

Generic delimitation in the *Gomesa* alliance (Orchidaceae, Oncidiinae) based on molecular and morphological evidence

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Summary: Molecular phylogenetics has now provided a new approach to the taxonomy of Oncidiinae and related taxa. The concepts of numerous previously accepted genera and their interrelations have been brought into question. One of the most significant changes in the systematics of *Oncidium*-like orchids concern the recognition of *Gomesa* and its closely allied genera. In this paper, a taxonomic revision of the *Gomesa* alliance is presented based on morphological and molecular analyses. We selected 20 morphological characters which, in our opinion, discriminate the group of species of the *Gomesa* clade. In all phenograms presented in this paper, there are some groups of genera which are characterized by a series of common characters – these similarities are discussed. Several subclades within *Gomesa* s.l. can be recognized in the phylogenetic trees: *Alatiglossum-Kleberella-Neoruschia-Nitidocidium*, *Carriella-Campaccia-Baptistonia*, *Rodrigueziopsis*, *Coppensia flexuosa*, *Ornithophora*, *Rodrigueziella-Gomesa*, *Brasilidium-Carenidium*, *Menezesiella-Coppensia varicosa* group, and *Rhinocidium*. Thirteen genera are recognized within the studied orchid group: *Alatiglossum*, *Baptistonia*, *Brasilidium*, *Carenidium*, *Carriella*, *Coppensia*, *Gomesa*, *Menezesiella*, *Neoruschia*, *Nitidocidium*, *Ornithophora*, *Rhinocidium* and *Rodrigueziopsis*. Section *Emarginata* of *Baptistonia* is elevated to the subgeneric rank. The genus *Rodrigueziella* is reduced to a section within *Gomesa*. Fourteen new combinations within *Alatiglossum*, *Coppensia*, *Brasilidium*, *Menezesiella*, *Nitidocidium*, and *Rhinocidium* are proposed. Each taxon is morphologically characterized and a dichotomous key is provided for the accepted genera.

Keywords: *Gomesa*, taxonomy, Orchidaceae, morphology, phylogeny

The orchid subtribe Oncidiinae has been an issue of debate among taxonomists in respect to its systematic position and internal classification for a long time. This taxon was proposed by BENTHAM (1881), who included numerous genera resembling *Oncidium* Sw. In Schlechter's classification system, Oncidiinae were divided into 12 subtribes (SCHLECHER 1926). The subsequent taxonomic concepts varied greatly regarding oncidoid orchids depending on the emphasized characters used in the classification (DRESSLER 1993; GARAY & STACY 1974; SZLACHETKO 1995; SENGHAS 1997). Some of the previously recognized sections within *Oncidium* were elevated to the generic rank, e.g. *Cohniella* Pfitzer (sect. *Teretifolia*), *Grandiphyllum* Docha Neto (sect. *Pulvinata* and part of sect. *Paucituberculata*), *Ampliglossum* Campacci (sect. *Synsepala*, *Verrucituberculata*, and *Oblongata*), *Caucaea* Schltr. (sect. *Cucullata*) or *Vitekorchis* Romowicz & Szlach. (sect. *Excavata*) or included in previously described genera, as e.g. *Baptistonia* Barb. Rod. (section *Waluewa*).

Molecular phylogenetics provides a new approach to the taxonomy of Oncidiinae and related taxa (GARAY & STACY 1974; SZLACHETKO 1995; SENGHAS 1997; WILLIAMS et al. 2001a, b; NEUBIG et al. 2012). The concepts of numerous previously accepted genera and their interrelations have been brought into question. One of the most significant changes in the systematics of *Oncidium*-like orchids concerns the recognition of *Gomesa* R. Br. and its closely allied genera.

The aim of the present study was to evaluate differences in several morphological characters between members of *Gomesa* s. str. and related groups of species and to critically evaluate their implication by comparing with previously published phylogenetic data.

Historical background on *Gomesa* and relatives

The genus *Gomesa* was described by BROWN (1815) in the beginning of 19th century based on *Gomesa recurva*. The author found this orchid different from other taxa in basally connate lateral sepals, sessile, entire, unspurred lip which is adnate to the gynostemium in the lower part and ornamented by two longitudinal lamellae in the free part. PFITZER (1887) included the genus in Odontoglossinae (originally Odontoglosseae) together with several other genera, i.e. *Oncidium*, *Solenidium* Lindl., *Sigmatostalix* Rchb. f., *Lockhartia* Hook. and *Zygostates* Lindl. In subsequent studies, *Gomesa* was placed within Oncidiinae (SAITOU & NEI 1987; STACE 1989; DRESSLER 1993; SZLACHETKO 1995). About 35 species were included in *Gomesa* until 2009, the last one was described in 1972. Six of them were included in *Rodrigueziella* Kuntze, two in *Binotia* Rolfe, one in *Rodriguezia* Ruiz & Pav. and *Notylia* Lindl. and about 6 others were synonymized with other *Gomesa* species (SENGHAS 1997).

The genus *Carenidium* was described by Baptista in 2006 (in DOCHA NETO et al. 2006) based on *Oncidium concolor* Hook. The author included here 10 species and in the same paper he elevated *Oncidium* sect. *Rhinoceroles* to generic rank under the name *Rhinocidium*. This taxon contained plants with subsimilar tepals, connate lateral sepals and discs ornamented with horn-like callus. In 2006 and 2007, the species *O. disciferum*, *O. fuchsii*, *O. ouricanense*, *O. paranense*, *O. raniferum* and *O. welteri* were transferred into this genus (DOCHA NETO et al. 2006; DOCHA NETO & BAPTISTA 2007). The concept of *Rhinocidium* was therefore modified and it included also plants with bipartite callus composed of two rounded plates. Meanwhile, the new genus *Menezesiella* Chiron & V.P. Castro (CHIRON & CASTRO-NETO 2006) was established for representatives of the *O. raniferum* complex which included *O. hookeri*, *O. loefgrenii*, *O. paranaensis*, and *O. raniferum*. Moreover, the genus *Baptistonia* Barb. Rodr. was restituted and revised by CHIRON & CASTRO-NETO (2004), CASTRO-NETO (2008), CHIRON (2008) and CHIRON et al. (2009).

The authors proposed numerous new combinations within this genus which in their concept embraced i.a. *O. venustum* which was first placed within *Carenidium* (Baptista in DOCHA NETO et al. 2006) and later transferred to the monospecific genus *Campaccia* (CAMPACCI et al. 2011). In 2006, an additional genus, *Ampliglossum* Campacci, was proposed (DOCHA NETO et al. 2006). It comprises plants similar to the *Baptistonia* representatives with rugose pseudobulbs, paniculate inflorescence, subsimilar tepals, broad lip with tuberculate callus and with glabrous gynostemium ornamented by inconspicuous wings. In *Ampliglossum*, the author included, among others, *O. welteri*. In the same year, Castro and Lacerda created the monospecific genus *Carriella* for *Baptistonia colorata* (Königer & J.G. Weinm.) Chiron (CASTRO-NETO 2006). A few months later, being unaware about Brazilian research, Szlachetko and colleagues (SZLACHETKO 2006; SZLACHETKO & MYTNIK-EJSMONT 2006; ROMOWICZ & SZLACHETKO 2006) published papers separating some genera from *Oncidium* s.l. All of them must now be treated as synonyms (Art. 11 International Code of Nomenclature).

Another monospecific taxon, *Nitidocidium* F. Barros & V.T. Rodrigues, was established in 2010. The only representative of this genus is *Nitidocidium gracile* (Lindl.) F. Barros & V.T. Rodrigues (≡

Oncidium gracile Lindl.) which differs from other species included in *Oncidium* sect. *Concoloria* by the gynostemium structure (column part nearly as long as the anther) and lip form (indistinctly 3-lobed, with rectangular, bifid callus at the base). Later, *O. paranense* was separated as the monospecific genus *Hardingia* Docha Neto & Baptista, as it did not fulfil the defined criteria for any existing genus (CAMPACCI et al. 2011). These orchids being somewhat similar to *Baptistonia*, which were recognized previously as representatives of *Oncidium* sect. *Crispa* Rchb. f. ex Pfitzer, were transferred into the new genus *Brasilidium* by DOCHA NETO et al. (2006). The specific composition of this taxon was later evaluated by BARROS & RODRIGUES (2010a), DOCHA NETO & CAMPACCI et al. (2011) and KLEIN VARELLA (2011).

The other group of *Oncidium*-like plants recognized within the *Gomesa* clade was included by Lindley in section *Barbata*. This taxon was elevated to generic rank and named *Alatiglossum* by DOCHA NETO et al. (2006). The concept of this genus was later revised by DOCHA NETO & BENELLI (2006), DOCHA NETO & BAPTISTA (2007) as well as by BAPTISTA & DOCHA NETO (2007). Shortly after formal description of *Alatiglossum*, CASTRO-NETO & CATHARINO (2006) segregated two other taxa from this genus: the monospecific *Neoruschia* and *Kleberiella*, including six species. The last group of *Oncidium*, which is included in the *Gomesa* clade, consists of orchids included by various authors in different sections of *Oncidium* and currently recognized as *Coppensia*. This genus was described by DUMORTIER (1835) based on *Oncidium bifolium* Sims and restituted by CAMPACCI (2006) who considered it similar to *Baptistonia*, characterized by compressed, ovoid, rugose pseudobulbs, inconspicuous sepals, lip ornamented by verrucose or lamellate callus and glabrous gynostemium with minute wings (BAPTISTA & DOCHA NETO 2006).

With the exception of all those mentioned species that were previously included in the various sections of *Oncidium*, the *Gomesa* clade includes representatives of two *Rodriguezia*-like genera. The first one, *Rodriguezella*, was formally proposed by KUNTZE (1891) based on *Theodorea* Barb. Rodr. The latest name was previously in use for a genus of Asteraceae. BARBOSA RODRIGUES (1882) considered *Theodorea gomezoides* as related to *Rodriguezia* and *Gomesa* based on floral characters. Six species have been described so far within *Rodriguezella*, the latest in 1976 (PABST 1976). The establishment of the genus *Rodrigueziopsis* was proposed by SCHLECHTER (1920), who considered *Rodriguezia eleutherosepala* Barb. Rodr. and *R. microphyta* Barb. Rodr. as different from other *Rodriguezia* species regarding lip and column structure. In respect to gynostemium morphology, Schlechter found *R. eleutherosepala* similar to *Trizeuxis* and *Capanemia*. From the time since the genus had been described, just one new species within *Rodrigueziopsis*, *R. antillensis* Withner (WITHNER 1971) was found; however, it was soon recognized as a representative of the monotypic *Antillanorchis* Garay (GARAY & STACY 1974).

The last taxon included in the *Gomesa* clade is *Ornithophora* described by BARBOSA RODRIGUES (1882) based on the Brazilian plant named *O. quadricolor*. This species was in the author's opinion different from the similar *Sigmatostalix* in respect to gynostemium structure and from *Ornithocephalus* and *Phymatidium* in respect to habit. Subsequent studies by GARAY & PABST (1951) revealed that *O. quadricolor* is conspecific with the previously described *Sigmatostalix radicans* Rchb. f. (REICHENBACH 1864) which was also transferred to *Ornithophora*.

All taxa mentioned above were included in *Gomesa* by Chase & Williams (in CHASE et al. 2009). There, the genus which previously contained less than 20 species and was restricted to Brazil, Paraguay and northeastern Argentina was reshaped into a large taxon with over 120 species

widely distributed in the Neotropics. CHASE et al. (2009) also did not propose any infrageneric classification of *Gomesa* and explained that this would serve little purpose in groups with high levels of parallelism. This concept of the genus was accepted by NEUBIG et al. (2012) who stated that almost all species included in *Gomesa* have fused lateral sepals, a trait that makes them easy to recognize despite their floral diversity.

Unfortunately, the genus cannot be clearly defined in regard to morphological features by this broad concept. Fused lateral sepals are not observed in numerous representatives of *Gomesa* s.l. On the other side, such connation is present in some other taxa, e.g. *Symphyglossum* Schltr. (considered by these authors as member of *Oncidium* Sw.), *Systemoglossum* Schltr. (*Miltonia* Lindl.), *Polyotidium* Garay or *Goniochilus* M.W. Chase (*Leochilus* Knowles & Westc.).

Materials and methods

Morphology

We examined over 5000 herbarium specimens and liquid preserved flowers of oncidoid orchids deposited in AMES, AMO, BM, COL, CUVC, F, FLAS, HB, HUA, JAUM, K, MBM, MO, NY, P, PMA, RB, SP, UGDA, VALLE and W (THIERS 2018) as well as living plants by standard procedures. Every studied specimen was photographed and data from the labels were taken. Both vegetative and generative characters of each plant were examined. The form and size of pseudobulbs and leaves were examined first, then inflorescence architecture and form and size of the floral bracts. Finally, flower morphology was studied after proper rehydration.

Numerical analyses

In our numerical study, 20 discriminative characters were used to describe the generative and vegetative structures of *Gomesa* s.l.; as an outgroup we selected *Oncidium altissimum* (Jacq.) Sw., a generic type of *Oncidium*. This approach was chosen on account of the recent concept of *Oncidium* being so broad, however, that its members are not discernible by morphology. Table 1 provides a complete list of the features included in the database as well as selected sets. We used the numerical 0-1-(2) system of character coding; it is univocal and the most commonly used approach in phenetic and cladistic analysis. The incorporation of each feature for each genus in the *Gomesa* complex resulted in a data matrix containing 360 units (Table 2). The PAST software was used to create hierarchic phenograms and cladograms (HAMMER et al. 2001). Cluster analysis is a typical procedure used in phenetic research (STACE 1989). A distance matrix was created using the Manhattan measure, an average subtraction measured across the dimensions $D = \sum_i |X_{ij} - X_{ik}|$. Several methods of clade amalgamation were used:

- 'middle links rule unweighted pair-group average' (UPGMA) as the most phenetical algorithm;
- neighbor joining (NJ) as the algorithm for optimizing a tree according to the balanced minimum evolution (SAITOU & NEI 1987);
- the parsimony method (maximum parsimony, MP) following the rule that the best solution is the easiest one and requiring the fewest *ad hoc* assumptions (SWOFFORD et al. 1996);
- Ward's minimum variance criterion with heuristic techniques of tree creation with parameter stepwise addition (adding taxa in varying orders: closest, furthest or mixed) and TBR parameter (with tree-bisection-reconnection, TBR, branch swapping), saving all the best trees and significantly using the highest number of 1000 trees.

Table 1. Features included in the database for numerical analyses.

| | |
|----|--|
| 1 | Rhizome: 0 – abbreviated; 1 – elongate |
| 2 | Pseudobulbs: 0 – smooth; 1 – sulcate |
| 3 | Pseudobulbs: 0 – unifoliate; 1 – bifoliate; 2 – 1- or 2-leaved |
| 4 | Sheaths: 0 – leafy; 1 – bladeless; 2 – obscurely leafy |
| 5 | Inflorescence: 0 – many-flowered; 1 – few-flowered |
| 6 | Lateral sepals: 0 – free to the base; 1 – connate basally |
| 7 | Lip: 0 – sessile; 1 – clawed |
| 8 | Lip: 0 – flat; 1 – geniculate |
| 9 | Lip: 0 – 3-lobed; 1 – unlobed or almost so |
| 10 | Isthmus: 0 – entire margins; 1 – fringed margins |
| 11 | Lip callus: 0 – lamellate; 1 – dissecting; 2 – pad-like; 3 – horn-like |
| 12 | Lip callus: 0 – glabrous; 1 – pubescent |
| 13 | Gynostemium vs lip: 0 – obtuse angle; 1 – right angle; 2 – acute angle; 3 – parallel |
| 14 | Column part: 0 – alate; 1 – wingless |
| 15 | Column part: 0 – free from the lip; 1 – fused with the lip margins |
| 16 | Column part: 0 – glabrous; 1 – glandular |
| 17 | Anther: 0 – subventral; 1 – subdorsal |
| 18 | Apical clinandrium: 0 – obscure; 1 – prominent |
| 19 | Receptive surface: 0 – large; 1 – narrow |
| 20 | Tabula infrastigmatica: 0 – absent; 1 – present |

Statistical application was used to carry out analyses (software products and solutions originally developed by StatSoft and acquired by Dell in March 2014). Multidimensional Scaling (MDS) was prepared first. In general, the goal of this analysis was to detect meaningful underlying dimensions to explain observed similarities or dissimilarities (distances) between taxa. All data from the dissimilarity matrix were analyzed in addition to correlation matrices. Resulting from the MDS analysis, a two-dimensional representation of the taxa was obtained along with a two-dimensional map. The actual orientations of the axes are arbitrary and can be rotated in any direction. The second step was to prepare a Principal Components & Classification Analysis (PCAA). PCAA can be used as a classification technique in which the taxa are plotted in space generated by the factor (distance) axes. In the graph, taxa fall in a circle, called the correlation circle, with the pair of factor axes as its axes. The variables, when projected onto this circle, reveal quite some information about themselves. The variables that are correlated with a particular factor can thus be identified, thereby providing information as to which variables can explain the given factor. The last step and process is called cluster analysis – a commonly used method of analysis in phenetic research (STACE 1989). The distance matrix was created using the most widely used type of correlation coefficient, Pearson's coefficient r , also called linear or product-moment correlation. The correlation coefficient determines the extent to which values of two variables are 'proportional' to each other. We also used single linkage (nearest neighbor) (SL), as an amalgamation rule.

Table 2. Data matrix for numerical analyses.

| | <i>Gomesa</i> s.s. | <i>Rodrigueziella</i> | <i>Rodrigueziopsis</i> | <i>Nitidocidium</i> | <i>Neoruschia</i> | <i>Kleberella</i> | <i>Alatiglossum</i> | <i>Cariella</i> | <i>Campaccia</i> | <i>Baptistonia</i> | <i>Basitidium</i> | <i>Carenidium</i> | <i>Ornithophora</i> | <i>Menezziella</i> | <i>Coppensia (varicosum)</i> | <i>Rhinocidium</i> | <i>Coppensia (flexuosum)</i> | <i>Oncidium (altissimum)</i> | |
|------------------------------|-------------------------|-------------------------|-------------------------|---------------------|-------------------|-------------------------|-------------------------|------------------|------------------|-------------------------|-------------------|-------------------|---------------------|--------------------|------------------------------|--------------------|------------------------------|------------------------------|------------------|
| Rhizome (1) | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | |
| Pseudobulbs (2–4) | 0 1 2 | 0 1 1 | 0 1 0 | 1 1 1 | 0 0 0 | 0 0 1 | 0 0 1 | 0 0 1 | 0 1 1 | 0 0 1 | 0 0 1 | 1 1 1 | 0 1 0 | 1 1 2 | 1 1 0 | 1 1 1 | 0 2 0 | 1 2 0 | 1 1 0 |
| Inflorescence (5) | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| Tepals (6) | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| Lip (7–10) | 0 1 1 0 | 0 1 1 0 | 1 0 0 0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 1 | 0 0 0 1 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 | 1 0 0 0 | 1 0 0 0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 |
| Lip callus (11–12) | 0 0 | 0 1 | 0 0 | 0 0 | 1 0 | 1 0 | 1 0 | 0 0 | 1 0 | 1 0 | 1 0 | 0 0 | 0 0 | 2 0 | 1 0 | 3 0 | 1 0 | 1 0 | 1 0 |
| Gynostemium (13–16) | 3 1 0 0 | 3 1 0 0 | 3 1 1 0 | 2 0 0 0 | 1 0 0 0 | 1 0 0 0 | 0 0 0 0 | 0 1 0 0 | 0 0 0 0 | 2 0 0 1 | 1 0 0 0 | 1 0 0 0 | 1 1 0 0 | 0 0 0 0 | 1 0 0 0 | 1 1 0 0 | 1 0 0 0 | 1 0 0 0 | 0 0 0 0 |
| Anther (17) | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Apical clinandrium (18) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Stigma (19) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| Tabula infra-stigmatica (20) | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 |

Phylogenetic analyses

We aligned data for 61/63 nucleotide sequences, one nuclear marker (ITS) and one plastid genome region (*matK*) representing the taxa of Oncidiinae Benth. as well as the outgroup. All sequences were taken from NCBI (<http://www.ncbi.nlm.nih.gov/genbank/>).

DNA sequences were aligned automatically by Seaview (GALTIER et al. 1996) using the MUSCLE algorithm (EDGAR 2004). Maximum parsimony analysis used a heuristic search strategy in PAUP*4.0b10 (SWOFFORD 2000) with tree-bisection-reconnection (TBR) branch swapping, activated MULTREES (holding multiple trees) option, simple addition, and ACCTRAN optimization. All characters were unordered and equally weighted (FITCH 1971). Missing data were coded as '?' and gaps were coded as '-'. All parsimonious trees (10,000) were used to determine the strict consensus tree. Tree length, consistency index (CI), retention index (RI), and homoplasy index (HI) were estimated. Internal support of clades was evaluated by character bootstrapping (FELSENSTEIN 1985) using 1000 replicates. For bootstrap support levels, we considered bootstrap percentages (BP) of 50–70% as weak, 71–85% as moderate, and >85% as strong (KORES et al. 2001).

Results

Morphological data

Data on the comparative morphology of the investigated taxa in *Gomesa* s.l. are presented in Appendix 1. We selected 20 morphological characters which in our opinion discriminate the group of species of the *Gomesa* clade. We present some phenograms in this paper (Figs 1–4). Based on some of the characters the genus, *Gomesa* s.l. can be divided into two groups (5 – inflorescence many-flowered vs few-flowered; 6 – lateral sepals free to the base vs connate basally; 7 – lip sessile vs clawed; 14 – column part alate vs wingless), others can be found in minor assemblages of species (1 – rhizome abbreviated vs elongated; 2 – pseudobulbs smooth vs sulcate; 8 – lip flat vs geniculate) or some are even unique for a single group (11 – character of lip callus; 15 – column part free or fused with lip margins; 16 – column part glabrous vs glandular; 17 – anther subventral vs subdorsal; 18 – apical clinandrium obscure vs prominent). In all phenograms presented in this paper (Figs 1–4), there are some groups of genera which are characterized by a series of common characters. Below we would like to discuss them briefly.

The pair *Gomesa-Rodrigueziella* (UPGMA) can be easily distinguished from other members of *Gomesa* s.l. by having an entire lip. In all other species of the *Gomesa* s.l. clade, the lip is distinctly lobed, although the type of lobation may vary between species. The lip is furnished with two more or less parallel lamellae, which are pubescent in *Rodrigueziella*. However, numerous weak differences between representatives of the two genera are noticeable. Lateral sepals of *Gomesa* s. str. are basally connate and in *Rodrigueziella* they are free to the base.



Figure 1. Morphological variation in *Gomesa* s.l. Dendrogram construction using the UPGMA algorithm and the Manhattan distance measures.



Figure 2. Morphological variation in *Gomesa* s.l. Scatterplot using Cartesian coordinates to display values for two dimensions.

Other differences concern the sheaths enclothing the pseudobulbs (bladeless in *Rodrigueziella* vs obscurely leafy in *Gomesa*) and the inflorescence (few-flowered in *Rodrigueziella* vs many-flowered in *Gomesa*). They are of minor taxonomic value, as they are distributed all over the species of this clade.

The second group (UPGMA) of genera includes *Ornithophora* and *Rodrigueziopsis*, which are characterized by having elongate aerial rhizomes between pseudobulbs. In other analyzed taxa within *Gomesa* s.l., this character can be found in the *Coppensia flexuosa* group only. The most symptomatic morphological differences are recorded for the gynostemium and lip of *Rodrigueziopsis*, varying in almost all aspects from cases observed in *Ornithophora*.

The gynostemium is elongate, wingless in both *Ornithophora* and *Rodrigueziopsis*, but in the former the gynostemium and lip form more or less a right angle, and in the latter both these structures are parallel, with the column part being connate with the lip margins. Along with the lamellate callus they both form a tube accessible for insects with long mouthparts. Such a position of the gynostemium versus the lip results in a reflexion of the anther and exposition of the rostellum and viscidium. In *Rodrigueziopsis*, the column produces two elongate projections on both sides of the rostellum, which are missing in *Ornithophora*. These differences between *Ornithophora* and *Rodrigueziopsis* undoubtedly reflect an adaptation to various pollination systems and support the recognition of both groups as distinct genera.

We could not detect any unique character of the pair *Nitidocidium* and *Carenidium* (UPGMA), but we have been able to identify some features which can be used in distinguishing both of them: the lip of *Nitidocidium* is sessile and geniculately bent near the middle, while this structure



Figure 3. Morphological variation in *Gomesa* s.l. Pincipal components and classification analysis (PCCA) using all variables for analysis.

is clawed and flat in *Carenidium*; a prominent tabula infrastigmatica is observed in *Nitidocidium* (vs missing in *Carenidium*); in both genera, lip and gynostemium are joined forming a somewhat different angle (acute in *Nitidocidium* vs right in *Carenidium*).

Although *Rhinocidium* and *Menezesiella* are superficially similar in flower appearance (UPGMA), both can be easily distinguished from each other by a series of characters. The structure, on which the generic name of *Rhinocidium* is based, is a horn-like callus in the lip center, which has not been found elsewhere in the *Gomesa* clade. The lip callus of *Menezesiella* is large and pad-like produced at the lip base. The lateral sepals of *Rhinocidium* are connate basally (vs free to the base in *Menezesiella*). In both genera, the gynostemium is wingless, short and joined with the lip at an obtuse angle in *Menezesiella*, while it is more elongate and slender forming a right angle with the lip in *Rhinocidium*. Additionally, a tabula infrastigmatica is observed in *Menezesiella*, but it is absent in *Rhinocidium*. In conclusion, we consider both groups as distinct.

Oncidium (represented in our analyses by *O. altissimum*) and both groups of *Coppensia* (UPGMA) are vegetatively rather similar, although the *Coppensia flexuosa* group is rather isolated by having an elongated rhizome (vs abbreviated) and smooth pseudobulbs (vs sulcate). On the other hand, the *Coppensia varicosa* group is the only one of the three groups with lateral sepals that are basally connate. There are also some differences in the angle between lip and gynostemium junction.

In our phenetic analyses, *Kleberella* is usually joined with *Neoruschia* or *Alatiglossum* in various combinations. Such an ensemble is rather difficult to define, as its genera can be easily distinguished by a series of morphological characters, concerning both vegetative, floral and reproductive structures.



Figure 4. Morphological variation in *Gomesa* s.l. Dendrogram construction using the single linkage algorithm and the Pearson r correlation distance measures.

Additionally, *Gomesa-Rodrigueziella*, *Ornithophora-Rodrigueziopsis* and *Nitidocidium-Carenidium* are variously grouped together by NJ and Ward methods.

Morphology-based cladograms offer somewhat different results, with three main units, which are not supported by any unique set of features.

The first group comprises the genera *Neoruschia*, *Kleberella*, *Carriella* and *Alatiglossum*. They are similar in habit, i.e. they possess bladeless sheaths enclathing pseudobulbs (except *Neoruschia*), and a usually few-flowered inflorescence (except *Alatiglossum*), although they are very difficult to be defined in respect to floral and reproductive organs. For example, *Kleberella* and *Alatiglossum* display a unique feature: fimbriate margins of the lip isthmus, not found elsewhere in the *Gomesa* s.l. clade. The lip callus is lamellate in *Carriella*, but in both *Kleberella* and *Alatiglossum* it is more complex and consists of dissected segments of various form. Additionally, the lip in the only species of this genus, *C. colorata* (Königer & J.G. Weinm.) V.P. Castro & K.G. Lacerda, is sessile (vs clawed in others). There are some other differences between some of the genera, summarized in Appendix 1.

Brasilidium and *Baptistonia* are easy to discern based on their gynostemium structure. Within *Gomesa* s.l., species of *Baptistonia* are particularly characterized by a glandular column part and prominent apical clinandrium exceeding the anther.

In contrast to *Ornithophora* and *Rodrigueziopsis*, there is a distinctly abbreviated rhizome in *Rodrigueziella*, and its pseudobulbs are basally enclathed in bladeless sheaths, the lip is sessile, more or less unlobed, and the lip callus is pubescent. On the other hand, the column part is fused with the lip in *Rodrigueziopsis* and the anther is subdorsal.



Figure 5. Fragment of single maximum likelihood tree resulting from analysis of the combined five-region data presented by NEUBIG et al. (2012).



Figure 6. One of the most parsimonious trees from ITS1-5.8S-ITS2 sequences. Length of branches is shown above; values below branches represent bootstrap support (≥ 50%); arrows indicate clades that collapse in the strict consensus tree; gi denotes the ID number of GenBank.

Neither phenograms nor cladograms based on morphological characters are congruent with the phylogenetic tree.

Molecular data

In the phylogenetic studies of CHASE et al. (2009), the authors analyzed 43 samples of *Gomesa* s.l., including five representatives of *Gomesa* s.str. Similar results were presented by NEUBIG et al. (2012) who investigated 60 samples of *Gomesa* s.l., including 46 species representing 16 of the genera mentioned above (Fig. 5). In our study, the statistics for two data matrices (ITS, *matK*) are separated by 'l'. The number of analyzed taxa were 61/63, respectively. The aligned length of the matrix was 776/1782 characters, of which 173/120 were parsimony informative. The results of maximum parsimony analyses were 229 (for the ITS matrix) and 10,000 (for the *matK*) parsimonious trees. All of them were used to determine the strict consensus tree. The tree length for one of the most parsimonious trees was 396/272, consistency index (CI) = 0.763/0.805 and retention index (RI) = 0.887/0.895. The only difference within the analyzed taxa between our study (Figs 6–7) and the paper by NEUBIG et al. (2012) is the position of *Gomesa chrysostoma* which is included in the *Gomesa* s.str. clade.

NEUBIG et al. (2012) stated that *Gomesa* s.l. vary greatly in regard to floral morphology. As *Gomesa* sensu NEUBIG et al. (2012) contains species previously classified in *Oncidium*, the authors tried to provide characters which make possible to distinguish both genera and they indicated the presence of fused lateral sepals in *Gomesa* s.l., “a trait that makes them easy to recognize despite their floral diversity”. According to these authors, the lateral sepals are usually free in *Oncidium* species. Unfortunately, this is not true and, in fact, fused or free lateral sepals are distributed in various species of *Gomesa* s.l. as well as in *Oncidium* s.l. Despite detailed analysis of morphological structure of *Gomesa* s.l. as well as of *Oncidium* s.l., we were not able to trace a single character unique for one or another group of the species. The only remaining criterion discriminating both genera sensu NEUBIG et al. (2012) seems to be their geographical distribution: most species of *Gomesa* s.l. are from Brazil, whereas *Oncidium* is found in the western parts of South and Central America.

Several subclades within *Gomesa* s.l. can be recognized in the phylogenetic tree (Figs 5–7). The group *Alatiglossum-Kleberrella-Neoruschia-Nitidocidium* is relatively uniform regarding the organization of their reproductive structures, i.e. gynostemium is alate, anther is ventral, stigmatic surface is rather large, apical clinandrium is obscure and a prominent tabula infrastigmatica is observed. But this set of characters can be found in any other Oncidiinae and cannot be treated as unique for this subclade. The relative uniformity of the gynostemium structure is in contrast to their vegetative parts. From the four genera mentioned, only representatives of *Nitidocidium* produce sulcate, bifoliate pseudobulbs, very obscurely 3-lobed lip with apical lobe being the largest and lamellate lip callus. Members of *Kleberrella* and *Alatiglossum* are unique in having fimbriate margins along the lip isthmus, as already mentioned. The gynostemium is almost parallel to the lip.

Within the subclade *Carriella-Campaccia-Baptistonia*, the genus *Baptistonia* is probably the most characteristic taxon by having a glandular column part and prominent apical clinandrium. Both of these are missing in other representatives of *Gomesa* s.l. Additionally, the lip and gynostemium form an acute angle, except in *Campaccia*. The gynostemium of *Carriella*, unlike the other two genera of this clade, is wingless, lateral sepals are free to the base and lip callus is lamellate.



Figure 7. One of the most parsimonious trees for *Gomesa* s.l. species of *marK* gene. Length of branches is shown above; values below branches represent bootstrap support ($\geq 50\%$); arrows indicate clades that collapse in the strict consensus tree; gi denotes the ID number of GenBank.

A unique character of *Campaccia* not found in *Cariella* or only occasionally in *Baptistonia* (i.e., *Baptistonia kautskyi*, *B. pabstii* and *B. pulchella*) is a bifoliate pseudobulb. The common character found in the three genera is a bladeless basal sheath of the pseudobulbs.

Long aerial stolons mark the very characteristic appearance of *Rodrigueziopsis*. This is similar in *Coppensia flexuosa* group and in *Ornithophora*, although in this case, they are much shorter. But the fusion between lip and column part as well as subdorsal anther are not found anywhere in *Gomesa* s.l., except in *Rodrigueziopsis*.

A unique feature of the subclade *Rodrigueziella-Gomesa* is the unlobed or obscurely 3-lobed lip, to which the gynostemium is almost parallel. The latter character is also found in *Rodrigueziopsis*. The differences between *Rodrigueziella* and *Gomesa* are related to the presence of pubescent lip calli in the former as well as bladeless sheaths (obscurely leafy in *Gomesa*), few-flowered inflorescence (many-flowered in *Gomesa*) and a fusion between lateral sepals (connate basally in *Gomesa*).

Delimitation between *Brasilidium* and *Carenidium* concerns the vegetative as well as floral characters. In *Brasilidium*, the predominantly unifoliate pseudobulbs are usually smooth (but see *B. crispum*, Campacii in DOCHA NETO et al. 2006) and produce many-flowered inflorescences (vs sulcate, bifoliate pseudobulbs and few-flowered inflorescences in *Carenidium*). The lip of *Brasilidium* is sessile and carries a dissecting callus, in contrast to the lip of *Carenidium* which is clawed, with lamellate callus. A tabula infrastigmatica is prominent in *Brasilidium*.

Before molecular data had become available, the genus *Ornithophora* was often treated as synonymous with *Sigmatostalix*. Both share similar structure of lip and gynostemium, apparently an example of convergent evolution. Among the members of *Gomesa* s.l., in particular, *Ornithophora* can be distinguished by the presence of prominent stolons (although much shorter than in *Rodrigueziopsis*), wingless, very elongate and slender gynostemium and flat large lip lamina originating on a prominent claw terminated with knob-like callus.

The genera of the subclade consisting of *Menezesiella*, the *Coppensia varicosa* group and *Rhinocidium* can be easily distinguished on the basis of lip callus shape, the most characteristic being the horn-like projection on the lip of *Rhinocidium*. The lip calli of *Menezesiella* consist of large thick pads of tissue at the lip base, in the *Coppensia varicosa* group the lip calli are similar to most of those of Oncidiinae, i.e. dissected into digitate segments. A tabula infrastigmatica is missing in *Rhinocidium* and the gynostemium of *Coppensia varicosa* group members is alate. Others characteristics are distributed in various combinations between these genera.

Members of the *Coppensia flexuosa* group are most similar to *Oncidium altissimum*, differing from the latter by having usually somewhat elongate stolons, smooth pseudobulbs and differently angled connections between lip and gynostemium.

The problem arises on how to delimit both groups of *Coppensia* along morphological means. The only character pair we could detect was caespitose vs rhizomatous habit, although it is not a permanent one. There are two possible scenarios of how to resolve problems with the classification of species falling in both of the aforementioned clades. The first one is to consolidate both *Coppensia* groups along with *Rhinocidium* and *Menezesiella*. A such defined *Coppensia* is morphologically undefinable, however. A second possibility is to maintain the status of separate genera for *Rhinocidium*, *Menezesiella* and *Coppensia* including the *C. flexuosa* and

C. varicosa groups, with the latter genus being paraphyletic. It appears that the rate of evolution of *Menezesiella* and *Rhinocidium* could be higher than in the case of *Coppensia* species. A similar situation was found in *Coelogyne* (GRAVENDEEL et al. 2001) and *Odontoglossum* (KOLANOWSKA & SZLACHETKO 2015).

Discussion

The circumscription of Oncidiinae proposed by NEUBIG et al. (2012) was based on nuclear ITS sequence analyses and on seven plastid regions. The authors recognized 61 clades at the generic level. Most genera are defined by a number of morphological characters. However, we think that some of the genera proposed by NEUBIG et al. (2012) are too broadly defined and cannot be easily recognized on morphological grounds (e.g. *Cyrtochilum* Kunth, *Oncidium* or *Gomesa*). We treated this problem in some previous articles (cf. KOLANOWSKA & SZLACHETKO 2013, 2015; SZLACHETKO & KOLANOWSKA 2014, 2015) as well as some other authors (DALSTRÖM & HIGGINS 2016). The wide concept of *Oncidium* and *Telipogon* Kunth is an issue further pursued in ongoing research.

NEUBIG et al. (2012) often emphasize that “floral morphology must be foregone in Oncidiinae as a basis for generic characters. (...) Floral traits in Oncidiinae are highly plastic and reflect evolutionary shifts in pollinators”. This statement is surprising especially in the case of such plants as orchids, which are highly dependent on pollinators and evolved under pollinator pressure. If floral traits are unimportant in orchid taxonomy, then what else? The authors’ answer: “We feel that it is better to use vegetative features in combination with a few floral traits to define broader genera” (NEUBIG et al. 2012). We tried to turn up such a combination of features for *Oncidium*, but in the end we did not find any. For *Cyrtochilum* s.l. they provided the following combination of features: “Vegetatively, *Cyrtochilum* are distinguished by dull pseudobulbs that are round or ovoid in cross section with two to four apical leaves and two to six leaf-bearing sheaths and relatively thick roots”. There is no need to point out that this combination of characters is not suitable to distinguish *Cyrtochilum*, because it can be found also in *Brassia* R. Br., for example. The situation is similar in the case of *Gomesa* s.l.

The feature that NEUBIG et al. (2012) selected to characterize *Gomesa* s.l., i.e. the presence of fused lateral sepals, is neither unique nor even stable for *Gomesa* species, as discussed in detail before. This character state is widely distributed in many Oncidiinae groups and by itself cannot be treated as discriminative.

The question arises whether it would be more appropriate to distinguish smaller, morphologically unified groups at the rank of genera. Molecular taxonomists are against such an action and argue that “recognition of these segregate genera would require creation of many new genera to maintain monophyly, and these new genera would be difficult to diagnose using floral or vegetative traits” (NEUBIG et al. 2012). But creation of large, highly polymorphic genera creates other problems.

We do not question monophyly of the *Gomesa* clade, at least as some markers indicate, but we hesitate to recognize taxa that are undefinable in respect of morphology. All the more, because it is rather easy to distinguish monophyletic and morphologically homogenous groups of species within *Gomesa* s.l. The question arises, whether one needs to assign a rank to the different genera for such groups. In our opinion, this is reasonable also from a practical point of view for most of them. However, some are better to be lumped with other ones. We will discuss this below. The

only exception is *Coppensia*, which appears to form a paraphyletic unit with *Rhinocidium* nested in this clade. Due to the lack of any permanent morphological character that could separate both groups of *Coppensia*, we prefer to leave them together. A list of species included in the *Gomesa* clade is presented in Appendix 2 together with information about the taxonomic treatment of each of these species by various authors.

Taxonomic treatment

Key to the genera

1. Lip entire to sub-entire, ovate to pandurate or subrhombic in outline 2
- 1* Lip 3-lobed or bipartite 3
2. Lip callus glabrous *Gomesa* sect. *Gomesa*
- 2* Lip callus pubescent *Gomesa* sect. *Rodrigueziella*
3. Lip isthmus more or less fringed *Alatiglossum*
- 3* Lip isthmus entire 4
4. Gynostemium wings obscure or absent 5
- 4* Gynostemium wings/appendages well developed 7
5. Lip bipartite, basal part claw-like *Ornithophora*
- 5* Lip 3-lobed 6
6. Pseudobulbs bifoliate, lip callus in form of massive tissue covering basal part of the lip *Menezesiella*
- 6* Pseudobulbs unifoliate, lip callus consisting of prominent keel running in the lower half and diverging in the apical part *Carriella*
7. Clinandrium exceeding the anther *Baptistonia* subgen. *Baptistonia*
- 7* Clinandrium not exceeding the anther 8
8. Lateral sepals free to the base 9
- 8* Lateral sepals connate at least at the base 10
9. Lip sessile, callus massive, consisting of some digitate and knob-like projections *Neoruschia*
- 9* Lip clawed, callus consisting of two parallel keels in the lower half *Rodrigueziopsis*
10. Pseudobulbs unifoliate *Brasilidium*
- 10* Pseudobulbs 2–3-leaved 11
11. Lip basal part narrower than apical part, lateral lobes much smaller than the middle lobe 12
- 11* Lip basal part wider than apical part, lateral lobes prominent 14
12. Gynostemium with digitate projections *Carenidium*
- 12* Gynostemium broadly winged 13
13. Pseudobulbs enclathed basally in bladeless sheaths, lip basally cuneate, callus consisting of thick pad of tissue, diverging towards the apex into two short keels *Nitidocidium*

- 13* Pseudobulbs basally enclathed in 1–2 leafy sheaths, lip basally 3-lobed, callus consisting of numerous tubercules, elongate projections or thickenings of various form *Coppensia*
14. Lip callus dissected into some plates and variously shaped projections *Baptistonia* subgen. *Emarginata*
- 14* Lip callus horn-like *Rhinocidium*

Nitidocidium F.Barros & V.T.Rodrigues, Bol. CAOB 77–78: 27 (26–29). 2010 [issued on 30 Jun 2010]; Generitype: *Nitidocidium gracile* (Lindl.) F.Barros & V.T.Rodrigues (≡ *Oncidium gracile* Lindl.).

Plants caespitose. Pseudobulbs clustered, large, somewhat flattened, ovoid, shallowly sulcate, bifoliate, enclathed basally in bladeless sheaths. Inflorescence laxly few-flowered. Sepals subsimilar, lateral sepals basally connate. Petals larger than sepals. Lip sessile, basally cuneate, apical lobe transversely elliptic, apically emarginated; callus in the basal part of the lip only, consisting of thick pad of tissue, diverging towards the apex into two short keels, glabrous. Gynostemium forms an acute angle with the lip, erect, rather short and stout. Column part broadly winged near the stigma, wings obliquely rhomboid, entire. Anther subventral. Pollinia 2, obovoid, slightly dorsiventrally flattened, hard, unequally and deeply cleft, empty inside. Apical clinandrium obscure. Stigma large, ovate, deeply concave. Rostellum short but relatively massive, conical-digitate in the middle, obtuse. Viscidium single, large, ellipsoid, very thick, fleshy. Tegula single, oblong, thin, lamellate, delicate, flat. Rostellum remnant bilobulate at the middle, canaliculate on the dorsal surface. Tabula infrastigmatica prominent (Fig. 8).

The genus is easily distinguishable by its peculiar lip form combined with bilamellate lip calli, caespitose habit, sulcate, bifoliate pseudobulbs enclathed basally with bladeless sheaths. A genus of two species known exclusively from Brazil.

- *Nitidocidium gracile* (Lindl.) F.Barros & V.T.Rodrigues
- *Nitidocidium barbaceniae* (Lindl.) Szlach. & Kolan., *comb. nov.*
Basionym: *Oncidium barbaceniae* Lindl., Fol. Orchid. 6/7(*Oncidium*): 32. 1855.

Neoruschia Cath. & V.P. Castro, Richardiana 6(3): 158. 2006 [issued on 30 Jun 2006]; Generitype: *Neoruschia cogniauxiana* (Schltr.) Cath. & V.P. Castro (≡ *Oncidium cogniauxianum* Schltr.).

Plants caespitose. Pseudobulbs clustered, laterally compressed, ovoid, smooth, unifoliate, enclathed in 1–2 leafy sheaths. Inflorescence laxly few-flowered. Flowers relatively large. Sepals subsimilar, lateral sepals basally free. Petals similar to the dorsal sepal. Lip sessile, basally cordate, prominently 3-lobed, the middle lobe transversely elliptic, apically emarginated, much larger than lateral lobes, lateral lobes dentate along upper margins; callus massive, consisting of some digitate and knob-like projections, more or less radiating, glabrous. Gynostemium forms a right angle with the lip, erect, rather short. Column part broadly winged near the stigma, wings obliquely elliptic-ovate, entire. Anther subventral. Pollinia 2, obovoid, slightly dorsiventrally flattened, hard, unequally and deeply cleft, empty inside. Apical clinandrium obscure. Stigma large, ovate, deeply concave. Rostellum short but relatively massive, conical-digitate in the middle, obtuse. Viscidium single, rather small, ellipsoid. Tegula single, oblong, thin, lamellate, delicate, flat. Rostellum remnant bilobulate at the middle, canaliculate on the dorsal surface. Tabula infrastigmatica inconspicuous (Fig. 9).



Figure 8. *Nitidocidium gracile* (Lindl.) F.Barros & V.T. Rodrigues (photo: M. Rosim).

It is similar and closely related to *Alatiglossum*, from which it differs by lacking fimbriate isthmus margins and having inconspicuous tabula infrastigmatica. Combining it with *Alatiglossum* would eventually cause problems with the definition of such a genus. *Neoruschia* is a monotypic genus restricted to SE Brazil:

- *Neoruschia cogniauxiana* (Schltr.) Cath. & V.P. Castro

Alatiglossum Baptista, Colet. Orquídeas Brasil. 3: 87. 2006 [issued on 10 Feb 2006]; Generitype: *Alatiglossum barbatum* (Lindl.) Baptista (≡ *Oncidium barbatum* Lindl.)

= *Kleberella* V.P. Castro & Cath., Richardiana 6(3): 158. 2006 [issued on 30 Jun 2006]; Generitype: *Kleberella uniflora* (Booth ex Lindley) V.P. Castro & Catharino (≡ *Oncidium uniflorum* Booth ex Lindley)

Plants caespitose. Pseudobulbs clustered, compressed, oblongoid to ovoid, rather smooth, single-leaved, enclathed in bladeless sheaths. Inflorescence subclaxly few- to many-flowered, branching. Sepals dissimilar, lateral sepals basally connate or free. Petals similar to the dorsal sepal. Lip sessile, distinctly 3-lobed, the middle lobe clawed, entire; lateral lobes prominent, with more or less fringed apical margins or entire but with fringed isthmus margins between lateral and middle lobes; callus rather small, consisting of some lobes, plates and/or digitate projections. Gynostemium forms an obtuse angle with the lip, erect, rather short, slender. Column part very narrowly alate near the stigma. Anther subventral. Pollinia 2, obovoid, slightly dorsiventrally flattened, hard, unequally and deeply cleft, empty inside. Apical clinandrium obscure. Stigma large, ovate, deeply concave. Rostellum short but relatively massive, conical-digitate in the middle, obtuse. Viscidium single, rather small, ellipsoid. Tegula single, oblong, thin, lamellate, delicate, flat. Rostellum remnant bilobulate at the middle, canaliculate on the dorsal surface. Tabula infrastigmatica prominent (Fig. 10).

BAPTISTA & DOCHA NETO (2006) classified under this name ca. 20 species known mostly from Brazil. His concept of *Alatiglossum* included also species that were transferred almost simultaneously by CASTRO-NETO & CATHARINO (2006) to the genera *Neoruschia* and *Kleberella*. BARROS & RODRIGUES (2010a) showed that the characters used by CASTRO-NETO & CATHARINO (2006) are not always relevant. They draw the conclusion that both genera should be regarded



Figure 9. *Neoruschia cogniauxiana* (Schltr.) Cath. & V.P. Castro (photo: R. Martins).

as synonyms of *Alatiglossum*. In another article, BARROS & RODRIGUES (2010b) created a new genus *Nitidocidium* to accommodate *Oncidium gracile* Lindl., previously treated as a member of *Carenidium* by Baptista (in DOCHA NETO et al. 2006), emphasizing the molecular results – placing *O. gracile* at the base of the *Alatiglossum* clade – and the absence of common morphological features between both entities.

We combine here *Kleberia* and *Alatiglossum* under the latter name because of priority. It can be easily identified by the fimbriate isthmus between the lip's middle and lateral lobes not found elsewhere in the clade.

The genus includes the following species:

- *Alatiglossum barbatum* (Lindl.) Baptista
- *Alatiglossum bohnkianum* (V.P. Castro & G.F. Carr) Baptista
- *Alatiglossum chrysopteranthum* (Lückel) Baptista
- *Alatiglossum chrysopterum* (Lindl.) Baptista
- *Alatiglossum ciliatum* (Lindl.) Baptista
- *Alatiglossum croesus* (Rchb. f.) Baptista
- *Alatiglossum culuenense* Docha Neto & Benelli
- *Alatiglossum emilii* (Schltr.) Baptista
- *Alatiglossum eurycline* (Rchb. f.) Szlach. & Kolan., *comb. nov.*
Basionym: *Oncidium eurycline* Rchb. f., Gard. Chron. 2: 812. 1883.
- *Alatiglossum fuscopetalum* (Hoehne) Baptista
- *Alatiglossum herzogii* (Schltr.) Docha Neto
- *Alatiglossum longipes* (Lindl. & Paxton) Baptista
- *Alatiglossum macropetalum* (Lindl.) Baptista
- *Alatiglossum medinense* Campacci
- *Alatiglossum micropogon* (Rchb. f.) Baptista
- *Alatiglossum psyche* (Schltr.) Baptista
- *Alatiglossum reductum* (Kraenzl.) Baptista



Figure 10. I. *Alatiglossum ciliatum* (Lindl.) Baptista (photo: L.F.Varella). II. *Alatiglossum longipes* (Lindl. & Paxton) Baptista (photo: L.F.Varella). III. *Alatiglossum croesus* (Rchb.f.) Baptista: gynostemium details. A – gynostemium, side view; B – gynostemium, bottom view; C – anther; D – pollinia, various views; E – tegula and viscidium, various views [Heidelberg BG O-20202, HEID].

- *Alatiglossum regentii* (V.P. Castro & G.F. Carr) Baptista
- *Alatiglossum trichodes* (Lindl.) Baptista
- *Alatiglossum uniflorum* (Booth ex Lindl.) Baptista

Carriella V.P. Castro & K.G. Lacerda, Icon. Orchid. Brasil. 2: t. 123. 2006 [issued Mar 2006]; Generitype: *Carriella colorata* (Königer & J.G. Weinm.) V.P. Castro & K.G. Lacerda (≡ *Oncidium coloratum* Königer & J.G. Weinm.). = *Carria* V.P. Castro & K.G. Lacerda Orchids (West Palm Beach) 74(9): 694. 2005 [issued on 17 Aug 2005], non *Carria* Gardner, Calcutta J. Nat. Hist. 7: 6. 1847 (Theaceae).

Plants caespitose. Pseudobulbs clustered, compressed, ovoid, smooth, unifoliate, encloded in bladeless sheaths. Inflorescence laxly few-flowered. Sepals and petals subsimilar, lateral sepals free to the base. Lip sessile, basally rounded and 3-lobed, the middle lobe oblong elliptic, larger than lateral lobes; callus consisting of prominent keel running in the lower half, apically somewhat diverging and upcurved, basally terminated with a pair of subglobose projections, glabrous. Gynostemium forms an obtuse angle with the lip, suberect, elongate, slender. Column part terete, wingless. Anther subventral, apically 3-lobed, papillate. Pollinia 2, obovoid, slightly dorsiventrally flattened, hard, unequally cleft. Apical clinandrium obscure. Stigma large, ovate, deeply concave. Rostellum short, conical-digitate in the middle, obtuse. Viscidium single, very small, ellipsoid, delicate. Tegula single, linear, thin, lamellate, very delicate, flat. Rostellum remnant bilobulate at the middle, canaliculate on the dorsal surface. Tabula infrastigmatica prominent (Fig. 11).

A monotypic genus easily separated from all other members of *Gomesa* clade by the following combination of characters: wingless gynostemium, lip middle lobe longer than wide and lip callus consisting of prominent keel running in the lower half, apically somewhat diverging and upcurved, basally terminated with a pair of subglobose projections.

CHIRON (2007) and CHIRON et al. (2009) postulated that both *Carriella* and *Campaccia* are better placed in *Baptistonia*. One these authors does not share that opinion about the status of this entity, which is a mere subgenus of *Baptistonia* in his opinion:

Baptistonia subgenus *Carriella* (V.P. Castro & K.G. Lacerda) Chiron, *comb. et stat. nov.* Basionym: *Carriella* V.P. Castro & K.G. Lacerda, *Icon. Orchid. Brasil. 2: t. 123. 2006.*

- *Carriella colorata* (Königer & J.G. Weinm.) V.P. Castro & K.G. Lacerda

Baptistonia Barb. Rodr., *Gen. Sp. Orchid. 1: 95. 1877*; Generitype: *Baptistonia echinata* Barb. Rodr.

= *Waluwewa* Regel, *Trudy Imp. St.-Petersb. Bot. Sada. 11: 390. 1990*; Generitype: *Waluwewa pulchella* Regel.

Plants caespitose. Pseudobulbs clustered, somewhat compressed, ovoid to oblongoid, smooth, 1–3-foliate, encloded in bladeless sheaths. Inflorescence laxly to densely few- to many-flowered, sometimes branching. Sepals and petals dissimilar, lateral sepals more or less connate. Lip sessile, 3-lobed, the middle lobe transversely elliptic, callus consisting of prominent, parallel keels running in the lower half, apically somewhat diverging or with more sophisticated pattern consisting of variously shaped projections. Gynostemium forms an acute or obtuse angle with the lip, elongate, rather slender, slightly arched. Column part glandular below stigma, with two obliquely triangular to falcate-lanceolate projections just above the middle. Anther subventral. Pollinia 2, obliquely obovoid, deeply cleft at the apex, hard. Apical clinandrium prominent or obscure, exceeding the anther, almost entire, glandular near the margin. Stigma relatively narrow, elliptic, deeply concave. Rostellum pendent, small, ligulate, blunt. Viscidium single, very small, ovate, thin, sticky on the outer surface. Tegula single, oblong triangular, thin, lamellate. Rostellum remnant with apical, oblique, shallow plate surrounded by two obscure triangular, acute lobules. Tabula infrastigmatica present (Fig. 12).

Baptistonia can be easily separated from *Carriella* of the same clade by having a glandular column part below the stigma, with two obliquely triangular projections just above the middle



Figure 11. *Carriella colorata* (Königer & J.G. Weinm.) V.P. Castro & K.G. Lacerda (photo: L.F. Varella).

and lip callus consisting of parallel keels running in the lower half, with more sophisticated pattern consisting of variously shaped projections. Additionally, lip middle lobe of *Baptistonia* is suborbicular to transversely elliptic. The genus *Campaccia* is similar in many respects to *Baptistonia*, but can be distinguishable from the latter by having 2–3-leaved pseudobulbs (vs 1-leaved), lip and gynostemium form an obtuse angle (vs acute angle) and apical clinandrium is obscure (vs prominent), otherwise both taxa are very similar. Therefore, we decided to amalgamate them maintaining the status of separate subgenera for both.

Subgenus *Baptistonia*

The subgenus in its narrow sense embraces up to 30 species, depending on the author.

Within this subgenus we recognize 4 sections as delimited by CHIRON (2008):

sect. *Baptistonia*

Type: *Baptistonia echinata* Barb. Rodr.

- *Baptistonia sarcodes* (Lindl.) Chiron & V.P. Castro
- *Baptistonia pulchella* (Regel) Chiron & V.P. Castro
- *Baptistonia uhlii* Chiron & V.P. Castro

sect. *Lamellaticallae* Chiron

Type: *Baptistonia widgrenii* (Lindl.) V.P. Castro & Chiron

- *Baptistonia albinoi* (Schltr.) Chiron & V.P. Castro
- *Baptistonia brieniana* (Rchb. f.) V.P. Castro & Chiron
- *Baptistonia leinigii* (Pabst) Chiron & V.P. Castro
- *Baptistonia pabstii* (Campacci & C. Espejo) Chiron & V.P. Castro
- *Baptistonia remotiflora* (Garay) Chiron & V.P. Castro
- *Baptistonia riograndense* (Cogn.) Chiron & V.P. Castro
- *Baptistonia velteniana* V.P. Castro & Chiron
- *Baptistonia verrucosissima* (Cogn.) V.P. Castro & Chiron

sect. *Laevicallae* Chiron

Type: *Baptistonia lietzei* (Regel) Chiron & V.P. Castro

- *Baptistonia cruciata* (Rchb. f.) Chiron & V.P. Castro
- *Baptistonia damacenoii* Chiron & V.P. Castro
- *Baptistonia kautskyi* (Pabst) V.P. Castro & Chiron
- *Baptistonia pubes* (Lindl.) Chiron & V.P. Castro
- *Baptistonia truncata* (Pabst) Chiron & V.P. Castro

sect. *Crassicallae* Chiron

Type: *Baptistonia cornigera* (Lindl.) Chiron & V.P. Castro

- *Baptistonia fimbriata* (Lindl.) Chiron & V.P. Castro
- *Baptistonia gutfreundiana* (Chiron & V.P. Castro) Chiron & V.P. Castro
- *Baptistonia nitida* (Barb. Rodr.) V.P. Castro & Chiron
- *Baptistonia silvana* (V.P. Castro & Campacci) V.P. Castro & Chiron

Incertae sedis

We were not able to gather sufficient information about *Baptistonia* species listed below and to classify them in an appropriate section.

- *Baptistonia calimaniorum* V.P. Castro
- *Baptistonia cipoensis* Laitano & V.P. Castro
- *Baptistonia pauloensis* V.P. Castro & Laitano

Subgenus *Emarginata* (Chiron.) Szlach. & Kolan., *comb. et stat. nov.*

Basionym: *Baptistonia* section *Emarginata* Chiron, *Richardiana* 8(3): 123. 2008; Type species: *Baptistonia venusta* (Drapiez) Chiron

= *Campaccia* Baptista, P.A. Harding & V.P. Castro, *Colet. Orquídeas Brasil*. 9: 316. 2011 [issued on 25 May 2011]; Generitype: *Campaccia venusta* (Drapiez) Baptista, P.A. Harding & V.P. Castro (≡ *Oncidium venustum* Drapiez).

This subgenus is similar in many respects to the nominal one, but can be distinguished from the latter by having 2–3-leaved pseudobulbs (vs 1-leaved), lip and gynostemium form an obtuse angle (vs acute angle) and the apical clinandrium is obscure (vs prominent). This monospecific taxon is restricted in distribution to the Brazilian States of Rio de Janeiro and Paraná:

- *Baptistonia venusta* (Drapiez) Docha Neto

Rodrigueziopsis Schltr., *Repert. Spec. Nov. Regni Veg.* 16: 427. 1920; Generitype (Garay & Sweet 1972: 527): *Rodrigueziopsis eleutherosepala* (Barb. Rodr.) Schltr. (≡ *Rodriguezia eleutherosepala* Barb. Rodr.).

Plants with long aerial stolons. Pseudobulbs spaced, compressed, bifoliate, subtended basally by leafy sheaths. Inflorescence elongate, laxly few-flowered. Sepals and petals dissimilar, lateral sepals free to the base. Lip clawed, 3-lobed near the middle, lateral lobes much smaller than the middle one, callus consisting of two parallel keels in the lower half. Gynostemium parallel with the basal lip part, elongate, slightly swollen and bent back at the apex, fused with the lip margins



Figure 12. I. *Baptistonias venusta* (Drapiez) Docha Neto (photo: L. F. Varela). II. *Baptistonias cornigera* (Lindl.) Chiron & V.P. Castro (photo: L. F. Varela). III. *Baptistonias pubes* (Lindl.) Chiron & V.P. Castro: gynostemium details. A – gynostemium, bottom view; B – gynostemium, side view; C–D – anther, various views; E – pollinia, various views [Chase 85119, DLSz]. IV. *Baptistonias pulchella* (Regel) Chiron & V.P. Castro: gynostemium details. A – gynostemium, side view; B – gynostemium, bottom view; C – anther; D – pollinia, various views; E – tegula and viscidium [Heidelberg BG O-19054, HEID].

up to the rostellum base. Column part ca. 1.5 times longer than anther, glabrous, with two wing-like projections on both sides of rostellum. Anther subdorsal. Pollinia 2, elipsoid-obovoid, cleft at the apex, hard. Apical clinandrium forms a narrow collar-like structure surrounding anther base. Stigma large, elliptic, concave. Rostellum erect, triangular-ligulate, rounded at the apex. Viscidium small, single, elliptic, fleshy, thick. Tegula single, obtriangular in the upper half, linear below, thin, lamellate. Rostellum remnant shallowly bilobed at the apex, with oblique, apical plate on the inner surface surrounded by fovea. Tabula infrastigmatica missing (Fig. 13).

The genus includes two Brazilian species, characterized by long aerial stolons, clawed lip, parallel with the gynostemium and adorned with a pair of parallel keels and glabrous gynostemium with wing-like projections:

- *Rodriguezopsis eleutherosepala* Schltr.
- *Rodriguezopsis microphyton* Schltr.



Figure 13. *Rodriguezziopsis eleutherosepala* Schltr. A – habit; B – flower closeup (photos: M. Rosim).

Gomesa R. Br., Bot. Mag. 42: t. 1748. 1815; Generitype: *Gomesa recurva* R. Br.

Plants caespitose. Pseudobulbs clustered, compressed, bifoliate, enclathed basally by few sheaths, of which the uppermost with obscure blade. Inflorescence many-flowered, usually dense. Sepals and petals subsimilar, lateral sepals more or less connate in the lower part. Lip sessile, unlobed to obscurely 3-lobed, more or less geniculate near the middle, callus consisting of two parallel lamellae in the lower part, glabrous or pubescent. Gynostemium somewhat diverging from the lip, erect or gently arched, elongate, slender. Column part wingless or obscurely winged in the upper half. Anther subapical or apical, incumbent. Pollinia 2, almost obliquely obovoid to obovoid-ellipsoid, hard, unequally and deeply cleft, empty inside. Apical clinandrium obscure. Stigma oblong elliptic, deeply concave. Rostellum elongate in the middle, ligulate, obtuse. Viscidium single, oblong-elliptic, thick. Tegula single, linear, thin, lamellate. Rostellum remnant bilobulate at the middle, with oblique shallowly concave plate between obscure, acute lobules. Tabula infrastigmatica missing.

The main difference between *Gomesa* and *Rodriguezziella* cited above (lateral sepals basally connate versus non-connate) seems to be irrelevant on the generic level. Therefore, we decided to merge both genera, but simultaneously maintaining the status of separate sections:

Section *Gomesa*

In our delimitation, this group comprises 10–15 species, depending on the accepted synonymies, which have glabrous lip calli (Fig. 14).

- *Gomesa barkeri* (Hook.) Rolfe
- *Gomesa brasiliensis* (Rolfe) M.W. Chase & N.H. Williams
- *Gomesa crispa* (Lindl.) Klotzsch ex Rchb. f.



Figure 14. I. *Gomesa recurva* R. Br. (photo: L.F.Varella). II. *Gomesa planifolia* Klotzsch ex Rchb. f.: gynostemium details. A – gynostemium, side view; B – gynostemium, bottom view; C – rostellum remnant; D – pollinia, various views [Kew RBG, K 12544]. III. *Gomesa planifolia* Klotzsch ex Rchb. f.: gynostemium details. A – pollinia, various views; B – tegula and viscidium, various views [Kew RBG, K, cult.]. IV. *Gomesa brasiliensis* (Rolfe) M.W. Chase & N.H. Williams: gynostemium details. A – gynostemium, bottom view; B – rostellum remnant; C – tegula and viscidium, side view; D – pollinia, various views [Kew RBG, K 47505].

- *Gomesa divaricata* Hoffmanns. ex Schltr.
- *Gomesa fischeri* Regel
- *Gomesa laxiflora* Klotzsch & Rchb. f.
- *Gomesa planifolia* Klotzsch ex Rchb. f.
- *Gomesa recurva* R. Br.
- *Gomesa sessilis* Barb. Rodr.
- *Gomesa undulata* Hoffmanns.

Section *Rodrigueziella* (Kuntze) Szlach., Kolan. & Chiron, *stat. et comb. nov.*

Basionym: *Rodrigueziella* Kuntze, Revis. Gen. Pl. 2: 649. 1891; Generitype: *Rodrigueziella gomezoides* (Barb. Rodr.) Berman (\equiv *Theodora gomezoides* Barb. Rodr.).

This group consists of 5–7 species with pubescent lip lamellae (Fig. 15).

- *Gomesa doeringii* (Hochne) Pabst
- *Gomesa gomezoides* (Barb. Rodr.) Pabst



Figure 15. I. *Gomesa gomezoides* (Barb. Rodr.) Pabst (photo: L.F.Varella). II. *Gomesa handroi* (Hoehne) Pabst (photo: L.F.Varella). III. *Gomesa gomezoides* (Barb. Rodr.) Pabst: gynoecium details. A – gynoecium, bottom view; B – gynoecium, side view; C – rostellum remnant; D – anther; E – pollinia, various views; F – tegula and viscidium, various views [Heidelberg BG O-7699, HEID].

- *Gomesa handroi* (Hoehne) Pabst
- *Gomesa jucunda* (Rchb. f.) M.W. Chase & N.H. Williams
- *Gomesa petropolitana* (Pabst) M.W. Chase & N.H. Williams
- *Gomesa verboonenii* Pabst

Brasilidium Campacci, Colet. Orquídeas Brasil. 3: 78. 2006 [issued on 10 Feb 2006]; Generitype: *Brasilidium crispum* (Lodd. ex Lindl.) Campacci (≡ *Oncidium crispum* Lodd. ex Lindl.).

= *Anettea* Szlach. & Mytnik, Polish Bot. J. 51(1): 49(–50). 2006 [issued on 21 Jul 2006]; Generitype: *Anettea crispa* (Lodd.) Szlach. & Mytnik (≡ *Oncidium crispum* Lodd.).

Plants caespitose. Pseudobulbs clustered, somewhat compressed, unifoliate, encloded with bladeless sheaths. Inflorescence elongate, branching, rather densely many-flowered. Flowers showy. Dorsal sepal and petals subsimilar, petals larger than sepals, lateral sepals more or less connate basally. Lip sessile, basally 3-lobed, lateral lobes much smaller than the middle one, callus limited to the basal part of the lip, consisting of two thick ridges and often some more projections. Gynoecium perpendicular to the lip lamina, erect or slightly arched, stout, short.

Column part slightly longer than anther, winged near the stigma, wings usually well-developed, flabellate or flat, entire or uneven and papillate on margins. Anther subventral, incumbent, papillate. Pollinia 2, oblong-obovoid to obovoid, dorsiventrally flattened, hard, unequally and deeply cleft, empty inside. Apical clinandrium usually obscure, occasionally forms a narrow collar-like structure surrounding the anther base. Stigma large, elliptic, deeply concave. Rostellum relatively short, conical-digitate in the middle, obtuse. Viscidium single, elliptic, thick, fleshy. Tegula single, oblong to oblong-elliptic, flat, sometimes more or less geniculate near the apex, thin, lamellate. Rostellum remnant bilobulate at the middle, canaliculate on the dorsal surface. Tabula infrastigmatica prominent (Fig. 16).

Brasilidium differs from *Carenidium* by having unifoliate pseudobulbs (vs bifoliate), sessile lip (vs clawed), and wing-like column appendages (vs digitate). The lip callus of *Brasilidium* species forms a more complicated pattern than in *Carenidium* consisting of a pair of thick ridges and additional projections. The lip calli of *Carenidium* are formed of a pair a keels. As originally proposed, the genus embraced ca. 12 Brazilian species. Later some more species have been added to *Brasilidium* (e.g. BARROS & RODRIGUES 2010a; CASTRO-NETO 2012; CHIRON 2014):

- *Brasilidium brunnipetalum* (Barb. Rodr.) Szlach. & Kolan., *comb. nov.*
Basionym: *Oncidium brunnipetalum* Barb. Rodr., Gen. Sp. Orchid. 2: 190. 1881.
- *Brasilidium colnagoi* (Pabst) Campacci
- *Brasilidium crispum* (Lodd.) Campacci
- *Brasilidium curtum* (Lindl.) Campacci
- *Brasilidium enderianum* (hort.) Szlach. & Kolan., *comb. nov.*
Basionym: *Oncidium enderianum* hort., Gard. Chron. 2: 75. 1883.
- *Brasilidium forbesii* (Hook.) Campacci
- *Brasilidium gardneri* (Lindl.) Campacci
- *Brasilidium gravesianum* (Rolfe) Campacci
- *Brasilidium imperatoris-maximilianii* (Rchb. f.) Szlach. & Kolan., *comb. nov.*
Basionym: *Oncidium imperatoris-maximilianii* Rchb. f., Bot. Ergebn. Maxim. Bras.: 154. 1866.
- *Brasilidium litum* (Rchb. f.) Campacci
- *Brasilidium marshallianum* (Rchb. f.) Campacci
- *Brasilidium novaesae* (Ruschi) Chiron
- *Brasilidium pectorale* (Lindl.) Campacci
- *Brasilidium praetextum* (Rchb. f.) Campacci
- *Brasilidium regentii* V.P. Castro & Marçal
- *Brasilidium riviereanum* (hort. ex Wibier) Campacci
- *Brasilidium scullyi* (Pabst & A.F. Mello) Campacci
- *Brasilidium tapiraiense* Campacci
- *Brasilidium zappii* (Pabst) Campacci

Carenidium Baptista, Colet. Orquídeas Brasil. 3: 90. 2006 [issued on 10 Feb 2006]; Generitype: *Carenidium concolor* (Hook.) Baptista (≡ *Oncidium concolor* Hook.).

≡ *Concocidium* Romowicz & Szlach., Polish Bot. J. 51(1): 44(–45). 2006 [issued on 21 Jul 2006]; Generitype: *Concocidium concolor* (Hook.) Romowicz & Szlach. (≡ *Oncidium concolor* Hook.).

Plants caespitose. Pseudobulbs clustered, somewhat compressed, sulcate, bifoliate, basally enclosed in bladeless sheaths. Inflorescence elongate, rather laxly several-flowered. Sepals



Figure 16. I. *Brasilidium praetextum* (Rchb.f.) Campacci (photo: L.F.Varella). II. *Brasilidium gardneri* (Lindl.) Campacci: gynoecium details. A – gynoecium, bottom view; B – gynoecium, side view; C – pollinarium [Chase 84508, DLSz].

and petals subsimilar, lateral sepals basally connate. Lip clawed, 3-lobed, lateral lobes smaller than middle lobe, disc with two keels restricted to the claw, lamina large, flat. Gynoecium perpendicular to the lip, rather short, stout, erect, forming a right angle with the lip lamina. Column part with two digitate projections near the stigma. Anther subventral, incumbent. Pollinia 2, oblong-obovoid, dorsiventrally flattened, hard, unequally and deeply cleft, empty inside. Apical clinandrium obscure. Stigma large, elliptic, deeply concave. Rostellum relatively short, conical-digitate in the middle, obtuse. Viscidium single, elliptic, thick, fleshy. Tegula



Figure 17. I. *Carenidium dasytyle* (Rchb. f.) Baptista (photo: Swiss Orchid Foundation). II. *Carenidium concolor* (Hook.) Baptista: gynostemium details. A – gynostemium, side view; B – gynostemium, bottom view; C – anther; D – pollinia, various views; E – tegula and viscidium, various views [Heidelberg BG O-15062E, HEID].

single, oblong, flat, thin, lamellate. Rostellum remnant bilobulate at the middle, canaliculate on the dorsal surface. Tabula infrastigmatica missing (Fig. 17).

Brasiliidium and *Carenidium* can be recognized by elliptic, laterally compressed pseudobulbs, paniculate inflorescence, sepals shorter than petals, lateral sepals free or connate only at the base, lateral lobes of the lip much smaller than the median lobe and a glabrous gynostemium, but the lip callus as well as gynostemium appendages are different. Therefore, we suggest to treat them as separate. *Carenidium* s. str. (i.e. without *Menezesiella*, *Nitidocidium*, the species classified within *Baptistonia* and *Oncidium itapetingense* transferred to *Ornithophora* by BARROS & RODRIGUES (2010a, b) is composed of two Brazilian species only:

- *Carenidium concolor* (Hook.) Baptista
- *Carenidium dasytyle* (Rchb. f.) Baptista

Ornithophora Barb. Rodr., Gen. Sp. Orchid. 2: 225. 1882; Generitype: *Ornithophora radicans* (Rchb. f.) Garay & Pabst (\equiv *Sigmatostalix radicans* Rchb. f. = *Ornithophora quadricolor* Barb. Rodr.).

Plants with elongate rhizome. Pseudobulbs somewhat compressed, bifoliate, subtended basally by some leafy sheaths. Inflorescence elongate, laxly few-flowered. Sepals and petals subsimilar, lateral sepals free to the base. Lip clawed, claw terminated by knob-like callus, lamina more or less transversely elliptic; callus lamellate. Gynostemium perpendicular to the lip, elongate, slender, somewhat arcuate. Column part terete, non-winged, slightly swollen just below the stigma base. Anther subventral, incumbent, operculate, obovoid-cordate, obscurely 2-chambered, papillate.



Figure 18. I. *Ornithophora radicans* (Rchb.f.) Garay & Pabst (photo: A. Avetta). II. *Ornithophora radicans* (Rchb.f.) Garay & Pabst: gynostemium details. A – gynostemium, side view; B – gynostemium, bottom view; C – rostellum remnant, front view; D – anther; E – pollinia, various views; F – tegula and viscidium, back view [Heidelberg BG O-433, HEID].

Pollinia 2, obliquely obovoid, hard, unequally and deeply cleft, empty inside. Apical clinandrium obscure. Stigma small, elliptic, deeply concave, partially hidden by rostellum. Rostellum elongate, rostrate, thick, bent down at the apex, obtuse. Viscidium single, oblong-ovate, thin, lamellate. Tegula single, linear, apically expanded, thin, lamellate. Rostellum remnant rostrate, bilobulate at the apex. Tabula infrastigmatica missing (Fig. 18).

A genus of 1–2 species known from Brazil, characterized by elongate stolons, clawed lip, with claw terminated by knob-like callus, lamina more or less transversely elliptic, lamellate callus and elongate, slender gynostemium.

- *Ornithophora itapetingensis* (V.P. Castro & Chiron) F. Barros & V.T. Rodrigues
- *Ornithophora radicans* (Rchb.f.) Garay & Pabst

Menezesiella Chiron & V.P. Castro, *Richardiana* 6(2): 103–106. 2006; Generitype: *Menezesiella ranifera* (Lindl.) Chiron & V.P. Castro (\equiv *Oncidium raniferum* Lindl.).

= *Castroa* Guiard, *Richardiana* 6(3): 161–164. 2006; Generitype: *Castroa calimaniiana* Guiard.

Plants caespitose. Pseudobulbs clustered, somewhat compressed, sulcate, bifoliate, sheaths bladeless or the uppermost leafy. Inflorescence much elongate, branching, rather laxly many-flowered. Sepals and petals subsimilar, lateral sepals free to the base. Lip sessile, deeply 3-lobed just above the base, lateral lobes ligulate, the middle lobe clawed, elliptic. Lip callus in form of massive tissue covering basal part of the lip. Gynostemium forms an obtuse angle with the lip lamina, erect, short. Column part obscurely winged in the upper half. Anther subapical, incumbent. Pollinia 2, almost obliquely obovoid, hard, unequally and deeply cleft, empty inside. Apical clinandrium obscure. Stigma oblong elliptic, deeply concave. Rostellum elongate in the middle, ligulate, obtuse. Viscidium single, small. Tegula single, linear, thin, lamellate. Rostellum remnant bilobulate at the middle, with oblique shallowly concave plate between obscure, acute lobules. Tabula infrastigmatica prominent (Fig. 19).

As discussed by GUIARD (2006), *Castroa* is not very different from *Menezesiella* and, in our opinion, does not deserve any taxonomic status. *Menezesiella* species were treated as members

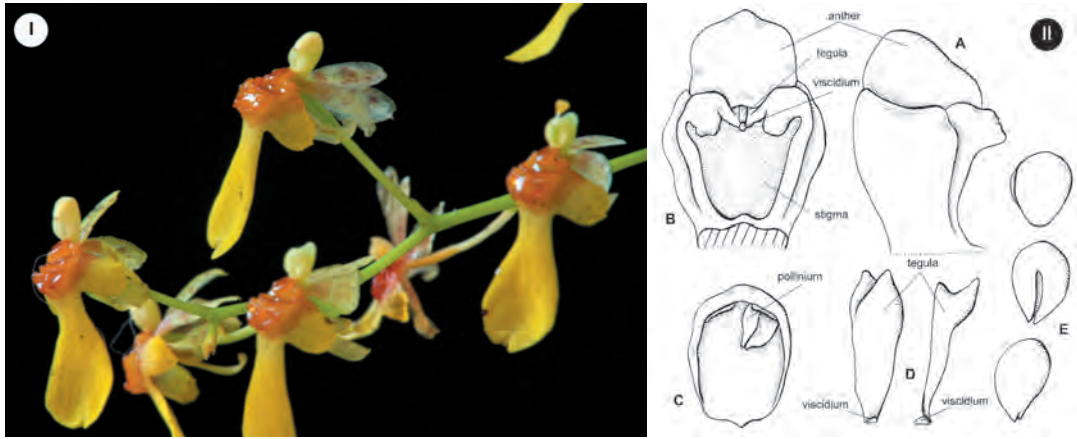


Figure 19. I. *Menezesiella ranifera* (Lindl.) Chiron & V.P. Castro (photo: L.F. Varella). II. *Menezesiella loefgrenii* (Cogn.) V.P. Castro & Chiron: gynostemium details. A – gynostemium, side view; B – gynostemium, bottom view; C – anther; D – tegula and viscidium; E – pollinia [Heidelberg BG O-6230, HEID].

of *Rhinocidium* by Baptista (in DOCHA NETO & BAPTISTA 2006). All these genera were lumped into *Coppensia* by BARROS & RODRIGUES (2010a) based on some common vegetative characters, such as narrowly piriform, sulcate, densely black-spotted, bifoliate pseudobulbs. The most characteristic features of *Menezesiella*, however, are sessile, deeply 3-lobed lip with massive callus in the basal part of the lip, gynostemium is relatively short and column part is obscurely winged. The genus comprises about 8 species known from Brazil:

- *Menezesiella calimaniana* (Guiard) Szlach. & Kolan., *comb. nov.*
Basionym: *Castroa calimaniana* Guiard, *Richardiana* 6: 162. 2006.
- *Menezesiella calimaniorum* V.P. Castro & G.F. Carr
- *Menezesiella discifera* (Lindl.) Szlach. & Kolan., *comb. nov.*
Basionym: *Oncidium disciferum* Lindl., *Folia Orchid. Oncidium*: 24. 1855.
- *Menezesiella hookeri* (Rolfe) V.P. Castro & Chiron
- *Menezesiella loefgrenii* (Cogn.) V.P. Castro & Chiron
- *Menezesiella neoparanaensis* Chiron & V.P. Castro
- *Menezesiella ouricanense* (V.P. Castro & Campacci) Szlach. & Kolan., *comb. nov.*
Basionym: *Oncidium ouricanense* V.P. Castro & Campacci, *Bol. CAOB* 4(1): 17. 1992.
- *Menezesiella ranifera* (Lindl.) Chiron & V.P. Castro
- *Menezesiella regentii* V.P. Castro
- *Menezesiella salesopolitana* V.P. Castro & Chiron

Coppensia Dumort., *Nouv. Mém. Acad. Roy. Sci. Bruxelles* 9(3): 10. 1835; Generitype: *Coppensia bifolia* (Sims) Dumort. (≡ *Oncidium bifolium* Sims).

= *Ampliglossum* Campacci, in DOCHA NETO et al. (2006). Generitype *Ampliglossum varicosum* (Lindl. & Paxton) Campacci (≡ *Oncidium varicosum* Lindl. & Paxton).

Plants caespitose or with stolons. Pseudobulbs somewhat compressed and sulcate, bifoliate, 1 or 2 upper sheaths leafy. Inflorescence much elongate, often branching. Sepals and petals subsimilar, lateral sepals basally connate. Lip sessile, much larger than tepals, basally 3-lobed, lateral lobes obscure, the middle lobe apically incised, callus at the base of the lip only, consisting of numerous



Figure 20. I. A – *Coppensia spilopectera* (Lindl.) Campacci (photo: L.F. Varella); B – *Coppensia varicosa* (Lindl. & Paxton) Campacci (photo: L.F. Varella). II. *Coppensia bifolia* (Sims) Dumort: gynostemium details. A – gynostemium, bottom view; B – gynostemium, side view; C – anther; D – pollinia, various views; E – tegula and viscidium, various views [Heidelberg BG O-826, HEID].

tubercules, elongate projections or thickenings of various forms. Gynostemium more or less perpendicular to the lip axis, rather short, somewhat arcuate. Column part alate, wings obliquely ovate, entire. Anther subapical, incumbent. Pollinia 2, almost obliquely obovoid, hard, unequally and deeply cleft, empty inside. Apical clinandrium obscure. Stigma elliptic-ovate, deeply concave. Rostellum elongate in the middle, ligulate, obtuse. Viscidium single, small. Tegula single, linear, thin, lamellate. Rostellum remnant bilobulate at the middle, with oblique shallowly concave plate between obscure, acute lobules. Tabula infrastigmatica prominent (Fig. 20).

The genus includes 25–30 species with lip much larger than tepals, large lip middle lobe and callus confined to the base of the lip and consisting of numerous tubercules. The gynostemium is short with obliquely ovate wings on both sides of the stigma.

- *Coppensia batemnianum* (Parm ex Knowles & Westc.) Campacci
- *Coppensia bicolor* (Lindl.) Campacci
- *Coppensia bifolia* (Sims) Dumort
- *Coppensia blanchetii* (Rchb. f.) Campacci
- *Coppensia caldensis* (Rchb. f.) Docha Neto
- *Coppensia chapadensis* (V.P. Castro & Campacci) Campacci

- *Coppensia chrysothyrsus* (Rchb. f. & Warm.) Szlach. & Kolan., *comb. nov.*
Basionym: *Oncidium chrysothyrsus* Rchb. f. & Warm., Sel. Orch. ser. 2 t. 5. 1865.
- *Coppensia doniana* (Batem. ex W. Baxt.) Campacci
- *Coppensia flexuosa* (Sims) Campacci
- *Coppensia fuscans* (Rchb. f.) Campacci
- *Coppensia hydrophila* (Barb. Rodr.) Campacci
- *Coppensia insignis* (Rolfe) Szlach. & Kolan., *comb. et stat. nov.*
Basionym: *Oncidium varicosum* var *insigne* Rolfe, Orchid Rev. 6: 27. 1898.
- *Coppensia isoptera* (Lindl.) Campacci
- *Coppensia mandonii* (Rchb. f.) Campacci
- *Coppensia martiana* (Lindl.) Campacci
- *Coppensia megaloptera* (Kraenzl.) Szlach. & Kolan., *comb. nov.*
Basionym: *Oncidium megalopterum* Kraenzl., Pflanzenreich: 156. 1922.
- *Coppensia paranapiacabense* (Hoehne) Campacci
- *Coppensia reichertii* Menezes & V.P. Castro
- *Coppensia sellowii* (Cogn.) Campacci
- *Coppensia sincorana* Campacci & Cath.
- *Coppensia spilloptera* (Lindl.) Campacci
- *Coppensia varicosa* (Lindl. & Paxton) Campacci
- *Coppensia viperina* (Lindl.) Campacci
- *Coppensia warmingii* (Rchb. f.) Campacci
- *Coppensia welteri* (Pabst) Campacci

Rhinocidium Baptista, Colet. Orquídeas Brasil. 3: 93. 2006 [issued on 10 Feb 2006]; Generitype: *Rhinocidium longicornu* (Mutel) Baptista (≡ *Oncidium longicornu* Mutel)

= *Rhinocerotidium* Szlach., Polish Bot. J. 51: 40. 2006 [issued on 21 Jul 2006]; Generitype: *Rhinocerotidium rhinoceros* (Rchb. f.) Szlach. (≡ *Oncidium rhinoceros* Rchb. f.).

Plants caespitose. Pseudobulbs clustered, compressed, sulcate, bifoliate, sheaths bladeless. Inflorescence elongate, branching, many-flowered. Sepals and petals subsimilar, lateral sepals connate in the basal half. Lip sessile, 3-lobed just above the base, the middle lobe much larger than both laterals. Callus in form of single, horn-like, upcurved projection, with transverse ridge above. Gynostemium perpendicular to the lip lamina, elongate, slender, terete. Column part winged near the stigma, wings entire and papillate on margins. Anther subventral, incumbent, papillate. Pollinia 2, subglobose, slightly dorsiventrally flattened, hard, unequally cleft at the apex, empty inside. Apical clinandrium obscure. Stigma rather small, ovate, deeply concave. Rostellum very short, digitate in the middle, obtuse. Viscidium single, elliptic, thick, fleshy. Tegula single, oblong, thin, lamellate. Rostellum remnant bilobulate at the middle. Tabula infrastigmatic missing (Fig. 21).

The genus with 2–3 species is confined to Brazil:

- *Rhinocidium longicornu* (Mutel) Baptista
- *Rhinocidium macronyx* (Rchb. f.) Baptista
- *Rhinocidium rhinoceros* (Rchb. f.) Szlach. & Kolan., *comb. nov.*
Basionym: *Oncidium rhinoceros* Rchb. f. Bot. Zeit. (Berlin) 14: 514. 1856.



Figure 21. I. *Rhinocidium longicornu* (Mutel) Baptista (photo: L.F.Varella). II. *Rhinocidium macronyx* (Rchb.f.) Baptista: gynostemium details. A – gynostemium, bottom view; B – gynostemium, side view; C – anther; D – pollinia, various views; E – tegula and viscidium, various views [Heidelberg BG O-20819, HEID].

Incertae sedis

Hardingia Docha Neto & Baptista, Colet. Orquídeas Brasil. 9: 342 (2011); Generitype *Hardingia paranaensis* (Kraenzl.) Docha Neto & Baptista (\equiv *Oncidium paranaense* Kraenzl.).

Plants caespitose. Pseudobulbs oblongoid, somewhat compressed, sulcate, 1(2)-foliate, subtended basally by non-foliaceous sheaths. Inflorescence multiflowered, paniculate. Sepals and petals dissimilar, lateral sepals basally connate. Lip 3-lobed at the apex, sessile, the middle lobe ligulate, both lateral lobes elliptic-ovate, concave, calli in form of 3 more or less parallel thick ridges running from the base down to the basal portion of the lip middle lobe, disc papillate. Gynostemium perpendicular to the lip, short and stout. Wings prominent, obliquely oblong rhombic. Anther incumbent. Pollinia 2, oblong-obovoid, dorsiventrally flattened, hard. Apical clinandrium obscure. Stigma very small, deeply concave. Rostellum relatively short, conical-digitate in the middle, obtuse. Viscidium single, elliptic, rather small, thick, fleshy. Tegula single, oblong oblanceolate, flat, thin, lamellate. Rostellum remnant bilobulate at the middle, canaliculate on the dorsal surface. Tabula infrastigmatic prominent.

We had no access to any material of this species that would have been suitable for molecular work. CHASE et al. (2009) transferred *Oncidium paranaense* Kraenzl. to *Gomesa* s.l. and BARROS & RODRIGUES (2010a) to *Coppensia*. Due to the unusual lip form combined with the *Gomesa*-type gynostemium and sulcate, oblongoid pseudobulbs, DOCHA NETO & BAPTISTA (2011) created the monospecific genus *Hardingia*.

Homoplasy

Homoplasy shows the independent evolutionary origin or loss of one or more features in different organisms. The appearance of homoplasy can affect the inference of phylogenetic relationships, joining similar groups, but not related taxa. Many researchers have discussed the relative extent of homoplasy in morphological and molecular data, and which data should be used to infer phylogeny (GIVNISH & SYTSMA 1992, 1997a, b; MIYAMOTO & FITCH 1995; DOYLE 1996). Main

problems arise, when morphology and molecules provide different results and cannot be used in understanding phylogeny and adaptive evolution. Most studies of homoplasy have focussed on patterns rather than on processes, as in the following problem.

Homoplasy is expressed in three patterns of features or character-state evolution: convergence, parallelism and reversal (HENNIG 1979; MCSHEA 1996; FUTUYMA 1997). If different organisms occupy a similar ecological niche, and they are pollinated by the same pollinators, it is difficult to determinate which morphology trait is an effect of convergence and which is inherited from the ancestor. On the other side, phylogenetic analysis establishes the relationships between genes or gene fragments by inferring the common history of the sequences. To achieve this, the sequences used for the studies need to be homologous (VANDAMME 2009). Theoretically, phylogenetic analyses should be able to resolve the issues above. However, if a particular character shows only a limited number of states (in respect to nucleotides in the DNA sequence), evolution will appear to proceed linearly. In that case, we are dealing with analogous but non-homologous mutations which can accumulate by chance in species that lack a recent common ancestor (GIVNISH & SYTSMAS 1992). However, nucleotide sequence reversal may occur when a substitution reverts back to the original nucleotide. Firstly, when we deal with multiple hits, the substitution will have occurred several times at the same nucleotide. Secondly, when we observe parallel substitutions, the same substitution may have happened in two different lineages (VANDAMME 2009). Such cases can lead to homoplasy in sequence alignments, and they can affect the inference of phylogeny.

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Appendix 1. Comparative morphology of *Gomesa* and its relatives.

| | <i>Gomesa</i> s. str. | <i>Rodrigueziiella</i> | <i>Rodrigueztopsis</i> | <i>Nitidodictium</i> | <i>Neoruschia</i> | <i>Kleberiiella</i> | <i>Alatiglossum</i> | <i>Cavriella</i> | |
|------------------------|---|--|---|--|---|---|--|--|--|
| Habit | caespitose | caespitose | plants with long aerial stolons | caespitose | caespitose | caespitose | caespitose | caespitose | |
| Pseudobulbs | clustered, compressed, bifoliate, enclothed basally by few sheaths, of which the uppermost with obscure blade | clustered, somewhat compressed, bifoliate, enclothed by bladeless sheaths | spaced, compressed, bifoliate, subtended basally by leafy sheaths | clustered, somewhat flattened, ovoid, shallowly sulcate, bifoliate, enclothed basally in bladeless sheaths | clustered, laterally compressed, ovoid, smooth, unifoliate, enclothed in 1–2 leafy sheaths | clustered, compressed, oblongoid to ovoid, smooth, unifoliate, enclothed in bladeless sheaths | clustered, compressed, oblongoid to ovoid, rather smooth, single-leaved, enclothed in bladeless sheaths | clustered, compressed, ovoid, smooth, unifoliate, enclothed in bladeless sheaths | |
| Inflorescence | usually dense, many-flowered | laxly to subdensely few-flowered | laxly few-flowered | laxly few-flowered | laxly few-flowered | laxly few-flowered | sublaxly many-flowered, branching | laxly few-flowered | |
| Tepals | subsimpliar, lateral sepals more or less connate in the lower part | dissimpliar, lateral sepals free to the base | dissimpliar, lateral sepals free to the base | subsimpliar, lateral sepals basally connate | subsimpliar, lateral sepals basally free | subsimpliar, lateral sepals free to the base | dissimpliar, lateral sepals basally connate | subsimpliar, lateral sepals free to the base | |
| Lip | sessile, unlobed to obscurely 3-lobed, more or less geniculate near the middle | sessile, geniculate reflexed near the middle, inconspicuously lobed or almost entire | clawed, 3-lobed near the middle, lateral lobes much smaller than the middle one | sessile, basally cuneate, apical lobe transversely elliptic, apically emarginated | sessile, basally cordate, prominently 3-lobed, middle lobe transversely elliptic, apically emarginated, much larger than lateral lobes, lateral lobes dentate along upper margins | clawed, 3-lobed, lateral lobes much smaller than the middle one, isthmus with fringed margins | clawed, 3-lobed, middle lobe clawed, entire, lateral lobes prominent, with more or less fringed apical margins or entire but with fringed isthmus margins between lateral and middle lobes | sessile, basally rounded and 3-lobed, middle lobe oblong elliptic, larger than lateral lobes | |
| Lip callus | consisting of two parallel lamellae in the lower part | lamellate, lamellae pubescent | consisting of two parallel keels in the lower half | consisting of thick pad of tissue, diverging towards the apex into two short keels | massive, consisting of some digitate and knob-like projections, more or less radiating, glabrous | prominent, massive, prominently dissected into oblong segments | consisting of some lobes, plates and/or digitate projections | consisting of prominent keel running in the lower half, apically somewhat diverging and upcurved, basally terminated with a pair of subglobose projections, glabrous | |
| Anther | subapical or apical, incumbent | subventral, incumbent, papillate | subdorsal, incumbent | subventral | subventral | subventral | subventral | subventral, apically 3-lobed, papillate | |
| Tabula infrastigmatica | absent | absent | absent | prominent | inconspicuous | prominent | prominent | prominent | |

Generic delimitation in the *Gomesa* alliance (Orchidaceae, Oncidiinae)

| <i>Campaccia</i> | <i>Baptistonia</i> | <i>Brasilidium</i> | <i>Carenidium</i> | <i>Ornithophora</i> | <i>Menesciella</i> | <i>Coppensia (varicosum)</i> | <i>Rhinocidium</i> | <i>Coppensia (flexuosum)</i> | <i>Oncidium (altissimum)</i> |
|--|--|---|---|--|---|--|--|--|---|
| caespitose | caespitose | caespitose | caespitose | rhizome elongate | caespitose | caespitose | caespitose | caespitose | caespitose |
| clustered, somewhat compressed, oblongoid, smooth, enclosed basally by bladeless sheaths, 2–3-leaved | clustered, somewhat compressed, ovoid to oblongoid, smooth, unifoliate, enclosed in bladeless sheaths | clustered, somewhat compressed, unifoliate, enclosed with bladeless sheaths | clustered, somewhat compressed, sulcate, bifoliate, basally enclosed in bladeless sheaths | not clustered, somewhat compressed, bifoliate, subtended basally by some leafy sheaths | clustered, somewhat compressed, sulcate, bifoliate, sheaths bladeless, or the uppermost leafy | somewhat compressed and sulcate, bifoliate, 1 or 2 upper sheaths leafy | clustered, compressed, sulcate, bifoliate, sheaths bladeless | well-separated one from another, 1- or 2-foliate, subtended basally by 1–2 leafy sheaths | clustered, compressed, bifoliate, enclosed basally by few leafy sheaths |
| densely many-flowered, branching | laxly to densely few- to many-flowered, sometimes branching | rather densely many-flowered, branching | rather laxly several-flowered | laxly few-flowered | rather laxly many-flowered, branching | subdensely many-flowered, often branching | many-flowered, branching | densely many-flowered, often branching | many-flowered, branching |
| dissimilar, lateral sepals connate at the base only | dissimilar, lateral sepals more or less connate | subsimilar, lateral sepals more or less connate basally | subsimilar, lateral sepals basally connate | subsimilar, lateral sepals free to the base | subsimilar, lateral sepals free to the base | subsimilar, lateral sepals basally connate | subsimilar, lateral sepals connate in the basal half | subsimilar, lateral sepals free to the base | subsimilar, lateral sepals free to the base |
| sessile, basally rounded and 3-lobed, the middle lobe transversely elliptic, lateral lobes smaller | sessile, 3-lobed, the middle lobe transversely elliptic; callus | sessile, basally 3-lobed, lateral lobes much smaller than the middle one | clawed, 3-lobed, lateral lobes smaller than middle lobe; callus | clawed, claw terminated by knob-like callus, lamina more or less transversely elliptic | sessile, deeply 3-lobed just above the base, lateral lobes ligulate, the middle lobe clawed, elliptic | sessile, much larger than tepals, basally 3-lobed, lateral lobes obscure, the middle lobe apically incised | sessile, 3-lobed just above the base, the middle lobe much larger than both laterals | sessile, 3-lobed just above the base, sessile | sessile, 3-lobed just above the base, the middle lobe much larger than the middle one, middle lobe apically incised |
| prominent, dissected into some plates and variously shaped projections | consisting of prominent, parallel keels running in the lower half, apically somewhat diverging or with more sophisticated pattern consisting of variously shaped projections | consisting of two thick ridges and often some more projections | in form two keels restricted to the claw, lamina large, flat | lamellate, lamellae thickened | in form of massive tissue covering basal part of the lip | consisting of numerous tubercles, elongate projections or thickenings of various forms | in form of single, horn-like, upcurved projection, with transverse ridge above | in form of rather complicated mix of various more or less elongate projections | in form of rather complicated mix of various more or less elongate projections |
| subventral | incumbent | subventral, incumbent, papillate | subventral, incumbent | subventral, incumbent, papillate | subapical, incumbent | subapical, incumbent | subventral, incumbent, papillate | subventral, incumbent | |
| prominent | present | prominent | absent | absent | prominent | prominent | absent | prominent | prominent |

Appendix 1 (Continuation). Comparative morphology of *Gomesa* and its relatives.

| | <i>Gomesa</i> s.str. | <i>Rodriguezella</i> | <i>Rodriguezopsis</i> | <i>Nitidodium</i> | <i>Neoruschia</i> | <i>Kleberella</i> | <i>Alatiglossum</i> | <i>Carriella</i> | |
|--------------------|---|---|--|--|---|--|--|---|--|
| Gynostemium | somewhat diverging from the lip, erect or gently arched, elongate, slender; column part wingless or obscurely winged in the upper half | parallel with the basal lip part, erect, elongate, slender; column part twice longer than anther, obscurely winged below stigma, minutely papillate on wings' margins, ciliate on two knob-like thickenings just below stigma | parallel with the basal lip part, fused with the lip margins up to the rostellum base, slightly swollen and bent back at the apex; column part ca. 1.5 times longer than anther, glabrous, with two wing-like projections on both sides of rostellum | forms an acute angle with the lip, erect, rather short and stout; column part broadly winged near the stigma, wings obliquely rhomboid, entire | forms a right angle with the lip, erect, rather short; column part broadly winged near the stigma, wings obliquely elliptic-ovate, entire | forms a right angle with the lip, erect, rather short; column part narrowly alate near the stigma | forms an obtuse angle with the lip, erect, rather short, slender; column part very narrowly alate near the stigma | forms an obtuse angle with the lip, suberect, elongate, slender; column part terete | |
| Apical clinandrium | obscure | obscure | forming narrow collar-like structure surrounding anther base | obscure | obscure | obscure | obscure | obscure | |
| Stigma | large, oblong-elliptic, deeply concave | rather large, elliptic, deeply concave | large, elliptic, concave | large, ovate, deeply concave | large, ovate, deeply concave | large, ovate, deeply concave | large, ovate, deeply concave | large, ovate, deeply concave | |
| Rostellum | elongate in the middle, ligulate, obtuse; remnant bilobulate at the middle, with oblique shallowly concave plate between obscure, acute lobules | rather short and stout, conical-digitate in the middle, obtuse; remnant bilobulate at the middle, with oblique shallowly concave plate between acute lobules | erect, triangular ligulate, rounded at apex; remnant shallowly bilobed at apex, with oblique, apical plate on inner surface surrounded by fovea | short but relatively massive, conical-digitate in the middle, obtuse; remnant bilobulate at the middle, canalicate on the dorsal surface | short but relatively massive, conical-digitate in the middle, obtuse; remnant bilobulate at the middle, canalicate on the dorsal surface | short but relatively massive, conical-digitate in the middle, obtuse; remnant bilobulate at the middle, canalicate on the dorsal surface | short but relatively massive, conical-digitate in the middle, obtuse; remnant bilobulate at the middle, canalicate on the dorsal surface | short, conical-digitate in the middle, obtuse; remnant bilobulate at the middle, canalicate on the dorsal surface | |
| Viscidium | single, oblong-elliptic, thick | single, oblong, thick, fleshy | single, small, elliptic, fleshy, thick | single, large, ellipsoid, very thick, fleshy | single, rather small, ellipsoid | single, rather small, ellipsoid | single, rather small, ellipsoid | single, very small, ellipsoid, delicate | |
| Tegula | single, linear, thin, lamellate | single, large, oblong obovate, thin, lamellate, flat | single, obtriangular in upper half, linear below, thin, lamellate | single, oblong, thin, lamellate, delicate, flat | single, oblong, thin, lamellate, delicate, flat | single, oblong, thin, lamellate, delicate, flat | single, oblong, thin, lamellate, delicate, flat | single, linear, thin, lamellate, very delicate, flat | |

Generic delimitation in the *Gomesa* alliance (Orchidaceae, Oncidiinae)

| | <i>Campaccia</i> | <i>Baptistonia</i> | <i>Brasilidium</i> | <i>Carenidium</i> | <i>Ornithophora</i> | <i>Menezeiella</i> | <i>Coppensia</i> (<i>varicosum</i>) | <i>Rhinocidium</i> | <i>Coppensia</i> (<i>flexuosum</i>) | <i>Oncidium</i> (<i>altissimum</i>) |
|--|--|---|---|--|--|---|---|---|--|--|
| | forms an obtuse angle with the lip, erect, rather short; column part with prominent, rather massive oblong projections near the stigma | forming an acute angle with the lip, elongate, rather slender, slightly arched; column part glandular below stigma, with two obliquely triangular projections just above the middle | perpendicular to the lip lamina, erect or slightly arched, stout, short; column part slightly longer than anther, winged near the stigma, wings usually well-developed, flabellate or flat, entire or uneven and papillate on margins | perpendicular to the lip, rather short, stout, erect, forming a right angle with the lip lamina; column part with two digitate projections near the stigma | perpendicular to the lip, elongate, slender, somewhat arcuate; column part terete, non-winged, slightly swollen just below the stigma base | forms an obtuse angle with the lip lamina, erect, short; column part obscurely winged in the upper half | more or less perpendicular to the lip axis, rather short, somewhat arcuate; column part alate, wings obliquely ovate, entire | perpendicular to the lip lamina, elongate, slender, terete; column part winged near the stigma, wings entire and papillate on margins | perpendicular to the lip lamina, rather short and stout, alate; wings prominent, elliptic to obliquely ovate | forms an obtuse angle with the lip, suberect, winged near the stigma, wings well-developed, flabellate, entire or uneven |
| | obscure | prominent, exceeding the anther, almost entire, glandular near the margin | usually obscure, occasionally forms a narrow collar-like structure surrounding the anther base | obscure | obscure | obscure | obscure | obscure | obscure | obscure |
| | rather small, ovate, deeply concave | relatively narrow, elliptic, deeply concave | large, elliptic, deeply concave | large, elliptic, deeply concave | small, elliptic, deeply concave, partially hidden by rostellum | small, oblong elliptic, deeply concave | elliptic-ovate, deeply concave | rather small, ovate, deeply concave | large, elliptic-ovate, deeply concave | large, elliptic-ovate, deeply concave |
| | short, conical-digitate in the middle, obtuse; remnant bilobulate at the middle, canaliculate on the dorsal surface | pendent, small, ligulate, blunt; remnant with apical, oblique, shallow plate surrounded by two obscure triangular, acute lobules | relatively short, conical-digitate in the middle, obtuse; remnant bilobulate at the middle, canaliculate on the dorsal surface | relatively short, conical-digitate in the middle, obtuse; remnant bilobulate at the middle, canaliculate on the dorsal surface | elongate, rostrate, thick, bent down at the apex, obtuse; remnant rostrate, bilobulate at the apex | elongate in the middle, ligulate, obtuse; remnant bilobulate at the middle, with oblique shallowly concave plate between obscure, acute lobules | elongate in the middle, ligulate, obtuse; remnant bilobulate at the middle, with oblique shallowly concave plate between obscure, acute lobules | very short, digitate in the middle, obtuse; remnant bilobulate at the middle | relatively short, conical-digitate in the middle, obtuse; remnant bilobulate at the middle, canaliculate on the dorsal surface | |
| | single, small, ellipsoid | single, very small, ovate, thin, sticky on the outer surface | single, elliptic, thick, fleshy | single, elliptic, thick, fleshy | single, oblong ovate, thin, lamellate | single, small | single, small | single, elliptic, thick, fleshy | single, elliptic, rather small, thick, fleshy | single, elliptic, rather small, thick, fleshy |
| | single, oblong, thin, lamellate, delicate, flat | single, oblong triangular, thin, lamellate | single, oblong-elliptic, flat, sometimes more or less geniculate near the apex, thin, lamellate | single, oblong, flat, thin, lamellate | single, linear, apically expanded, thin, lamellate | single, linear, thin, lamellate | single, linear, thin, lamellate | single, oblong, thin, lamellate | single, oblong, flat, thin, lamellate | single, oblong, flat, thin, lamellate |

Appendix 2. Taxonomic treatment of representatives of the *Gomesa* alliance.

| Species | Original placement | Morphological approach* (chronological order) | | | | Molecular approach# | Present paper |
|-----------------------|---------------------|---|---|--|--|---------------------|-----------------------|
| <i>adamantina</i> | <i>Oncidium</i> | <i>Coppensia adamantina</i> (Marçal & Cath.) Cath. 2008 | | | | <i>Gomesa</i> | <i>Rodriguezopsis</i> |
| <i>albinoi</i> | <i>Oncidium</i> | <i>Baptistonia amicta</i> (Lindl.) Chiron & V.P. Castro 2004 | | | | <i>Gomesa</i> | <i>Baptistonia</i> |
| <i>alpina</i> | <i>Gomesa</i> | | | | | | <i>Gomesa</i> |
| <i>amictum</i> | <i>Oncidium</i> | <i>Baptistonia amicta</i> (Lindl.) Chiron & V.P. Castro 2004 | | | | | <i>Baptistonia</i> |
| <i>barbaceniae</i> | <i>Oncidium</i> | <i>Ampliglossum barbaceniae</i> (Lindl.) Campacci 2006 | <i>Coppensia barbaceniae</i> (Lindl.) Campacci 2006 | | | <i>Gomesa</i> | <i>Nitidocidium</i> |
| <i>barbatum</i> | <i>Oncidium</i> | <i>Alatiglossum barbatum</i> (Lindl.) Baptista 2006 | | | | <i>Gomesa</i> | <i>Alatiglossum</i> |
| <i>barkeri</i> | | | | | | <i>Gomesa</i> | <i>Gomesa</i> |
| <i>batemaniana</i> | <i>Oncidium</i> | <i>Ampliglossum batemanianum</i> (Parm. ex Knowles & Westc.) Campacci 2006 | <i>Coppensia batemaniana</i> (Parm. ex Knowles & Westc.) Campacci 2006 | | | | <i>Coppensia</i> |
| <i>bicolor</i> | <i>Oncidium</i> | <i>Ampliglossum bicolor</i> (Lindl.) Campacci 2006 | <i>Coppensia bicolor</i> (Lindl.) Campacci 2006 | | | <i>Gomesa</i> | <i>Coppensia</i> |
| <i>bifolia</i> | <i>Oncidium</i> | <i>Coppensia bifolia</i> (Sims) Dumort. 1835 | <i>Ampliglossum bifolium</i> (Sims) Campacci 2006 | | | <i>Gomesa</i> | <i>Coppensia</i> |
| <i>binotii</i> | <i>Gomesa</i> | | | | | <i>Gomesa</i> | <i>Gomesa</i> |
| <i>blanchetii</i> | <i>Oncidium</i> | <i>Ampliglossum blanchetii</i> (Rchb. f.) Campacci 2006 | <i>Coppensia blanchetii</i> (Rchb. f.) Campacci 2006 | | | <i>Gomesa</i> | <i>Coppensia</i> |
| <i>bohnikianum</i> | <i>Oncidium</i> | <i>Kleberella bohnikiana</i> (V.P. Castro & G.F. Carr) V.P. Castro & Cath. 2006 | <i>Alatiglossum bohnikianum</i> (V.P. Castro & G.F. Carr) Baptista 2007 | | | | <i>Alatiglossum</i> |
| <i>brachyandrum</i> | <i>Oncidium</i> | <i>Concocidium brachyandrum</i> (Lindl.) Romowicz & Szlach 2006 | | | | | <i>Carenidium</i> |
| <i>brasiliensis</i> | <i>Cochlioda</i> | | | | | <i>Gomesa</i> | <i>Gomesa</i> |
| <i>brieniana</i> | <i>Oncidium</i> | <i>Baptistonia brieniana</i> (Rchb. f.) V.P. Castro & Chiron 2004 | | | | | <i>Baptistonia</i> |
| <i>brunnipetala</i> | <i>Oncidium</i> | <i>Ampliglossum brunnipetalum</i> (Barb. Rodr.) Campacci 2006 | <i>Coppensia brunnipetala</i> (Barb. Rodr.) Campacci 2006 | | | | <i>Brasilidium</i> |
| <i>caldense</i> | <i>Oncidium</i> | <i>Coppensia caldensis</i> (Rchb. f.) Docha Neto 2006 | | | | | <i>Coppensia</i> |
| <i>calimaniana</i> | <i>Castroa</i> | <i>Coppensia calimaniana</i> (Guiard) F. Barros & V.T. Rodrigues 2010 | | | | | <i>Menezesiella</i> |
| <i>calimaniorum</i> | <i>Menezesiella</i> | <i>Coppensia calimaniorum</i> (V.P. Castro & G.F. Carr) F. Barros & V.T. Rodrigues 2010 | | | | | <i>Menezesiella</i> |
| <i>calimaniorum</i> | <i>Baptistonia</i> | | | | | | <i>Baptistonia</i> |
| <i>carlosregentii</i> | | | | | | <i>Gomesa</i> | <i>Alatiglossum</i> |

Appendix 2 (Continuation). Taxonomic treatment of representatives of the *Gomesa* alliance.

| Species | Original placement | Morphological approach* (chronological order) | | | | Molecular approach# | Present paper |
|-------------------------|--------------------|---|--|--|--|---------------------|---------------------|
| <i>chapidensis</i> | <i>Oncidium</i> | <i>Ampliglossum chapadense</i> (V.P. Castro & Campacci) Campacci 2006 | <i>Coppensia chapadensis</i> (V.P. Castro & Campacci) Campacci 2006 | | | | <i>Coppensia</i> |
| <i>chrysopteranthum</i> | <i>Oncidium</i> | <i>Alatiglossum chrysopteranthum</i> (Lückel) Baptista 2006 | | | | | <i>Alatiglossum</i> |
| <i>chrysopterum</i> | <i>Oncidium</i> | <i>Alatiglossum chrysopterum</i> (Lindl.) Baptista 2006 | | | | | <i>Alatiglossum</i> |
| <i>chrysothapsis</i> | | | | | | <i>Gomesa</i> | <i>Baptistonia</i> |
| <i>chrysostoma</i> | <i>Gomesa</i> | | | | | | <i>Gomesa</i> |
| <i>chrysothysus</i> | <i>Oncidium</i> | | | | | | <i>Coppensia</i> |
| <i>ciliatum</i> | <i>Oncidium</i> | <i>Alatiglossum ciliatum</i> (Lindl.) Baptista 2006 | | | | <i>Gomesa</i> | <i>Alatiglossum</i> |
| <i>cogniauxianum</i> | <i>Oncidium</i> | <i>Alatiglossum cogniauxianum</i> (Schltr.) Baptista 2006 | <i>Neoruschia cogniauxiana</i> (Schltr.) Cath. & V.P. Castro 2006 | | | <i>Gomesa</i> | <i>Neoruschia</i> |
| <i>colnagoi</i> | <i>Oncidium</i> | <i>Brasilidium colnagoi</i> (Pabst) Campacci 2006 | | | | | <i>Brasilidium</i> |
| <i>coloratum</i> | <i>Oncidium</i> | <i>Carriella colorata</i> (Königer & J.G. Weinm. bis) V.P. Castro & K.G. Lacerda 2006 | <i>Baptistonia colorata</i> (Königer & J.G. Weinm.) Chiron 2008 | | | <i>Gomesa</i> | <i>Carriella</i> |
| <i>concolor</i> | <i>Oncidium</i> | <i>Carenidium concolor</i> (Hook.) Baptista 2006 | <i>Brasilidium concolor</i> (Hook.) F. Barros & V.T. Rodrigues 2010 | <i>Concocidium concolor</i> (Hook.) Romowicz & Szlach. 2006 | | <i>Gomesa</i> | <i>Carenidium</i> |
| <i>cornigerum</i> | <i>Oncidium</i> | <i>Baptistonia cornigera</i> (Lindl.) Chiron & V.P. Castro 2004 | | | | <i>Gomesa</i> | <i>Baptistonia</i> |
| <i>crispum</i> | <i>Rodriguezia</i> | <i>Brasilidium crispum</i> (Lodd.) Campacci 2006 | <i>Anettea crispa</i> (Lodd.) Szlach. & Mynnik 2006 | | | | <i>Gomesa</i> |
| <i>croesus</i> | <i>Oncidium</i> | <i>Alatiglossum croesus</i> (Rchb. f.) Baptista 2006 | <i>Kleberella croesus</i> (Rchb. f.) V.P. Castro & Cath. 2006 | | | | <i>Alatiglossum</i> |
| <i>cruciata</i> | <i>Oncidium</i> | <i>Baptistonia cruciata</i> (Rchb. f.) Chiron & V.P. Castro 2004 | | | | | <i>Baptistonia</i> |
| <i>culuenense</i> | <i>Oncidium</i> | <i>Alatiglossum culuenense</i> Docha Neto & Benelli 2006 | | | | | <i>Alatiglossum</i> |
| <i>curtum</i> | <i>Oncidium</i> | <i>Brasilidium curtum</i> (Lindl.) Campacci 2006 | <i>Anettea curta</i> (Lindl.) Szlach. & Mynnik 2006 | | | <i>Gomesa</i> | <i>Brasilidium</i> |
| <i>damacenoii</i> | <i>Baptistonia</i> | | | | | | <i>Baptistonia</i> |
| <i>dasytyle</i> | <i>Oncidium</i> | <i>Carenidium dasytyle</i> (Rchb. f.) Baptista 2006 | <i>Brasilidium dasytyle</i> (Rchb. f.) F. Barros & V.T. Rodrigues 2010 | <i>Concocidium dasytyle</i> (Rchb. f.) Romowicz & Szlach. 2006 | | <i>Gomesa</i> | <i>Carenidium</i> |
| <i>densiflora</i> | <i>Gomesa</i> | | | | | | <i>Gomesa</i> |
| <i>diamantinensis</i> | <i>Coppensia</i> | | | | | | <i>Coppensia</i> |
| <i>disciferum</i> | <i>Oncidium</i> | <i>Rhinocidium disciferum</i> (Lindl.) Docha Neto 2007 | <i>Concocidium disciferum</i> (Lindl.) Romowicz & Szlach. 2006 | | | | <i>Menezesiella</i> |

Appendix 2 (Continuation). Taxonomic treatment of representatives of the *Gomesa* alliance.

| Species | Original placement | Morphological approach* (chronological order) | | | | Molecular approach# | Present paper |
|------------------------|----------------------|---|--|--|--|---------------------|-------------------------|
| <i>divaricata</i> | <i>Gomesa</i> | | | | | | <i>Gomesa</i> |
| <i>doeringii</i> | <i>Theodorea</i> | | | | | | <i>Gomesa</i> |
| <i>doniana</i> | <i>Oncidium</i> | <i>Ampliglossum donianum</i> (Bateman ex W. Baxter) Campacci 2006 | <i>Coppensia doniana</i> (Bateman ex W. Baxter) Campacci 2006 | | | <i>Gomesa</i> | <i>Coppensia</i> |
| <i>duseniana</i> | <i>Gomesa</i> | | | | | | <i>Gomesa</i> |
| <i>echinata</i> | <i>Baptistonia</i> | | | | | <i>Gomesa</i> | <i>Baptistonia</i> |
| <i>edmundoi</i> | <i>Oncidium</i> | <i>Ampliglossum edmundoi</i> (Pabst) Campacci 2006 | <i>Coppensia edmundoi</i> (Pabst) Campacci 2006 | | | | <i>Coppensia</i> |
| <i>eleutherosepala</i> | <i>Rodriguezia</i> | | | | | | <i>Rodrigueziaopsis</i> |
| <i>emilii</i> | <i>Oncidium</i> | <i>Alatiglossum emilii</i> (Schltr.) Baptista 2006 | | | | | <i>Alatiglossum</i> |
| <i>enderianum</i> | <i>Oncidium</i> | <i>Anettea enderiana</i> (auct.) Szlach. & Mytnik 2006 | | | | | <i>Brasilidium</i> |
| <i>endocharis</i> | <i>Oncidium</i> | <i>Concocidium endocharis</i> (Rchb. f.) Romowicz & Szlach. 2006 | | | | | <i>Carenidium</i> |
| <i>erectiflora</i> | <i>Gomesa</i> | | | | | | <i>Caucaea</i> |
| <i>eurycline</i> | <i>Oncidium</i> | | | | | | <i>Alatiglossum</i> |
| <i>fimbriata</i> | <i>Oncidium</i> | <i>Baptistonia fimbriata</i> (Lindl.) Chiron & V.P. Castro 2004 | | | | | <i>Baptistonia</i> |
| <i>fischeri</i> | <i>Gomesa</i> | | | | | | <i>Gomesa</i> |
| <i>flexuosum</i> | <i>Oncidium</i> | <i>Ampliglossum flexuosum</i> (Lodd.) Campacci 2006 | <i>Coppensia flexuosa</i> (Lodd.) Campacci 2006 | | | <i>Gomesa</i> | <i>Coppensia</i> |
| <i>foliosa</i> | <i>Pleurothallis</i> | | | | | | <i>Gomesa</i> |
| <i>forbesii</i> | <i>Oncidium</i> | <i>Brasilidium forbesii</i> (Hook.) Campacci 2006 | <i>Anettea forbesii</i> (Hook.) Szlach. & Mytnik 2006 | | | <i>Gomesa</i> | <i>Brasilidium</i> |
| <i>fuscans</i> | <i>Oncidium</i> | <i>Ampliglossum fuscans</i> (Rchb. f.) Campacci 2006 | <i>Coppensia fuscans</i> (Rchb. f.) Campacci 2006 | <i>Heteranthocidium fuscans</i> (Rchb. f.) Szlach., Mytnik & Romowicz 2006 | | <i>Gomesa</i> | <i>Coppensia</i> |
| <i>fuscopetalum</i> | <i>Oncidium</i> | <i>Alatiglossum fuscopetalum</i> (Hoehne) Baptista 2006 | | | | | <i>Alatiglossum</i> |
| <i>gardneri</i> | <i>Oncidium</i> | <i>Brasilidium gardneri</i> (Lindl.) Campacci 2006 | <i>Anettea gardneri</i> (Lindl.) Szlach. & Mytnik 2006 | | | <i>Gomesa</i> | <i>Brasilidium</i> |
| <i>gilva</i> | <i>Epidendrum</i> | | | | | <i>Gomesa</i> | <i>Gomesa</i> |
| <i>glaziovii</i> | <i>Gomesa</i> | | | | | <i>Gomesa</i> | <i>Gomesa</i> |
| <i>gomezoides</i> | <i>Theodorea</i> | | | | | <i>Gomesa</i> | <i>Rodriguezella</i> |
| <i>gracile</i> | <i>Oncidium</i> | <i>Carenidium gracile</i> (Lindl.) Baptista 2006 | <i>Nitidocidium gracile</i> (Lindl.) F. Barros & V.T. Rodrigues 2010 | <i>Concocidium gracile</i> (Lindl.) Romowicz & Szlach. 2006 | | <i>Gomesa</i> | <i>Nitidocidium</i> |
| <i>graminifolium</i> | <i>Cyrtochilum</i> | <i>Concocidium graminifolium</i> (Lindl.) Romowicz & Szlach. 2006 | | | | | <i>Carenidium</i> |
| <i>gravesianum</i> | <i>Oncidium</i> | <i>Brasilidium gravesianum</i> (Rolfe) Campacci 2006 | <i>Anettea gravesiana</i> (Rolfe) Szlach. & Mytnik 2006 | | | <i>Gomesa</i> | <i>Brasilidium</i> |
| <i>guinlei</i> | <i>Theodorea</i> | | | | | | <i>Gomesa</i> |

Appendix 2 (Continuation). Taxonomic treatment of representatives of the *Gomesa* alliance.

| Species | Original placement | Morphological approach* (chronological order) | | | Molecular approach# | Present paper |
|---|----------------------|---|---|--|---------------------|---------------------|
| <i>gutfreundiana</i> | <i>Oncidium</i> | <i>Baptistonia gutfreundiana</i> (Chiron & V.P. Castro) Chiron & V.P. Castro 2004 | | | | <i>Baptistonia</i> |
| <i>handroi</i> | <i>Theodorea</i> | | | | <i>Gomesa</i> | <i>Gomesa</i> |
| <i>herzogii</i> | <i>Oncidium</i> | <i>Alatiglossum herzogii</i> (Schltr.) Docha Neto 2007 | | | | <i>Alatiglossum</i> |
| <i>hookeri</i> | <i>Oncidium</i> | <i>Carenidium hookeri</i> (Rolfe) Baptista 2006 | <i>Menezesiella hookeri</i> (Rolfe) V.P. Castro & Chiron 2006 | <i>Coppensia bookeri</i> (Rolfe) F. Barros & L.R.S. Guim. 2010 | <i>Gomesa</i> | <i>Menezesiella</i> |
| <i>hydrophilum</i> | <i>Oncidium</i> | <i>Ampliglossum hydrophilum</i> (Barb. Rodr.) Campacci 2006 | <i>Coppensia hydrophila</i> (Barb. Rodr.) Campacci 2006 | | <i>Gomesa</i> | <i>Coppensia</i> |
| <i>imperatoris-maximiliani</i> | <i>Oncidium</i> | <i>Anettea imperatoris-maximiliani</i> (Rchb. f.) Szlach. & Mytnik 2006 | | | <i>Gomesa</i> | <i>Brasilidium</i> |
| <i>intermedia</i> | <i>Gomesa</i> | | | | | <i>Gomesa</i> |
| <i>insigne</i> (varicosum var. <i>insigne</i>) | <i>Oncidium</i> | <i>Ampliglossum insigne</i> (Rolfe) Campacci 2006 | <i>Coppensia varicosa</i> (Lindl.) Campacci var. <i>insignis</i> (Rolfe) Campacci 2006 | | | <i>Coppensia</i> |
| <i>isopterum</i> | <i>Oncidium</i> | <i>Ampliglossum isopterum</i> (Lindl.) Campacci 2006 | <i>Coppensia isoptera</i> (Lindl.) Campacci 2006 | | | <i>Coppensia</i> |
| <i>itapetingensis</i> | <i>Oncidium</i> | <i>Carenidium itapetingens</i> (V.P. Castro & Chiron) Baptista 2006 | <i>Ornithophora itapetingensis</i> (V.P. Castro & Chiron) F. Barros & V.T. Rodrigues 2010 | | | <i>Ornithophora</i> |
| <i>jucunda</i> | <i>Mesospinidium</i> | | | | <i>Gomesa</i> | <i>Gomesa</i> |
| <i>kautskyi</i> | <i>Oncidium</i> | <i>Baptistonia kautskyi</i> (Pabst) V.P. Castro & Chiron 2004 | | | <i>Gomesa</i> | <i>Baptistonia</i> |
| <i>laxiflora</i> | <i>Gomesa</i> | | | | <i>Gomesa</i> | <i>Gomesa</i> |
| <i>leinigii</i> | <i>Oncidium</i> | <i>Baptistonia leinigii</i> (Pabst) Chiron & V.P. Castro 2004 | | | | <i>Baptistonia</i> |
| <i>lietzei</i> | <i>Oncidium</i> | <i>Baptistonia lietzei</i> (Regel) Chiron & V.P. Castro 2004 | | | <i>Gomesa</i> | <i>Baptistonia</i> |
| <i>loefgrenii</i> | <i>Oncidium</i> | <i>Carenidium loefgrenii</i> (Cogn.) Baptista 2006 | <i>Menezesiella loefgrenii</i> (Cogn.) V.P. Castro & Chiron 2006 | <i>Coppensia loefgrenii</i> (Cogn.) F. Barros & V.T. Rodrigues 2010 | <i>Gomesa</i> | <i>Menezesiella</i> |
| <i>longicornu</i> | <i>Oncidium</i> | <i>Rhinocidium longicornu</i> (Mutel) Baptista 2006 | <i>Rhinocerotidium longicornu</i> (Mutel) Szlach. 2006 | <i>Coppensia longicornu</i> (Mutel) F. Barros & V.T. Rodrigues 2010 | <i>Gomesa</i> | <i>Rhinocidium</i> |
| <i>longipes</i> | <i>Oncidium</i> | <i>Alatiglossum longipes</i> (Lindl.) Baptista 2006 | <i>Kleberella longipes</i> (Lindl.) V.P. Castro & Cath. 2006 | | <i>Gomesa</i> | <i>Alatiglossum</i> |
| <i>macronyx</i> | <i>Oncidium</i> | <i>Rhinocidium macronyx</i> (Rchb. f.) Baptista 2006 | <i>Rhinocerotidium macronyx</i> (Rchb. f.) Szlach. 2006 | <i>Coppensia macronyx</i> (Rchb. f.) F. Barros & V.T. Rodrigues 2010 | <i>Gomesa</i> | <i>Rhinocidium</i> |

Appendix 2 (Continuation). Taxonomic treatment of representatives of the *Gomesa* alliance.

| Species | Original placement | Morphological approach* (chronological order) | | | | Molecular approach# | Present paper |
|------------------------|---------------------|---|---|--|---|---------------------|-------------------------|
| <i>macropetalum</i> | <i>Oncidium</i> | <i>Alatiglossum macropetalum</i> (Lindl.) Baptista 2006 | | | | <i>Gomesa</i> | <i>Alatiglossum</i> |
| <i>majeuskyae</i> | <i>Oncidium</i> | <i>Ampliglossum majeuskyi</i> (Toscano & V.P. Castro) Campacci 2006 | <i>Coppensia majeuskyi</i> (Toscano & V.P. Castro) Campacci 2006 | | | | <i>Coppensia</i> |
| <i>mandonii</i> | <i>Oncidium</i> | <i>Ampliglossum mandonii</i> (Rchb. f.) Campacci 2006 | <i>Coppensia mandonii</i> (Rchb. f.) Campacci 2006 | | | | <i>Coppensia</i> |
| <i>mantiqueirensis</i> | <i>Coppensia</i> | | | | | | <i>Coppensia</i> |
| <i>margaritae</i> | <i>Gomesa</i> | | | | | | <i>Gomesa</i> |
| <i>marshallianum</i> | <i>Oncidium</i> | <i>Brasilidium marshallianum</i> (Rchb. f.) Campacci 2006 | <i>Anettea marshalliana</i> (Rchb. f.) Szlach. & Mytnik 2006 | | | | <i>Brasilidium</i> |
| <i>martiana</i> | <i>Oncidium</i> | <i>Ampliglossum martianum</i> (Lindl.) Campacci 2006 | <i>Coppensia martiana</i> (Lindl.) Campacci 2006 | | | <i>Gomesa</i> | <i>Coppensia</i> |
| <i>megalopterum</i> | <i>Oncidium</i> | | | | | | <i>Coppensia</i> |
| <i>messmeriana</i> | <i>Binotia</i> | <i>Gomesa messmeriana</i> (Campacci) Laitano 2010 | | | | | <i>Gomesa</i> |
| <i>microphyton</i> | <i>Rodriguezia</i> | | | | | | <i>Rodrigueziaopsis</i> |
| <i>micropogon</i> | <i>Oncidium</i> | <i>Alatiglossum micropogon</i> (Rchb. f.) Baptista 2006 | | | | | <i>Alatiglossum</i> |
| <i>montanum</i> | <i>Oncidium</i> | <i>Ampliglossum montanum</i> (Barb. Rodr.) Campacci 2006 | <i>Coppensia montana</i> (Barb. Rodr.) Campacci 2006 | | | <i>Gomesa</i> | <i>Coppensia</i> |
| <i>neoparanaensis</i> | <i>Menezesiella</i> | | | | | <i>Gomesa</i> | <i>Menezesiella</i> |
| <i>nitida</i> | <i>Oncidium</i> | <i>Baptistonia nitida</i> (Barb. Rodr.) V.P. Castro & Chiron 2004 | | | | <i>Gomesa</i> | <i>Baptistonia</i> |
| <i>novaesae</i> | <i>Oncidium</i> | <i>Gomesa novaesae</i> (Ruschi) Fraga & A.P. Fontana 2011 | <i>Brasilidium novaesae</i> (Ruschi) Chiron 2014 | | | | <i>Brasilidium</i> |
| <i>orthostates</i> | <i>Oncidium</i> | <i>Ampliglossum orthostates</i> (Ridl.) Campacci 2006 | <i>Coppensia orthostates</i> (Ridl.) Campacci 2006 | | | | <i>Coppensia</i> |
| <i>ottonis</i> | <i>Oncidium</i> | <i>Concocidium ottonis</i> (Schltr.) Romowicz & Szlach. 2006 | | | | | <i>Carenidium</i> |
| <i>ouricanensis</i> | <i>Oncidium</i> | <i>Carenidium ouricanense</i> (V.P. Castro & Campacci) Baptista 2006 | <i>Rhinocidium ouricanense</i> (V.P. Castro & Campacci) Docha Neto 2007 | <i>Coppensia ouricanensis</i> (V.P. Castro & Campacci) F. Barros & V.T. Rodrigues 2010 | | | <i>Menezesiella</i> |
| <i>pabstii</i> | <i>Oncidium</i> | <i>Baptistonia pabstii</i> (Campacci & C. Espejo) Chiron & V.P. Castro 2004 | | | | | <i>Baptistonia</i> |
| <i>paranaense</i> | <i>Oncidium</i> | <i>Carenidium paranaense</i> (Kraenzl.) Baptista 2006 | <i>Rhinocidium paranaense</i> (Kraenzl.) Docha Neto 2007 | <i>Hardingia paranaensis</i> (Kraenzl.) Docha Neto & Baptista 2011 | <i>Coppensia paranaensis</i> (Kraenzl.) F. Barros & V.T. Rodrigues 2010 | | <i>Incertae sedis</i> |
| <i>paranaensis</i> | <i>Gomesa</i> | | | | | | <i>Gomesa</i> |

Appendix 2 (Continuation). Taxonomic treatment of representatives of the *Gomesa* alliance.

| Species | Original placement | Morphological approach* (chronological order) | | | | Molecular approach# | Present paper |
|--------------------------|-----------------------|--|---|---|--|------------------------|------------------------|
| <i>paranaensis</i> | <i>Menezesiella</i> | | | | | | <i>Menezesiella</i> |
| <i>paranana</i> | <i>Gomesa</i> | <i>Coppensia paranana</i> (M.W. Chase & N.H. Williams) F. Barros & V.T. Rodrigues 2010 | | | | | <i>Menezesiella</i> |
| <i>paranapiacabensis</i> | <i>Oncidium</i> | <i>Ampliglossum paranapiacabense</i> (Hochne) Campacci 2006 | <i>Coppensia paranapiacabensis</i> (Hochne) Campacci 2006 | | | | <i>Coppensia</i> |
| <i>pardoglossa</i> | <i>Oncidium</i> | | | | | <i>Gomesa</i> | - |
| <i>pauciflora</i> | <i>Gomesa</i> | | | | | | <i>Gomesa</i> |
| <i>pectoralis</i> | <i>Oncidium</i> | <i>Brasilidium pectorale</i> (Lindl.) Campacci 2006 | <i>Anettea pectoralis</i> (Lindl.) Szlach. & Mytnik 2006 | | | <i>Gomesa</i> | <i>Brasilidium</i> |
| <i>petropolitana</i> | <i>Rodrigueziella</i> | | | | | <i>Gomesa</i> | <i>Gomesa</i> |
| <i>pirarensis</i> | <i>Oncidium</i> | <i>Ampliglossum pirarensis</i> (Rchb. f.) Campacci 2006 | <i>Coppensia pirarensis</i> (Rchb. f.) Campacci 2006 | | | <i>Noba-williamsia</i> | <i>Noba-williamsia</i> |
| <i>planifolia</i> | <i>Gomesa</i> | | | | | | <i>Gomesa</i> |
| <i>polymorpha</i> | <i>Gomesa</i> | | | | | | <i>Gomesa</i> |
| <i>praetextum</i> | <i>Oncidium</i> | <i>Brasilidium praetextum</i> (Rchb. f.) Campacci 2006 | <i>Anettea praetexta</i> (Rchb. f.) Szlach. & Mytnik 2006 | | | <i>Gomesa</i> | <i>Brasilidium</i> |
| <i>psyche</i> | <i>Oncidium</i> | <i>Alatiglossum psyche</i> (Schltr.) Baptista 2006 | | | | | <i>Alatiglossum</i> |
| <i>pubes</i> | <i>Oncidium</i> | <i>Baptistonia pubes</i> (Lindl.) Chiron & V.P. Castro 2004 | | | | <i>Gomesa</i> | <i>Baptistonia</i> |
| <i>pulchella</i> | <i>Waluwewa</i> | <i>Baptistonia pulchella</i> (Regel) Chiron & V.P. Castro 2004 | | | | | <i>Baptistonia</i> |
| <i>radicans</i> | <i>Sigmatostalix</i> | <i>Ornithophora radicans</i> (Rchb. f.) Garay & Pabst 1951 | | | | <i>Gomesa</i> | <i>Ornithophora</i> |
| <i>ramosa</i> | <i>Oncidium</i> | <i>Ampliglossum ramosum</i> (Lindl.) Campacci 2006 | <i>Coppensia ramosa</i> (Lindl.) Campacci 2006 | | | | <i>Coppensia</i> |
| <i>raniferum</i> | <i>Oncidium</i> | <i>Carenidium raniferum</i> (Lindl.) Baptista 2006 | <i>Menezesiella ranifera</i> (Lindl.) Chiron & V.P. Castro 2006 | <i>Rhinocidium raniferum</i> (Lindl.) Baptista 2007 | <i>Coppensia ranifera</i> (Lindl.) F. Barros & V.T. Rodrigues 2010 | <i>Gomesa</i> | <i>Menezesiella</i> |
| <i>reclinata</i> | <i>Gomesa</i> | | | | | | <i>Gomesa</i> |
| <i>recurva</i> | <i>Gomesa</i> | | | | | | <i>Gomesa</i> |
| <i>reductum</i> | <i>Oncidium</i> | <i>Alatiglossum reductum</i> (Kraenzl.) Baptista 2006 | | | | | <i>Alatiglossum</i> |
| <i>regentii</i> | <i>Menezesiella</i> | <i>Alatiglossum regentii</i> (V.P. Castro & G.F. Carr) Baptista 2007 | <i>Kleberella regentii</i> (V.P. Castro & G.F. Carr) V.P. Castro & Cath. 2006 | | | | <i>Alatiglossum</i> |
| <i>reichertii</i> | <i>Coppensia</i> | | | | | | <i>Coppensia</i> |
| <i>remotiflora</i> | <i>Oncidium</i> | <i>Baptistonia remotiflora</i> (Garay) Chiron & V.P. Castro 2004 | | | | | <i>Baptistonia</i> |

Appendix 2 (Continuation). Taxonomic treatment of representatives of the *Gomesa* alliance.

| Species | Original placement | Morphological approach* (chronological order) | | | | Molecular approach# | Present paper |
|------------------------|---------------------|---|---|--|--|---------------------|---------------------|
| <i>rhinoceros</i> | <i>Oncidium</i> | <i>Rhinocerotidium rhinoceros</i> (Rchb. f.) Szlach. 2006 | | | | | <i>Rhinocidium</i> |
| <i>riograndensis</i> | <i>Oncidium</i> | <i>Baptistonia riograndense</i> (Cogn.) Chiron & V.P. Castro 2004 | | | | <i>Gomesa</i> | <i>Baptistonia</i> |
| <i>riviereanum</i> | <i>Oncidium</i> | <i>Brasilidium riviereanum</i> (hort. ex Wibier) Campacci 2006 | | | | | <i>Brasilidium</i> |
| <i>rupestris</i> | <i>Coppensia</i> | | | | | | <i>Coppensia</i> |
| <i>sarcodes</i> | <i>Oncidium</i> | <i>Baptistonia sarcodes</i> (Lindl.) Chiron & V.P. Castro 2004 | <i>Anettea sarcodes</i> (Lindl.) Szlach. & Mytnik 2006 | | | <i>Gomesa</i> | <i>Baptistonia</i> |
| <i>scandens</i> | <i>Gomesa</i> | | | | | | <i>Gomesa</i> |
| <i>schlechteri</i> | <i>Theodora</i> | | | | | | <i>Gomesa</i> |
| <i>scullyi</i> | <i>Oncidium</i> | <i>Brasilidium scullyi</i> (Pabst & A.F. Mello) Campacci 2006 | | | | | <i>Brasilidium</i> |
| <i>sellowii</i> | <i>Oncidium</i> | <i>Ampliglossum sellowii</i> (Cogn.) Campacci 2006 | <i>Coppensia sellowii</i> (Cogn.) Campacci 2006 | | | | <i>Coppensia</i> |
| <i>salesopolitana</i> | <i>Menezesiella</i> | | | | | | <i>Menezesiella</i> |
| <i>sessilis</i> | <i>Gomesa</i> | | | | | | <i>Gomesa</i> |
| <i>silvanum</i> | <i>Oncidium</i> | <i>Baptistonia silvana</i> (V.P. Castro & Campacci) V.P. Castro & Chiron 2004 | | | | <i>Gomesa</i> | <i>Baptistonia</i> |
| <i>sincorana</i> | <i>Coppensia</i> | | | | | | <i>Coppensia</i> |
| <i>spilopterum</i> | <i>Oncidium</i> | <i>Ampliglossum spilopterum</i> (Lindl.) Campacci 2006 | <i>Coppensia spiloptera</i> (Lindl.) Campacci 2006 | | | <i>Gomesa</i> | <i>Coppensia</i> |
| <i>stricta</i> | <i>Gomesa</i> | | | | | | <i>Rodriguezia</i> |
| <i>tenuiflora</i> | <i>Gomesa</i> | | | | | | <i>Notylia</i> |
| <i>theodora</i> | <i>Gomesa</i> | | | | | | <i>Gomesa</i> |
| <i>trichodes</i> | <i>Oncidium</i> | <i>Alatiglossum trichodes</i> (Lindl.) Baptista 2006 | | | | | <i>Alatiglossum</i> |
| <i>truncata</i> | <i>Oncidium</i> | <i>Baptistonia truncata</i> (Pabst) Chiron & V.P. Castro 2004 | | | | | <i>Baptistonia</i> |
| <i>ublii</i> | <i>Baptistonia</i> | | | | | | <i>Baptistonia</i> |
| <i>undulata</i> | <i>Gomesa</i> | | | | | | <i>Gomesa</i> |
| <i>unicolor</i> | <i>Oncidium</i> | <i>Alatiglossum unicolor</i> (Rolfe) Baptista 2006 | <i>Kleberella unicolor</i> (Rolfe) V.P. Castro & Cath. – <i>Richardiana</i> 6(3): 159. 2006 [issued on 30 Jun 2006] | | | | <i>Alatiglossum</i> |
| <i>uniflorum</i> | <i>Oncidium</i> | <i>Alatiglossum uniflorum</i> (Booth ex Lindl.) Baptista 2006 | <i>Kleberella uniflora</i> (Booth ex Lindl.) V.P. Castro & Cath. 2006 | | | | <i>Alatiglossum</i> |
| <i>varicosum</i> | <i>Oncidium</i> | <i>Ampliglossum varicosum</i> (Lindl. & Paxton) Campacci 2006 | <i>Coppensia varicosa</i> (Lindl. & Paxton) Campacci 2006 | | | <i>Gomesa</i> | <i>Coppensia</i> |
| <i>vasconcelosiana</i> | <i>Coppensia</i> | | | | | | <i>Coppensia</i> |
| <i>velteniana</i> | <i>Baptistonia</i> | | | | | | <i>Baptistonia</i> |

Appendix 2 (Continuation). Taxonomic treatment of representatives of the *Gomesa* alliance.

| Species | Original placement | Morphological approach* (chronological order) | | | | Molecular approach# | Present paper |
|-----------------------|--------------------|---|---|--|--|---------------------|--------------------|
| <i>venustum</i> | <i>Oncidium</i> | <i>Carenidium venustum</i> (Drap.) Baptista 2006 | <i>Baptistonia venusta</i> (Drap.) Chiron 2008 | <i>Campaccia venusta</i> (Drapiez) Baptista, P.A. Harding & V.P. Castro 2011 | | <i>Gomesa</i> | <i>Baptistonia</i> |
| <i>verboonenii</i> | <i>Gomesa</i> | | | | | | <i>Gomesa</i> |
| <i>verrucosissima</i> | <i>Oncidium</i> | <i>Baptistonia verrucosissima</i> (Cogn.) V.P. Castro & Chiron 2004 | | | | | <i>Baptistonia</i> |
| <i>viperinum</i> | <i>Oncidium</i> | <i>Ampliglossum viperinum</i> (Lindl.) Campacci 2006 | <i>Coppensia viperina</i> (Lindl.) Campacci 2006 | | | <i>Gomesa</i> | <i>Coppensia</i> |
| <i>virescens</i> | <i>Gomesa</i> | | | | | | <i>Gomesa</i> |
| <i>warmingii</i> | <i>Oncidium</i> | <i>Ampliglossum warmingii</i> (Rchb. f.) Campacci 2006 | <i>Coppensia warmingii</i> (Rchb. f.) Campacci 2006 | | | <i>Gomesa</i> | <i>Coppensia</i> |
| <i>welteri</i> | <i>Oncidium</i> | <i>Ampliglossum welteri</i> (Pabst) Campacci 2006 | <i>Coppensia welteri</i> (Pabst) Campacci 2006 | <i>Rhinocidium welteri</i> (Pabst) Baptista 2007 | | <i>Gomesa</i> | <i>Rhinocidium</i> |
| <i>widgrenii</i> | <i>Oncidium</i> | <i>Baptistonia widgrenii</i> (Lindl.) V.P. Castro & Chiron 2004 | | | | <i>Gomesa</i> | <i>Baptistonia</i> |
| <i>williamsii</i> | <i>Oncidium</i> | <i>Ampliglossum williamsii</i> (Schltr.) Campacci 2006 | <i>Coppensia williamsii</i> (Schltr.) Campacci 2006 | | | | <i>Coppensia</i> |
| <i>zappii</i> | <i>Oncidium</i> | <i>Brasilidium zappii</i> (Pabst) Campacci 2006 | <i>Anettea zappii</i> (Pabst) Szlach. & Mytnik 2006 | | | | <i>Brasilidium</i> |

* BAPTISTA & DOCHA NETO (2006, 2007); BARROS & RODRIGUES (2010a,b); CAMPACCI (2006); CAMPACCI et al. (2011); CASTRO-NETO (2006, 2008); CASTRO-NETO & CATHARINO (2006); CHIRON (2008); CHIRON & CASTRO-NETO (2004, 2006); DOCHA NETO & BAPTISTA (2006, 2007); DOCHA NETO & BENELLI (2006); DOCHA NETO & KLEIN VARELA (2011); DOCHA NETO et al. (2006); LAITANO (2010); CHIRON & BOLSANELLO (2014); ROMOWICZ & SZLACHETKO (2006); SZLACHETKO (2006); SZLACHETKO & MYTNIK-EJSMONT (2006).

CHASE et al. (2009); NEUBIG et al. (2012)

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Artikel/Article: [Generic delimitation in the Gomesa alliance \(Orchidaceae, Oncidiinae\) based on molecular and morphological evidence 79-131](#)