NEW COMBINATIONS AND TRANSFERS TO *ODONTOGLOSSUM* ONCIDIINAE (ORCHIDACEAE): AVOID CREATING NEW NAMES

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Abstract. A generic transfer of eight species from *Oncidium* to *Odontoglossum* is made here, supported by molecular and morphologic evidence. Homotypic synonyms are listed. These transfers make it possible to maintain a monophyletic genus *Odontoglossum* without creating any new generic names. Quotes from authors that favor a larger and morphologically indefinable *Oncidium* are included and responded to by the authors of this paper, who are in favor of maintaining a more conservative and traditional, as well user-friendly and visually workable taxonomic classification.

Keywords: Oncidiinae, Odontoglossum, Oncidium, species transfers, taxonomy

Many attempts have been made by various authors to solve the complicated taxonomy in Oncidiinae in general, and to classify or delineate the genus *Odontoglossum* Kunth in particular, but without lasting or entirely convincing results; Kunth (1816: 350), Lindley (1852), Beer (1854: 274–295), Pfitzer (1887: 106–107), Bockemühl (1984: 213–218; 1989: 15–29), Chase et al. (2008), Pridgeon et al. (2009: 212–220), Neubig (2012), and Kolanowska and Szlachetko (2016). For a variety of reasons and from a taxonomic point of view, this is not an easy group of plants to deal with. Traditionally, in this particular case, taxonomists have focused on a few morphologic features, generally associated with some flower details, particularly the angle between the column and the lip. Species with similar looking flowers, with regards to the chosen important taxonomic features favored at the time, have ended up in the same genus despite displaying many different-looking features otherwise, such as vegetative and micro-morphologic structures. Since molecular research focusing on DNA sequencing has arrived on the scene as an additional tool for systematists, we realize that vegetative features are very important in revealing close or distant relationships. Also micro-morphology has an important role to play here, while flower color, odor and general shape can be misleading and appear to be evolutionary plastic adaptations to available pollinators.

POLLINATION SYNDROMES

Very little is documented about pollination of *Odontoglossum* species. Van der Pijl and Dodson (1966: 80–81; figure 53 on page 80) report the following: "In the case of *Odontoglossum kegeljani* E.Morren [= *Odontoglossum lehmannii* Rchb.f.; authors' note] in Ecuador, male bees of *Bombus robustus* var. *hortulans* Friese come to the flowers and attempt to reach nectar in the false nectarines. The teeth of the callus act to impede the advance into the flower and in their struggles they detach the viscidium of the pollinarium with their heads. The stipe curves downward, carrying the pollinia to a position in front of the head and in visiting a subsequent flower they leave the pollinia on the sticky surface of the stigma."

This may be the only photographically supported report of the pollination of an *Odontoglossum* species. But it probably represents what happens to most "typical" odontoglossums since the basic flower morphology is very similar. In the case of the "*Cochlioda* Lindl., group" in *Odontoglossum* (members of the former genus *Cochlioda*, Dalström, 2012), however, the brightly rosy red to magenta or orange-colored flowers suggest a different pollination syndrome, and hummingbird pollination of Odontoglossum (as Cochlioda) vulcanicum (Rchb.f.) Dalström is reported by van der Pijl and Dodson (1966: 89, 95). These authors continue: "A point which has been generally overlooked in taxonomy in the orchids is that the characters which result from adaptations to bird-pollination are often striking. These characters are commonly employed by taxonomists in separating genera, with the result that closely related species may be placed in distinct genera. Examples are the Cochlioda-Odontoglossum-Oncidium and the Sophronitis-Laelia-Cattleya complexes where the enormous numbers of artificial hybrids are mute evidence of the failure of taxonomists to understand the ecological background of speciation in these groups." (van der Pijl and Dodson, 1966: 94). The conclusion is that we should widen our generic concepts and be ready to accept that groups of species with rather different looking flowers may still be rather closely related. A true close relationship, however, can generally be seen in similar vegetative features.

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Another case of a deviating pollination syndrome for a small species complex within a larger complex is represented by the "Solenidiopsis Senghas group" in Odontoglossum (members of the former genus Solenidiopsis, Dalström 2012). These miniature Odontoglossum species are vegetatively indistinguishable from their larger "cousins," but have developed very different looking flowers. Actually, the flowers are structurally similar to members of the "Cochlioda group," but are non-resupinate and rather drab in yellow to dark brown colors. While flowers of "cochliodas" display color as an attractant, the members of the "Solenidiopsis group" have distinct flower odors, which suggest an entirely different pollination syndrome, probably performed by smaller bees. Hence members of different but still closely related Odontoglossum groups or sub-genera can co-exist sympatrically without interspecific cross-pollination. Cross-pollination among similar-looking members within the same group of the more typical species complexes, however, is a different story altogether and rather frequent (Rolfe, 1893; Dalström, 2003).

When Chase and others (2008) transferred orchid genera Cochlioda, Odontoglossum, Sigmatostalix Rchb.f., and Solenidiopsis to Oncidium Sw., based on molecular evidence, a rather strange situation developed, seen from a taxonomic point of view. Many plants with very different vegetative features as well as floral features ended up in the same genus, together with some members of what clearly belong to the genus Cyrtochilum Kunth, such as Odontoglossum contaypacchaense D.E.Benn. & Christenson, Odontoglossum machupicchuense D.E.Benn. & Christenson, Odontoglossum pseudomelanthes D.E.Benn. Christenson and Odontoglossum rubrocallosum & D.E.Benn. & Christenson. In fact, even without these mistakenly transferred Cyrtochilum species (which probably were transferred without molecular evidence), the members of the generously extended Oncidium (sensu Chase et. al., 2008) are so different from each other that it becomes virtually impossible to visually define the genus Oncidium and to separate it from many other genera in the Oncidiinae. Therefore, some of the arguments used by Chase et al. (2008), Pridgeon et al. (2009), and later Neubig et al., (2012) to justify this transfer are worth analyzing.

"If *Odontoglossum* is to be maintained as a distinct genus, then many more genera will need to be created or some long-known species with typical *Oncidium* floral morphology (e.g., *O. chrysomorphum* Lindl., *O. obryzatum* Rchb.f.) will have to be transferred into *Odontoglossum*, which removes any hope of morphological distinctiveness for *Odontoglossum*." (Chase et al., 2008).

No additional new names are needed to maintain *Odontoglossum* as a distinct genus once the vegetative *Odontoglossum*-looking "*Oncidium chrysomorphum*" and "*O. obryzatum*" complexes are transferred into *Odontoglossum*. This is clearly a more conservative and stabilizing alternative than lumping everything into *Oncidium*, which will effectively eliminate any possibility

of distinguishing it as a genus. What DNA research has taught us is that flower morphology is not entirely reliable as a basis for taxonomic decisions, but vegetative features are.

"After these changes [the removal of many *Cyrtochilum* species from *Odontoglossum* by Dalström (2001a)], there still remains a core group of *Odontoglossum* species that DNA studies have indicated are monophyletic, but these are deeply embedded in *Oncidium*." (Chase et al., 2008).

By studying the "...single maximum likelihood tree resulting from analysis of the combined five-region data set for 736 individuals" (Figure 8, in Neubig *et al.* 2012). We can see that an extended *Odontoglossum* is not actually "deeply embedded" in *Oncidium* at all, but a monophyletic sister-group to *Oncidium* (*sensu stricto*), even when the latter includes other distinguishable and monophyletic groups that have been described as separate genera, such as *Heteranthocidium* Szlach., Mytnik & Romowicz, *Chamaeleorchis* Senghas & Lückel, and *Sigmatostalix* Rchb.f.

"In addition, *Cochlioda* Lindl. and *Symphyglossum* [as "*Symphyloglossum*"] Schltr. are hummingbird-pollinated species of *Oncidium* and also deeply imbedded in *Oncidium/Odontoglossum*, so these too are transferred." (Chase et al., 2008).

Symphyglossum sanguineum (Rchb.f.) Schltr., as the sole species from that genus was transferred to Odontoglossum in 2001 based on molecular evidence and vegetative features, and is not deeply embedded in Oncidium (sensu stricto). It is, however, deeply embedded in the monophyletic and extended Odontoglossum (Dalström 2001b). The other former Symphyglossum species; S. distans (Rchb.f.) Garay & Dunsterv., and S. umbrosum (Rchb.f.) Garay & Dunsterv., belong in Cyrtochilum. Whether Odontoglossum sanguineum is hummingbird-pollinated or not is probably pure speculation. We are not aware of any scientific documentation for this phenomenon.

"Sigmatostalix is another such case. These often-tiny plants produce oil on their lip calli and are recorded to be pollinated by oil-collecting bees, as are the great majority of species in *Oncidium*. Size alone is not suitable for generic delimitation, and in all other ways the species of *Sigmatostalix* are similar to those in *Oncidium*. These also we transfer to *Oncidium*." (Chase et al., 2008).

Sigmatostalix Rchb.f., is a monophyletic complex of species that are easily distinguished from the bulk of Oncidium species (sensu stricto), and from most other Oncidiinae members for that matter, by the combination of a miniature growth, strongly flattened pseudobulbs generally with papery thin leaves, and the morphologic unique and rather bizarre–looking flowers. It makes sense to maintain this genus for the same reasons as for maintaining Odontoglossum. "We feel that it is better to use vegetative features in combination with few floral traits to define broader genera... *Oncidium* is perhaps the best example of our contention 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." (Neubig et al., 2012).

We agree that vegetative features can and should be used in defining genera, in combination with molecular evidence, and where possible also floral and any other available traits. The species transferred to Odontoglossum in this paper share more vegetative and molecular features with other species in that genus than with members of Oncidium (sensu stricto), but have switched to different pollination syndromes and therefore form a separate group within the genus, just like the "Cochlioda group" and the "Solenidiopsis group." The "when" and "why" this switch has taken place are unknown of course, but some indications suggest that ancient hybridization between members of genus Heteranthocidium (the "Oncidium heteranthum Poepp. & Endl., complex") and some Odontoglossum species may have taken place. Members of both genera are frequently sympatric in the Andean region and flower simultaneously, where few Oncidium (sensu stricto) species occur. The species that are transferred from Oncidium to Odontoglossum in this paper (the "Oncidium chrysomorphum" and "O. obryzatum"

complexes) display features from both Heteranthocidium and Odontoglossum. They sometimes, but apparently not always, produce abortive flowers. The flowers in general and the pollination apparatus in particular of the transferred species are very similar to Heteranthocidium flowers, with an elongate, elephant-trunk-like rostellum and very narrow stipe on a minute ovoid viscidium. The inflorescence shapes are similar to some Heteranthocidium species, but the glossy, strongly flattened and the generally purple-mottled pseudobulbs are common Odontoglossum characteristics (Fig. 1). Members of the "Oncidium chrysomorphum" and "O. obryzatum" complexes are also characterized by having strictly unifoliate pseudobulbs, which makes them easily identified as a group even without flowers. Molecular evidence demonstrates that the here transferred species belong to the "base" of an extended Odontoglossum clade (Neubig et al. 2012). These hybridization speculations may seem far-fetched at first but we need to keep in mind that natural hybridization in Odontoglossum (Rolfe, 1893) is quite common and may be a much more active factor in the speciation process than we previously have acknowledged.

In addition to the already DNA sequenced species, which are transferred to *Odontoglossum* below, there are a few other taxa that may have to be transferred as well. It is unclear at this time, however, whether they really represent valid species or are just synonyms of the ones treated in this paper. In other words, more work is needed to complete this task.

Nomenclature

Odontoglossum boothianum (Rchb.f.) Dalström & W.E.Higgins *comb. nov.*

- Basionym: Oncidium boothianum Rchb.f., Bonplandia (Hannover) 2: 14. 1854. TYPE: VENEZUELA. Carabobo: H. Wagener s.n. (Holotype: W-48679). Fig. 2.
- Homotypic synonyms: *Heteranthocidium boothianum* (Rchb.f.) Szlach., Mytnik & Romovicz. Polish Bot. J. 51: 54. 2006.
 - *Vitekorchis boothianus* (Rchb.f.) Romovicz & Szlach., Polish Bot. J. 51: 46 (2006).

The identification of the DNA voucher representing this species (*Whitten 1732, 2447* and 2505, FLAS) was verified by Dalström.

Odontoglossum chrysomorphum (Lindl.) Dalström & W.E.Higgins *comb. nov*.

Basionym: *Oncidium chrysomorphum* Lindl., Fol. Orchid. 6: 54. 1855. TYPE: "Caraccas" (Lindl., 1855) Probably Colombia: Santa Martha, *W. Purdie s.n.* (holotype: K, not seen).

The identification of the DNA voucher representing this species (*Whitten* 1671, FLAS) was verified by Dalström.

Odontoglossum obryzatoides (Kraenzl.) Dalström & W.E.Higgins *comb. nov*.

Basionym: Oncidiumobryzatoides Kraenzl., in H.G.A.Engler (ed.), Pflanzenr., IV, 50(80): 240. 1922. TYPE: COSTA RICA. A. R. Endres 325 (holotype: W-13227). The identification of the DNA voucher representing this species (N 639 = Chase 11754, K) was not verified. However, the vegetative features in particular and floral features in general of this species correspond very well with the other species included here to justify the transfer.

Odontoglossum obryzatum (Rchb.f. & Warsz.) Dalström & W.E.Higgins *comb. nov*.

Basionym: Oncidium obryzatum Rchb.f. & Warsz., Bonplandia (Hannover) 2: 108. 1854. TYPE: PERU. J. von Warscewicz s.n. (Holotype: W-48672).

Vitekorchis obryzata (Rchb.f. & Warsz.) Romovicz & Szlach., Polish Bot. J. 51: 46. 2006.

The identification of the DNA voucher representing this species (*Whitten 2343*, at FLAS) was verified by Dalström. The floral features of this species are very similar to the lesser known but earlier described species that follows immediately below, and they may prove to be synonymous when more material has been analyzed.

Odontoglossum pictum (Kunth) Dalström & W.E.Higgins *comb. nov.*

Basionym: Oncidium pictum Kunth in F.W.H.Humboldt, A.J.A.Bonpland & K.S.Kunth, Nov. Gen. Sp. 1: 346.
1816. TYPE: COLOMBIA. Cauca: Popayan, between El Naranjo and Roldanilla, alt. 540 m, A. J. A. Bonpland & F. W. H. von Humboldt 1893 (Holotype: P). Fig. 3.

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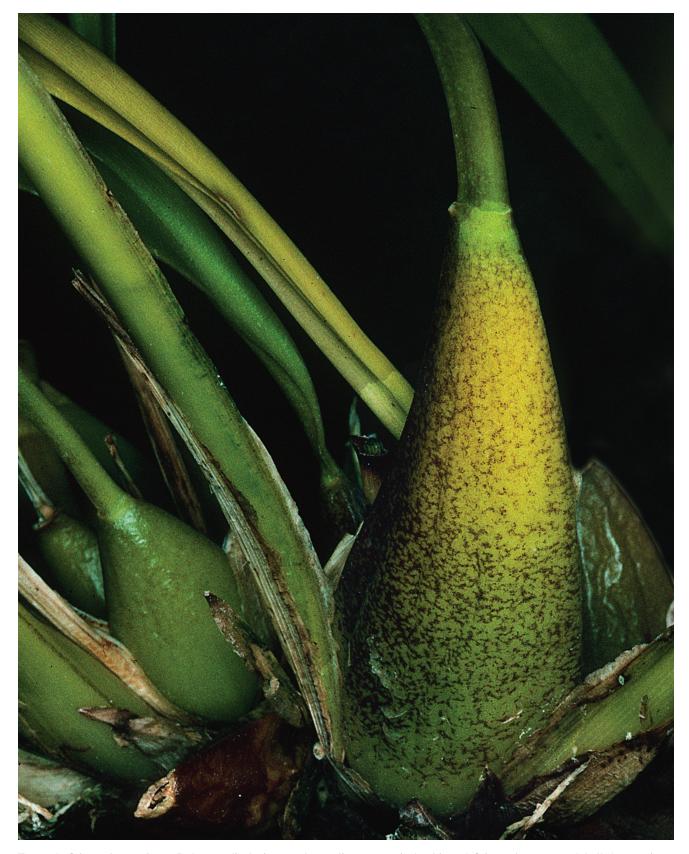


FIGURE 1. Odontoglossum hirtzii Dalström, displaying purple mottling on a typical cultivated Odontoglossum pseudobulb (no specimen made). Photograph by Stig Dalström.



FIGURE 2. Odontoglossum boothianum (Rchb.f.) Dalström & W.E.Higgins (based on S. Dalström 3716 (USM). Photograph by Stig Dalström.

No DNA sample of this species is known to us or has appeared in any published phylogenetic analysis, but it may prove to be an older name for *O. obryzatum*. The illustration of *Odontoglossum pictum* (as "*Oncidium*") that appears in the original publication (Kunth 1816: t. 81) shows a bifoliate pseudobulb. The type specimen in Paris from which the drawing is made has a unifoliate pseudobulb (Fig. 3), however, which appears to be typical for this group of species.

Odontoglossum tipuloides (Rchb.f.) Dalström & W.E.Higgins *comb. nov*.

Basionym: Oncidium tipuloides Rchb.f., Bot Zeitung (Berlin) 10: 856. 1852. TYPE: PERU. Huanuco: Cuchero, January 1830, E. F. Pöppig 1635 (Holotype: W). Fig. 4.

The identification of the DNA vouchers representing this species (*Whitten 1676* and 2421, FLAS, both previously incorrectly identified as cf. "*schmidtianum*") was verified by Dalström.

Odontoglossum trinasutum (Kraenzl.) Dalström & W.E.Higgins *comb. nov*.

Basionym: Oncidium trinasutum Kraenzl., in H.G.A.Engler (ed.), Pflanzenr., IV, 50(80): 194. 1922. TYPE: ECUADOR. Pichincha: W. Jameson s.n. (Holotype: W-44522).

The identification of the DNA voucher representing this species ("N335" = Williams 335, FLAS) was verified by Dalström.

Odontoglossum zelenkoanum (Dressler & Pupulin) Dalström & W.E.Higgins *comb. nov.*

Basionym: Oncidium zelenkoanum Dressler & Pupulin, Lankesteriana 8: 37. 2003. TYPE: PANAMA. Bocas del Toro: Culebra (Velorio), 1000 m, November 2000, flowered in cultivation July 2001, A. Maduro & E. Olmos 195 (Holotype: MO; Isotype PMA). Fig. 5.

The identification of the DNA voucher representing this species ("N 552" = *Whitten 3471*, at FLAS) was verified by Dalström.



FIGURE 3. Oncidium pictum Kunth. Holotype (P). Photograph by Muséum National d'Histoire Naturelle (P), provided by SEL.



FIGURE 4. Odontoglossum tipuloides (Rchb.f.) Dalström & W.E.Higgins (based on S. Dalström 2358 (SEL). Photograph by Stig Dalström.

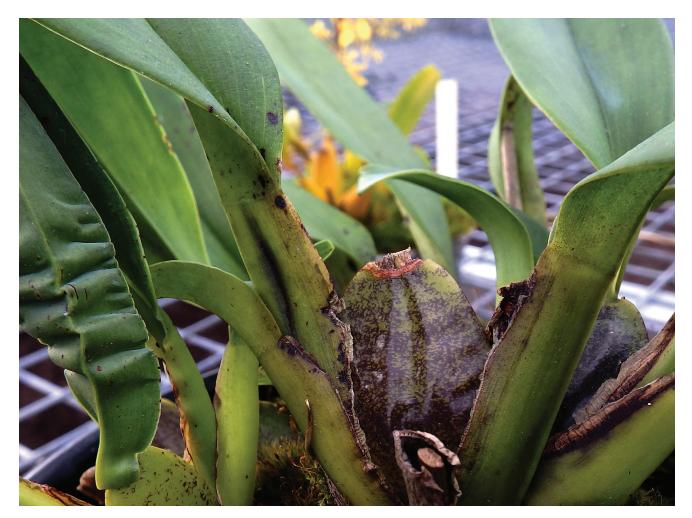


FIGURE 5. Odontoglossum zelenkoanum (Dressler & Pupulin) Dalström & W.E.Higgins (based on S. Dalström 3791 (USM). Photograph by Stig Dalström.

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