, deceit pollination, *Gomesa*, ITS, *matK*, oil-collecting bees, *Oncidium*, Oncidiinae, Orchidaceae.

INTRODUCTION

Oncidium Sw. (Oncidiinae; Cymbidieae; Orchidaceae) is one of the most conspicuous genera of neotropical orchids. Their mostly bright-yellow flowers often marked with brown are

commonly called *lluvia de oro* (golden rain) in Spanish or ‘dancing ladies’ in English. They are mostly epiphytic and frequently seen in cultivation. In its broadest circumscription, *Oncidium* has over 400 species. Delimitation of *Oncidium* and related genera has been the subject of much controversy and inconsistency (Dressler and Williams, 1975; Garay and

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Stacy, 1974). In simplest terms, *Oncidium* has always been a genus of convenience, but if a set of circumscribing characters were to be proposed these would include: a spurless (non-rewarding) flower with the lip (labellum) attached at a 90° or greater angle to the column and a complex tuberculate callus and tabula infrastigmatica (a fleshy structure on the base of the column; Fig. 1). Given the clear arbitrariness of the primary character, that of the angle of lip/column attachment and heterogeneity of vegetative traits and chromosome numbers in *Oncidium* when circumscribed using this character (Chase, 1986, 1987), no one was at all surprised that the early restriction endonuclease studies of plastid DNA showed that *Oncidium* was polyphyletic (Chase and Palmer, 1992). Subsequent studies of plastid and nuclear DNA sequences (Williams *et al.*, 2001a, b) have further detailed the extent of problems with delimitation of *Oncidium*, and the process of generic recircumscription to achieve monophyly has been started, resulting in the description of *Cyrtochiloides*

N.H.Williams & M.W.Chase and *Zelenkoa* M.W.Chase & N.H.Williams, resurrection of *Cyrtochilum* Kunth, and expansion of *Caucaea* Schltr., *Miltonia* Lindl., *Otoglossum* Garay & Dunsterville and *Trichocentrum* Poeppig & Endl. We have also amalgamated into *Oncidium* the other genera of *Oncidiinae* that are embedded in that clade; these include *Cochlioda*, *Odontoglossum* and *Symphyglossum* (Chase *et al.*, 2008). This is the fourth installment of a series of papers recircumscribing genera in *Oncidiinae*. Here the focus is on the Brazilian species that have previously been included in *Oncidium*.

In their synopsis of *Oncidium*, Garay and Stacy (1974) recognized several sections of *O.* subgenus *Oncidium* that were either endemic to Brazil (often most diverse in the *Mata Atlantica* vegetation) or had their greatest species diversity there. These include nearly all sections of the genus with a synsepal (fused lateral sepals): *O.* sections *Barbata* Lindl., *Concoloria* Kraenzl. *pro parte*, *Crispa* Rchb.f., *Rhinocerotes* Garay & Stacy, *Synsepsala* Pfitzer and *Waluwewa* (Regel) Schltr. In addition, some species of *O.* section *Paucituberculata* Lindl., which some authors have recognized as *O.* section *Ranifera* Kraenzl., also have a synsepal. Garay and Stacy (1974) also included in *O.* section *Paucituberculata* species with thickened leaves and reduced pseudobulbs, such as *O. hians* Lindl., that are morphologically similar to the species of *O.* section *Pulvinata*, the Brazilian mule-ear species of *Oncidium* (named for their long, flat, thickened leaves and reduced pseudobulbs; these species are now placed in *Grandiphyllum* Docha Neto) that have entirely free lateral sepals. Species of *O.* section *Ranifera* (e.g. *O. raniferum* Lindl., *O. paranaense* Kraenzl. and *O. hookeri* Rolfe) have larger pseudobulbs (relative to their size) and thin leaves compared with *O. hians*.

Some species of *O.* section *Verrucituberculata* Lindl., such as *O. batemanianum* Parm ex Knowl. & Westc., have a synsepal and are principally distributed in Brazil, whereas others lack the synsepal and are found outside of Brazil (e.g. *O. auriferum* Rchb.f. from Colombia). The key character of *O.* section *Verrucituberculata* (*sensu* Garay and Stacy) is the presence of a few tubercles isolated on the lip away from the main callus, but these species are otherwise similar to species in other sections of the genus. *Oncidium* section *Concoloria* also contains some non-Brazilian species, such as *O. hyphaematicum* Rchb.f. and *O. brachyandrum* Lindl., that lack a synsepal but do have the section-defining lip without lateral lobes and an even number of parallel tubercles. Another 'odd-ball' Brazilian species, *O. venustum* Drapiez (synonym *O. trulliferum* Lindl.), is vegetatively similar to the members of *O.* section *Waluwewa*, but it lacks the floral traits typical of this group (a pilose column and synsepal). It was treated as a member of *O.* section *Rostrata* by Garay and Stacy (1974) because it has a beaked column, but it is out of place in this group vegetatively and geographically (it is the sole species of this section found in Brazil). Chiron (2008) recently transferred this species to *Baptistonia*.

In addition, there are a number of other principally Brazilian genera that have a synsepal; these are *Baptistonia* Barb.Rodr. (monospecific or recently with additional species transferred from *Oncidium*; Chiron and Castro Neto, 2004), *Binotia* Rolfe (monospecific), the newly described *Carriella*

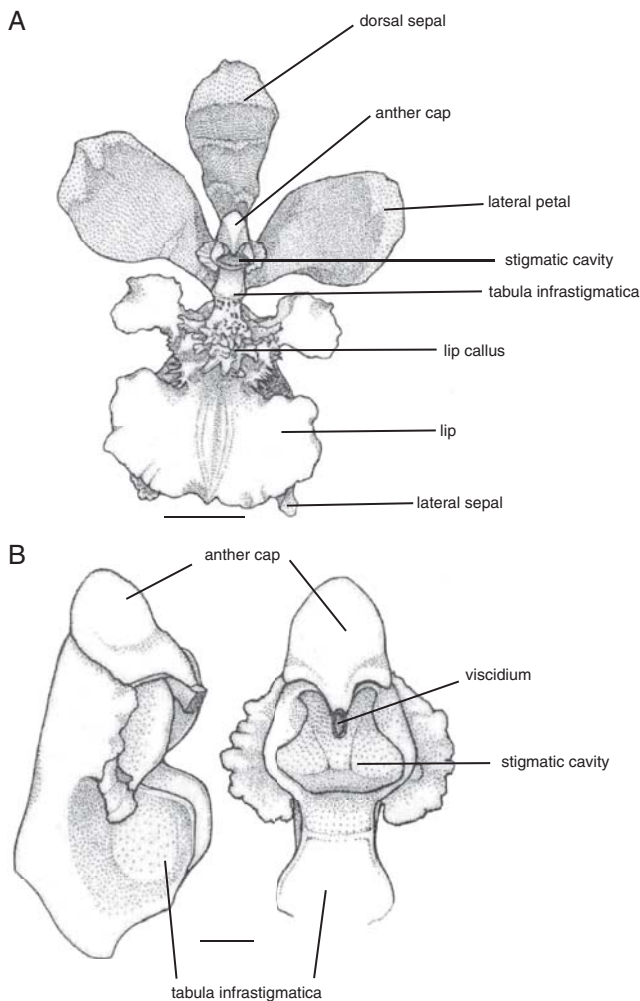


FIG. 1. Floral morphology of *Gomesa* (*Oncidium/Klaberiella*) *longipes* (*Oncidiinae*; Orchidaceae). This species has been treated as a member of *O.* section *Barbata* (Garay and Stacy, 1974) and has a synsepal that is fused to about one-third of its length. Scale bars: 0.5 cm (upper), 0.1 cm (lower). (Drawing: Rodrigo B. Singer).

V.P. Castro & K.G. Lacerda (monospecific; Castro and Lacerda, 2005, 2006), *Gomesa* Lindl., *Ornithophora* Barb. Rodr. (monospecific), *Rodrigueziella* Kuntze (synonym *Theodora* Barb. Rodr. non Cass.; two species) and *Rodrigueziopsis* Schltr (two species). Both *Coppensia* Dumort. and *Waluwewa* Regel were based on species with a synsepal, and these species were included by Garay and Stacy (1974) in *O.* sections *Synsepalata* and *Waluwewa*, respectively. A synsepal is relatively rare in Oncidiinae outside Brazil, but this trait does appear in *Caucaea* Rchb.f. (Andes), *Symphloglossum* Schltr. (Andes), *Systeloglossum* Schltr. (Andes to Central America) and *Tolumnia* Raf. (Caribbean), which were found in previously published studies not to be related to the Brazilian groups with this trait (Williams *et al.*, 2001a, b). In addition to a synsepal, the Brazilian groups fold the perianth parts differently in the bud (the lip is often pushed through the tepals before they unfold), hold their buds on a flexed rather than straight pedicle and have a different inflorescence structure in which the bracts (one at each node) are not closely held to the developing raceme, such that their tips project outward and away from the apex of the raceme, whereas in groups of *Oncidium* related to the type species, tips of these bracts are tightly appressed to the emerging raceme. These traits also vary among species, and ones such as the protruding lip are much more pronounced in species with large lips, such as *O. varicosum* Lindl. and *O. insigne* (Rolfe) Christenson. Most Brazilian groups also have a glaucous cast to their leaves so that even in the vegetative state most species can be separated from those of *Oncidium* proper.

All these differences from the type group of *Oncidium*, which is diverse in Andean South America, Central America, the Caribbean and Mexico rather than Brazil, had been previously noted, but the floral morphology of all groups included in *Oncidium* is more or less stereotypical, mostly bright yellow with brown spotting/bars on sepals and petals with the typical lip/column arrangement. The Brazilian groups also have the most common chromosome number in *Oncidium* and Oncidiinae, $2n = 56$, but they were known not to produce hybrids when crossed to other sections of the genus (Sanford, 1964, 1967). However, interfertility is not useful in determining generic limits in Orchidaceae, as Garay and Stacy (1974) pointed out: ‘The fact that one *Oncidium* species will or will not cross with another *Oncidium* species is quite inconsequential as far as this whole alliance is concerned, for genetic compatibility among species is the rule rather than the exception in the entire orchid family. The mere placing of a pollinium from a given plant onto the stigma of another does not convey any information to the vector whether it be a human being or a member of the insect world.’

In earlier studies (Williams *et al.*, 2001a, b), two approaches were used to investigate generic relationships in Oncidiinae: (1) a combined data set of all DNA regions from the plastid and nuclear genomes; and (2) separate analyses of each region to determine if they produce congruent results. The first matrix was assembled to provide well-supported (by the bootstrap; Felsenstein, 1985) estimates of relationships because none of the individual matrices on their own provided enough variable sites to obtain clear patterns. This same procedure is used in this paper but to *matK* are added three other plastid regions, two portions of the highly variable

ycf1 gene (5' and 3', 1098 and 1569 bp, respectively) and the *psbA-trnH* spacer, to further increase the number of variable sites included in analyses.

MATERIALS AND METHODS

Total DNA was extracted from fresh or silica-gel dried samples of leaves or flowers (Chase and Hills, 1991) using a modified 2X CTAB protocol (Doyle and Doyle, 1987), except that some of the samples were purified by caesium chloride/ethidium bromide density-dependent centrifugation (1.5 g mL^{-1}). All samples were vouchered by herbarium specimens or pickled flowers (Appendix).

Production of DNA sequences for *matK* and ITS used protocols and primers described in Williams *et al.* (2001a) and Whitten *et al.* (2000). Primers and protocols for *ycf1* and *psbA-trnH* are described in Neubig *et al.* (2009) and Xu *et al.* (2000), respectively. Raw electropherograms were assembled and checked for agreement of both strands using Sequencher 4.8 (Genecodes, Inc.). Sequences were aligned manually in PAUP* version 4.0b10 (Swofford, 2001) following the guidelines for insertion of gaps described by Kelchner (2000). No computer algorithm is capable of estimating insertion/deletion events for the different categories of change in DNA sequences; only the human eye can accomplish this task, so no computerized algorithm was used to align the sequences. Data matrices are available from M.W.C. and N.H.W. upon request (m.chase@kew.org; orchid@flmnh.ufl.edu); all sequences have been deposited in GenBank (Appendix).

Parsimony analyses

The following heuristic tree search strategy in PAUP* was used for all analyses. In a first phase, 1000 replicates of random-taxon entry order were used with tree-bisection-reconnection (TBR) swapping and a tree limit of ten trees per step to eliminate having to swap on large numbers of trees. The shortest trees found in these 1000 replicates were then used as starting trees in another round of swapping with no tree limit, and all shortest trees found were swapped on to completion. To produce estimates of internal support, 500 replicates of the bootstrap were used with the following settings: simple addition, TBR swapping and a tree limit of ten trees per step. The bootstrap consensus tree and one of the individual trees with branch lengths proportional to the amount of change are illustrated.

Searches were performed on three matrices: (1) a combined plastid matrix for 60 taxa for which all data were present for all taxa (Fig. 2A; but *Cariella colorata* König & J.G. Weinm. bis is missing 5' *ycf1*); (2) ITS for 59 taxa (*Gomesa handroi* (Hoehne) Pabst was missing for ITS; Fig. 2B); and (3) a combined matrix of for all 60 taxa (*G. handroi* and *G. colorata* for which ITS and 5' *ycf1* were coded as missing data, respectively). For plastid regions, there are no reasons to expect incongruence for different parts of that non-recombining, uniparentally inherited genome so these were directly combined without performing separate analyses. For the various parts of the ITS/5.8S nrDNA region, a similar argument can be made, although it is possible for other portions of the large

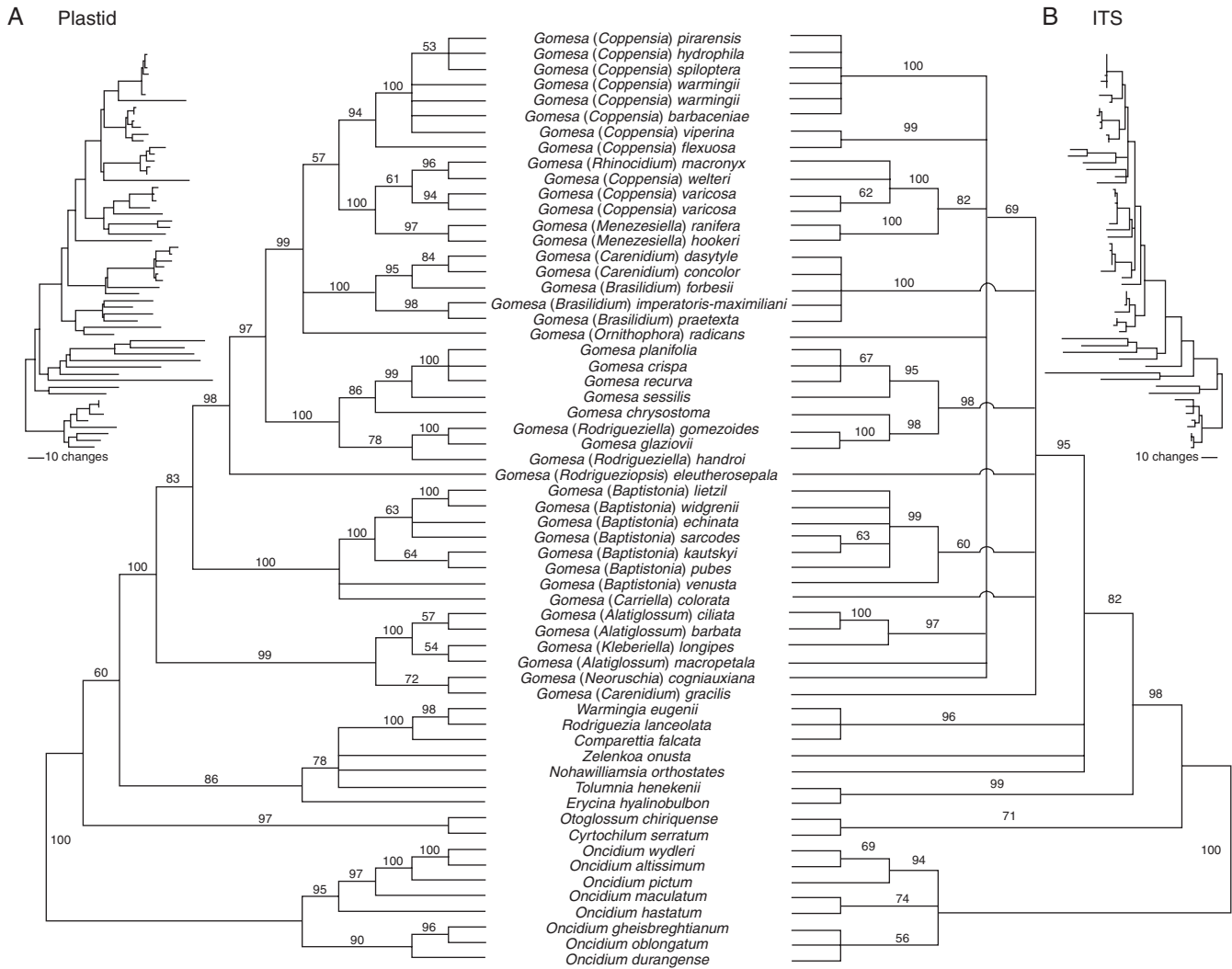


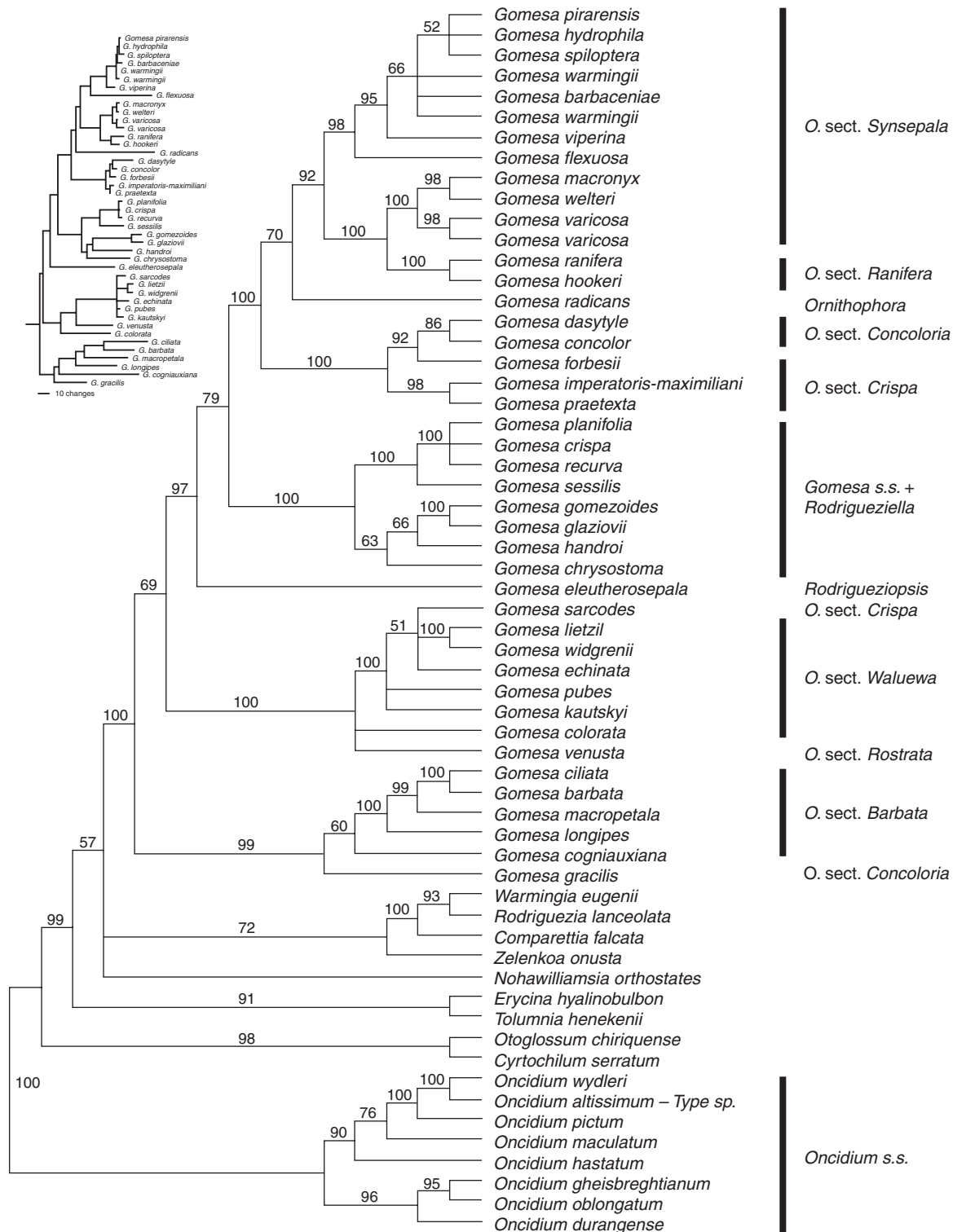
FIG. 2. Comparison of bootstrap consensus trees from separate plastid (A) and nr ITS (B) analyses; bootstrap percentages greater than 50 are indicated above branches. Single trees with proportional branch lengths (DELTRAN optimization) are illustrated in the uppermost corners to demonstrate low levels of divergence within some clades. Alternative recent circumscriptions are indicated in brackets. The type species of *Oncidium* s.s. is *O. altissimum* (seventh species from the bottom).

ribosomal subunit to exhibit differential patterns of inheritance, e.g. in *Caulerpa* (Durand *et al.*, 2002) and *Drosophila* (Polanco *et al.*, 1998). Direct combination of the plastid and nuclear ribosomal regions and their degree of congruence in Oncidiinae have been covered in Williams *et al.* (2001a, b). No cases of strongly supported incongruence that could be attributed to genealogical discordance were detected here (Fig. 2), so direct combination is appropriate. The positions of *Oncidium* (*Carenidium*) *gracile* Lindl. are discordant in the plastid and ITS results, but there was no strong support for its position in either analysis.

RESULTS

Due to similarity of the separate ITS and plastid trees (Fig. 2), with the noted exception only relationships observed in the combined analysis (Fig. 3) will be described. The

ITS matrix had 869 characters, of which 212 (24%) were potentially parsimony-informative; the 17 ITS trees had 750 steps with a consistency index (CI) of 0.59 (including autapomorphies) and a retention index (RI) of 0.77. The combined plastid matrix had 5184 characters, of which 445 (9%) were potentially parsimony-informative; the seven plastid trees had 1677 steps with a CI of 0.68 and an RI of 0.79. Analysis of the combined matrix produced three trees of 2464 steps with a CI of 0.65 and an RI of 0.77. The species representing *Oncidium* sections *Barbata*, *Concoloria*, *Crispa*, *Ranifera*, *Rhinocerotus*, *Synsepala* and *Waluwewa* (sections are indicated to the right of the cladogram; Fig. 3) and most of the Brazilian species of *Verrucituberculata* form a clade [100% bootstrap percentage (BP)] in which *Baptistonia*, *Carriella*, *Gomesa*, *Ornithophora*, *Rodriguezella* and *Rodriguezopsis* are embedded (Fig. 3). The larger clade is well supported (100 BP) as distinct from the type section of *Oncidium* (the



Gomesa s.l.

FIG. 3. Bootstrap consensus tree from the combined analysis of plastid and nrITS DNA; bootstrap percentages greater than 50 are indicated above branches. A single tree with proportional branch lengths (DELTRAN optimization) is illustrated in the upper left-hand corner to demonstrate low levels of divergence within some clades. Previously recognized genera and the sectional classification of *sensu* Garay and Stacy (1974) are indicated by the bar on the right. The type species of *Oncidium* s.s. is *O. altissimum* (seventh species from the bottom).

type is the Caribbean species, *O. altissimum* Sw.; Figs 2 and 3), and species representing other major clades of Oncidiinae are well supported in intercalating positions.

In Fig. 2, the generic assignments of these taxa in the system of Docha Neto *et al.* (2006) and Chiron and Castro Neto (2004) are indicated in brackets. *Baptistonia* may be

monophyletic if *Carriella* is sister to the rest of the species (but it is unresolved in our analyses; Figs 2 and 3), but none of the other recently described genera with two or more species is monophyletic. The sections of *Oncidium sensu* Garay and Stacy (1974) are indicated on Fig. 3; none is monophyletic; if *Baptistonia echinata* Barb.Rodr., *O. venustum* Drapiez and *O. sarcodes* Lindl. (section *Crispa*) are included, *O.* section *Waluwewa* is monophyletic. There are few differences in the ITS and plastid sequences between species in this clade, e.g. the sequence for *B. echinata* is identical to that of *Oncidium lietzei* Regel and *Oncidium widgrenii* Lindl. Similarly low levels of variation are observed within several other species clusters: these are centred around *Coppensia barbaceniae* (Lindl.) Campacci, *Coppensia varicosa* (Lindl.) Campacci, *Rhinocidium macronyx* (Rchb.f.) Baptista and *Brasilidium crispum* (Lodd.) Carpacci [= *Anettea imperatoris-maximiliani* (Rchb.f.) Szlach. & Mytnik.].

DISCUSSION

Nearly all species of Oncidiinae are pollinated by insects that receive no reward for visiting these plants (pollinator relationships are reviewed by Chase in Pridgeon *et al.*, 2009). Exceptions are the members of the twig epiphyte clade, many of which have a spur or cavity into which nectar is secreted by a horn at the base of the lip or simply the lip base itself (e.g. *Comparettia* Poeppig & Endl., *Rodriguezia* Ruiz & Pavón and *Leochilus* Knowles & Westc.). Floral fragrances may be collected from some genera by male euglossine bees (e.g. *Notylia* Lindl.). Some taxa in the Brazilian group (e.g. species of *O.* sections *Ranifera*, *Rhinocerotus* and *Waluwewa*) appear to produce varying amounts of oil on the lip callus, which may be collected by *Centris* bees that mix it with pollen collected from other species and feed it to their larvae (no orchid pollen has ever been observed to be used in this manner; van der Pijl and Dodson, 1966). There is sufficient oil present on lips of some species to collect it with a capillary tube (Faria, 2004), and thus it is possible that this is offered as a reward for pollination. In many *Oncidium* species, we question whether there is sufficient oil present to function as anything other than an attractant, in which case this would be another instance of deceit pollination, but this situation requires further study. The structure of the oil present in these species has been worked out to be acylglycerols in *Oncidium pubes* Lindl. and free fatty acids, non-volatile isoprenoids (triterpene squalene) and steroids (stigmasterol and clionasterol) in *O. flexuosum* Sims (Reis *et al.*, 2000; Faria, 2004). Studies in the field are needed to characterize this pollination syndrome more accurately.

Other research (Powell, 2008) has shown that the yellow-flowered species with typical *Oncidium* morphology (regardless of whether they are members of type group of *Oncidium* or the *Gomesa* clade) have floral UV-absorption patterns that mimic those of similarly coloured species of Malpighiaceae, which have sepal glands that produce oil collected by *Centris* bees. No other yellow flowers have been shown to have this same pattern of light absorbance (Powell, 2008). Thus, we may have a continuum of taxa that mimic malpigh flowers in colour but offer no reward to some that

appear to be producing enough oil to reward a pollinator. Some of the latter, such as *O. raniferum* Lindl., are not the typical 'malpigh yellow', but UV absorption patterns in these species have yet to be studied. Observations of oil bees visiting *Oncidium* species (reviewed in van der Cingel, 2001) have recorded that these bees use their mandibles to grab the tabula infrastigmatica and then attempt to scrap oil from the lip callus with their legs, paralleling the situation in malpigh species in which bees use their mandibles to hold onto the banner petal (the one at 90° to the rest of the petals) and scrape oil from sepal glands with their legs. This observation explains the presence of the tabula infrastigmatica, which otherwise appears to be an enigmatic structure of *Oncidium*.

In any case, the typical malpigh-mimicking species of Oncidiinae have floral traits associated with *Oncidium*, and thus it is clear that *Oncidium* as a genus has historically been defined by a floral syndrome related to its pollination biology. It should therefore come as no great surprise that such floral traits are subject to convergence, and the taxa they characterize are unlikely to be monophyletic. Given that these species are all members of a single subtribe and closely related, then such convergence would be difficult to separate from cases in which similarity of floral morphology was due to common ancestry. Floral traits in Oncidiinae should largely be ignored when considering generic limits, and instead chromosome number and vegetative characters should be emphasized. For example, when identifying the species to be circumscribed into a resurrected concept of *Cyrtochilum* (Williams *et al.*, 2001a), floral traits had to be disregarded; these had led previous taxonomists [e.g. Garay and Stacy (1974) among many] to place these species in several genera (e.g. *Buesiella* C.Schweinf., *Oliveriana* Rchb.f., *Oncidium* and *Odontoglossum* Kunth). Instead, we emphasized vegetative traits, in this case pseudobulbs that were round in cross-section (rather than laterally compressed as in most Oncidiinae) with many leaves subtending pseudobulbs rather than one or two as in the great majority of Oncidiinae (Williams *et al.*, 2001a). Previous authors had used other floral traits (e.g. a trilobed lip in which the apical lobe was smaller than the side lobes and often reflexed) in circumscribing *Cyrtochilum* (Kraenzlin, 1922), but this also did not produce a natural group. For example, it included two species of the mule-ear group, *Trichocentrum*: *T. flavovirens* (L.O.Williams) M.W.Chase & N.H.Williams and *T. microchilum* (Bateman ex Lindl.) M.W.Chase & N.H.Williams. When recircumscribing *Trichocentrum*, lower chromosome numbers ($2n = 42$ or less rather than $2n = 56$) and reduced pseudobulbs with succulent leaves were emphasized (Williams *et al.*, 2001b). A parallel to this situation is to be found in *Moraea* (Iridaceae), in which Goldblatt (1998) had to downplay floral traits in circumscribing genera. In many groups of plants, pollination syndromes confound efforts to create a taxonomic scheme based on monophyletic groups.

We propose here to merge the principally Brazilian groups of *Oncidium* with *Gomesa*, which we are certain will come as surprise to many people familiar with *Gomesa*. Although vegetatively compatible, flowers of *Gomesa* are completely different in morphology (the lip parallels the column, as in

many species of *Odontoglossum*) and colour (mostly pale green); Dressler (1981) reported that *Gomesa* is pollinated by bees, but did not specify which sort. *Gomesa* has a synsepal, the leaf character (a glaucous surface), outwardly pointing inflorescence bracts and flexed pedicels, and in spite of general appearances it is fairly easy to diagnose *Gomesa* as a member of this expanded genus based on these characters.

Gomesa had previously been considered to be closely related to *Oncidium* (Pabst and Dungs, 1977), but of course saying this does not help much since the latter is polymorphic and polyphyletic. Dressler (1981) considered that *Gomesa* might be congeneric with *Ada* Lindl., *Brachtia* Rchb.f. and *Mesospinidium* Rchb.f., presumably because of the similar lip/column relationships of these taxa. A relationship to *Binotia* Rolfe, *Rodrigueziella* and *Rodrigueziopsis* is easy to imagine because of their floral similarity to *Gomesa*, although vegetatively all three are distinctive due to the relatively elongate rhizome between growths and their reduced size.

Oncidium brunleesianum Rchb.f. (syn *Baptistonia echinata*) is a particularly unusual member of *Oncidium* section *Waluwewa*; it has a lip that projects forward with the broad side lobes enveloping the column, which are unusual traits for a member of *Oncidium*. This trait led Szlachetko (1995) to consider it to be a member of his subtribe Trichopiliinae and not at all a close relative of either *Gomesa* or *Oncidium*. *Carriella colorata* (Königer & J.G.Weinm.bis) V.P.Castro & K.G.Lacerda, although described in *Oncidium* (Königer and Weinmann, 2003), was segregated from *Oncidium* because it is similar to *Baptistonia*, but it differs in floral traits as well, the justification given for not including it in an expanded concept of *Baptistonia* (Castro and Lacerda, 2005). In terms of habit, *B. echinata* and *Carriella colorata* are typical members of *O.* section *Waluwewa*, and recently Chiron (2008) transferred the latter to *Baptistonia*.

Chiron and Castro Neto (2004) transferred *O. sarcodes* (section *Crispa*) to *Baptistonia*; its floral morphology is 'intermediate' between *O.* sections *Waluwewa* and *Crispa*, but the present analysis shows that Chiron and Castro Neto were correct; it is a member of *O.* section *Waluwewa*. Garay and Stacy (1974) considered *O. venustum* (as *O. trulliferum* Lindl., a well-known later synonym) a member of *O.* section *Rostrata* because it has the typical beaked column of this section, but this structure is a part of some oil-bee syndromes and also occurs in otherwise unrelated groups of orchids with other pollination syndromes (e.g. *Phalaenopsis* Blume, tribe Vandaeae). The present results show that *O. venustum* is also embedded in the *Gomesa* clade, perhaps sister to *Baptistonia* s.l. with high bootstrap support (Fig. 2). Chiron (2008) also has recently transferred this species to *Baptistonia*.

Ornithophora radicans (Rchb.f.) Garay & Pabst was long been considered problematic and perhaps to have a relationship to *Sigmatostalix* Rchb.f. (Reichenbach originally placed it in that genus). Production of oil and pollination by *Centris* bees is accompanied by reduction in size of both flowers (which makes sense given the small sizes of the bees) and plants, as well as a long, beak-like column apex, which curves out over the lip callus. Why this syndrome should involve reduced vegetative stature is unclear, but *G. radicans* is a good example of this (the bees are small, so floral reduction makes sense). Most species of *Sigmatostalix* (now included

in *Oncidium* s.s.; Chase et al., 2008) are similarly small. A relationship to the Brazilian sections of *Oncidium* was never envisioned for this species; it was always viewed as either a member of *Sigmatostalix* or the sole member of *Ornithophora*. There are a number of similarities in the beak-like column of this species to those of *Sigmatostalix* and *Ornithocephalus*, which share this type of the oil-bee syndrome. In 2003, Castro Neto and Chiron described a new species in *Oncidium* section *Rostrata*, *O. itapetingense* V.P.Castro & Chiron, which Baptista (in Docha Neto et al., 2006) transferred to *Carenidium*. The floral morphology of this species, with a beaked rostellum, is highly reminiscent of *G. radicans*, and if material of this species becomes available we predict that it will fall as sister to *G. radicans*.

We do not propose a sectional classification of *Gomesa* here because we believe that this serves little purpose in groups in which parallelism is so rife; in practical terms this means that neat boxes upon which such classifications have been typically founded do not exist. Some of the sections of Garay and Stacy (1974) do hold up reasonably well. For example, *O.* section *Waluwewa* has all of the species included there by Garay and Stacy, but *Baptistonia echinata*, *Carriella colorata*, *O. sarcodes* and *O. venustum* also belong here. However, other sections like *O.* section *Concoloria* are grossly polyphyletic. Characters for *O.* section *Concoloria* are a simple lip with a callus composed of a series or parallel keels and no side lobes, and some of the species included here by Garay and Stacy (1974) are members of *Miltonia* or *Oncidium* s.s. Of the ten species Garay and Stacy included here, only *O. dasytyle* Rchb.f., *O. concolor* Hook. and *O. gracile* Lindl. fall in the *Gomesa* clade; the first two form a sister pair embedded among members of *O.* section *Crispa*, whereas the last is related to *O.* section *Barbata* (Fig. 3). To a large extent, knowing something about phylogenetic relationships makes natural subgeneric categories either extremely difficult to create (as well as for which to write keys) or it renders them artificial due to abandoning monophyly as the primary guiding principle. Looking at the patterns of relationships in Figs. 2 and 3, one can see that there are well-supported subclades within *Gomesa* s.l., but it is not possible to identify clear sets of characters that could be used to serve as the basis for constructing a workable classification within the clade. Thus, we abandon the sections of Garay and Stacy (1974) as unworkable and prefer not to set up such a system ourselves. Szlachetko and colleagues transferred sections of *Oncidium* sensu Garay and Stacy (1974) to segregate genera: in the case of Brazilian groups these were *O.* section *Crispa* to *Anettea* Szlach. & Mytnik, *O.* section *Concoloria* to *Concocidium* Romowicz & Szlach. and *O.* section *Rhinocerotes* to *Rhinocerotidium* Szlach. (Romowicz and Szlachetko, 2006; Szlachetko, 2006; Szlachetko and Mytnik-Ejsmont, 2006). Also in 2006, Campacci (in Docha Neto et al., 2006) established the genus *Brasilidium* for the species of section *Crispa*, but he included a different set of species in his genus than Szlachetko and Mytnik-Ejsmont (2006) included in *Anettea* (both cited the type species as *Oncidium crispum*, so they are taxonomic synonyms in spite of differing species composition). For example, Szlachetko and Mytnik-Ejsmont (2006) included *O. sarcodes* in *Anettea*, but Chiron and Castro Neto (2004) had transferred

this species to *Baptistonia*; Campacci did not include *O. sarcodes* in *Brasilidium* in parallel with the treatment by Chiron and Castro Neto (2004). Similarly, Baptista described *Carenidium* based on the same type species as Romowicz and Szlachetko (2006) had used for *Concocidium*, the type of *Oncidium* section *Concoloria* (*O. concolor*), but they did not circumscribe the species of these genera in the same way; Romowicz and Szlachetko (2006) included there as well species such as *O. hyphaematicum* Rchb.f., which is a member of *Oncidium* s.s. Baptista at least excluded the non-Brazilian species from *Carenidium*, but he included in his concept two species, *O. hookeri* Rolfe and *O. raniferum* Lindl. (*O.* section *Raniferum* sensu Garay and Stacy), that are unrelated to the rest of *Carenidium* (Figs 2 and 3). This problem was rectified by Chiron and Castro Neto (2006), who segregated this group into *Menezesiella*. The species of *Menezesiella* are indeed not related to those in *Carenidium*, but instead they are embedded in *Coppensia* (Fig. 3).

Docha Neto *et al.* (2006) described several other new genera to accommodate these mostly Brazilian groups, many of which belong to the *Gomesa* clade, but these new genera are not monophyletic, even though they stated that phylogeny should be the basis of taxonomic practice. For example, in *Brasilidium*, Campacci did not include *O. concolor* or *O. dasytyle*, even though both are members of this clade in the present analyses; instead Baptista placed them in *Carenidium*. Campacci transferred all names he made in *Ampliglossum* to *Coppensia* when he (probably) mistakenly thought that *O. varicosum* was related to *O. bicolor*. In the present results, *O.* section *Synsejala* is not monophyletic, and given the relationships shown in Figs 2 and 3, *Ampliglossum* could still apply to a group of species related to *O. varicosum* because they are not related to the group in which we presume *O. bicolor* would fall (the clade containing *O. warmingii*, in which the rest of the species of *O.* section *Synsejala* fall). *Oncidium varicosum*, *O. weteri* Pabst and *O. insigne* (Rolfe) Christenson would then be the members of *Ampliglossum*, which are well supported as related to *O. macronyx* Rchb.f., for which Baptista (in Docha Neto *et al.*, 2006) described *Rhinocidium* (Figs 2 and 3) and Szlachetko (2006) later described *Rhinocerotidium*. The potential for confusion caused by differing generic concepts of these various authors boggles even the minds of people who are reasonably familiar with these taxa.

However, the story of confusion does not end here. Soon after Baptista (in Docha Neto *et al.*, 2006) described a new genus, *Alatiglossum* Baptista, for the former members of *O.* section *Barbata*, Castro Neto and Martins Catharino (2006) described two other genera, *Kleberella* V.P.Castro & Cath. and *Neoruschia* Cath. & V.P.Castro, based on *O. uniflorum* Booth ex Lindl. and *O. cogniauxianum* Schltr., respectively, which had been included in *Alatiglossum* by Baptista. Also in 2006, Chiron and Castro Neto described *Menezesiella* Chiron & V.P.Castro for three of the species, *O. hookeri*, *O. loefgrenii* Cogn. and *O. raniferum*, that Baptista had included in *Carenidium*. Chiron and Castro Neto were correct that these species are not related to those of *O.* section *Concoloria*, and if we are to use the segregate genera, then use of this name would be appropriate. Finally (we hope) in 2008, Castro Neto and colleagues (including

Chiron) transferred another three species to *Menezesiella*, even though they must certainly have been aware of these at the time they described the genus (Castro Neto *et al.*, 2008). One of these newly transferred species was *M. calimaniorum* (Guiard) V.P.Castro & G.F.Carr, which was the type species for *Castroa* Guiard, published in 2006 with a photograph of the species in the same journal in which Chiron (who is also the chief editor) and Castro described *Menezesiella* (Guiard, 2006); from the photograph it is clear that *Castroa calimaniora* is a member of *Menezesiella*. Some workers might prefer to continue the process started by Chiron and Castro Neto (2004, 2005a, b) and Docha Neto *et al.* (2006) in which successively new sets of genera would be established for the Brazilian members of *Oncidium*, but once we publish our results it seems certain that someone will decide to make further changes to those that have already been published and another new wave of synonyms will appear. From a simple inspection of the results presented here (Figs 2 and 3), to produce a reasonable (monophyletic) system of classification at least 15 genera must be recognized (some not yet described; e.g. a new genus would be needed for *Oncidium gracile*). If such fine splitting at the generic level were to be extended to the whole of Oncidiinae, then there would be double the number of genera to be recognized, from 70 in Pridgeon *et al.* (2009) to well over 120. We prefer instead to recognize larger and inevitably more heterogeneous generic limits rather than narrower but more homogeneous genera because this ultimately makes the classification easier for most people to use; only experts are able to tell apart the narrowly circumscribed taxa in the *Gomesa* clade. It is telling that the Brazilians who claimed to know these taxa well did not manage to circumscribe monophyletic genera and have published successive transfers of the same species into new genera. Furthermore, Szlachetko and colleagues fared no better with their reliance on column morphology in establishing monophyletic taxa. In effect, all these workers have relied upon characters that are highly integrated into pollination syndromes; this reliance prevented them from understanding relationships and erecting natural taxa.

In previous classifications, there were two other species of *Oncidium* that are known to occur in Brazil. *Oncidium phymatochilum* Lindl. is a vegetatively anomalous species, but it has been shown by Williams *et al.* (2001b) to be sister to the species of *Miltonia*, into which these authors transferred it. Morphologically, this species is no more similar to *Miltonia* than it is to *Oncidium*, but Williams *et al.* (2001b) stated that monotypic genera are a redundancy in classification and therefore decided to lump it with its sister taxon *Miltonia*. Later, Christenson (2005) transferred it into its own genus, *Phymatochilum* Christenson; in any case, it is no longer a member of *Oncidium*. The other species, *Oncidium orthostates* Ridl., occurs from the tepuis of the Guyana Highlands in Venezuela (Amazonas and Bolivar) into Brazil (Amazonas, Goiás, Rondônia, Roraima and Tocantins). This is a peculiar distribution for a member of *Oncidium* or *Gomesa*; there are no other members of these two genera in that region. It is also a peculiar species in *Oncidium* or *Gomesa* due to absence of a tabula infrastigmatica, although it otherwise looks enough like section *Synsejala* for Campacci (in Docha Neto *et al.*, 2006) to transfer it into *Ampliglossum* and later

into *Coppensia*. In the present analyses, this species falls neither with *Oncidium* nor *Gomesa*, but rather in an isolated position between these two major clades (Fig. 3). Florally, it is similar to *Zelenkoa onusta* (Lindl.) M.W.Chase & N.H.Williams, but it differs in habit and does not fall with that species in any of the present analyses. A new genus for it is described below. With the removal of this species from *Oncidium*, *O. baueri* becomes the only member of *Oncidium* in Brazil.

TAXONOMIC TREATMENT

Gomesa R.Br., Bot. Mag. t. 1748. 1815. Type species: *Gomesa recurva* R.Br.

Synonyms:

Coppensia Dumort., Nouv. Mém. Acad. Roy. Sci. Bruxelles **9**: 10. 1835. Type species: *Coppensia bifolia* (Sims) Dumort. (basonym: *Oncidium bifolium* Sims).

Baptistonia Barb.Rodr., Gen. Sp. Orchid. **1**: 95. 1877. Type species: *Baptistonia echinata* Barb.Rodr.

Theodorea Barb.Rodr. (non Cass.), Gen. Sp. Orchid. **1**: 144. 1877. Type species: *Theodorea gomezoides* Barb.Rodr.; this is a later homonym of *Theodorea* Cass., a genus of Asteraceae.

Ornithophora Barb.Rodr., Gen. Sp. Orchid. **2**: 225. 1882. Type species: *Ornithophora quadricolor* Barb.Rodr. (= *Ornithophora radicans* (Rchb.f.) Garay & Pabst).

Waluwewa Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada **11**: 309. 1890. Type species: *Waluwewa pulchella* Regel.

Rodrigueziella Kuntze, Rev. Gen. 649. 1891. Type species: *Rodrigueziella gomezoides* (Barb.Rodr.) Kuntze (basonym: *Theodorea gomezoides* Barb.Rodr.).

Binotia Rolfe, *Orchid Rev.* **13**: 296. 1905. Type species: *Binotia brasiliensis* Rolfe.

Rodrigueziopsis Schltr., Repert. Spec. Nov. Regni Veg. **16**: 427. 1920. Type species: *Rodrigueziopsis eleutherosepala* (Barb.Rodr.) Schltr.

Hellerorchis A.D.Hawkes, *Orchid J.* **3**: 275. 1959. Type species: *Hellerorchis gomezoides* (Barb.Rodr.) A.D.Hawkes (basonym: *Rodrigueziella gomezoides* Barb.Rodr.).

Carria V.P.Castro & K.G.Lacerda (non Gardn.), *Orchids* **74**: 694. 2005. Type species: *Carria colorata* (Königer & J.G.Weinm.bis) V.P.Castro & K.G.Lacerda (basonym: *Oncidium coloratum* Königer & J.G.Weinm.bis). *Carria* Castro & Lacerda is a later homonym of *Carria* Gardn., a genus in Ternstroemiaceae.

Carriella V.P.Castro & K.G.Lacerda, *Icon. Orchid. Brasil.* **2**, t. 123. 2006. Type species: *Carriella colorata* (Königer & J.G.Weinm.bis) V.P.Castro & K.G.Lacerda (basonym: *Oncidium coloratum* Königer & J.G.Weinm.bis).

Alatiglossum D.H.Baptista, *Colet. Orq. Bras.* **3**: 87. 2006. Type species: *Alatiglossum barbatum* (Lindl.) D.H.Baptista (basonym: *Oncidium barbatum* Lindl.).

Ampliglossum Campacci, *Colet. Orq. Bras.* **3**: 83. 2006. Type species: *Ampliglossum varicosum* Campacci (basonym: *Oncidium varicosum* Lindl. & Paxton).

Anettea Szlach. & Mytnik, *Pol. J. Bot.* **51**: 49. 2006. Type species: *Anettea crispa* (Lodd.) Szlach. & Mytnik (basonym: *Oncidium crispum* Lodd.).

Brasilidium Campacci, *Colet. Orq. Bras.* **3**: 78. 2006. Type species: *Brasilidium crispum* Campacci (basonym: *Oncidium crispum* Lindl.).

Carenidium D.H.Baptista, *Colet. Orq. Bras.* **3**: 90. 2006. Type species: *Carenidium concolor* (Hook.) D.H.Baptista (basonym: *Oncidium concolor* Hook.).

Castroa Guiard, *Richardiana* **6**: 162. 2006. Type species: *Castroa calimaniana* Guiard.

Concocidium Romowicz & Szlach., *Pol. Bot. J.* **51**: 44. 2006. Type species: *Concocidium concolor* (Hook.) Romowicz & Szlach. (basonym: *Oncidium concolor* Hook.).

Kleberiella V.P.Castro & Catharino, *Richardiana* **6**: 158. 2006. Type species: *Kleberiella uniflora* (Booth ex Lindl.) V.P.Castro & Catharino (basonym *Oncidium uniflorum* Booth ex Lindl.).

Menezesiella Chiron & V.P.Castro, *Richardiana* **6**: 103. 2006. Type species: *Menezesiella ranifera* (Lindl.) Chiron & V.P.Castro (basonym: *Oncidium raniferum* Lindl.).

Neoruschia Catharino & V.P.Castro, *Richardiana* **6**: 58. 2006. Type species: *Neoruschia cogniauxiana* (Schltr.) Catharino & V.P.Castro (basonym: *Oncidium cogniauxianum* Schltr.).

Rhinocidium D.H.Baptista, *Colet. Orq. Bras.* **3**: 93. 2006. Type species: *Rhinocidium longicornu* (Mutel) D.H.Baptista (basonym: *Oncidium longicornu* Mutel).

Rhinocerotidium Szlach., *Pol. Bot. J.* **51**: 40. 2006. Type species: *Rhinocerotidium longicornu* (Mutel) Szlach. (basonym: *Oncidium longicornu* Mutel).

Gomesa × *amicta* (Lindl.) M.W.Chase & N.H.Williams, **comb. nov.**; basonym: *Oncidium* × *amictum* Lindl., *Bot. Reg. t.* 66. 1847. (*G. sarcodes* × *G. lietzei*).

Gomesa × *colnagoi* (Pabst) M.W.Chase & N.H.Williams, **comb. nov.**; basonym: *Oncidium* × *colnagoi* Pabst, *Bradea* **2**: 4. 1976. (*G. forbesii* × *G. zappii*).

Gomesa × *lita* (Rchb.f.) M.W.Chase & N.H.Williams, **comb. nov.**; basonym: *Oncidium* × *litum* Rchb.f., *Gard. Chron.*, n.s. 20: 3328. 1883.

Gomesa × *regentii* (V.P.Castro and Chiron) M.W.Chase & N.H.Williams, **comb. nov.**; basonym: *Baptistonia* × *regentii* V.P.Castro & Chiron, *Richardiana* **5**: 187. 2005.

Gomesa × *scullyi* (Pabst & Mello) M.W.Chase & N.H.Williams, **comb. nov.**; basonym: *Oncidium* × *scullyi* Pabst & Mello, *Bradea* **2**: 187(-188), fig. D. 1977. (*G. curta* × *G. gravesiana*).

Gomesa × *wheatleyana* (W.H.Gower) M.W.Chase & N.H.Williams, **comb. nov.**; basonym: *Oncidium* × *wheatleyanum* W.H.Gower, *The Garden*, 154: 227. 1893. (*G. imperatoris-maximimiliana* × *G. dasytyle*).

Gomesa adamantina (Marçal & Cath.) M.W.Chase & N.H.Williams, **comb. nov.**; basonym: *Oncidium adamantinum* Marçal & Cath., *Richardiana* **6**: 119. 2006.

Gomesa albinoi (Schltr.) M.W.Chase & N.H.Williams, **comb. nov.**; basonym: *Oncidium albinoi* Schltr., *Repert. Spec. Nov. Regni Veg.* **23**: 63. 1926.

Gomesa barbaciae (Lindl.) M.W.Chase & N.H.Williams, **comb. nov.**; basonym: *Oncidium barbaciae* Lindl., *Fol. Orch. Oncid.* **6**: 32. 1855.

Gomesa barbata (Lindl.) M.W.Chase & N.H.Williams, **comb. nov.**; basonym: *Oncidium barbatum* Lindl., *Coll. Bot. t.* 27. 1821.

- Gomesa batemanni* (Parm. ex Knowles & Westc.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium batemanni* Parm. ex Knowles & Westc., Fl. Cab. 3: 183. 1840.
- Gomesa bicolor* (Lindl.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium bicolor* Lindl., Bot. Reg. 66. 1843.
- Gomesa bifolia* (Sims) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium bifolium* Sims, Bot. Mag. 36: t. 1491. 1812.
- Gomesa blanchetii* (Rchb.f.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium blancheti* Rchb.f., Linnaea 22: 845. 1850.
- Gomesa bohnkiana* (V.P.Castro & G.F.Carr) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium bohnkianum* V.P.Castro & G.F.Carr, Orchid Digest 70: 88. 2006.
- Gomesa brasiliensis* (Rolfe) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Binotia brasiliensis* Rolfe, Orchid Rev. 13: 296. 1905.
- Gomesa brieniana* (Rchb.f.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium brienianum* Rchb.f. Gard. Chron. nov. ser. 15: 40. 1881.
- Gomesa brunnipetala* (Barb.Rodr.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium brunnipetalum* Barb.Rodr., Gen. Sp. Orchid. 2: 190. 1881.
- Gomesa caldensis* (Rchb.f.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium caldense* Rchb.f., Linnaea, 22: 846. 1849.
- Gomesa calimani* (Guiard) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Castroa calimani* Guiard, Richardiana 6: 162. 2006.
- Gomesa chapadensis* (V.P.Castro & Campacci) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium chapadense* V.P.Castro & Campacci, Orquidário 6: 150. 1992.
- Gomesa chrysoptera* (Lindl.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium macropetalum* var. *chrysoptera* Lindl., Fol. Orch. Oncid. 16. 1855.
- Gomesa chrysopterantha* (Lückel) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium chrysopteranthum* Lückel, Orchidee (Hamburg) 49: 43. 1998.
- Gomesa chrysothapsis* (Rchb.f.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium chrysothapsis* Rchb.f. Gard. Chron. ser. 3, 3: 72. 1888. Probably a synonym of *G. cornigera*.
- Gomesa chrysothyrsus* (Rchb.f. ex Warn.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium chrysothyrsus* Rchb.f. ex Warn., Sel. Orch. Ser. II. t. 5. 1864.
- Gomesa ciliata* (Lindl.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium ciliatum* Lindl., Gen. Sp. Orch. 200. 1833.
- Gomesa cogniauxiana* (Schltr.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium cogniauxianum* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 9: 175. 1921.
- Gomesa colorata* (Königer & J.G.Weinm.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium coloratum* Königer & J.G.Weinm.bis.
- Gomesa concolor* (Hook.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium concolor* Hook., Bot. Mag. t. 3752. 1839.
- Gomesa cornigera* (Lindl.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium cornigerum* Lindl., Edwards's Bot. Reg. 18: t. 1542. 1832.
- Gomesa croesus* (Rchb.f.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium croesus* Rchb.f., Hamb. Garten-Blumenzeitung 13: 314. 1857.
- Gomesa cruciata* (Rchb.f.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium cruciatum* Rchb.f., Gard. Chron. 1: 138. 1878.
- Gomesa cuneata* (Scheidw.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium cuneatum* Scheidw., Allg. Gartenzeitung 10: 309. 1842.
- Gomesa curta* (Lindl.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium curtum* Lindl., Edwards's Bot. Reg. 33: t. 68. 1847.
- Gomesa damaceno* (Chiron & V.P.Castro) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Baptisia damaceno* Chiron & V.P.Castro, Richardiana 4: 124. 2004.
- Gomesa dasytyle* (Rchb.f.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium dasytyle* Rchb.f., Gard. Chron. 253. 1873.
- Gomesa discifera* (Lindl.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium disciferum* Lindl., Fol. Orch. Oncid. 24. 1855.
- Gomesa doeringii* (Hoehne) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Theodora doeringii* Hoehne, Arq. Bot. Estado São Paulo, n.s., f.m., 1: 86. 1942.
- Gomesa doniana* (Batem. ex W.Baxt.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium donianum* Batem. ex W.Baxt., J.C. Loudon Suppl. Hort. Brit. 3: 598. 1850.
- Gomesa echinata* (Barb.Rodr.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Baptisia echinata* Barb.Rodr., Gen. Sp. Orchid. 1: 95. 1877.
- Gomesa edmundoi* (Pabst) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium edmundoi* Pabst, Bradea 1: 172, tab. 1, fig. B. 1972.
- Gomesa eleutherosepala* (Barb.Rodr.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Rodriguezia eleutherosepala* Barb.Rodr., Gen. Spec. Orchid. 2: 240. 1881.
- Gomesa emilii* (Schltr.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium emilii* Schltr., Repert. Spec. Nov. Regni Veg. 16: 449. 1920.
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- Gomesa eurycline* (Rchb.f.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium eurycline* Rchb.f., Gard. Chron. 2: 812. 1883.
- Gomesa flexuosa* (Sims) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium flexuosum* Sims, Bot. Mag. t. 2203. 1821.
- Gomesa forbesii* (Hook.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium forbesii* Hook., Bot. Mag. 65: t. 3705. 1839.
- Gomesa fuscans* (Rchb.f.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium fuscans* Rchb.f., Otia Bot. Hamb. 86. 1881.
- Gomesa fuscopetala* (Hoehne) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium*

macropetalum Lindl. var. *fuscopetalum* Hoehne, Relat. Commiss. Linhas. Teleg. Estrateg. Matto Grosso Amazonas 5: 61, pl. 56, f. 2. 1910.

Gomesa gardneri (Lindl.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium gardneri* Lindl., in Hook., Lond. J. Bot. 2: 662. 1843.

Gomesa gilva (Vell.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Epidendrum gilvum* Vell., Fl. Flum. lx. t. 33. 1831.

Gomesa gracilis (Lindl.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium gracile* Lindl., Edwards's Bot. Reg. 23: t. 1920. 1837.

Gomesa gracillima (Schltr.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium gracillimum* Cogn., in Mart. Fl. Bras. 3(6): 401. 1906.

Gomesa gravesiana (Rolfe) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium gravesianum* Rolfe, Gard. Chron. ser. 3, 11: 650. 1892.

Gomesa gutfreundiana (Chiron & V.P.Castro) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium gutfreundianum* Chiron & V.P.Castro, Richardiana 3: 122. 2003.

Gomesa hookeri (Rolfe) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium hookeri* Rolfe, Gard. Chron. ser. 3, 2: 520. 1941.

Gomesa hydrophila (Barb.Rodr.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium hydrophilum* Barb.Rodr., Gen. Sp. Orchid. 1: 92. 1877.

Gomesa insignis (Rolfe) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium varicosum* Lindl. var. *insigne* (Rolfe), Orchid Rev. 6: 27. 1898.

Gomesa imperatoris-maximiliani (Rchb.f.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium imperatoris-maximiliani* Rchb.f., in H.R.vanFernseeWawra, Bot. Ergebn.: 154. 1866. Synonym: *Oncidium crispum* Lodd. Gen. Sp. Orch. Pl. 197. 1833. Note: the epithet *crispa* is already occupied in *Gomesa*, so we have used a later name for this species in *Gomesa*.

Gomesa isoptera (Lindl.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium isoptera* Lindl., Edwards's Bot. Reg. 23: t. 1920. 1837.

Gomesa itapetingensis (V.P.Castro & Chiron) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium itapetingense* V.P.Castro & Chiron, Richardiana 3: 25. 2003.

Gomesa jucunda (Rchb.f.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Mesospinidium jucundum* Rchb.f., Gard. Chron. (n. s.) 6: 580. 1876.

Gomesa kautskyi (Pabst) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium kautskyi* Pabst, Bradea 2(14): 90, t. 2, E. 1976.

Gomesa leinigii (Pabst) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium leinigii* Pabst, Bradea 1(20): 182, t. 3, f. B. 1972.

Gomesa lietzei (Regel) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium lietzei* Regel, Act. Hort. Petrop. 7: 387. 1880.

Gomesa loefgrenii (Cogn.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium loefgrenii* Cogn., in Mart. Fl. Bras. 3, pt. 6: 381, pl. 90, fig. 1. 1905.

Gomesa longicornu (Mutel) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium longicornu* Mutel, Mem. Scarpe. 13. 1838.

Gomesa longipes (Lindl. & Paxt.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium longipes* Lindl. & Paxt., Fl. Gard. 1: 46. 1850.

Gomesa macronyx (Rchb.f.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium macronyx* Rchb.f., Otia Bot. Hamb. 95. 1881.

Gomesa macropetala (Lindl.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium macropetalum* Lindl., Sert. Orch. sub t. 48. 1841.

Gomesa majevskyi (Toscano & V.P.Castro) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium majevskyi* Toscano & V.P.Castro, Bradea 3: 349. 1983.

Gomesa mandonii (Rchb.f.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium mandonii* Rchb.f., Xenia Orch. 3: 21. 1878.

Gomesa marshalliana (Rchb.f.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium marshallianum* Rchb.f., Gard. Chron. 1866: 682. 1866.

Gomesa martiana (Lindl.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium martianum* Lindl., Edwards's Bot. Reg. 23: t. 1920. 1837.

Gomesa megaloptera (Kraenzl.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium megalopterum* Kraenzl., in Engler, Pflanzenz. 4, Fam. 50: 156. 1922.

Gomesa microphyta (Barb.Rodr.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Rodriguezia microphyta* Barb.Rodr., Rev. Engenh. 3: 144. 1881.

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Gomesa montana (Barb.Rodr.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium montanum* Barb.Rodr., Gen. Sp. Orch. Nov. 1: 93. 1877.

Gomesa neoparanaensis (Chiron & V.P.Castro) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Menezesiella neoparanaensis* Chiron & V.P.Castro, Richardiana 8: 51. 2008.

Gomesa nitida (Barb.Rodr.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium nitidum* Barb.Rodr., Gen. Sp. Orch. Nov. 2: 193. 1882.

Gomesa ouricanensis (V.P.Castro & Campacci) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium ouricanense* V.P.Castro & Campacci, Bol. CAOB 4: 17. 1992.

Gomesa pabstii (Campacci & C.Espejo) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium pabstii* Campacci & C.Espejo, Orquideophilo 6: 36. 1998.

Gomesa paranaensis (Kraenzl.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium paranaense* Kraenzl., in Svensk. Vet. Akad. Handl. XLVI, 10: 84. 1911.

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Gomesa pardoglossa (Rchb.f.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium pardoglossum* Rchb.f., Gard. Chron. 1: 516. 1886.

Gomesa pectoralis (Lindl.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium pectorale* Lindl., Sert. Orch. t. 39. 1840.

Gomesa petropolitana (Pabst) M. W. Chase and N. H. Williams, **comb. nov.**; basionym: *Rodrigueziella petropolitana* Pabst, *Bradea* 22: 87. 1976.

Gomesa pirarensis (Rchb.f.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium pirarense* Rchb.f., *Linnaea* 22: 846. 1850.

Gomesa praetexta (Rchb.f.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium praetextum* Rchb.f., *Gard. Chron.* 1873: 1206. 1873.

Gomesa psyche (Schltr.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium psyche* Schltr., *Repert. Spec. Nov. Regni Veg.* 17: 16. 1921.

Gomesa pubes (Lindl.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium pubes* Lindl., *Bot. Reg.* t. 1007. 1826.

Gomesa pulchella (Regel) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Waluwewa pulchella* Regel, *Trudy Imp. S.-Peterburgsk. Bot. Sada* 11: 309. 1890. Synonym: *Oncidium waluwewa* Schltr., *Repert. Spec. Nov. Regni Veg.* 15: 215. 1918. Note: in *Oncidium*, the epithet *pulchella* is occupied, so Schlechter published a new name for this species, but in *Gomesa* it must have its original epithet.

Gomesa radicans (Rchb.f.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Sigmatostalix radicans* Rchb.f., *Walp. Ann.* 6: 859. 1849.

Gomesa ramosa (Lindl.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium ramosum* Lindl., *Edwards's Bot. Reg.* 23: t. 1920. 1837.

Gomesa ranifera (Lindl.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium raniferum* Lindl., *Bot. Reg.* sub t. 1920, t. 48. 1838.

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Gomesa reichertii (L.C.Menezes & V.P.Castro) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Coppensia reichertii* L.C.Menezes & V.P.Castro, *Richardiana* 8: 21. 2008.

Gomesa remotiflora (Garay) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium remotiflorum* Garay, *Taxon* 19: 454. 1970.

Gomesa rhinoceros (Rchb.f.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium rhinoceros* Rchb.f., *Bot. Zeit.* 14: 514. 1856.

Gomesa riograndensis (Cogn.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium riograndense* Cogn., *Fl. Bras. (Martius)* 3, pt. 6: 446, pl. 89, fig. 2. 1906.

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Gomesa salesopolitana (V.P.Castro & Chiron) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Menezesiella salesopolitana* V.P.Castro & Chiron, *Richardiana* 6: 200. 2006.

Gomesa sarcodes (Lindl.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium sarcodes* Lindl., *Journ. Hort. Soc.* 4: 266. 1849.

Gomesa sellowii (Cogn.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium sellowii* Cogn., in *Mart. Fl. Bras.* 3, pt. 6: 404. 1906.

Gomesa silvana (V.P.Castro & Campacci) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium silvanum* V.P.Castro & Campacci, *Orquidário* 5: 22. 1991.

Gomesa sincorana (Campacci & Cath.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Coppensia sincorana* Campacci & Cath., *Bol. CAOP* 64: 124. 2006.

Gomesa spiloptera (Lindl.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium spilopterum* Lindl., *Edwards's Bot. Reg.* 30 Misc.: 75. 1844.

Gomesa trichodes (Lindl.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium trichodes* Lindl., *Fol. Orch. Oncid.* 6: 15. 1855.

Gomesa truncata (Pabst) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium truncatum* Pabst, *Orquidea (Rio de Janeiro)* 17: 45. 1955.

Gomesa uhlii (Chiron & V.P.Castro) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Baptistonia uhlii* Chiron & V.P.Castro, *Richardiana* 6: 21. 2006.

Gomesa unicolor (Rolfe) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium unicolor* Rolfe, *Orchid Rev.* 1: 266. 1893.

Gomesa uniflora (Booth ex Lindl.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium uniflorum* Booth ex Lindl., *Edwards's Bot. Reg.* 29: t. 43. 1843.

Gomesa varicosa (Lindl.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium varicosum* Lindl., *Edwards's Bot. Reg.* 23: t. 1920. 1837.

Gomesa velteniana (V.P.Castro & Chiron) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Baptistonia velteniana* V.P.Castro & Chiron, *Richardiana* 5: 80. 2005.

Gomesa venusta (Drapiez) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium venustum* Drapiez, *Hort. Belge* 3: 28. 1836.

Gomesa viperina (Lindl.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium viperinum* Lindl., *Gen. Sp. Orch.* 197. 1833.

Gomesa warmingii (Rchb.f.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium warmingii* Rchb.f., *Otia Bot. Hamb.* 86. 1881.

Gomesa welteri (Pabst) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium welteri* Pabst, *Arch. Jard. Bot. Rio de Janeiro* 14: 25, tab. 7B. 1956.

Gomesa widgreni (Lindl.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium widgreni* Lindl., *Fol. Orch. Oncid.* 6: 17. 1855.

Gomesa williamsii (Schltr.) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium williamsii* Schltr., *Repert. Spec. Nov. Regni Veg.* 10: 459. 1912.

Gomesa zappii (Pabst) M.W.Chase & N.H.Williams, **comb. nov.**; basionym: *Oncidium zappii* Pabst, *Bradea* 2(22): 3. 1976.

Not transferred: *Oncidium kraenzlinianum* Cogn. because it does not appear to be a member of this group, even though Garay put it in *O.* section *Synsepalia*. From its description, it could be *Caucaea radiata*.

We describe below a new genus for the singular species, *Oncidium orthostates* Ridl., which differs in floral traits from all other genera of Oncidiinae. This species has a peculiar distribution in the Guyana Highlands of Venezuela, Guyana and Brazil. The species is sister to clades of other genera and is not resolved as sister to any other single taxon. It is most similar florally to *Zelenkoa onusta* (Lindl.) M.W.Chase & N.H.Williams., the single species of that genus, but it never

comes out exclusively with it. We name the new genus in honour of Norris H. Williams, who has spent his botanical career studying members of Oncidiinae and pollination biology of neotropical orchids.

***Nohawilliamsia* M.W. Chase & Whitten, gen. nov.**

Plantae terrestres vel lithophyticae, parvae, pseudobulbi lati oblongi, 1 vel 2 bracteis foliiferis subtenti, folio apicali 1 vel 2. Folia crassa. Inflorescentia lateralis, racemosa, plerumque non ramosa, floribus numerosis. Structura floris Oncidio similis, sed tabula infrastigmatica carenti atque columna brevi. Pollinia dua.

Small, perennial, caespitose **herbs**, terrestrial to lithophytic, with pseudobulbs clustered on a short rhizome. **Pseudobulbs** oblong to elliptical-oblong in outline, weakly ancipitous, weakly ridged longitudinally, usually with 1–2 terminal leaves, composed of a single internode, lower portions concealed by 3–4 sheathing bracts, the uppermost 1–2 with a lamina. **Leaves** elliptic-lanceolate, coriaceous, glabrous, conduplicate, margins entire, eventually deciduous. **Inflorescences** produced laterally from the base of the pseudobulb, subtended by a sheathing bract, much longer than leaves, racemose (rarely sparsely branched), many-flowered, in some cases producing plantlets at nodes after flowering. **Flowers** showy, resupinate, pedicellate ovary twisted, glabrous. **Sepals** free, more or less equal in size to the petals, shortly elliptic, dorsally carinate and shortly acuminate. **Petals** free, same shape as sepals; lip broadly attached to column, trilobed with the apical lobe much larger than the lateral lobes and apically cleft, with a basal trilobed callus. **Column** shorter than dorsal sepal, swollen apically, with a pair of lateral wings on the sides of the stigma; stigma round; anther terminal operculate, incumbent, one-celled; pollinarium with two, hard, waxy pollinia with an obvious, abaxial suture, attached to the head of an elongate stipe by irregularly shaped viscin (caudicles); viscidium oval in outline. **Capsules** and **seeds** not seen. **Seedlings** not seen.

There is at this time only a single species in this genus, and we here transfer it formally to *Nohawilliamsia*.

***Nohawilliamsia orthostates* (Ridl.) M.W.Chase & Whitten, comb. nov.;** basionym: *Oncidium orthostates* Ridl., *Timehri* 5: 204. 1886.

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APPENDIX

Taxa, vouchers and GenBank accession numbers

Species	Authors	Voucher	Herbarium/ number	GenBank ITS	GenBank <i>matK</i>	GenBank <i>3' ycf1</i>	GenBank <i>5' ycf1</i>	GenBank <i>trnH-psbA</i>
<i>Comparettia falcata</i>	Poepp. & Endl.	Whitten 2688	FLAS	FJ565601	FJ565090	FJ563757	FJ563043	FJ564609
<i>Cyrtorchilum serratum</i>	(Lindl.) Kraenzl.	Whitten 3427; Whitten 91289	FLAS	AF432961	AF239494	FJ563260	FJ562567	FJ564123
<i>Erycina hyalinobulbon</i>	(Llave & Lex.) N.H. Williams & M.W. Chase	Chase 83395	K	AF350536	AF350615	EU490744	FJ562474	FJ564026
<i>Gomesa barbaceniae</i>	(Lindl.) M.W.Chase & N.H.Williams	Faria 23	UEC	FJ565420	FJ564911	FJ563545	FJ562837	FJ564397
<i>Gomesa barbata</i>	(Lindl.) M.W.Chase & N.H.Williams	Semir sn	UEC	FJ565431	FJ564924	FJ563558	FJ562849	FJ564410
<i>Gomesa chrysostoma</i>	Hoffmanns.	Faria et al. s.n.	UEC	FJ565408	FJ564899	FJ563533	FJ562825	FJ564385
<i>Gomesa ciliata</i>	(Lindl.) M.W.Chase & N.H.Williams	Chase O-137	K	FJ565217	FJ564730	FJ563205	FJ562514	FJ564066
<i>Gomesa cogniauxiana</i>	(Schltr.) M.W.Chase & N.H.Williams	UEC 103-073	UEC	FJ565409	FJ564900	FJ563534	FJ562826	FJ564386
<i>Gomesa colorata</i>	(Königer & J.G.Weinm.bis) M.W.Chase & N.H.Williams	Gerlach 03/2467	M	FJ565242	FJ564754	FJ563246		FJ564107
<i>Gomesa concolor</i>	(Hook.) M.W.Chase & N.H.Williams	Williams N341	FLAS	FJ565323	FJ564816	FJ563406	FJ562704	FJ564261
<i>Gomesa crispa</i>	(Lindl.) Klotzsch ex Rchb.f.	Faria & Pansarin 1022	UEC	FJ565415	FJ564906	FJ563540	FJ562832	FJ564392
<i>Gomesa dasystyle</i>	(Rchb.f.) M.W.Chase & N.H.Williams	Chase O-210	K	AF350551	AF350630	FJ563220	FJ562529	FJ564080
<i>Gomesa echinata</i>	(Rchb.f.) M.W.Chase & N.H.Williams	Faria et al. s.n.	UEC	FJ565406	FJ564897	FJ563531	FJ562823	FJ564383
<i>Gomesa eleutherosepala</i>	(Barb.Rodr.) M.W.Chase & N.H.Williams	Chase 83426	K	FJ565203	FJ564717	FJ563171	FJ562478	FJ564030
<i>Gomesa flexuosa</i>	(Sims) M.W.Chase & N.H.Williams	Chase O-98	K	AF350552	AF350631	FJ563189	FJ562497	FJ564049
<i>Gomesa forbesii</i>	(Hook.) M.W.Chase & N.H.Williams	Faria & Ribeiro 1039	UEC	FJ565429	FJ564922	FJ563556	FJ562847	FJ564408
<i>Gomesa glaziovii</i>	Cogn.	Faria et al 1034	UEC	FJ565433	FJ564926	FJ563560	FJ562851	FJ564412
<i>Gomesa gomezoides</i>	(Barb.Rodr.) Pabst	Chase O-151	K	AF350553	AF350632	FJ563213	FJ562522	FJ564074

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APPENDIX *Continued*

Species	Authors	Voucher	Herbarium/ number	GenBank ITS	GenBank <i>matK</i>	GenBank <i>3' ycf1</i>	GenBank <i>5' ycf1</i>	GenBank <i>trnH-psbA</i>
<i>Gomesa gracilis</i>	(Lindl.) M.W.Chase & N.H.Williams	<i>Faria et al</i> 975	UEC	FJ565411	FJ564902	FJ563536	FJ562828	FJ564388
<i>Gomesa handroi</i>	(Hoehne) Pabst	<i>Koehler s.n.</i>	UEC		FJ564928	FJ563562	FJ562853	FJ564414
<i>Gomesa hookeri</i>	(Rolfe) M.W.Chase & N.H.Williams	<i>Faria et al</i> 1020	UEC	FJ565427	FJ564920	FJ563554	FJ562845	FJ564406
<i>Gomesa hydrophila</i>	(Barb.Rodr.) M.W.Chase & N.H.Williams	<i>Singer et al</i> <i>s.n.</i>	UEC	FJ565419	FJ564910	FJ563544	FJ562836	FJ564396
<i>Gomesa imperatorismaximiliani</i>	(Rechb.f.) M.W.Chase & N.H.Williams	<i>Chase 84504</i>	K	FJ565207	FJ564720	FJ563181	FJ562489	FJ564041
<i>Gomesa kautskyi</i>	(Pabst) M.W.Chase & N.H.Williams	<i>Faria 37</i>	UEC	FJ565423	FJ564914	FJ563548	FJ562839	FJ564400
<i>Gomesa lietzei</i>	(Regel) M.W.Chase & N.H.Williams	<i>Whitten</i> 3001	FLAS	FJ565625	FJ565117	FJ563786	FJ563071	FJ564638
<i>Gomesa longipes</i>	(Lindl. & Paxt.) M.W.Chase & N.H.Williams	<i>Pansarin</i> 725	UEC	FJ565417	FJ564908	FJ563542	FJ562834	FJ564394
<i>Gomesa macronyx</i>	(Rechb.f.) M.W.Chase & N.H.Williams	<i>Chase 85121</i>	K	FJ565199	FJ564713	FJ563160	FJ562465	FJ564017
<i>Gomesa macropetala</i>	(Lindl.) M.W.Chase & N.H.Williams	<i>Faria et al.</i> <i>s.n.</i>	UEC	FJ565424	FJ564915	FJ563549	FJ562840	FJ564401
<i>Gomesa pirarensis</i>	(Rechb.f.) M.W.Chase & N.H.Williams	<i>Faria et al.</i> <i>s.n.</i>	UEC	FJ565418	FJ564909	FJ563543	FJ562835	FJ564395
<i>Gomesa planifolia</i>	Klotzsch ex Rechb.f.	<i>Chase 83424</i>	K	AF350554	AF350633	FJ563159	FJ562464	FJ564016
<i>Gomesa praetexta</i>	(Rechb.f.) M.W.Chase & N.H.Williams	<i>Faria &</i> <i>Ribeiro 1036</i>	UEC	FJ565412	FJ564903	FJ563537	FJ562829	FJ564389
<i>Gomesa pubes</i>	(Lindl.) M.W.Chase & N.H.Williams	<i>Chase 85119</i>	K	FJ565190	FJ563836	FJ563139	FJ562444	FJ563995
<i>Gomesa radicans</i>	(Rechb.f.) M.W.Chase & N.H.Williams	<i>Whitten</i> 2988, <i>Whitten</i> 99254	FLAS	FJ565624	FJ565116	FJ563785	FJ563070	FJ564637
<i>Gomesa ranifera</i>	(Lindl.) M.W.Chase & N.H.Williams	<i>Chase 85122</i>	K	FJ565200	FJ564714	FJ563161	FJ562466	FJ564018
<i>Gomesa recurva</i>	Lodd.	<i>Faria et al</i> 1042	UEC	FJ565435	FJ564929	FJ563563	FJ562854	FJ564415
<i>Gomesa sarcodes</i>	(Lindl.) M.W.Chase & N.H.Williams	<i>Pansarin</i> 315	UEC	FJ565422	FJ564913	FJ563547	FJ562838	FJ564399
<i>Gomesa sessilis</i>	Barb.Rodr.	<i>Faria et al</i> 116	UEC	FJ565434	FJ564927	FJ563561	FJ562852	FJ564413
<i>Gomesa spiloptera</i>	(Lindl.) M.W.Chase & N.H.Williams	<i>Faria et al.</i> 98/32	UEC	FJ565428	FJ564921	FJ563555	FJ562846	FJ564407
<i>Gomesa varicosa</i>	(Lindl.) M.W.Chase & N.H.Williams	<i>Faria et al</i> 1043	UEC	FJ565432	FJ564925	FJ563559	FJ562850	FJ564411
<i>Gomesa varicosa</i>	(Lindl.) M.W.Chase & N.H.Williams	<i>Whitten</i> 3611	FLAS	FJ565668	FJ565161	FJ563829	FJ563113	FJ564682
<i>Gomesa venusta</i>	(Lindl.) M.W.Chase & N.H.Williams	<i>Williams</i> N522 MSBG 1981–1050A	FLAS	FJ565358	FJ564850	FJ563458	FJ562754	FJ564310
<i>Gomesa viperina</i>	(Lindl.) M.W.Chase & N.H.Williams	<i>Gerlach 98/</i> 2080	M	FJ565347	FJ564841	FJ563446	FJ562742	FJ564298
<i>Gomesa warmingii</i>	(Rechb.f.) M.W.Chase & N.H.Williams	<i>Chase 86211</i>	K	FJ565226	FJ564739	FJ563228	FJ562539	FJ564089
<i>Gomesa warmingii</i>	(Rechb.f.) M.W.Chase & N.H.Williams	<i>Costa 049/</i> 2003	UEC	FJ565430	FJ564923	FJ563557	FJ562848	FJ564409
<i>Gomesa welteri</i>	(Pabst) M.W.Chase & N.H.Williams	<i>Faria et al</i> 1015	UEC	FJ565416	FJ564907	FJ563541	FJ562833	FJ564393
<i>Gomesa widgrenii</i>	(Lindl.) M.W.Chase & N.H.Williams	<i>Whitten</i> 3559	FLAS	FJ565658	FJ565150	FJ563818	FJ563103	FJ564671
<i>Nohawilliamsia orthostates</i>	(Ridl.) M.W. Chase & Whitten	<i>Chase 8175</i>	K	FJ565399	FJ563950	FJ563521	FJ562816	FJ564373
<i>Oncidium altissimum</i>	(Jacq.) Sw.	<i>Atwood 5602</i>	FLAS	FJ565295	FJ563914	FJ563363	FJ562663	FJ564220
<i>Oncidium durangense</i>	Hagsater	<i>Whitten</i> 99246	FLAS	AF350811	FJ564941	FJ563587	FJ562876	FJ564438

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APPENDIX *Continued*

Species	Authors	Voucher	Herbarium/ number	GenBank ITS	GenBank <i>matK</i>	GenBank 3' <i>ycf1</i>	GenBank 5' <i>ycf1</i>	GenBank <i>trnH-psbA</i>
<i>Oncidium ghiesbreghtianum</i>	A. Rich. & Galeotti	<i>Chase 86117</i>	K	AF350563	AF350642	FJ563190	FJ562498	FJ564050
<i>Oncidium hastatum</i>	(Ruiz & Pavon) Mansf.	<i>Whitten 3016</i>	FLAS	AF350812	FJ564787	FJ563350	FJ562652	FJ564209
<i>Oncidium maculatum</i>	(Lindl.) Lindl.	<i>Atwood 5604</i>	FLAS	AF350806	FJ563917	FJ563366	FJ562666	FJ564223
<i>Oncidium oblongatum</i>	Lindl.	<i>Williams N220</i>	FLAS	AF350820	FJ563912	FJ563358	FJ562659	FJ564216
<i>Oncidium reichenbachii</i>	Lindl.	<i>Atwood 5605</i>	FLAS	AF350805	FJ563916	FJ563365	FJ562665	FJ564222
<i>Oncidium wydleri</i>	Rchb.f.	<i>Chase 86069</i>	K	AF350801	FJ563849	FJ563187	FJ562495	FJ564047
<i>Otoglossum chiriquense</i>	(Rchb.f.) Garay & Dunst.	<i>Chase 86242</i>	K	AF432977	AF433036	FJ563174	FJ562481	FJ564033
<i>Rodriguezia lanceolata</i>	Ruiz & Pav.	<i>Chase 83002</i>	K	AF350542	AF350621	FJ563162	FJ562467	FJ564019
<i>Tolumnia henekenii</i>	(R.H. Schomb. ex Lindl.) Nir	<i>Whitten 3017</i>	FLAS	AF350535	AF350614	FJ563275	FJ562582	FJ564137
<i>Warmingia eugenii</i>	Rchb.f.	<i>Chase 84460</i>	K	FJ565196	FJ563841	FJ563154	FJ562459	FJ564011
<i>Zelenkoa onusta</i>	(Lindl.) N.H. Williams & M.W. Chase	<i>Chase 83170</i>	K	AF350555	AF350634	FJ563178	FJ562485	FJ564037