

# Problems with generic delimitation in the *Odontoglossum* complex (Orchidaceae, Oncidiinae) and an attempt for a solution

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Received: 7 March 2015 / Accepted: 25 September 2015 / Published online: 23 November 2015  
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**Abstract** Concepts of the generic delimitation in the *Odontoglossum* complex are revised. Comparative morphology of previously recognized genera: *Cochlioda*, *Collare-stuartense*, *Odontoglossum*, *Solenidiopsis*, and *Symphyglossum* is presented. Differences between those taxa are compared with the results of molecular studies. A new combination within *Collare-stuartense* is proposed.

**Keywords** *Collare-stuartense* · Neotropics · *Odontoglossum* · *Symphyglossum* · Taxonomy

## Introduction

The Neotropical genus *Odontoglossum* (Orchidaceae, Oncidiinae) was described by Carl Kunth in 1815 based on the plant collected by Humboldt and Bonpland in southern Ecuador. The author found this orchid similar to *Epidendrum* L., but with the gynostemium apically free from the lip, and named it *O. epidendroides* (Kunth 1815). Thirty-five years after formal description of the genus, about 70 names have already been linked with *Odontoglossum*. In the mid-XIX century, Lindley (1852) divided the genus into six sections based on the form of column appendages and clinandrium, the type of connation between lip and gynostemium, and the presence or lack of sepals fusion. Many of the species considered by Lindley as

representatives of *Odontoglossum* were later transferred to different genera, e.g., *Oncidium* Sw., *Cyrtochilum* Kunth., *Cochlioda* Lindl., *Osmoglossum* (Schltr.) Schltr., and *Otoglossum* (Schltr.) Garay & Dunst. The second major revision of the genus *Odontoglossum* was presented by Pfitzer (1888) who recognized eight sections including two adopted from Lindley. Also, orchids included by Pfitzer in the genus are currently comprised in other taxa, e.g., *Rossioglossum* (Schltr.) Garay & G.C.Kenn., *Miltonioides* Brieger & Lückel, and *Rhynchostele* Rchb.f. The most recent infrageneric classification of *Odontoglossum* was proposed by Bockemühl (1984, 1989) who accepted 58 species, which were embraced in six subgenera: nominal one, *Serratolaminata*, *Lindleyana*, *Erectolobata*, *Nevadensia*, and *Unguisepala*. Those taxa are distinguishable based on the form of lip-column adnation, shape of the lip base as well as anther and rostellum structure.

Pfitzer (1887) included *Odontoglossum* together with inter alia (“among others”) (i.a.) *Oncidium*, *Miltonia* Lindl., *Brassia* R.Br., *Solenidium* Lindl., *Sigmatostalix* Rchb.f., and *Gomesa* R.Br. in the subtribe Odontoglosseae (orig. orth.), and in all subsequent classification systems the genus was placed within Oncidiinae (Dressler 1993; Szlachetko 1995; Chase et al. 2003). Chase et al. (2008) decided to merge *Odontoglossum* together with i.a. *Symphyglossum* Schltr., *Cochlioda*, *Solenidiopsis* Senghas, *Collare-stuartense* Senghas & Bockemühl, *Chamaeleorchis* Senghas & Lückel, *Miltonioides*, *Mexicoa* Garay, and *Sigmatostalix* under *Oncidium*. In the phylogenetic tree presented by Neubig et al. (2012), species of *Oncidium* sensu Chase et al. (2008) form several clades. The first one that includes *Oncidium* s.s. is grouped along with *Miltonioides*, *Mexicoa*, *Vitekorchis* Romowicz & Szlach. p.p., *Chamaeleorchis*, and *Heteranthocidium* Szlach., Mytnik & Romowicz. The second embraces representatives of

Handling editor: Ricarda Riina.

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*Odontoglossum* and *Symphyglossum*, and it is sister to the clade composed of *Cochlioda*, *Solenidiopsis*, and *Collare-stuartense*. This large group is related to several species of *Oncidium* s.s. and *Vitekorchis* p.p. Lastly, sister to the above *Oncidium* s.l. there is a clade formed by representatives of *Sigmatostalix*. Neubig et al. (2012) stated that the recognition of these segregated 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,” and they suggested to keep monophyletic *Oncidium* clade as a single genus. Neubig et al. (2012) stated “that it is better to use vegetative features in combination with a few floral traits to define broader genera. The molecular analyses demonstrate the high levels of homoplasy in pollinator-related traits.” Unfortunately, the authors did not provide any vegetative character distinguishing *Oncidium* sensu *latissimo* from other clades of Oncidiinae. Our extensive examination of large number of representatives of this clade, both conserved and living specimens, has not identified such characters.

In the Neubig et al.’s (2012) approach, *Oncidium* includes over 500 species and it is not possible to define in terms of morphology only. The case of *Paphiopedilum* Pfitzer and *Phragmipedium* Rolfe is a good illustration of an analogous situation. Albert and Pettersson (1994) based on the results of a molecular study proposed lumping both genera under the priority name *Paphiopedilum*. The subsequent, well-sampled genetic research did not support this proposal (e.g., Cox et al. 1997), and the morphological-based generic delimitation within cypripedioid orchids is

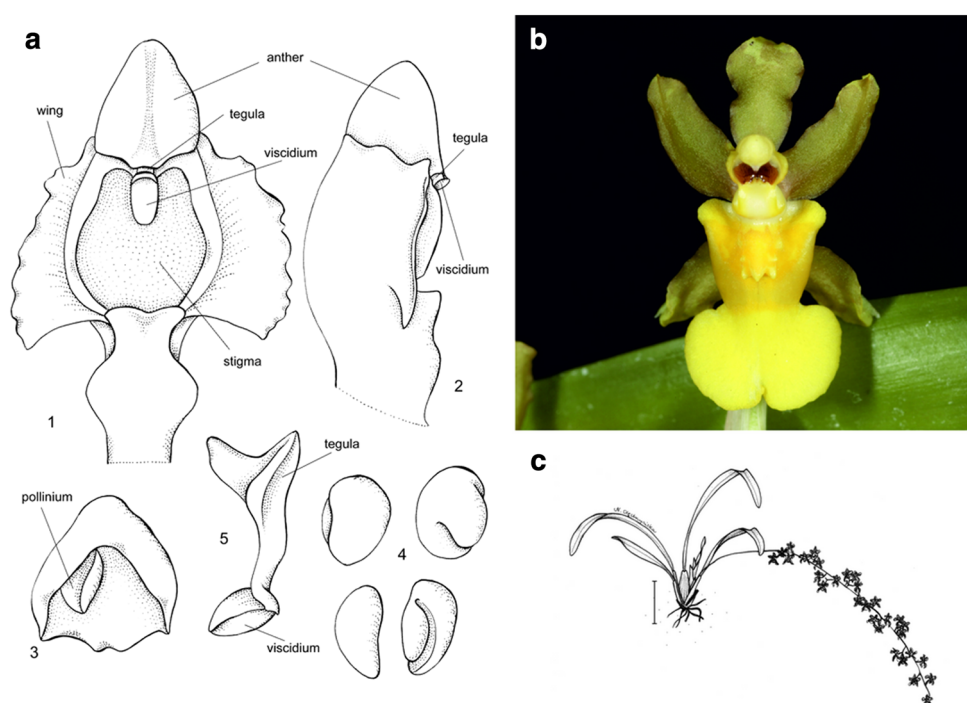
widely accepted. The other case is the subtribe Pleurothallidinae which is also monophyletic and was broken up into some major clades (Pridgeon et al. 2001). Few, however, propose resurrection of *Pleurothallis* s.l. or *Masdevallia* s.l. and smaller, but morphologically well-defined, genera, e.g., *Dracula* Luer, which gained general acceptance.

The arguments quoted by Neubig et al. (2012) can be equally well exploited to support fragmentation of *Oncidium* sensu *latissimo* and segregation of smaller genera. *Oncidium* according to the concept proposed by the aforementioned authors is exactly “difficult to diagnose using floral or vegetative traits”. Both groups (*Oncidium* and *Odontoglossum*) are distinguishable by i.a. the lip position (basal part perpendicular to the column in *Oncidium*), viscidium size, and viscidium/tegula ratio. Separation of *Oncidium* (Fig. 1) and *Odontoglossum* was also suggested by Dalström (2012); however, so far none of the modern taxonomists presented results of comprehensive morphological study supporting this segregation. The aim of our study is to evaluate morphological differences within taxa of *Odontoglossum* complex taking into account the outcomes of molecular phylogenetic studies.

## Materials and methods

A total of over 5000 herbarium and liquid-preserved specimens of orchids representing *Oncidium* s.l., *Odontoglossum* s.l., and related oncidoid genera deposited in AMES, AMO, B, BM, C, COL, CUV, F, FLAS, HUA, JAUM,

**Fig. 1** **a** Gynostemium of *Oncidium altissimum* (Jacq.) Sw. 1 Gynostemium, bottom view; 2 gynostemium, side view; 3 anther; 4 pollinia, various views; 5 tegula and viscidium (Szlachetko and Mytnik-Ejsmont 2009). **b** Flower of *Oncidium chrysomorphum* Lindl. Photo by T. Kusibab. **c** *Oncidium niesseniae*—habit. Scale bar 5 cm. Redrawn by N. Ołędryńska from Königer (1996)



K, MO, NY, P, PMA, RPSC, UGDA, VALLE, and W (Thiers 2015) were examined according to the standard procedures. Every studied specimen was photographed and the data from the labels were taken. Both vegetative and generative characters of each plant were examined. The shape and size of the pseudobulbs and leaves were examined first. Then inflorescence architecture and the shape and size of the floral bracts were studied. Finally, flower morphology was examined after its softening in boiling water.

**Results**

**Morphological data**

The studies revealed differences between examined taxa in both their vegetative and floral characters. Only *Symphyglossum* and *Odontoglossum tenuifolium* produce aggregated pseudobulbs. The inflorescence is produced from the bases of the pseudobulbs (*Odontoglossum* s.s., *O. tenuifolium*) or from the axil of the upper leaf-sheath. With the exception of *Solenidiopsis*, flowers of the studied orchids are resupinate. Connate lateral sepals are always observed in *Symphyglossum* and *O. tenuifolium*, while in *Odontoglossum* s.s. they are sometimes, at the most, shortly connate. Sepals and petals of other genera are free. The differences are also observed in the adnation of the basal lip portion with gynostemium, lip callus structure, and shape and size of the gynostemium appendages as well as clinandrium and tegula form. The comparative morphology of the analyzed taxa is presented in Table 1.

**Molecular data**

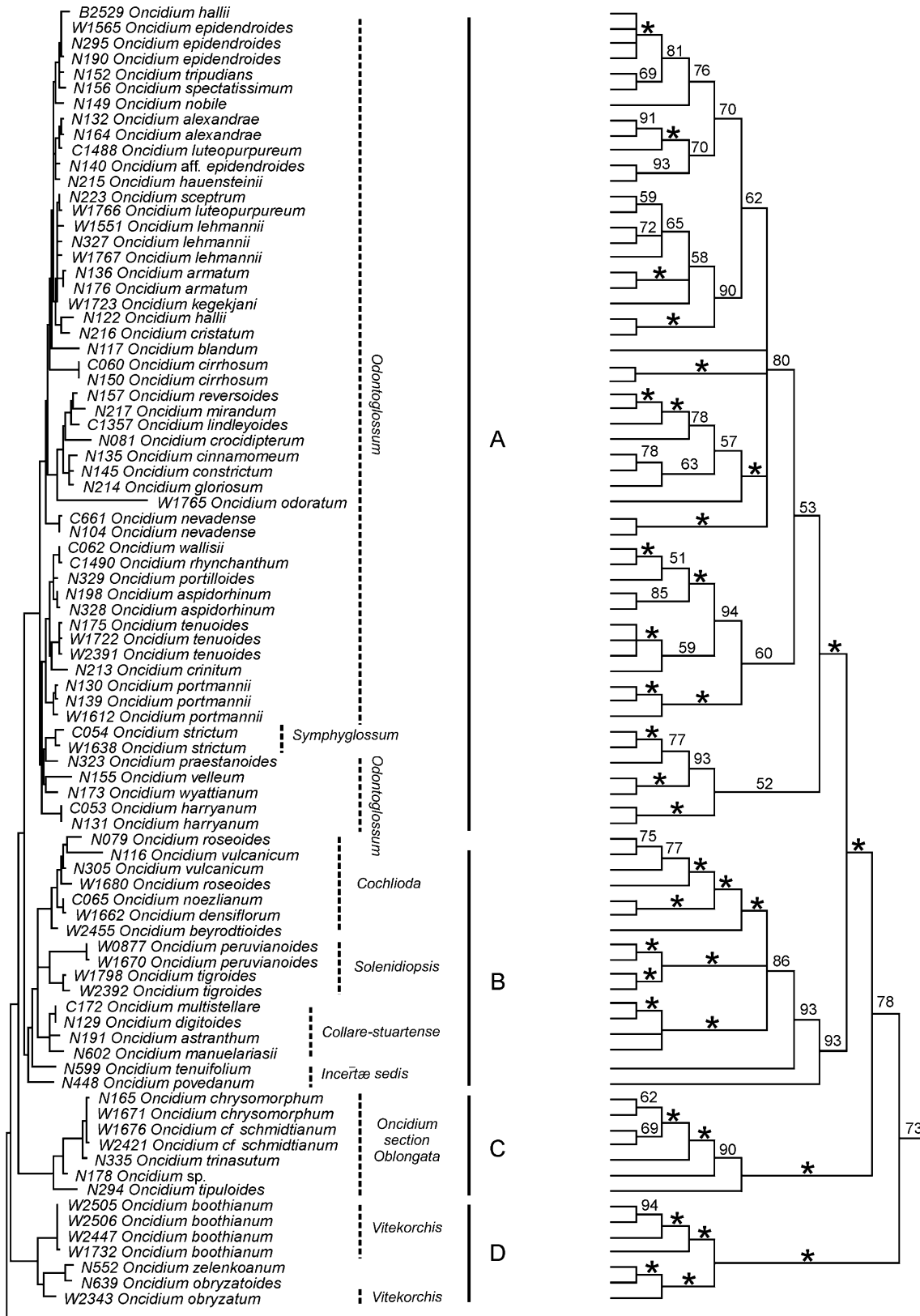
In the phylogenetic tree presented by Neubig et al. (2012), clade “*Odontoglossum*” is weakly supported and a polytomy is observed in one of the subclades (Fig. 2—subclade A). The same situation is observed in the analysis that included exclusively plastid regions (Fig. 3 in Neubig et al. 2012). *Odontoglossum hallii* Lindl. appears in two different branches of the tree provided by Neubig et al. (2012)—most probably due to incorrect identification of the samples. The representatives of previously recognized subgenera of *Odontoglossum* seem not to be closely related.

The following subclades can be distinguished in the *Odontoglossum* clade (Fig. 2):

- *Odontoglossum* s.s. intermixed with a single species of *Symphyglossum*, *S. sanguineum* (Rchb.f.) Schltr. (= *Oncidium strictum* (Cogn.) M.W.Chase & N.H. Williams), included in the analysis. It appears to be closely related to representatives of *Odontoglossum* subgen. *Nevadensia* and *O. praestanoides* (Fig. 2—subclade A).

**Table 1** Comparative morphology of *Odontoglossum* s.s., *Symphyglossum*, *Cochlioda*, *Solenidiopsis*, and *Collare-stuartense*

	<i>Odontoglossum</i> s.s.	<i>Symphyglossum</i>	<i>Cochlioda</i>	<i>Solenidiopsis</i>	<i>Collare-stuartense</i>
Pseudobulbs	Approximate	Aggregated	Approximate	Approximate	Approximate
Apical leaves	1–3	2	1–2	1–3	1–2
Flowers	Resupinate	Resupinate	Resupinate	Non-resupinate	Resupinate
Sepals and petals	Usually free	Lateral sepals connate to about the middle, petals adnate to the gynostemium	Free	Free	Free
Lip	Continuous with the base of the gynostemium	Basally adnate to the gynostemium	United with the gynostemium down the middle	Fused to the base of gynostemium through a short, central keel	Free from the gynostemium
Lip callus	Variously cristate, denticulate, lamellate	A pair of plates at the base of lip free part	Two pairs of diverging lamellae	Two pairs of diverging lamellae	Several short, diverging lamellae
Gynostemium	Obscurely winged near the stigma, or with various appendages near or just above the stigma	Winged near the stigma	Obscurely winged near the stigma	With prominent wings on both anther sides	Obscurely winged near the stigma, with two digitate projections just below the stigma
Column part	1.5–3.5 times longer than the anther	Twice as long as the anther	5 times longer than the anther	3 times longer than the anther	2.5 times longer than the anther
Clinandrium	Narrow	Narrow	Prominent	Obscure	Prominent
Tegula	Oblong	Oblong	Obtriangular-obovate	Oblong, pocket-like at apex	Linear, forming narrowly triangular projection



**Fig. 2** Tree on the left side of the figure is a fragment of single maximum likelihood tree presented by Neubig et al. (2012, their Fig. 8, p 130). The tree on the right side of the figure displays bootstrap (BS) support >50 %; asterisks indicate 95–100 % BS support



**Fig. 3** **a** Gynostemium of *Cochlioda vulcanica* (Rchb.f.) Benth. & Hook.f. ex B.D.Jacks. **1** Gynostemium apical part, *side view*; **2** gynostemium, apical part, *bottom view*; **3** anther, *back view*; **4** pollinia, various views; **5** tegula and viscidium, various views

(Szlachetko and Mytnik-Ejsmont 2009). **b** Flower of *Cochlioda noezliana* (Mast. ex L.Linden) Rolfe. Photo by Guido Deburghgraeve. **c** *Cochlioda densiflora*—habit. Scale bar 5 cm. Redrawn by N. Ołędzińska from Bennett and Christenson (1998)

- The second subclade (Fig. 2—subclade B) composed of representatives of *Cochlioda*, *Solenidiopsis*, and *Collare-stuartense* is well separated from *Odontoglossum*–*Symphyglossum* subclade. Most of the known species of *Cochlioda*, both known taxa of *Solenidiopsis*, and four of about seven *Collare-stuartense* species were included in the genetic studies (Neubig et al. 2012). The three genera form a distinct group in the phylogenetic tree. *Odontoglossum tenuifolium* and *O. povedanum* successively are sisters to other representatives of this subclade.
- The third subclade (Fig. 2—subclade C) includes *Oncidium chrysomorphum* Lindl., *O. schmidtianum* Rchb.f., *O. trinasutum* Kraenzl., and *O. tipuloides* Rchb.f.
- The fourth subclade (Fig. 2—subclade D) embraces *Oncidium boothianum* Rchb.f., *O. obryzatum* Rchb.f., *O. obryzatooides* Kraenzl., and *O. zelenkoanum* Dressler & Pupulin, i.e., species classified by taxonomists in the genus *Oncidium*.

## Discussion

As highlighted by Hillis (1987) a primary objective of phylogenetic studies is to reconstruct the evolutionary history of organisms on the basis of the analysis of their

genomes. Since the organisms under study share a single history, “systematic studies of any set of genetically determined characters should be congruent with other such studies based on different sets of characters”. Phylogenetic relationships could be sometimes incongruent with taxonomic classifications based on morphological data. The disadvantage of the first type of analysis is the difficulty for taxonomists to verify species identification of the sampled taxa in the molecular study, while the problem associated with the second method is the occurrence of convergence and the possibility of misidentification of some diagnostic features. Hereby, the optimal approach would be to use both morphological and molecular data, which is what we are intending to do in this paper.

All species of the first subclade (A) of *Odontoglossum* s.l. mentioned in the previous section, i.e., *Odontoglossum* s.s., except *Symphyglossum* can be characterized by a series of common characters. The lip is divided into two parts. The basal one is channel formed and parallel with the gynostemium, and the apical part is bent in a knee-like manner, thereby perpendicular to the lower one. The apical part is geniculate, denticulate, and undulate along margins, and at the base of lamina adorned with various, usually horn-like to digitate projections showing a complex pattern. Other segments of the flower are usually subsimilar, narrower than lip, and undulate along margins. The gynostemium is erect or gently arched, stout, narrowly

alate along the column part and terminated with digitate or fringed projections on both sides of the rostellum. The basal part of the gynostemium is variously fused with the lip. *Symphyglossum* is a genus of two species, of which only *S. sanguineum* was represented in Neubig et al.'s (2012) analyses. The species is embedded in *Odontoglossum* subclade (A), but differs from all other species of the group in having simple lip callus consisting of two keels running from the lip center toward the gynostemium, hence forming a channel, basally connate lateral sepals, and gynostemium devoid of any projections. These modifications in the lip and gynostemium structure could eventually evolve under pollinator pressure, in this case hummingbirds (cf. Stpiczńska and Davies 2006).

Shared characters for the second subclade (B) are rather difficult to identify. In all species of this subclade sampled in the phylogenetic tree (Fig. 2), the column part is prominently alate. Apical clinandrium is well developed and usually forms a prominent collar at the back and sides of the anther. The gynostemium is connate in the lower part with the lip along midvein in species of *Cochlioda* and *Collare-stuartense*. The stigmatic surface is divided into two parts by a strongly hook-bent rostellum in both *Cochlioda* and *Solenidiopsis* (cf. Szlachetko and Mytnik-Ejsmont 2009; Dalström 1999, 2001). This last character is missing in all the other species of this subclade (B). In general, however, there are more characters which differentiate alliances of the species within this subclade. *Cochlioda* species can be identified by purple, pink, or red flowers, which are adapted to hummingbird pollination. The lip callus consists of 2 or 4 papillate or ciliate keels running from the lamina center toward the gynostemium, together forming a tube accessible for pollinators. The elongate gynostemium is arched and parallel to the equally arched lip along its entire length. *Solenidiopsis* is the only genus included in this subclade (B) with non-resupinate flowers, probably being the result of adaptation to pollinator behavior. The lip and gynostemium of *Solenidiopsis* are relatively short, and the gynostemium is adorned with two large, elongate projections exceeding the anther. The shortly clawed lip possesses some thickened ridges on the upper surface and is papillate on its major part. In general, flower morphology of species of *Collare-stuartense* reminds somewhat *Odontoglossum* s.s. In both groups, the lip is ornamented with horn-like or digitate projections, and it is adnate with the lower part of the gynostemium along the midvein. Differences between *Collare-stuartense* and *Odontoglossum* s.s. concern gynostemium structure. In *Collare-stuartense*, there are no fringed or digitate projections. Instead, there are two wing-like structures being lateral lobes of prominent apical clinandrium and additional wings terminated with elliptic or ovate terminal lobes below stigmatic surface. As mentioned above, *O.*

*tenuifolium* is sister to other representatives of this subclade, and *O. povedanum* is sister to all above-mentioned species. In both these species, the gynostemium is relatively short and massive and parallel to the lip somewhat reminiscent of *Solenidiopsis*. Despite the latter, however, there are no elongate projections at the top of the gynostemium in neither of the considered species. In both *O. povedanum* and *O. tenuifolium*, the lip callus is rather similar to the one found in *Cochlioda* and like in this genus it forms along with the gynostemium a kind of tube.

The third subclade (C) includes species usually classified under *Oncidium* section *Oblongata* (Kraenzlin 1922). In general flower morphology, they share many features that are characteristic of *Oncidium* s.s., i.e., lip much larger than other perianth segments, prominently 3-lobed, with the middle lobe being the largest and apically split into two lobules, with complicated basal callus and gynostemium forming obtuse angle with the lip. The last subclade (D) comprises species which Romowicz and Szlachetko (2006) initially included in the genus *Vitekorchis*. Neubig et al. (2012) revealed, however, that the genus as circumscribed by those authors was polyphyletic and proposed a new and narrower concept of *Vitekorchis*. The species of this subclade have typical oncidoid flowers, i.e., with prominent tabula infrastigmatica and stigma sheltered by large, wing-like staminodes. Those wings are deeply dissected in *Oncidium zelenkoanum*, but otherwise this species is similar to the rest in subclade D. Morphological characters of *Oncidium chrysomorphum* and *O. boothianum* alliances (subclade C) as well as *Vitekorchis* (subclade D) will be dealt and discussed in detail in a future study dedicated to the classification of *Oncidium* s.s.

There is no consensus on the recognition of genera within the *Odontoglossum* complex, and generic concepts are changing as new data become available. For example, while initially Dalström recognized *Cochlioda* and *Solenidiopsis* as separated genera (Dalström 1999, 2001), he changed the concept in 2012 (Dalström 2012) and included both genera in *Odontoglossum*.

Detailed analyses of morphology of the species included in phylogenetic analyses conducted by Neubig et al. (2012) indicated that the *Odontoglossum* clade consists of some genera easily distinguishable morphologically. We propose to maintain *Cochlioda*, *Solenidiopsis*, *Collare-stuartense*, *Symphyglossum*, and *Odontoglossum* as separate genera, and therefore we postulate to reject Chase et al.'s (2008) proposal to include the *Odontoglossum* complex in *Oncidium*. In our view, nodes defining genera include morphological synapomorphies that permit recognition of their members.

In our approach, *Odontoglossum* is paraphyletic, with species falling into at least two poorly supported clades. The two species groups are separated by *Symphyglossum strictum*. A similar situation was recognized within

*Coelogyne* Lindl. (Gravendeel et al. 2001). In this case, the authors recognized that the morphology of the studied groups did not correspond to the three topologies probably as a result of convergent evolution of morphological characters and they decided to maintain a polyphyletic *Coelogyne*. In the case of the *Odontoglossum* complex, it could be proposed to lump *Odontoglossum* s.s. with *Symphyglossum*; however, in our opinion flower morphology of *Symphyglossum*, i.a. connation of the lateral sepals, adnation of the petals to the gynostemium, lip basally adnate to the gynostemium, and callus form allow to preserve it as a separated genus.

Another option for classification of the second subclade (B) mentioned above would be to unite *Collare-stuartense*, *Cochlioda*, and *Solenidiopsis* together with *Odontoglossum tenuifolium* and *O. povedanum* in one genus; however, such taxon would not be possible to identify morphologically. As we revealed above, just two gynostemium characters are common for *Collare-stuartense*, *Cochlioda*, and *Solenidiopsis*; however, all those plants are similar in their vegetative characters as they produce approximate, flattened pseudobulbs. On the other hand, the pseudobulbs of *Odontoglossum tenuifolium* are aggregated to alternate and unlike the three genera above and *O. povedanum*, its sepals are connate to about 1/3 of their length. Only in *Odontoglossum tenuifolium* and *O. povedanum* the column part is pubescent, at the base in the former and below the stigma in the latter. More differences between representatives of the five taxa are observed in their flower morphology, e.g., flower resupination, fusion of the lip with the gynostemium, and lip ornamentation.

As mentioned before, the concept of *Oncidium* s.l. proposed by molecular taxonomists is ill-defined in morphological terms and the *Odontoglossum* complex is not the only controversial group included in *Oncidium* s.l. A similar situation is observed i.a. in *Sigmatostalix* and *Heteranthocidium* (Szlachetko and Kolanowska in press). The generic limits within *Oncidium* s.l. is the subject of an ongoing study.

## Conclusions

While we do not underestimate the importance of molecular data in phylogenetic research, the results of molecular studies should be taken with caution in classification of organisms to avoid creation of ill-defined taxonomic units. Recognition of distinctive characters which have evolved in a group is essential to understand evolution (Brummitt 2006). This point of view is shared by numerous authors (e.g., Sosef 1997; Brummitt and Sosef 1998; Brummitt 2003; Dias et al. 2005; Nordal and Stedje 2005) who state that traditional classification is the optimal tool for cataloging biodiversity and requires recognition of paraphyletic

taxa. As highlighted by Brummitt (2014), “confusion has arisen in systematics from the failure to appreciate that taxonomy, which groups organisms into ranked taxa (families, genera, etc.), is essentially different from grouping them into clades. (...) Merely because one taxon falls phylogenetically within the clade of another taxon at the same rank does not necessarily mean that it must be included in it taxonomically.” Ultimately, neither cladogram nor a phylogenetic tree is a classification. Subjective decisions must always be taken to impose the limits and rank of taxa (Brummitt 1996).

It is difficult to accept the rather categorical statement by Chase (2009) and Neubig et al. (2012) that floral morphology has to be forgone in Oncidiinae because it is highly plastic and subject to shifts in pollinators. While pollinator-mediated selection has been suggested to play a major role for the origin and maintenance of the species diversity in orchids (Johnson 2006; Schiestl 2012; Xu et al. 2012), it should be noted that in situ observations of pollination of oncidoid orchids are rather scarce and the assumptions about the animals transferring their pollen are based mostly on flower morphology which has been proven to be misleading in numerous plant species (e.g., Williams and Adam 2010; Waser et al. 1996), including orchids (e.g., Kolanowska 2012).

Chase (2009) postulated that the vegetative traits in combination with a few floral characters should constitute the basis for generic delimitation, but the delineation within Oncidiinae proposed by the authors does not comply with this approach. According to Chase (2009), “the only reliable distinction between *Cyrtorchilum* and *Oncidium*/*Odontoglossum* is their habit; in *Cyrtorchilum*, pseudobulbs are round in cross section with numerous leaves subtending them as well as two or more apically (...) whereas in *Oncidium*/*Odontoglossum* they are ancipitous, usually without subtending leaves, and only 1–2 apically.” This is incorrect—in most of *Odontoglossum* species the pseudobulbs are subtended by foliaceous sheaths and the bifoliate pseudobulbs are often observed in both *Cyrtorchilum* and *Oncidium*/*Odontoglossum*. On the other hand, Williams et al. (2001) based on molecular data decided to incorporate representatives of *Psycmorchis* Dodson & Dressler and *Stacyella* Szlach. into *Erycina* Lindl. despite obvious vegetative dissimilarities between those taxa. Unlike *Stacyella* and *Erycina*, species of *Psycmorchis* s.s. do not produce pseudobulbs. Pseudobulbs of *Stacyella* representatives are subtended by several foliaceous bracts and the apical leaf lacks articulation, while *Erycina* produces several papyraceous sheaths and the leaf/leaves are articulate at the base (Kolanowska and Szlachetko 2014). Another orchid taxon lately discussed in the context of the generic delimitation, *Fernandezia* s.l., consists of monopodial plants growing in montane and high-montane habitats (Kolanowska and Szlachetko in press). These

orchids share general habit form—their stems are concealed by the leaf sheaths, the leaves are conduplicate, distichous, and articulate. The differences are observed in the inflorescence arrangement and flower morphology (i.a. gynostemium structure, perianth segments' connation).

In our opinion, floral characters are still important taxonomic and diagnostic attributes in orchid taxonomy and specifically in Oncidiinae provided that they are studied carefully. As there is no vegetative character defining *Oncidium* sensu latissimo, we postulate to reject the broad concept of *Oncidium* presented by Chase et al. (2008).

## Taxonomic treatment

### Key to taxa of the *Odontoglossum* alliance

- 1a. Stigma partially hidden by rostellum, hence appears to be bilobed ..... 2  
 1b. Stigma unlobed ..... 3  
 2a. Flowers resupinate ..... *Cochlioda*  
 2b. Flowers non-resupinate ..... *Solenidiopsis*  
 3a. Clinandrium 3-lobed, middle lobe exceeding the anther ..... *Collare-stuartense*  
 3b. Clinandrium obscure, not exceeding the anther ..... 4  
 4a. Lateral sepals connate for over third of their length ..... *Symphoglossum*  
 4b. Lateral sepals free or shortly connate ..... 5  
 5a. Gynostemium pubescent ..... 6  
 5b. Gynostemium glabrous ..... 7  
 6a. Lip apical half abruptly recurved .....  
 ..... *Odontoglossum tenuifolium*  
 6b. Lip apical part deflexed .....  
 ..... *Odontoglossum povedanum*  
 7a. Lip basal part parallel to the gynostemium ..... *Odontoglossum* s.s.  
 7b. Lip basal part perpendicular to the gynostemium ..... 8  
 8a. Tabula infrastigmatica missing, staminodes digitate ..... *O. chrysomorphum* group  
 8b. Tabula infrastigmatica prominent, staminodes ear-like ..... *O. obryzatum* group

*Cochlioda* Lindl. Fol. Orchid. 4: 1. 1853. —TYPE: *Cochlioda densiflora* Lindl. Fig. 3.

Pseudobulbs approximate, oblong to ovate, flattened, 1–2-foliolate, at the base with several sheaths. Leaves coriaceous or fleshy. Inflorescence produced from the axil of the upper leaf-sheath, few-flowered. Flowers resupinate. Sepals and petals subsimilar, free, spreading. Lip 3-lobed, united with the gynostemium down the middle; lateral lobes oblong to subquadrate; middle lobe ovate; disk with two pairs of diverging lamellae. Gynostemium elongate,

erect, stout. Column part ca. 5 times longer than anther, almost terete, fused with lip along midvein almost to stigma base. Anther incumbent, operculate, dorsiventrally slightly compressed, ellipsoid, 2-chambered. Connective narrow, rather thick. Pollinia 2, obliquely obovoid-ellipsoid, deeply and unequally cleft, hollow inside, hard. Apical clinandrium prominent, 3-lobed, exceeding anther, margin entire. Stigma transversely elliptic, deeply concave, partially hidden by rostellum, hence appears to be bilobed. Rostellum pendent, digitate, built of thick tissue, rounded at apex. Viscidium single, oblong, multilayered, sticky on outer surface. Tegula single, obtriangular-obovate, thin, lamellate. Rostellum remnant with apical, oblique, shallow plate surrounded by fovea.

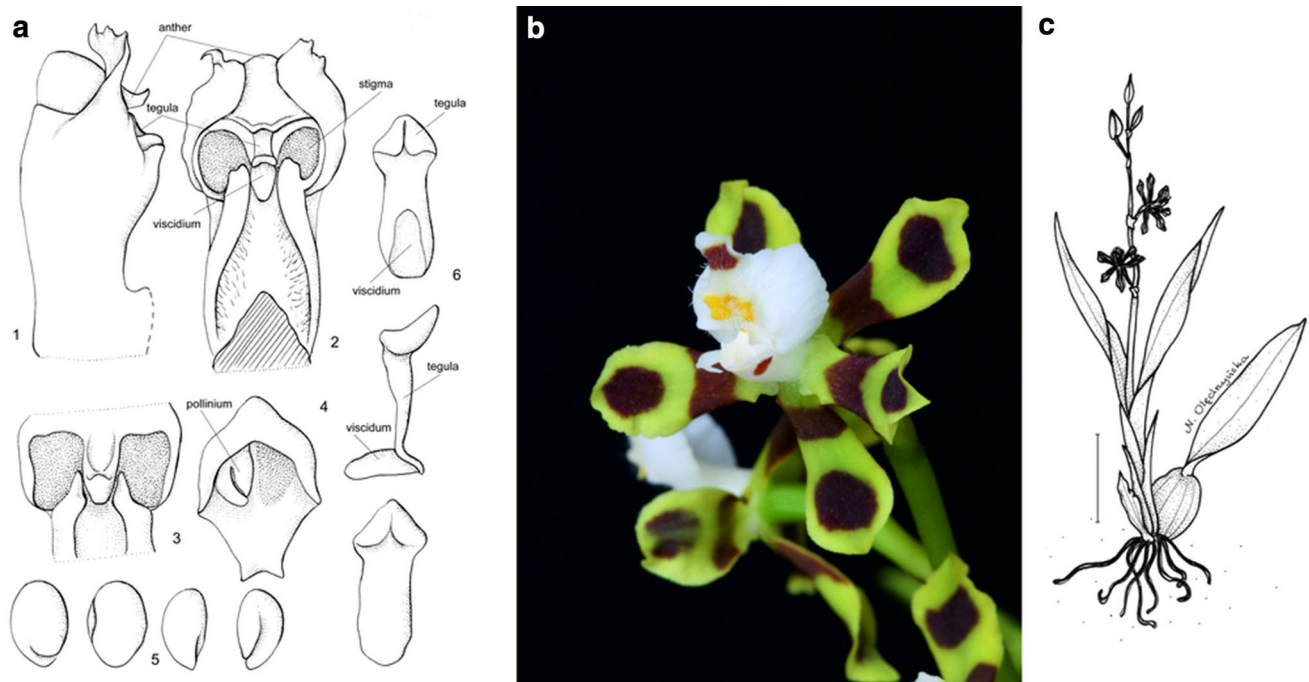
*Notes:* The species of this genus share similar characters in the gynostemium structure with *Solenidiopsis*, especially receptive surface divided into two parts by a pendent rostellum. Both genera, however, can be easily separated by the torsion of the flowers (resupinate in *Cochlioda* and non-resupinate in *Solenidiopsis*) and flower coloration (bright in *Cochlioda* and dull brownish-green in *Solenidiopsis*), which is probably caused by adaptation to different pollinators. Previously postulated synonymization of *C. beyrodtiana* under *C. densiflora* (Dalström 2001) should be rejected based on the outcomes of analysis of Neubig et al. (2012) which indicates that *C. beyrodtiana* is sister to all other representatives of the genus.

A genus of about six Andean species distributed from Ecuador to Peru and Bolivia. Populations were found growing at the altitudes of 1800–2700 m; however, some plants were reported from lower elevations of about 1200 m.

*Solenidiopsis* Senghas, Orchidee (Hamburg) 37: 274. 1986. —TYPE: *Solenidiopsis tigroides* (C.Schweinf.) Senghas. Fig. 4.

Pseudobulbs approximate, pyriform to ovate, flattened, 1–3-leaved, at the base with several sheaths. Leaves coriaceous or fleshy. Inflorescence produced from the axil of the upper leaf-sheath, several- to many-flowered. Flowers non-resupinate. Sepals and petals subsimilar, spreading, free. Lip 3-lobed, fused to the base of gynostemium through a short, central keel; lateral lobes ovate to subquadrate; middle lobe ovate; disk with two pairs of diverging lamellae. Gynostemium elongate, erect, robust. Column part ca. 3 times longer than anther, fused with lip along midvein in lower third, ventral surface below stigma grooved and pubescent, with prominent wings on both anther sides, wings thin, delicate, more or less denticulate on margins. Anther subapical, incumbent, operculate, dorsiventrally compressed, ellipsoid-ovoid, 2-chambered. Connective narrow, apically elongate. Pollinia 2, almost ellipsoid, slightly dorsiventrally flattened, unequally cleft, empty inside, hard. Apical





**Fig. 4** **a** Gynostemium of *Solenidiopsis tigroides* (C.Schweinf.) Senghas. 1 Gynostemium, side view; 2 gynostemium, bottom view; 3 rostellum remnant; 4 anther; 5 pollinia, various views, 6 Tegula and viscidium, various views (Szlachetko and Mytnik-Ejsmont 2009).

**b** Flower of *Solenidiopsis tigroides*. Photo by Guido Deburghgraeve. **c** *Solenidiopsis flavobrunnea*—habit. Scale bar 3 cm. Redrawn by N. Ołędryńska from Bennett and Christenson (1993)

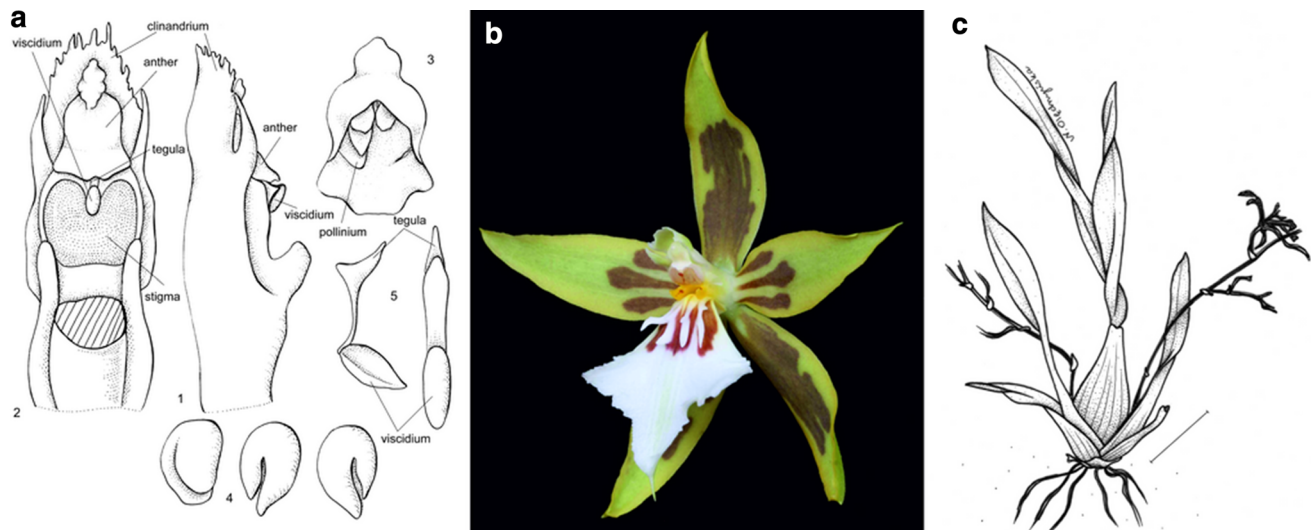
clinandrium obscure. Stigma transversely elliptic, deeply concave, partially divided by rostellum into two lobes, hence appears to be bilobed. Rostellum pendent, digitate, built of thick tissue, rounded at apex. Viscidium single, oblong, sticky, soft. Tegula single, oblong, thin, lamellate, pocket-like at apex. Rostellum remnant with apical, oblique, shallow plate surrounded by narrow fovea, canaliculated on dorsal surface.

*Notes:* This is the only representative of the *Odontoglossum* clade with non-resupinate flowers. The lip morphology of *Solenidiopsis* species reminds somewhat those of *Cochlioda* and *Odontoglossum povedanum*. Their lip is 3-lobed with callus consisting of two pairs of diverging lamellae. Unlike *Solenidiopsis*, flowers of *Cochlioda* and *O. povedanum* are resupinate. Furthermore, those genera can be easily distinguished by the gynostemium structure. In *Solenidiopsis* and *Cochlioda*, the receptive surface is split into two parts and it is entire in *O. povedanum*. Also, only in *O. povedanum* the gynostemium is pubescent. In *Solenidiopsis*, the apical, prominent wings on both anther sides are delicate, with more or less denticulate margins. They prominent wings are missing in both *Cochlioda* and *O. povedanum*.

A genus of about five (Dalström 1999) Peruvian species growing at altitudes of 2000–3100 m.

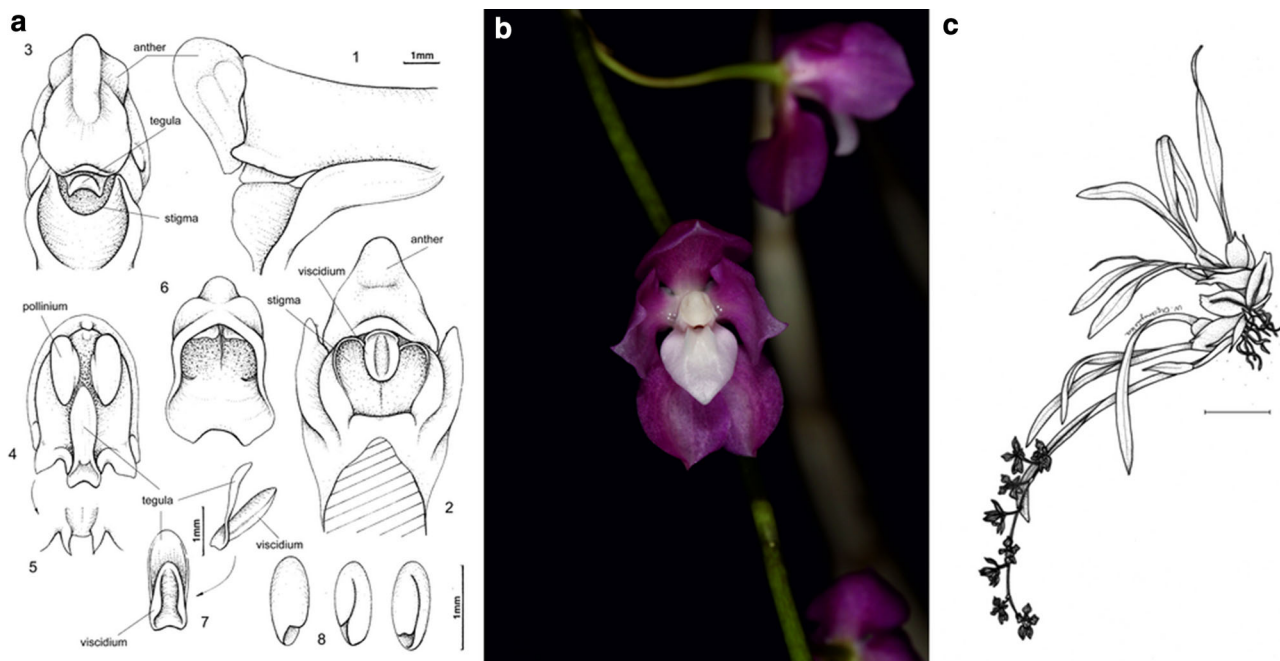
*Collare-stuartense* Senghas and Bockemühl, J. Orchideenfr. 4: 73. 1997. —TYPE: *Collare-stuartense multi-stellare* (Rchb.f.) Senghas & Bockemühl. Fig. 5.

Pseudobulbs approximate, ovate, flattened, 1–2-leaved, at the base with several sheaths. Leaves coriaceous or fleshy. Inflorescence produced from the axil of the upper leaf-sheath, several- to many-flowered. Flowers resupinate. Sepals and petals subsimilar, free, spreading. Lip 3-lobed, free from the gynostemium; lateral lobes ovate to subquadrate; middle lobe ovate; callus consisting of several short, diverging lamellae. Gynostemium erect, elongate, slender. Column part 2.5 times longer than anther, fused at its basal third with lip, obscurely winged near stigma, with two digitate projections just below stigma, glabrous. Anther subventral, incumbent, operculate, ellipsoid-ovoid, dorsoventrally flattened, obscurely 2-chambered. Connective narrow, slightly apically elongate, with thick knob-like appendix at top. Pollinia 2, almost ellipsoid-obovoid, hard, unequally and deeply cleft. Apical clinandrium prominent, exceeding anther, irregularly dentate on margins with two digitate projection at anther apex. Stigma large, elliptic, deeply concave. Rostellum shortly conical-digitate in middle, ligulate, blunt, pendent. Viscidium single, rather small, oblong-elliptic, thick. Tegula single, linear, thin, lamellate, laterally squeezed at apex, forming narrowly triangular



**Fig. 5** **a** Gynostemium of *Collare-stuartense multistellare* (Rchb.f.) Senghas & Bockemühl. **1** Gynostemium, side view; **2** gynostemium, bottom view; **3** anther; **4** pollinia, various views; **5** tegula and viscidium, various views (Szlachetko and Mytnik-Ejsmont 2009).

**b** Flower of *Collare-stuartense multistellare* (Rchb.f.) Senghas & Bockemühl. Photo by Guido Deburghgraeve. **c** *Collare-stuartense multistellare*—habit. Scale bar 5 cm. Redrawn by N. Ołędryńska from Dodson (1984)



**Fig. 6** **a** Gynostemium of *Symphyglossum sanguineum* (Rchb.f.) Schltr. **1** Gynostemium, side view; **2** gynostemium, bottom view; **3** gynostemium, front view; **4** gynostemium, front view, anther removed; **5** rostellum remnant; **6** anther; **7** tegula and viscidium,

various views; **8** pollinia, various views (Szlachetko and Mytnik-Ejsmont 2009). **b** Flower of *Symphyglossum strictum* (Cogn.) Schltr. Photo by J. Varigos. **c** *Symphyglossum ecuadorensis*—habit. Scale bar 6 cm. Redrawn by N. Ołędryńska from Dodson and Dodson (1980)

projection. Rostellum remnant bilobulate at middle, with oblique shallowly concave plate between acute lobules.

**Notes:** *Collare-stuartense* and *Odontoglossum* share similar characters of the lip, especially in the structure of the callus, which consists of several mostly digitate projections. Both genera can be easily distinguished by the

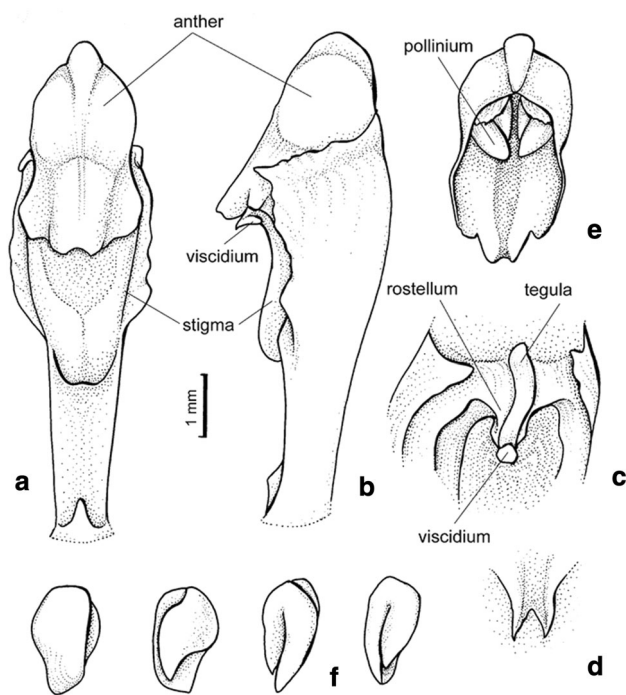
gynostemium morphology, especially the clinandrium, which is prominent, 3-lobed in *Collare-stuartense*, with the middle lobe exceeding the anther. The apical clinandrium of *Odontoglossum* is narrow and obscure.

A genus of about seven species distributed from Ecuador to Peru and Bolivia. The altitudinal range extends from



**Fig. 7** **a** Gynostemium of *Odontoglossum odoratum* Lindl. 1 Gynostemium, side view; 2 gynostemium, bottom view; 3 rostellum, side view; 4 anther; and 5 pollinia, various views (Szlachetko and Mytnik-Ejsmont 2009). **b** Flower of *Odontoglossum epidendroides* Lindl.

Photo by Guido Deburghgraeve. **c** *Odontoglossum epidendroides*—habit. Scale bar 10 cm. Redrawn by N. Ołędryńska from Dodson and Bennett (1989)



**Fig. 8** Gynostemium of *Odontoglossum crinitum* Rchb.f. **a** Gynostemium, bottom view; **b** gynostemium, side view; **c** rostellum; **d** rostellum remnant, front view; **e** anther; and **f** pollinia, various views (Szlachetko and Mytnik-Ejsmont 2009)

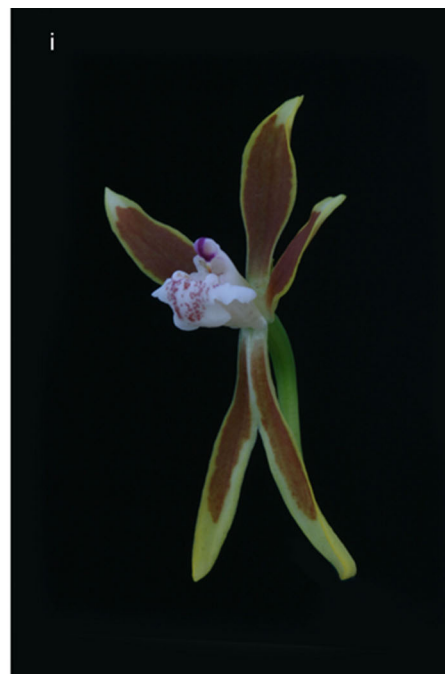
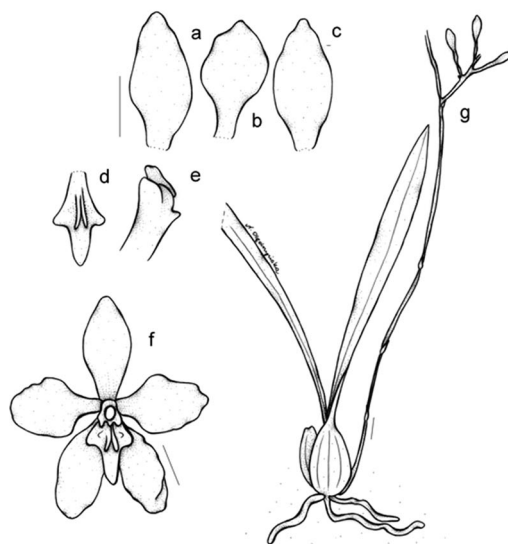
2000 to 2800 m. The revision of the available material indicated the necessity for one additional transfer to *Collare-stuartense*.

*Collare-stuartense ariasii* (Dalström) Szlach. & Kolan., **comb. nov.**  $\equiv$  *Odontoglossum ariasii* Dalström, Selbyana 22: 137. 2001. —TYPE: Peru, Junín, cloud forest near Huasahuasi, ca. 2600 m a. s. l., field collected by M. Arias, 20 Feb 2001, *S. Dalström 2502* (holotype: SEL [n.v.]

*Symphyglossum* Schltr., Orchis 13: 8. 1919. —TYPE: *Symphyglossum sanguineum* (Rchb.f.) Schltr. Fig. 6.

Pseudobulbs aggregated, oblong-ovoid, flattened, 2-leaved, at the base with several sheaths. Leaves coriaceous or fleshy. Inflorescence produced from the axil of the upper leaf-sheath, few- to many-flowered. Flowers resupinate. Sepals and petals subsimilar, lateral sepals connate to about the middle, petals adnate to the gynostemium. Lip entire, basally adnate to the gynostemium; lateral lobes ovate to subquadrate; middle lobe ovate; callus consisting of a pair of plates at the base of lip free part. Gynostemium elongate, gently upcurved in upper half, rather robust. Column part ca. twice as long as anther, fused with lip just below stigma, winged near stigma, wings with margins entire. Anther subapical, operculate, ellipsoid, slightly dorsiventrally flattened, obscurely 2-chambered. Connective narrow,

**Fig. 9** *Odontoglossum povedanum* P.Ortiz. *a* Lateral sepal, *b* petal, *c* dorsal sepal, *d* lip, *e* gynostemium, and *f* flower. Scale bars 10 mm. *g* Habit. Scale bar 20 mm. Redrawn by N. Ołędryńska from Ortiz Valdivieso (1997). *h* Flower. Photo by Guido Deburghgraeve



**Fig. 10** *Odontoglossum tenuifolium* Dalström *a* Habit. Scale bar 5 cm. *b* Petal, *c* dorsal sepal, *d* lateral sepals, and *e* flower. Scale bars 5 mm. *f*, *g* Gynostemium various views. Scale bars 3 mm. *h* Flower.

Scale bar 5 mm. Redrawn by N. Ołędryńska from Dalström (1996). *i* Flower. Photo by Guido Deburghgraeve

thickened on dorsal surface and apically elongate. Pollinia 2, oblong-ellipsoid, hard, unequally and deeply cleft. Apical clinandrium narrow. Stigma relatively small, elliptic, slightly concave. Rostellum rather short, ovate, rounded at apex. Viscidium single, oblong-ellipsoid, thick, fleshy, grooved on outer surface. Tegula single, longer than viscidium, oblong, thin, lamellate, flat. Rostellum remnant bilobulate at apex, canaliculated on dorsal surface.

*Notes:* This is the only genus of the *Odontoglossum* clade with simple lip. Moreover, both lateral sepals are connate to about the middle, and both petals are adnate to the gynostemium forming a kind of funnel, which probably plays a role in pollination.

A genus of about six species distributed from Ecuador to Peru between 1200 and 2600 m of altitude.

***Odontoglossum*** Kunth, Nov. Gen. Sp. 1: 350. 1816. —TYPE: *Odontoglossum epidendroides* Kunth. Figs. 7, 8.

Pseudobulbs approximate, usually ovoid or elliptic-oblong, compressed, 1–3-leaved, the bases enveloped in a few distichous, papery or foliaceous sheaths. Leaves coriaceous or fleshy. Inflorescences produced from the bases of the pseudobulbs, usually elongate, erect or arching, few- to many-flowered racemes or panicles. Flowers resupinate. Sepals subequal, usually spreading, usually free. Petals usually subequal to the dorsal sepal but sometimes broader. Lip 3-lobed or entire, the base continuous with the base of the gynostemium; lateral lobes (if present) spreading or erect, middle lobe usually deflexed, less frequently spreading; callus at the base of the lip variously cristate, denticulate, lamellate. Gynostemium elongate, erect to gently arched near middle, slender. Column part ca. 1.5–3.5 times longer than anther, obscurely winged near stigma, with various appendages near or just above stigma. Anther subapical to subventral, incumbent, operculate, ellipsoid, obscurely 2-chambered. Connective narrow, more or less thickened and apically elongate, occasionally forms a dorsal crest. Pollinia 2, obliquely ellipsoid, dorsiventrally flattened, hard, unequally and deeply cleft. Apical clinandrium narrow. Stigma elliptic, deeply concave, partially hidden by rostellum. Rostellum rather short, conical-digitate in middle, ligulate, pendent, obtuse. Viscidium single, oblong-ellipsoid, thick, fleshy. Tegula single, slightly longer than viscidium, oblong, thin, lamellate, flat. Rostellum remnant bilobulate at middle, with oblique shallowly concave plate between acute lobules, canaliculated on dorsal surface.

**Notes:** The genus can be confused with *Collare-stuartense*, from which however it can be separated by gynostemium morphology.

### Incertae sedis

As mentioned before, two species, *Odontoglossum tenuifolium* and *O. povedanum*, are not closely related to other representatives of the subclade B. Also their morphology does not allow their classification in any of the existing genera. It is possible that each of these two species could be placed in its own genus, but we think it is premature considering current available data.

***Odontoglossum povedanum*** P.Ortiz, Orquideologia 20: 321. 1997. —TYPE: Colombia, Santander, Suaita. Vado Real, ca. 2000 m a. s. l., collected by E. Poveda in Dec 1995, flowering in Bogotá in May 1996, *P. Ortiz 1070* (holotype: HPUJ [n.v.]). Fig. 9.

**Notes:** This species described as *Odontoglossum* was transferred to *Collare-stuartense* by Szlachetko and Górniak (2006); however, unlike *Odontoglossum* and *Collare-stuartense*, in *O. povedanum* the column part below the stigma is pubescent. While in the original drawing presented by Ortiz

Valdivieso (1997) the pseudobulbs are not subtended by foliaceous sheaths, the photographs of this species taken by G. Deburghgraeve show that these structures occur in *O. povedanum*. According to information provided by Deburghgraeve, the flowering of this plant starts from the most distal part of the inflorescence and the side branches gradually develop from the most proximal internodes. The simple lip callus with pubescent disk places it in a rather isolated position within *Odontoglossum* clade that is also supported by molecular analyses (Neubig et al. 2012).

***Odontoglossum tenuifolium*** Dalström, Lindleyana 11: 114. 1996. —TYPE: Bolivia, Chapare, between Cochabamba and Villa Tunari, 1950 m a. s. l., 7 Jan 1994, S. Dalström and J. Sönnemark 2012 (holotype: SEL [n.v.]; isotype: K [n.v.]). Fig. 10.

**Notes:** This species differs from all other members of *Odontoglossum* clade by its flower morphology, especially the abruptly recurved apical half of the lip with two digitate appendages. It is noteworthy that *O. tenuifolium* is similar to *Rusbyella* and *Dasyglossum* in both vegetative and floral characters. It differs, however, from both genera in having the lower part of the gynostemium pubescent. Additionally, it is easily separable from *Rusbyella* by the lip morphology. It would be a good example of convergence in flower morphology between rather distantly related genera if subsequent molecular studies confirm this situation.

**Acknowledgments** We are grateful to anonymous reviewers for their valuable comments on the manuscript. The curators and staff of the cited herbaria are thanked for their kind hospitality and assistance during visits. We are grateful to Natalia Ołędryńska for preparing line drawings. Guido Deburghgraeve, Tadeusz Kusibab, and John Varigos are thanked for providing us photographs. The project has been supported by the Polish Ministry of Science and Higher Education (Research Grant No. 5819/B/PO1/2010/39). This study was made possible thanks to the support of the Foundation for Polish Science (Fundacja na rzecz Nauki Polskiej, FNP).

### Compliance with ethical standards

The authors declare that there are no conflicts of interest. This article does not contain any studies with human participants or animals performed by any of the authors. Informed consent was obtained from all individual participants included in the study.

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