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Assembling  
the Tree of  
Life:  
Orchidaceae

## ONCIDIINAE (ORCHIDACEAE)



This study expands our previous work on subtribes [Maxillariinae](#), [Oncidiinae](#), [Zygopetalinae](#), and Stanhopeinae.

### INTRODUCTION TO ONCIDIINAE (ORCHIDACEAE)

This web site is based on our paper Neubig, K.M., W. M. Whitten, N. H. Williams, M. A. Blanco, L. Endara, J. G. Burleigh, K. Silvera, J. C. Cushman, & M. W. Chase. 2012. Generic recircumscriptions of Oncidiinae (Orchidaceae: Cymbidieae) based on maximum likelihood analysis of combined DNA datasets. *Botanical Journal of the Linnean Society* 168: 117-146. For this web site I have modified some of the text, added a few references, and added a large number of photographs. I also provide an interesting method of viewing [PHYLOGENETICS](#), an updated section on [REFERENCES](#), photographic [IMAGES](#) for a number of species, files that can be [DOWNLOADED](#) for you to examine on your computer, a list of [PEOPLE](#) involved in this project, [LINKS](#) to a number of interesting and useful web sites, and [ACKNOWLEDGMENTS](#) for all of the people, institutions, and organizations that helped with this project.

In our 2001 paper (Williams, et al., 2001a) we had 77 in-group taxa. We have increased taxon sampling to approximately 600 species (represented by 736 samples). We recovered the same clades as in our 2001 paper, with the following additions and exceptions.

**Clade A**, the *Fernandezia*-*Ornithocephalus*-*Telipogon* clade was represented by 8 species. We have increased sampling in this group to 96 OTU's and recover the same three major groupings: the *Telipogon* clade is sister to the *Fernandezia* clade + the *Ornithocephalus* clade. Members of the *Ornithocephalus* and *Telipogon* clades have four pollinia, whereas traditional members of the Oncidiinae have only two pollinia. *Pachyphyllum* and *Raycadenko* are lumped into *Fernandezia* and all have two pollinia. The presence of four pollinia appears to be a reversal from the two pollinia condition. *Hofmeisterella* is sister to the remainder of the *Telipogon* clade. The only chromosome counts that have been reported for members of this clade are for a member of the *Ornithocephalus* clade (2n=56), the most common number in the Oncidiinae.

**Clade B**, the *Brassia*-*Miltonia*-*Aspasia* clade, had 13 taxa, which is now increased to 53 OTU's. Within this clade, we recovered the following recognized genera: *Miltonia*, *Systeloglossum*, *Oliveriana*, *Cischweinfia*, *Brassia*, and *Aspasia*. *Miltonia* (100% BS) is sister to the remainder of this group, with the following relationships all well supported: (*Systeloglossum* + *Oliveriana*; 100% BS) is sister to *Cischweinfia* (100% BS); *Ada*, *Brachtia*, and *Mesospinidium* are embedded in *Brassia* and that clade is sister to *Aspasia* (100% BS). Chromosome numbers of members of this clade are usually 2n=56, although a wide range of numbers have been reported for *Brassia* (2n=18, 50, 52-58, 60), *Aspasia* (2n=56, 58, 60), and *Miltonia* (2n=48, 56, 59, 60, 86, 98, 112, although 60 is the most commonly reported number in *Miltonia*). No chromosome counts have been reported for other members of this clade.

**Clade C**, the *Cyrtorchilum* clade (86% BS, including *Miltoniopsis* and *Otoglossum*) had six taxa in our earlier sampling, which is now increased to 93 OTU's and we recovered the same clades: *Otoglossum*, *Cyrtorchilum*, *Miltonioides*, *Caucaea*, and *Cyrtorchiloides*; although we lacked material of *Cyrtorchiloides* in the first 2001 paper, we included it in the second 2001 paper (Williams, et al., 2001b). The relationships are: *Otoglossum* (79% BS) sister to the remainder, followed by *Cyrtorchiloides* (100% BS), *Miltoniopsis* (100% BS), *Caucaea* (100% BS), and finally *Cyrtorchilum* (99% BS). Our data do not support maintaining *Trigonochilum* or *Dasyglossum* as distinct genera.

**Clade D** in the first paper included *Rhynchostele*, *Erycina*, and *Tolumnia*, but with only 12 taxa and 84% bootstrap support. With increased sampling, Clade D breaks into two groups: the *Tolumnia* clade (100% BS) which is sister to the "twig-epiphyte" group (100% BS) in Clade E, and the *Rhynchostele* + *Erycina* clade (100% BS) which is sister to the "twig-epiphyte" + *Tolumnia* + *Gomesa* clade (93% BS).

**Clade E**, originally the "twig-epiphyte" clade plus *Zelenkoa* plus the *Gomesa* group (although at that time not recognized as just one genus), has been expanded from a taxon size of 15 to approximately 146 OTU's. The combined older clades D and E are now recognized as being broken into several different groups: (1) the "twig-epiphytes" sister to *Tolumnia* and several unresolved genera: *Solenidium*, *Capanemia*, *Zelenkoa*, *Notyliopsis*, and *Nohawilliamsia*; (2) the "twig-epiphytes" + *Tolumnia* + the unresolved genera sister to *Gomesa*; and (3) a *Rhynchostele* + *Erycina* clade sister to the above clades.

**Clade F**, the *Oncidium*/*Odontoglossum* clade, with 100% BS support (including *Cochlioda*, *Collare-stuartense*, *Heteranthodium*, *Sigmatostalix*, *Solenidiopsis*, *Symphyglossum*, *Mexicoa*, and *Miltonioides*) has been lumped into one genus (Chase, et al., 2008). As we pointed out earlier, the distinction between *Oncidium* and *Odontoglossum* has long been a source of contention. Much of the confusion and causes of concern have been resolved with the earlier transfer of species to other genera, such as *Rhynchostele*, *Otoglossum*, *Rossioglossum*, and *Cyrtorchilum*. Unfortunately, many apparently distinct groups are embedded within *Oncidium*/*Odontoglossum*. For example, *Cochlioda* and *Symphyglossum*, with their distinctive bird pollinated flowers, are deeply embedded in *Oncidium*/*Odontoglossum*. Although it has distinctive oil producing flowers (often quite small), *Sigmatostalix* is also deeply embedded within *Oncidium*/*Odontoglossum*. If we were to try to maintain *Oncidium*, *Odontoglossum*, *Sigmatostalix*, *Cochlioda*, and *Symphyglossum*, we would need to erect approximately 20 new genera, none of which we would be able to define on morphological grounds.

**Clade G**, *Lockhartia*, remains separate from other groups.

**Clade H**, the *Trichocentrum* s.l. group, now includes a number of clades for which we earlier had no material, including the *Rossioglossum* clade (including *Chelyorchis* and *Ticoglossum*) sister to *Cuitlauzina* (including *Osmoglossum* and *Palumbina*), the *Grandiphyllum* group (the Brazilian "mule-ear" oncidiums; 100% BS), and *Saundersia*. Although the entire clade has only weak support (57% BS), the individual clades all have strong support. *Rossioglossum* (100% BS) + *Cuitlauzina* (100% BS; 97% BS for the two) is sister to the remainder of the group, with a series of grades of *Grandiphyllum*, *Saundersia*, and *Trichocentrum* (100% BS).

**Clade I**, the *Trichopilia* clade (100% BS) is the same, although with larger taxon sampling. This clade includes *Psychopsis*, *Psychopsiella*, and *Trichopilia* (including *Helcia*, *Leucohyale*, and *Neoscobaria*).

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## THE ONCIDIINAE

Oncidiinae (Cymbidieae) are one of the most diverse subtribes of Orchidaceae, with a wide range of floral and vegetative morphologies. They include the greatest diversity of pollination systems and the widest range of chromosome numbers known for Orchidaceae (greater than the rest of the orchid family combined). They also form major components of the Neotropical flora, ranging from sea level to nearly 4,000 meters in the Andes; several species of *Brassia*, *Miltonia*, *Miltoniopsis*, and *Oncidium* are important ornamental crops. Oncidiinae are members of a Neotropical clade that includes subtribes Coeliopsidinae, Maxillariinae, Stanhopeinae, and Zygopetalinae; these five subtribes are each clearly monophyletic and collectively are sister to Eriopsidinae, but relationships among the five subtribes are still poorly resolved.

Largely following the generic concepts of Chase (2009b), subtribe Oncidiinae includes 62 genera (Table 1 in the **PHYLOGENETICS** section) and approximately 1,600 species. Prior to molecular phylogenetic studies, subtribal delimitation varied widely, from the relatively broad concept of Dressler (1993) to the narrow concepts of Szlachetko (1995), with the latter splitting out approximately 20 subtribes based largely on column morphology (including their complex pollinaria).

Previous classifications of Oncidiinae were intuitively based mainly on floral morphology and to a lesser extent chromosome number, and all were produced without cladistic methodology (Dressler, 1993; Garay & Stacy, 1974; Senghas, 1997). Recent molecular studies have helped resolve and define Oncidiinae, as well as circumscribe many genera (Chase & Palmer, 1987; Sandoval-Zapotitla, et al., 2010; Williams, et al., 2001a; Williams, Chase, & Whitten, 2001b). Subtribes Ornithocephalinae and Telipogoninae, long held separate on the basis of their four pollinia (vs. two in Oncidiinae), plus the monopodial Pachyphylliinae (two pollinia), were shown to nest within Oncidiinae.

Dressler (1993) emphasized seed characters, velamen type, and number of nodes per pseudobulb in his concepts of Cymbidieae and Maxillarieae. However, molecular data (van den Berg, et al., 2005) indicated that Cymbidieae sensu Chase (Chase, et al., 2003) are likely to be paraphyletic to Maxillarieae, and the two might be regarded as a single tribe. In the current circumscription, Oncidiinae include taxa with both two and four pollinia.

Oncidiinae exhibit an enormous diversity in form and function that makes them attractive subjects for evolutionary studies. Floral size ranges several orders in magnitude, and flowers evolved to utilize a diverse array of pollinators. Floral rewards include nectar, oils, and fragrances, but deceit flowers are the most common pollination strategy.

Chromosome numbers range from the lowest known in orchids of  $2n=10$  to  $2n=168$  (Tanaka & Kamemoto, 1984) and genome size spans at least a seven-fold range (Chase, et al., 2005). Vegetatively, plants range from large long-lived perennials with 1 kg pseudobulbs (or more) to highly reduced twig epiphytes the size of a thumbnail with rapid life cycles (several months). Most species are epiphytes and CAM photosynthesis is thought to have arisen repeatedly (Silvera, et al., 2009; Silvera, et al., 2010).

Understanding the evolution of this range of form, function, and biogeographic patterns depends upon a reliable phylogenetic hypothesis of relationships for hundreds of species. Generic boundaries and relationships within Oncidiinae have been highly contentious, and several genera have been viewed as taxa of convenience (non-monophyletic; Garay, 1963). Previous evolutionary studies have been hampered by the choice of non-monophyletic groups and by lack of reliable phylogenetic hypotheses. Our goal is to use combined plastid and nrITS data to produce a densely sampled phylogenetic estimate of relationships within Oncidiinae and to use this to underpin a stable generic classification (Chase, 2009b) that can be used as a framework for more focused studies.

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## POLLINATION AND FLORAL MIMICRY IN ONCIDIINAE

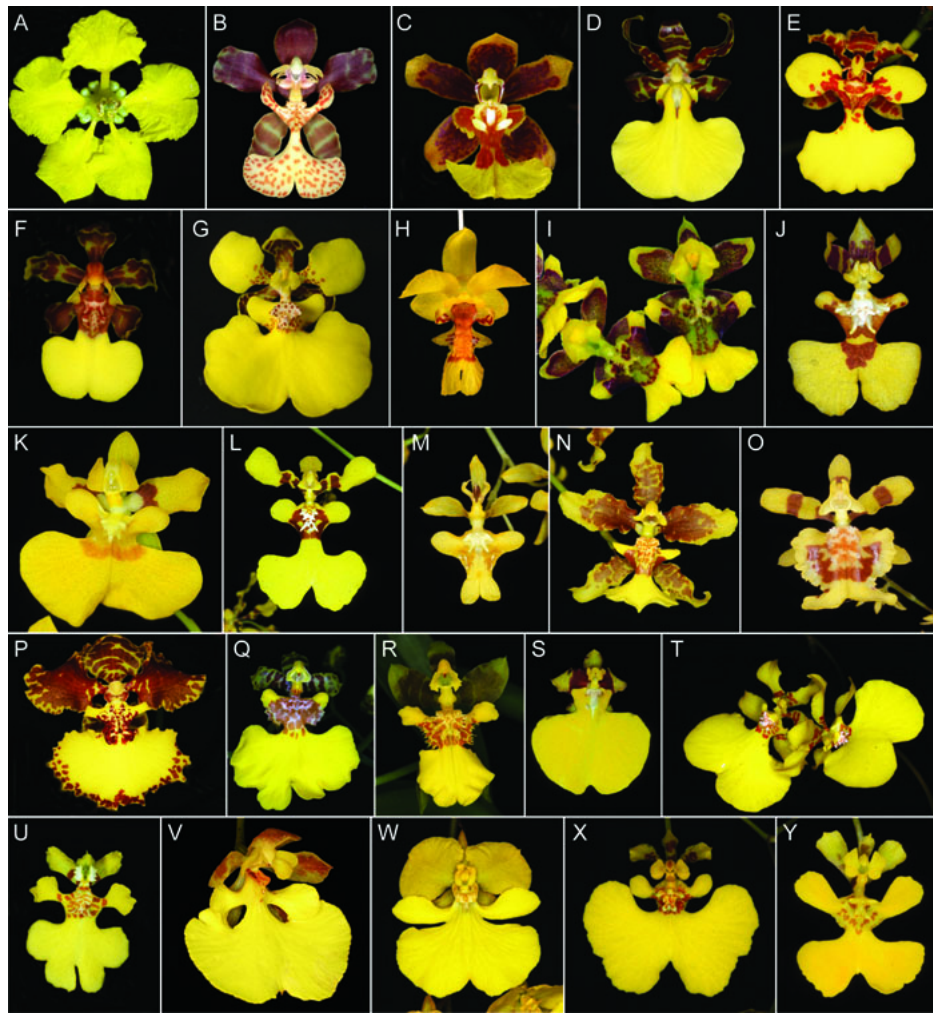
Historically, many of the difficulties with generic circumscription in Oncidiinae are likely the result of homoplasy and mimicry in flower shape and color. Generic boundaries have long been contentious in both the botanical and horticultural communities (Braem, 2010; Garay, 1963). As in most orchid groups, generic concepts traditionally have emphasized floral characters and neglected vegetative ones. In Oncidiinae, floral traits and pollination systems appear to be especially labile, which has undoubtedly fostered much of the confusion in generic boundaries and resulted in many polyphyletic genera. Floral rewards in Oncidiinae include nectar, oils, and fragrances. Pollen is never offered as a reward, and pseudopollen and resin rewards are unknown in Oncidiinae.

Nectar is a reward for bees, Lepidoptera, and hummingbirds and usually is presented in a nectariferous spur formed by the lip or the adnation of lip and column. However, nectar deceit is common, and the presence of a spur does not always indicate nectar. Relatively few species produce a fragrance reward consisting of monoterpenes, sesquiterpenes, and simple aromatics. These fragrances are collected by male euglossine bees (Apidae: Euglossini) and they are thought to serve a role in sexual selection by female euglossine bees (Bembe, 2004; Eltz, Roubik, & Lunau, 2005; Zimmermann, et al., 2009).

Most Oncidiinae species have flowers that either produce an oil reward or are mimics of oil-producing flowers of Malpighiaceae ("malpighs"; Carmona-Díaz & García-Franco, 2009; Reis, et al., 2000; Reis, et al., 2007; Sigris & Sazima, 2004; Silvera, 2002). **Figure 1**. These oil flowers attract a variety of female bees of various sizes of several different genera in the tribes Centridini, Tapinostapidiini, and Tetrapediini of the family Apidae (formerly assigned to a separate family, Anthophoridae, and still occasionally referred to as "anthophorid" bees). The female bees collect oil from specialised glands (elaiophores) on the flowers and use the oils as provisions and/or waterproofing for larval cells (Cane, et al., 1983; Melo & Gaglianone, 2005; Roubik, 1989).

Numerous species of Oncidiinae that are putative mimics of malpighs exhibit a suite of characters that include bright yellow (**Figure 1**) or purple (**Figure 2 A-E**) flowers, elaiophores consisting of epidermal pads on the lateral lobes of the lip or pads of trichomes on the lip callus and a tabula infrastigmatica (a fleshy ridge at the base of the column that is grasped by the bee's mandibles, freeing their front and middle legs to collect oil). Many Oncidiinae also possess prominent elaiophores (**Figure 2 F-J**); [e.g., *Oncidium cheiroporum* Rchb.f., *Oncidium sotoanum* R. Jiménez & Høegsater, *Trichocentrum cavendishianum* (Bateman) M.W. Chase & N.H. Williams, various *Gomesa* spp. (Aliscioni, et al., 2009; Davies & Stpieczynska, 2009; Pansarin, Castro, & Sazima, 2009; Stpieczynska & Davies, 2008; Stpieczynska, Davies, & Gregg, 2007)]. Parra-Tabla et al. (2000) reported that *Trichocentrum ascendens* (Lindl.) M.W. Chase & N.H. Williams is pollinated primarily by female *Trigona* bees collecting the oily floral secretions for nest construction. Species with prominent elaiophores represent legitimate oil reward flowers (**Figure 2 F-O**). We examined floral color and shape convergence in Neotropical plant communities, focusing on certain food-deceptive Oncidiinae orchids (e.g., *Trichocentrum ascendens* and *Oncidium nebulosum*) and rewarding species of Malpighiaceae. We showed that the species from these two distantly related families are often more similar in floral color and shape than expected by chance and propose that a system of multifarious floral mimicry—a form of Batesian mimicry that involves multiple models and is more complex than a simple one model—one mimic system—operates in these orchids (Papadopoulos et al., 2013).

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**Figure 1. Various genera and species of Oncidiinae displaying hypothetical mimicry of yellow Malpighiaceae flowers.**

A) *Malpighia* sp.; B) *Psychopsiella limminghei*; C) *Grandiphyllum auriculatum*; D) *Trichocentrum nanum*; E) *Trichocentrum cebolleta*; F) *Trichocentrum ascendens*; G) *Rossioglossum ampliatus*; H) *Lockhartia lepticaula*; I) *Fernandezia ecuadorensis*; J) *Vitekorchis excavata*; K) *Oncidium cultratum*; L) *Oncidium obryzatum*; M) *Oncidium* sp.; N) *Oncidium sphacelatum*; O) *Oncidium heteranthum*; P) *Gomesa gardneri*; Q) *Gomesa insignis*; R) *Gomesa longipes*; S) *Otoglossum harlingii*; T) *Otoglossum scansor*; U) *Erycina pusilla*; V) *Nohawilliamsia orthostates*; W) *Zelenkoa onusta*; X) *Tolumnia urophylla*; Y) *Tolumnia quadriloba*. Photos by W. Mark Whitten.





**Figure 2. Oncidiinae displaying various pollination syndromes.**

Row 1 A-E: Hypothetical purple Malpighiaceae mimics. A) *Malpighia glabra*; B) *Oncidium sotoanum*; C) *Cyrtorchilum edwardii*; D) *Tolumnia hawkesiana*; E) *Cyrtorchilum ioplocon*; Rows 2 (all) and 3 (all), Oncidiinae that secrete oil from localized elaiophores: F) *Lockhartia longifolia*; G-H) *Cyrtorchilum serratum* (arrow denotes elaiophore); I-J) *Oncidium cheirophorum* (arrow denotes elaiophore); K) *Ornithocephalus cochleariformis*; L) *Ornithocephalus dalstroemii*; M) *Ornithocephalus dressleri*; N) *Phymatidium falcifolium*; O) *Oncidium* sp.; (*Sigmatostalix* clade); Row 4 P-S, putative hummingbird-pollinated species: P) *Fernandezia subbiflora*; Q) *Brassia aurantiaca*; R) *Brassia andina*; S) *Oncidium* (*Cochlidia*) *beyrodtioides*; Row 4 T-U, pseudocopulatory species: T) *Tolumnia henekenii*; U) *Trichoceros antennifer*; Row 5 V-Y, species pollinated by nectar-foraging insects: V) *Trichocentrum longicalcaratum*; W) *Comparettia macroplectron*; X) *Rodriguezia* sp.; Y) *Trichopilia rostrata*; Row 5, Z, floral fragrance reward flower pollinated by male euglossine bees: Z) *Macroclinium dalstroemii*. Photo E courtesy Guido Deburghgraeve; all others by W. Mark Whitten.

Perhaps a larger percentage of Oncidiinae possess flowers with similar malpigh-mimicking color (bee-UV-green; Powell, 2008), morphology, and tabula infrastigmatica, but lack clearly demonstrable elaiophores. These species represent oil deceit flowers that lure oil-collecting bees but fail to produce a legitimate reward (**Figure 1**). Oncidiinae floral morphology is probably the result of a complex mixture of Batesian and M $\ddot{u}$ llerian mimicry (Roy & Widmer, 1999). Powell (2008) used spectral reflectance analyses to demonstrate that many Oncidiinae with yellow flowers closely match the color of yellow malpigh flowers [*Byrsonima crassifolia* (L.) Kunth] and thus satisfy criteria for Batesian mimicry. By mapping these traits onto a phylogenetic tree of Oncidiinae, he estimated at least 14 independent origins of putative malpigh mimicry within Oncidiinae. Carmona-D $\ddot{u}$ az and Garc $\acute{a}$ -a-Franco (2009) demonstrated that the rewardless *Trichocentrum cosymbephorum* (C. Morren) R. Jim $\acute{e}$ nez & Carnevali is pollinated by the same oil-collecting *Centris* bees that pollinate *Malpighia glabra* L., and the orchid has greater reproductive success in the presence of the malpigh than in isolated clumps. Vale, Rojas, and  $\acute{I}$ varez (2011) showed that the rewardless and self-incompatible *Tolumnia guibertiana* (A. Rich.) Braem, endemic to western Cuba, is completely dependent on oil-gathering female bees (*Centris poecila* Lepelletier) for fruit production. This bee species is also the pollinator of two other yellow-flowered plants in the area: the pollen and oil producing malpigh *Stigmaphyllon diversifolium* (Kunth) A. Juss. and the polliferous and buzz-pollinated *Ouratea agrophylla* (Tiegh.) Urb. (Ochnaceae).

Sazima and Sazima (1988) showed that some eglandular Malpighiaceae (lacking sepal elaiophores) are possible mimics of glandular forms. There likely are complex mimicry relationships between Malpighiaceae species, oil-producing Oncidiinae, and oil-deceit Oncidiinae. We also suspect that some Oncidiinae mimic oil-producing *Calceolaria* (Calceolariaceae), since they occur at high elevations where malpighs are absent or rare and *Calceolaria* species are common. For example, *Otoglossum harlingii* (Stacy) N.H. Williams & M.W. Chase (**Fig. 1 S**) bears a striking visual similarity to sympatric species of *Calceolaria*.

Some oil-secreting species with relatively small, greenish white or yellow flowers (e.g., *Ornithocephalus*, *Phymatidium*; **Figs. 2 K-N**) attract a subset of oil-foraging bees with smaller body size and do not appear to be involved in mimicry.

This extensive homoplasy in oil flower morphology has contributed to grossly polyphyletic classifications of Oncidiinae, especially in clades that contain species with bright yellow "oncidioid" flowers. Floral morphology, including detailed structure of the column (Szlachetko, 1995), is clearly unreliable as the sole basis for generic circumscription. A robust phylogenetic framework based on molecular data can help diagnose polyphyletic groups and inform a new clade-based classification.



## MATERIALS AND METHODS

**Taxon sampling** - Specimens were obtained from wild-collected or cultivated plants ([Appendix S1](#)). Most taxon names follow the generic concepts of Chase (2009b). Sampling of Oncidiinae included 738 accessions from a total of 590 ingroup species. We included seven outgroup taxa from other subtribes of Cymbidieae (Cameron, 2004; Cameron, Chase, Whitten, Kores, Jarrell, Albert, Yukawa, Hills, & Goldman, 1999). We were unable to obtain DNA of the following genera: *Caluera* Dodson & Determann, *Centroglossa* Barb.Rodr., *Cypholoron* Dodson & Dressler, *Dunstervillea* Garay, *Platyrrhiza* Barb.Rodr., *Quekettia* Lindl., *Rauhiella* Pabst & Braga, *Sanderella* Kuntze, *Suarezia* Dodson, and *Thysanoglossa* Porto & Brade.

**Extractions, amplification, and sequencing** - All freshly collected material was preserved in silica gel (Chase & Hills, 1991). Genomic DNA was extracted using a modified cetyl trimethylammonium bromide (CTAB) technique (Doyle & Doyle, 1987), scaled to a 1 mL volume reaction. Approximately 10 mg of dried tissue were ground in 1 mL of CTAB 2X buffer and 2.0  $\mu$ L of either B-mercaptoethanol or proteinase-K (25 micrograms/mL; Promega, Inc., Madison, Wisconsin USA). Some total DNAs were then cleaned with QIAquick PCR (Qiagen, Valencia, California, USA) purification columns to remove inhibitory secondary compounds. Amplifications were performed using an Eppendorf Mastercycler EP Gradient S thermocycler (Hauppauge, New York, USA) and Sigma brand reagents (St. Louis, Missouri, USA) in 25  $\mu$ L volumes with the following reaction components for ITS: 0.5-1.0  $\mu$ L template DNA (~10-100 ng), 11.0  $\mu$ L water, 6.5  $\mu$ L 5M betaine, 2.5  $\mu$ L 10X buffer, 3.0  $\mu$ L  $MgCl_2$  (25 mM), 0.5  $\mu$ L of 10  $\mu$ M dNTPs, 0.5  $\mu$ L each of 10  $\mu$ M primers, and 0.5 units *Taq* DNA polymerase. For the plastid regions, the following reaction components were used: 0.5-1.0  $\mu$ L template DNA (~10-100 ng), 16-18  $\mu$ L water, 2.5  $\mu$ L 10X buffer, 2-3  $\mu$ L  $MgCl_2$  (25 mM), 0.5  $\mu$ L of 10  $\mu$ M dNTPs, 0.5  $\mu$ L each of 10  $\mu$ M primers, and 0.5 units (0.2  $\mu$ L) *Taq* DNA polymerase.

**nrITS (ITS 1 + 5.8S rDNA + ITS 2)** - This region was amplified with a touchdown protocol using the parameters 94°C, 2 min; 15X (94°C, 1 min; 76°C, 1 min, reducing 1°C per cycle; 72°C, 1 min); 21X (94°C, 1 min; 59°C, 1 min; 72°C, 1 min); 72°C, 3 min with the primers 17SE and 26SE from Sun et al. (1994). Betaine was added to eliminate secondary structure typical of the ribosomal DNA, so that active ITS copies would predominate in the PCR product. Except for nrITS, all other regions sequenced are plastid regions.

**matK-trnK** - This region includes the entire *matK* gene and the flanking 3'*trnK* spacer and is roughly 1800 base-pairs (bp) in length. This region was amplified with the parameters 94°C, 3 min; 33X (94°C, 45 sec; 60°C, 45 sec; 72°C, 2 min); 72°C, 3 min, with primers -19F (Molvray, Kores, & Chase, 2000) and *trnK* 2R (Johnson & Soltis, 1994). Internal sequencing primers were *matK* intF (TGAGCGAACACATTCTATGG) and *matK* intR (ATAAGGTTGAAACCAAAAGTG). Some samples were amplified using the primers 56F and 1520R (Whitten, Williams, & Chase, 2000) that yielded a shorter, but nearly complete sequence of the *matK* exon (missing the 3'*trnK* spacer).

**psaB** - This region includes roughly 1700 bp of the protein-coding exon for a subunit of photosystem I. It was amplified with the parameters 94°C, 3 min; 33X (94°C, 30 sec; 55°C, 30 sec; 72°C, 2 min); 72°C, 4 min, with the primers NY159 and NY160 from Cameron (2004).

**rbcL** - This region (ca. 1350 bp) was amplified with the same parameters as for *psaB*, but with primers NY35 and NY149 from Cameron (2004).

**trnH-psbA** - This region includes about 800 bp of the intergenic spacer and a short exon, *rps19*. This region was amplified with the parameters 94°C, 3 min; 33X (94°C, 1 min; 58°C, 1 min; 72°C, 1 min, 20 sec); 72°C, 6 min, with the primers F and R from Xu et al. (2000).

**ycf1** - We sequenced two non-contiguous portions of *ycf1* (Neubig, Whitten, Carlswald, Blanco, Endara, Williams, & Moore, 2009) including ca. 1200 bp from the 5' end and ca. 1500 bp from the 3' end. Both were amplified using a "touchdown" protocol with the parameters 94°C, 3 min; 8X (94°C, 30 sec; 60-51°C, 1 min; 72°C, 3 min); 30X (94°C, 30 sec; 50°C, 1 min; 72°C, 3 min); 72°C, 3 min. Primers for the 5' portion are 1F (ATGATTTTAAATCTTTCTACTAG) and 1200R (TTGTGACATTTTCATTGCGTAAAGCCTT). Primers for the 3' portion are 3720F (TACGTATGTAATGAACGAATGG) and 5500R (GCTGTATTGGCATCAAACCAATAGCG). Additional internal sequencing primers are intF (GATCTGGACCAATGCACATAT T) and intR (TTTGATTGGGATGATCCAAGG).

PCR products were cleaned with Microclean (The Gel Company, San Francisco, California, USA) following the manufacturer's protocols, eluted with 50.0  $\mu$ L of 10 mM Tris-HCl (pH 8.5) and stored at 4°C. Purified PCR products were then cycle-sequenced using the parameters 96°C, 10 sec; 25X (96°C, 10 sec; 50°C, 5 sec; 60°C, 4 min), with a mix of 3.0  $\mu$ L water, 1.0  $\mu$ L fluorescent Big Dye dideoxy terminator, 2.0  $\mu$ L Better Buffer (The Gel Company), 1.0  $\mu$ L template and 0.5  $\mu$ L primer. Cycle sequencing products were cleaned using ExoSAP (USB Corporation, Cleveland, Ohio, USA) following the manufacturer's protocols. Purified cycle sequencing products were directly sequenced on an ABI 377, 3100, or 3130 automated sequencer according to the manufacturer's protocols (Applied Biosystems, Foster City, California, USA). Electropherograms were edited and assembled using Sequencher 4.9 (GeneCodes, Ann Arbor, Michigan, USA). All sequences were deposited in GenBank ([Appendix 1](#)).

**Data analyses** - We constructed two data matrices. The first included seven DNA regions (nrITS, *trnH-psbA*, 3'*ycf1*, 5'*ycf1*, *matK*, *rbcL*, and *psaB*) for 122 taxa. This smaller restricted data set included two relatively conserved plastid genes (*rbcL* and *psaB*) with the goal of providing increased resolution and support for the deeper nodes of the tree. The outgroup for this data set was *Rudolfiella* Hoehne sp.

The second matrix included five DNA regions (nrITS, *trnH-psbA*, 5'*ycf1*, 3'*ycf1*, and *matK*) for 737 samples representing approximately 600 species. Outgroup taxa were *Eriopsis biloba* Lindl., *Eulophia graminea* Lindl., *Cyrtidiorchis stumpsflei* (Garay) Rauschert, *Rudolfiella* Hoehne sp., *Stanhopea jenishiana* F. Kramer ex Rehb.f., and *Stanhopea trigrina* Bateman ex Lindl. Data matrices are available from the FLMNH public ftp site (<ftp://ftp.flmnh.ufl.edu/public/ncids>).

Maximum likelihood (ML) phylogenetic analyses were performed on both data sets using RAxML version 7.0.4 (Stamatakis, 2006). We ran analyses that included 1) only ITS, 2) only the plastid loci, and 3) all loci. All ML analyses used the general time-reversible model of evolution (GTR; Tavare, 1986) with among-site rate variation modeled using the "CAT" discrete rate categories option. For the analyses of the plastid loci and all loci, we further partitioned the ML model based on DNA region. Specifically, we estimated substitution model parameters for each region as well as region-specific branch lengths. To find the optimal tree for each data set, we performed 5 runs of the ML tree heuristic search and we performed 200 non-parametric bootstrap replicates to assess clade support in the tree (Felsenstein, 1985).

## RESULTS

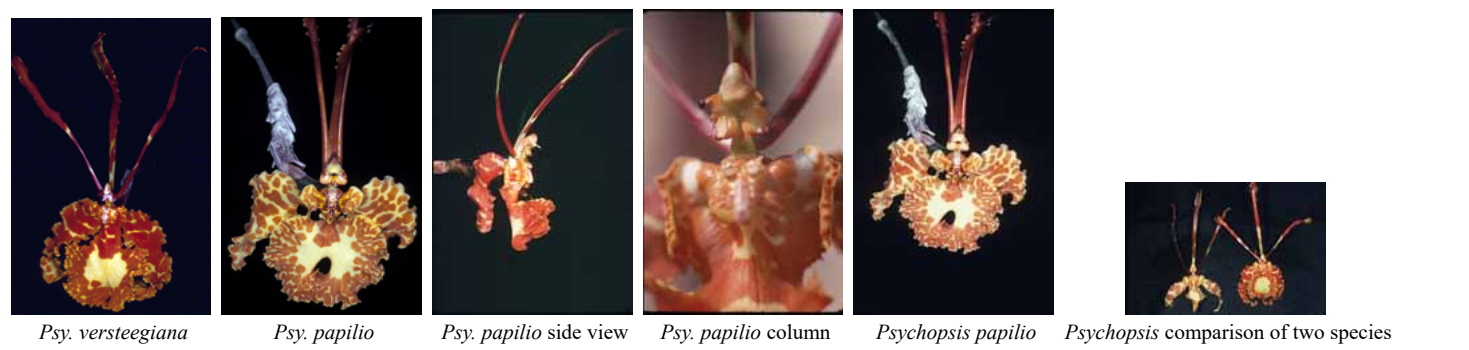
**Seven-locus data set** ([Fig. 3](#), [Fig. 4](#)). Both the plastid and the nrITS trees recover the same major clades, although there are some differences in the topology along the spines of the trees. There is conflict between the topology of the trees resulting from plastid and nuclear DNA sequences in the relationships of *Psychopsis*, *Psychopsiella*, and *Trichopilia*; *Psychopsis* and *Psychopsiella* are strongly supported as sister in the nrITS tree, whereas *Psychopsis* is strongly supported as sister to *Psychopsiella* and *Trichopilia* in the plastid tree. *Vitekorchis* is isolated in both nuclear and plastid trees. It is weakly supported as sister to *Oncidium* + all remaining taxa in the plastid tree, but is unresolved at a deeper node in nrITS trees. *Tolumnia* is strongly supported as sister to *Erycina* + *Rhynchosstele* in nrITS results, but plastid data place *Tolumnia* as a well-supported member of a derived clade (*Nohawilliamsia* to *Comparettia*). Many of these discrepancies in the deeper nodes may be due to potential alignment error or possible saturation of nrITS. Most of the plastid regions exhibit few or no apparent alignment problems (with the exception of large portions of *trnH-psbA* that were excluded from the analyses). The combined plastid + nrITS seven-region analysis of 122 taxa ([Fig. 4](#)) is largely consistent with the analysis of the larger five-locus data (736 taxa; Figs. 5-12), but the addition of *rbcL* and *psaB* data provide slightly more support for the spine of the tree.

**Five-locus data set (Figs. 5-12).** Many species are represented by two or more samples. In most cases, multiple accessions of a single species form a unique group (e.g., *Erycina*, Fig. 10). In a few cases, plants from putatively the same species do not fall together (e.g., *Cyrtochilum cimiciferum*, Fig. 9). Some of these may be due to errors in determinations, but usually these represent taxonomically confusing groups with poorly defined species boundaries. We recognize 62 clades in this tree at the generic level (Table 1, in the PHYLOGENETICS section). All of the clades that we recognize at the generic level are strongly supported, and there is also strong support for nearly all supra-generic nodes in the tree. Exceptions are the monotypic genera *Zelenkoa*, *Notyliopsis*, and *Nohawilliamsia* (Fig. 11). These taxa form a poorly supported grade that is sister to *Tolumnia* and the twig epiphyte clade (all taxa in Fig. 12). Other genera with weak support for generic topology include *Schunkea*, *Trizeuzis*, *Seegeriella*, and *Warmingia*.

# DISCUSSION

Genera are discussed in order of their appearance in the cladograms (Figs. 5-12). Generic concepts generally follow those of Chase (2009b) with a few exceptions; more detailed information for each genus is presented in that work.

***Psychopsis*** Raf. (5 spp.; Fig. 5) ranges from Costa Rica south through the Andes to Peru. Chase (2005) lumped the monotypic *Psychopsiella* into *Psychopsis* on the basis of their sister relationship in the nrITS tree to avoid creation of a monotypic genus, but analysis of the combined data sets place *Psychopsiella* sister to *Trichopilia* Lindl. Chromosome numbers also differ for *Psychopsis*  $2n=38$  (Dodson, 1957) versus  $2n=56$  for *Psychopsiella* and *Trichopilia* (Charanasri & Kamemoto, 1975). Both *Psychopsiella* and *Psychopsis* have yellow and brown flowers with a tabula infrastigmatica, suggestive of oil-reward flowers, although Dodson (2003) reported pollination of *Psychopsis krameriana* (Rchb.f.) H.G. Jones by *Heliconius* butterflies, but his observations have not been replicated.



***Psychopsiella*** Lckel & Braem (1 sp.; Fig. 1B; Fig. 5) is monotypic and vegetatively resembles a dwarf *Psychopsis*, but it lacks the elongate dorsal sepal and petals of the latter. It is restricted to Brazil and has been reported from Venezuela, near Caracas, but this may have been an escape from cultivation. It shares a chromosome number of  $2n=56$  with its sister, *Trichopilia*.



***Trichopilia*** Lindl. (approximately 26 spp.; Fig. 2Y ; Fig. 5) is largely characterized by having a lip that enfolds and is fused basally to the column, in some species forming a deep tubular structure suggestive of nectar reward or deceit, although Dodson (1962) reported pollination of one species by fragrance-collecting male euglossine bees. Some species of *Cattleya* and *Sobralia* have similar flowers, and they also are visited by male euglossine bees. Vegetatively, plants of *Trichopilia* are similar to the preceding two genera. *Helcia* Lindl., *Leucohyale* Klotzch, and *Neoscobaria* Garay are embedded within *Trichopilia*. These differ primarily in the lack of lip/column fusion and have previously been recognized by some authors as members of *Trichopilia*.





*T. (Leucohyle) subulata* *T. (Leucohyle) subulata* *T. (Leucohyle) subulata*

**Rossioglossum** (Schltr.) Garay & G.C. Kenn. (10 spp.; Fig. 5), as circumscribed here, includes *Ticoglossum* Lucas Rodr. ex Halb. and *Chelyorchis* Dressler & N.H. Williams. This genus also includes considerable floral diversity, suggestive of pollination by a variety of bees, but pollination data are mostly lacking. *Rossioglossum ampliatus* (Lindl.) M.W. Chase & N.H. Williams (Fig. 1G) has numerous bright yellow (bee-UV-green; Powell, 2008) *Oncidium*-like flowers that are malpigh mimics, whereas other *Rossioglossum* (e.g., *R. insleyi* and *R. grande*) bear relatively few, large flowers barred with yellow and brown. All species share vegetative similarities of rounded, ancipitous pseudobulbs topped by a pair of leathery leaves. Van der Pijl and Dodson (1966) reported pollination of *R. grande* by *Centris* bees. Their floral features, particularly the presence of a tabula infrastigmatica, indicates oil-bee pollination, although their floral absorbance has not been investigated. Recognition of *Chelyorchis*, due to its floral distinctiveness within this clade, would result in a paraphyletic *Rossioglossum*. The genus ranges mostly from Mexico to Central America, with *Chelyorchis pardoii* Carnevali & G. A. Romero extending further south to Trinidad and Tobago, Colombia, and Venezuela (Fernandez-Concha, et al., 2009). This species currently lacks a combination in *Rossioglossum*.



**Cuitlauzina** Lex. (10 spp.; Fig. 5), as circumscribed here, includes *Dignathe* Lindl., *Osmoglossum* (Schltr.) Schltr., and *Palumbina* Rehb.f. and collectively ranges from Mexico to Panama in Central America. Because floral morphology is so divergent within this genus, the close relationships between *Cuitlauzina* s.s., *Palumbina*, *Dignathe*, and *Osmoglossum* were previously unsuspected, although Ayensu and Williams (1972) showed that *Palumbina* and *Osmoglossum* shared some leaf anatomical features, and Williams (1972b) mentioned that there were similarities between the pollinaria of *Palumbina* and *Osmoglossum*, as well as vegetative and floral similarities. All four genera were segregated by various authors from *Odontoglossum*. *Cuitlauzina pendula* Lex. has a tabula infrastigmatica, but its pollinator is unknown; its color (white or pink) makes it unlikely to be an oil-bee flower. In spite of their gross floral disparity, they share a prominent clinandrial hood and similar pollinarium morphology (Sosa, et al., 2001).



*Cuit. pendula* white form *Cuit. pendula* pink form *Cuit. (Palumbina) candida* *Cuit. (Palumbina) candida* *Cuit. (Palumbina) candida* *Cuit. (Osmoglossum) pulchella*

**Grandiphyllum** Docha Neto (10 spp.; Fig. 1C; Fig. 5; Brazilian "mule-ear" oncidiums) is restricted to Brazil and northern Argentina, and the species were formerly placed as members of two sections of *Oncidium*. They have large leathery leaves and floral morphology typical of *Oncidium* with an oil-bearing callus or dense pad of trichomes and a tabula infrastigmatica, but they lack the complex tubularized pollinarium stipe (Chase, 1986b) typical of *Oncidium* s.s. Except for the placement of *Saundersia* (Fig. 5), these might have better been included in *Trichocentrum*; however, this also would have involved transferring *Saundersia*, which seems to share little with the other two clades.



*Grandiphyllum auriculatum*

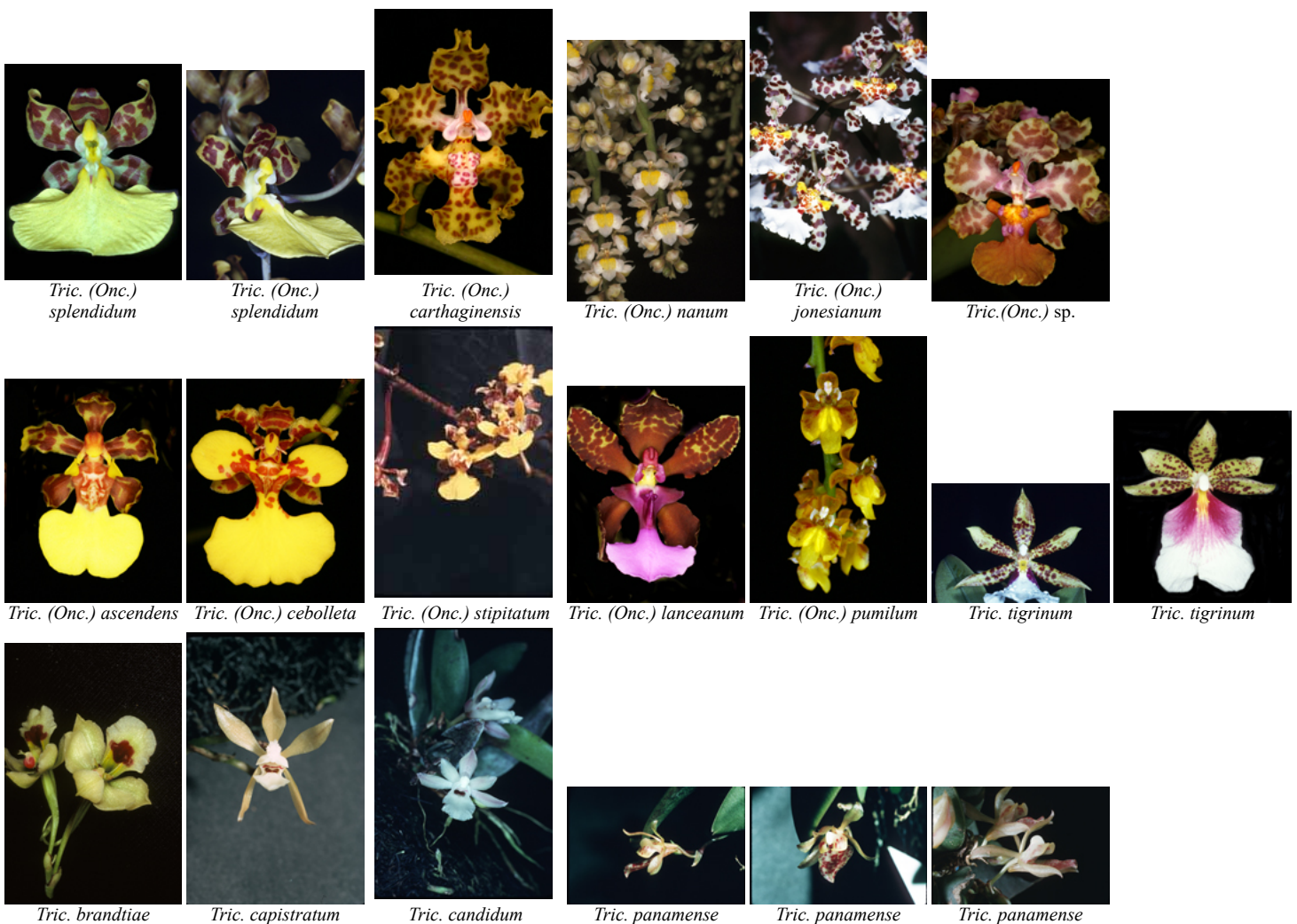


*Saundersia* Rchb.f. (2 spp.; Fig. 5) is restricted to Brazil. These small plants have relatively leathery "mule-ear" leaves and small flowers borne in a dense pendent raceme with a short column that lacks a tabula infrastigmatica. The roots, ovary, and sepals bear dense indumentum, a feature unique within this clade and rare in the entire subtribe (but found in some species of *Ornithocephalus*, which is not closely related; Fig. 6).

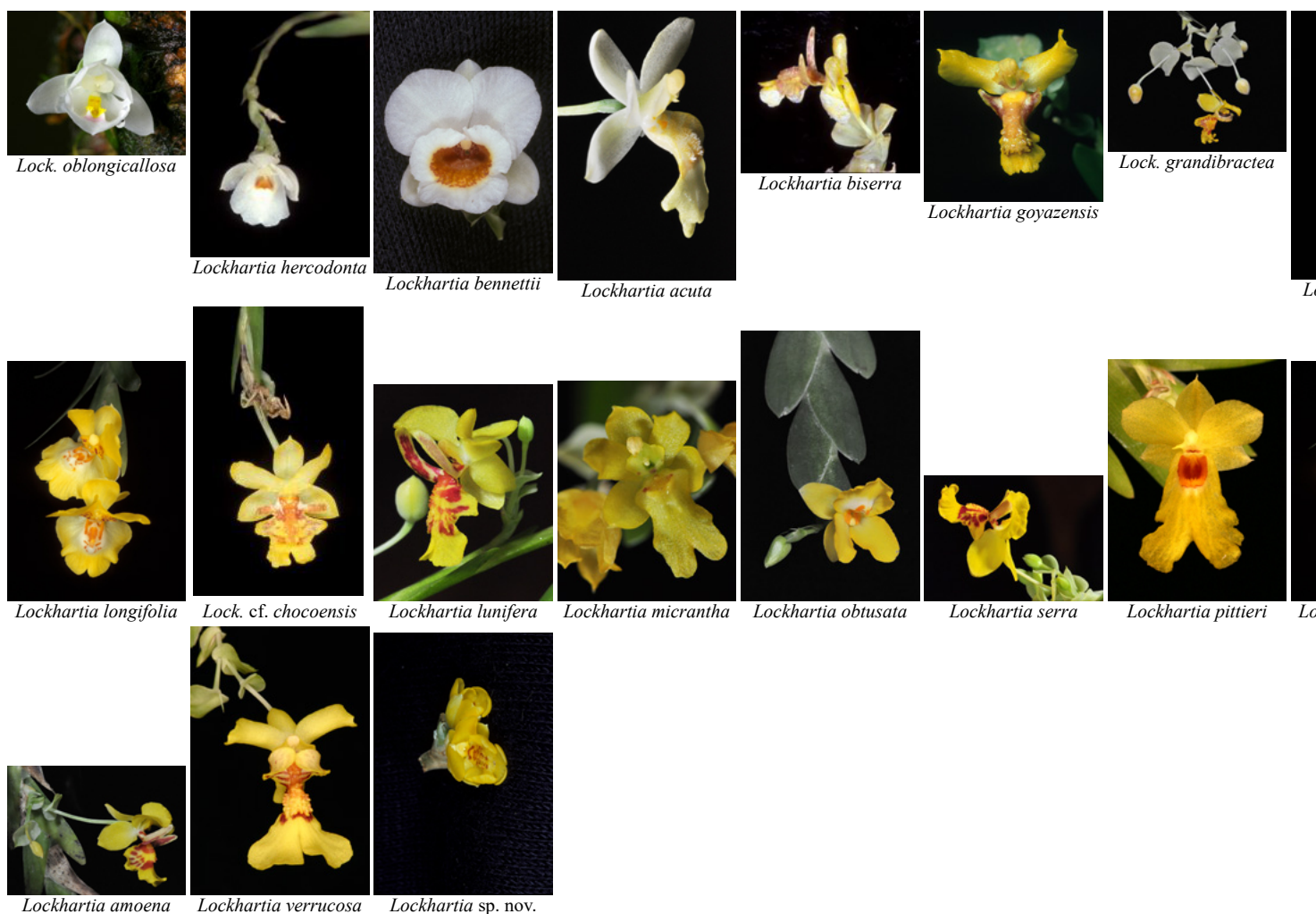
*Trichocentrum* Poepp. & Endl. (approximately 70 spp.; Figs. 1D,E,F, 2V; Fig. 5), as broadly circumscribed by Chase (2009b), also includes *Lophiaris* Raf. ("mule-ear" oncidiums), *Cohniella* Pfitzer ("rat-tail" oncidiums), and *Lophiarella* Szlach., Mytnik & Romowicz (*Trichocentrum microchilum* (Bateman ex Lindl.) M.W. Chase & N.H. Williams and *T. pumilum* (Lindl.) M.W. Chase & N.H. Williams). This clade also includes great floral diversity, but the species are linked by vegetative succulence. The leaves are thick and leathery, and in one clade the leaves are terete ("rat-tail" oncidiums).

Most species have yellow to brown flowers that are either true oil-rewarding or resin-rewarding species: *T. stipitatum* (Lindl. ex Benth.) M.W. Chase & N.H. Williams, visited by *Centris* and *Paratetrapedia* bees (Silvera, 2002); *T. ascendens* (Lindl.) M.W. Chase & N.H. Williams, pollinated by *Trigona* and *Centris* (Parra-Tabla, et al., 2000), and some are oil-deceit-flowers. Species of *Trichocentrum* s.s. typically have a spur (Fig. 2V), although nectar has never been observed. Most *Trichocentrum* s.s. with spurs might be deceit flowers, attracting nectar-foraging euglossine bees or other long-tongued bees. At least one species, *T. tigrinum* Linden & Rchb.f., has a strong fragrance and attracts fragrance-collecting male euglossine bees (van der Pijl & Dodson, 1966). Chromosome number varies greatly within this clade, forming a continuum from  $2n=24$  to  $2n=72$  that does not correlate well with subclades. Chase and Olmstead (1988) hypothesized that the range of numbers is the result of chromosomal condensation and does not involve polyploidy.

Some workers (Braem, 1993; Christenson, 1999; Fernandez-Concha, et al., 2010) favor a narrow circumscription of *Trichocentrum* (restricted to those species with a spur) and recognition of *Lophiaris* and *Cohniella*. These generic segregates are monophyletic with respect to our molecular data if one species of *Lophiarella* (*T. pumilum* (Lindl.) M.W. Chase & N.H. Williams) is included in *Lophiaris*, but *Lophiarella* should also include *T. flavovirens* (L.O. Williams) M.W. Chase & N.H. Williams and *T. splendidum* (A. Rich. ex Duch.) M.W. Chase & N.H. Williams, if *Lophiarella* is to be monophyletic. Chase (2009b) argued for lumping all these into a broader *Trichocentrum* on the basis of pollinarium and vegetative characters (Sandoval-Zapotitla & Terrazas, 2001), which also avoids recognition of a large number of genera.



*Lockhartia* Hook. (35 spp.; Figs. 1H, 2F; Fig. 5) has confused orchidologists for decades and has been placed in a number of suprageneric taxa. The genus ranges throughout much of the Neotropics. The flowers are mostly bright yellow and bear oil-secreting trichomes, similar to many others in Oncidiinae, but they lack a tabula infrastigmatica. The pollinaria have elongate caudicles that partially replace a stipe (similar to *Pachyphyllum* = *Fernandezia*), and all but one species have a "braided" vegetative habit with pseudomonopodial stems lacking pseudobulbs and tightly overlapping, unifacial, non-articulate leaves. The capsules have apical dehiscence instead of lateral dehiscence. These unusual features led some workers to place *Lockhartia* in a separate subtribe, Lockhartiinae Schltr., but molecular data strongly support its position within Oncidiinae. The unusual vegetative features are best explained as pedomorphic traits common to many seedlings of Oncidiinae (Chase, 1986b). One species (*L. genegeorgei* D.E. Benn. & Christenson) has prominent pseudobulbs with articulated, bifacial leaves; the lack of pedomorphic traits in this species led Senghas (2001) to describe a new genus, *Neobennettia* Senghas. We were unable to obtain a DNA sample of this taxon for inclusion in our analyses, but we feel its segregation into a monotypic genus is unwarranted. It may be a natural intergeneric hybrid between *Lockhartia* (probably *L. lepticaula* D.E. Benn. & Christenson) and a species of *Oncidium* or *Vitekorchis*; the elongate, non-bifid pollinarium stipe of *L. genegeorgei* is very different from that of other Lockhartias.



The following seven genera include taxa formerly segregated from Oncidiinae as the monopodial subtribes Pachyphyllinae (pollinia with two long stipes/caudicles) and Ornithocephalinae (four pollinia).

**Fernandezia** Lindl. (approximately 50 spp.; Figs. 1I, 2P; [Fig. 6](#)) has recently been re-circumscribed to include both *Pachyphyllum* Kunth and *Raycadenco* Dodson (Chase & Whitten, 2011). The monotypic *Raycadenco* has yellow and brown flowers with a tabula infrastigmatica typical of many oil-bee pollinated species of *Oncidium*, but the plants are monopodial (and therefore lack pseudobulbs), a habit shared with others in this clade. *Raycadenco* is sister to *Fernandezia* (including *Pachyphyllum*). These two genera (*Fernandezia* and *Pachyphyllum*) were previously distinguished on the basis of flower size and color. *Pachyphyllum* has tiny white, pink, or yellow flowers for which pollinators are unknown, whereas *Fernandezia* s.s. has larger flowers that are bright red or orange and are hummingbird pollinated. The two genera are not reciprocally monophyletic in our trees, lending support to our decision to lump *Pachyphyllum* into *Fernandezia*. Given the rampant parallelism in floral morphology and in particular the frequent occurrence of oil-bee flowers in Oncidiinae, it makes no sense to keep *Raycadenco* separate just because it has oil-bee flowers when we disregard different pollination syndromes in other genera (e.g., *Cyrtorchilum*, *Gomesa*, *Oncidium*, etc.).







*Frn. (Pachyphyllum) cuencae*



*Frn. (Pachyphyllum) hispidulum*

*Frn. (Pachyphyllum) sp.*



*Frn. (Pachyphyllum) sp.*



*Frn. (Pachyphyllum) sp.*



*Frn. (Raycadenco) ecuadorensis*

The genera we sampled comprising the former Ornithocephalinae are monophyletic in our trees, although several are represented by only a single sample (Figs. 2K,L M,N; Fig. 6): *Phymatidium* Lindl. (10 spp.), *Zygostates* Lindl. (20 spp.), *Chytroglossa* Rchb.f. (3 spp.), *Eloyella* P.Ortiz (7 spp.), *Hintonella* Ames (1 sp.), and *Ornithocephalus* Hook. (50 spp.). These genera possess tiny green to yellow to white flowers that secrete oil via labellar elaiophores and are pollinated by smaller genera of oil-collecting bees (Buchmann, 1987). Toscano de Brito and Dressler (2000) transferred all species of *Sphyrastylis* Schltr. into *Ornithocephalus*, and *Dipteranthus* Barb. Rodr. is not separable from *Zygostates* (Chase, 2009b). Genera of the former Ornithocephalinae not sampled in our study include *Centroglossa* Barb. Rodr. (5 spp.), *Caluera* Dodson & Determann (3 spp.), *Rauhiella* Pabst & Braga (3 spp.), *Platyrrhiza* Barb. Rodr. (1 sp.), and *Thysanoglossa* Porto & Brade (2 spp.). An unpublished analysis of nrITS data (Toscano de Brito, pers. comm.) shows that *Centroglossa* is embedded within *Zygostates*, and thus these two should be merged. The new combinations in *Zygostates* have not been made and *Centroglossa* was still listed in the Kew World Checklist of Monocotyledons when this manuscript was revised (17 August 2011). His (Toscano de Brito) results also confirm the monophyly and inclusion in this clade of the other four genera.



*Ornithocephalus* sp.  
plant



*Ornithocephalus* sp.



*Ornithocephalus* sp.



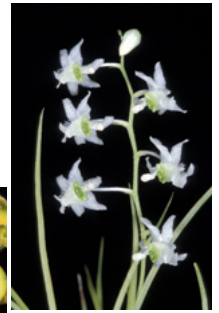
*Orn. (Sphyrastylis) sp.*



*Orn. (Sphyrastylis) sp.*



*Orn. (Sphyrastylis) sp.*



*Phymatidium*  
*tillandsioides*



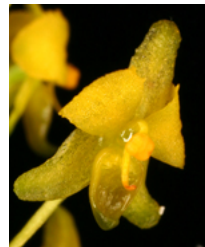
*Chytroglossa*  
*marileonniae*



*Chytroglossa*  
*marileonniae*



*Chytroglossa*  
*marileonniae*



*Chytroglossa*  
*marileonniae*



*Chytroglossa*  
*marileonniae*

*Hofmeisterella* Rchb.f. (1 sp.; Fig. 6), *Trichoceros* Kunth (9 spp.; Fig. 2U; Fig. 6), and *Telipogon* Kunth (170 spp.; Fig. 6) include species formerly regarded as subtribe Telipogoninae on the basis of four pollinia (vs. two in Oncidiinae) and pseudocopulatory flowers (that are pollinated by male tachinid flies) with furry columns and lip calli. Within this clade, monotypic *Hofmeisterella* is sister to *Trichoceros* (high elevation species with thick, succulent leaves, and pseudobulbs) and *Telipogon* (intermediate to high elevation species with thin leaves with reduced or absent pseudobulbs). Previous molecular studies of this clade showed that *Stellilabium* Schltr. is biphyetic and embedded within *Telipogon*. One Central American clade of *Stellilabium* is sister to a Central American clade of *Telipogon*, and these are embedded in a South American grade (Williams, Whitten, & Dressler, 2005).



*Telipogon andicola*



*Telipogon* sp.1





*Hof. eumicroscopica*

*Trichoceros* sp.



*Trichoceros antennifer*

*Telipogon andicola*



*Tel. klotzscheanus*



*Telipogon* sp. 2



*Tel. (Stellilabium)* sp.



*Tel. (Stellilabium)* sp.



*Tel. (Stellilabium)* sp.  
plant

*Vitekorchis* Romowicz & Szlach. (4 spp; Fig. 1J; Fig. 7) is an Andean genus that is sister to *Oncidium* in our trees but without strong BS support. The floral similarity to *Oncidium* and chromosome counts of  $2n=56$  are evidence supporting their lumping into *Oncidium*, but without stronger molecular support we prefer to maintain generic status for this clade at present. Their most distinguishing features are relatively large, sharply-ridged pseudobulbs with numerous subtending leaves, massive inflorescences, and small stipes relative to the pollinia. Our circumscription of *Vitekorchis* differs greatly from that of Szlachetko. His circumscription includes several species that should be retained in *Oncidium* (*O. boothianum* Rchb.f., *O. iricolor* Rchb.f., and *O. obryzatum* Rchb.f., among others).



*Vitekorchis excavata*

*Oncidium* Sw. (approximately 520 spp; Figs. 1I-J,O,S; 2B; Fig. 7, Fig. 8), as broadly circumscribed here, includes many previously recognized genera such as *Cochlioda* Lindl., *Mexicoa* Garay, *Miltonioides* Brieger & Lückel, *Odontoglossum* Kunth, *Sigmatostalix* Rchb.f., *Solenidiopsis* Senghas, and *Symphyglossum* Schltr., as well as a number of recent, minor segregates such as *Chamaeleorchis* Senghas & Lückel, *Collare-stuartense* Senghas & Bockemuhl, and *Heteranthocidium* Szlach., Mytnik, & Romowicz. With this broad circumscription, it is the largest genus of the subtribe. *Oncidium* species range from Mexico and Florida through the Caribbean, Central America south to Bolivia and Peru, with only one species in Brazil (*O. baueri* Lindl.). There are many chromosome counts of  $2n=56$  (Tanaka & Kamemoto, 1984).

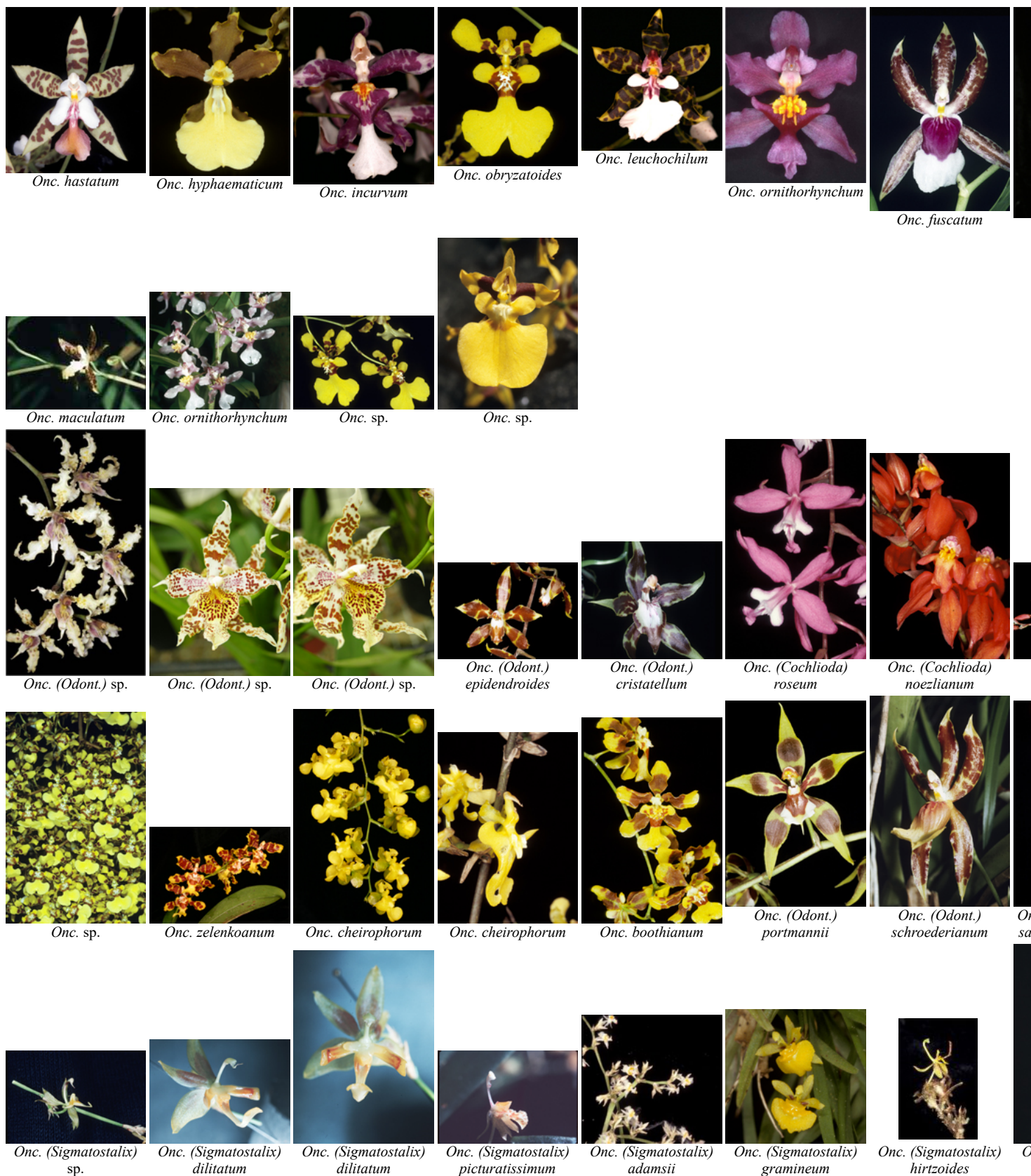
The circumscription of *Oncidium* has been highly contentious, especially among horticulturalists. For many years, the angle of attachment of the lip to column was used to distinguish *Oncidium* from *Miltonia* and *Odontoglossum*, but such angles form a continuum and use of this single-character to define genera resulted in highly artificial classifications, as was pointed out by Dressler and Williams (1975). *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 subject to shifts in pollinators. The traditional emphasis on floral features has resulted in many polyphyletic genera. Nearly fifty years ago, Garay (1963) admitted the artificiality of many generic boundaries within Oncidiinae: "To the taxonomist as well as the horticulturalist, it appears to be a serious and unpleasant thought to unite all these genera with *Oncidium*, but this course seems to be inevitable, since the information gained from experiments in hybridization and from cytological studies strongly points in that direction."

And as Dodson stated in *Orchid Flowers: Their Pollination and Evolution*, van der Pijl and Dodson, 1966, page 94:

◆ A point which has been generally overlooked in taxonomy in the orchids is that the characters which result from adaptation 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 *Sophranitis*-*Laelia*-*Cattleya* complexes where the enormous number of artificial hybrids are mute evidence of the failure of taxonomists to understand the ecological background of speciation in these groups. ◆

We feel 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. Most members of *Oncidium* s.s. are characterized by flowers that are adapted for pollination by relatively large oil-collecting bees (e.g., *Centris*), and many species possess prominent elaiophores on the side lobes of the lip together with a tabula infrastigmatica (Figs. 21,J). *Cochlioda* and *Symphyglossum* represent adaptations for hummingbird pollination, with bright red/pink/purple tubular flowers (Fig. 2S).

The lumping of *Sigmatostalix* into *Oncidium* seems initially inappropriate, but the vegetative habit of the two taxa differs only in size, and the flowers of *Sigmatostalix* are diminutive relative to most *Oncidium* species (Fig. 2O), reflecting adaptations to different groups of smaller oil-collecting bees as pollinators. Although many of the traditionally recognized segregate genera are monophyletic in our trees (e.g., *Sigmatostalix*, one clade of *Odontoglossum*), they are embedded within a larger clade of *Oncidium* species with diverse floral morphologies and pollination systems. Recognition of these segregate genera would require creation of many new genera to maintain monophyly, and these new genera would be difficult or impossible to diagnose using floral or vegetative traits.

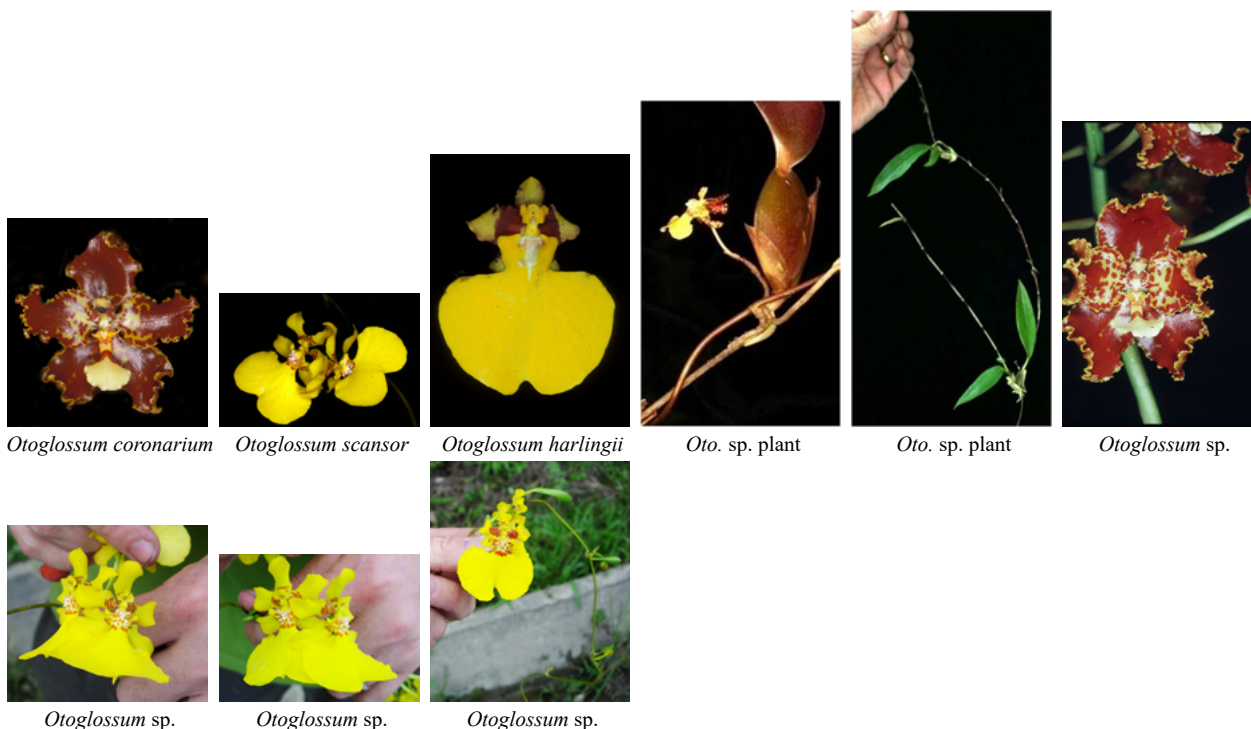


A few species of *Oncidium* (e.g., *O. abortivum* Rchb.f., *O. echinops* König, *O. heteranthum* Poepp. & Endl.; Fig. 2) produce branched inflorescences with terminal normal flowers on the branches, but the proximal flowers are abortive and sterile, consisting of only a cluster of yellow tepals that function as osmophores (W.M. Whitten, pers. obs.). In other species (*O. pentadactylon* Lindl.), abortive flowers are terminal, with all other proximal flowers being normal. Szlachetko, Mytnik-Ejsmont, & Romowicz (2006) described *Heteranthodium* to accommodate these species, but their genus is not monophyletic in our trees. Moreover, several of the 15 species they placed in the genus do not possess dimorphic flowers and are widely scattered in our trees (e.g., *O. boothianum*, *O. exaltatum* Høegsater, *O. fuscans* Rchb.f., *O. iricolor* Rchb.f.). All heteranthous species sampled here form a clade of 16 accessions (*O. retusum* Lindl. to *O. heterodactylum* Kraenzl., Fig. 2), but not all the species in this clade bear dimorphic flowers (*O. retusum*, *O. cultratum* Lindl., *O. lancifolium* Lindl. ex Benth.). Species delimitation is difficult within this clade, and there appears to have been multiple loss or gains of the heteranthous trait, coupled with its erratic phenotypic expression.



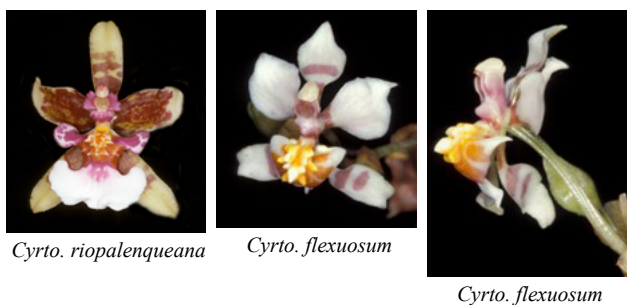


**Otoglossum** (Schltr.) Garay & Dunst. (13 spp; Figs. 1S,T; [Fig. 9](#)) was originally regarded as a subgenus of *Odontoglossum* by Schlechter, but the floral characters agree most closely with *Oncidium*. Distribution is primarily Andean, extending north to Costa Rica, with one species on tepuis of the Guyanan shield. It was probably their large, bright reddish-brown flowers and occurrence at higher elevations that caused them to be placed in *Odontoglossum*. As broadly circumscribed here, *Otoglossum* includes *Oncidium* sect. *Serpentia* (Kraenzl.) Garay, *Brevilongium* Christenson, and *Ecuadorella* Dodson & G.A. Romero. Prior to molecular data, a close relationship between *Otoglossum* s.s. and *Oncidium* sect. *Serpentia* was totally unsuspected. *Otoglossum* s.s. bear many-flowered inflorescences arising laterally from pseudobulbs widely spaced on woody rhizomes (Jenny, 2010), whereas *Oncidium* sect. *Serpentia* exhibits a unique vining habit (many meters long) that was interpreted by Christenson (2006) as an indeterminate inflorescence that periodically produces flowering plantlets at the nodes. We regard these elongate, vining structures as stems, not inflorescences, making their habit the same as in *Otoglossum* s.s. The molecular data strongly support *Oncidium* sect. *Serpentia* and *Otoglossum* s.s as sister taxa, and together they are sister to *Otoglossum harlingii* (Stacy) N.H. Williams & M.W. Chase, an unusual former *Oncidium* with an odd upright habit with long internodes and dichotomously forking woody rhizomes. Dodson and Romero created a monotypic genus (*Ecuadorella*) for this taxon. The inclusion of all these clades in *Otoglossum* reveals elongate rhizomes as a local synapomorphy for the genus (this trait occurs elsewhere in Oncidiinae, e.g., some species of *Cyrtorchilum*, to which *Otoglossum* is closely related).



**Cyrtorchiloides** N.H. Williams & M.W. Chase (4 spp.; Fig. 1J, [Fig. 9](#)) flowers have typical *Oncidium*-like morphology and were considered members of *Oncidium* until molecular data revealed their distinctiveness (Williams, et al., 2001b). Florally, they are only divergent from *Oncidium* in their pollinaria with smaller stipes, larger pollinia, and well-developed, stalked caudicles. The generic names alludes to the vegetative similarity of the plants to *Cyrtorchilum*. *Cyrtorchilum* and *Cyrtorchiloides* both have ovoid pseudobulbs rounded in cross-section (not angled) with 2-6 leaf-bearing subtending bracts.





*Cyrto. riopalenqueana*

*Cyrto. flexuosum*

*Cyrto. flexuosum*

**Milioniopsis** God.-Leb. (5 spp.; Fig. 9) was split from *Miltonia* and the name reflects their similar floral shapes. The species of *Milioniopsis* are distributed from Central America, Venezuela south to Peru, but absent from Brazil, whereas species of *Miltonia* are predominately Brazilian (and all are non-Andean). The flowers of *Milioniopsis* have broad, flat lips, and at least one species is reported to be pollinated by night-flying ptiloglossine bees (*Ptiloglossa ducalis* Smith; Dodson, 1965), rather than by oil-collecting anthophorid bees.



*Milioniopsis roezlii*

*Milioniopsis roezlii*

*Milioniopsis vexillaria*

*Milioniopsis vexillaria*

*Milioniopsis bismarkii*

**Caucaea** Schltr. (5-20 spp.; Fig. 9) was previously known as the *Oncidium cucullatum* Lindl. group, a set of poorly defined, high-elevation Andean species with showy flowers. Their phylogenetic distance from *Oncidium* and their relationships to the small-flowered, monotypic *Caucaea radiata* (Lindl.) Mansf. were unsuspected until molecular data revealed their close relationship (Williams, et al., 2001b) and they were lumped into *Caucaea*. In spite of the floral similarity to *Oncidium*, they are not closely related. *Caucaea* is sister to *Cyrtorchilum*, a relationship that was unexpected on the basis of gross floral shape. The two genera do share subtle traits, including pseudobulbs that are rounded (not strongly ancipitous or two-sided) and pollinaria with relatively short stipes and large caudicles. Both genera also occur in cool, high-elevation Andean cloud forests.



*Caucaea radiata*

*Caucaea andigena*

*Caucaea phalaenopsis*

*Caucaea nubigena*

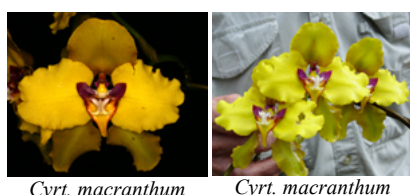
*Caucaea rhodosticta*

*Caucaea olivacea*

*Caucaea sanguinolenta*

**Cyrtorchilum** Kunth (approximately 120 spp.; Figs. 2C,E,G,H; Fig. 9) is restricted to the high Andes of Colombia and Venezuela south to Peru, with a single species, *C. meirax* (Rchb.f.) Dalström (and a putative related species) occurring in the Caribbean (Dalström, 2001). Many species have long (3-4 m), vining inflorescences and large showy flowers (some with prominent elaiophores; Figs. 2G,H), but a few species have diminutive plants and flowers. Vegetatively, *Cyrtorchilum* are distinguished by dull pseudobulbs that are round or ovoid in cross section with 2-4 apical leaves and 2-6 leaf-bearing bracts and relatively thick roots; in contrast, *Oncidium* species have glossy, ancipitous (2-edged) pseudobulbs and thin roots (Dalström, 2001). Dalström (2001) and Chase (2009b) discussed the tangled taxonomic history of the genus. Previous workers relied almost exclusively on floral traits, resulting in confusion with concepts of *Odontoglossum* and *Oncidium*.

Lindley, in a series of transfers over a period of years (1837-1842) in *Sertum Orchidaceum*, eventually sunk both *Odontoglossum* and *Cyrtorchilum* into *Oncidium*. Kraenzlin resurrected the genus *Cyrtorchilum* in 1922. *Dasyglossum* Kuhniger & Schildhauer and *Trigonochilum* Kuhniger & Schildhauer were created to accommodate some of the smaller flowered *Cyrtorchilum* species, but the authors repeatedly transferred taxa between the two genera because they could not decide where they fit on the basis of floral morphology. Senghas (1997) transferred all *Dasyglossum* into *Trigonochilum* because he could not reliably distinguish them. Neither genus is monophyletic in our DNA trees. Similarly, *Buesiella* C. Schweinf., *Neodryas* Rchb.f., *Rusbyella* Rolfe ex Rusby, and *Siederella* Mytnik, Górnjak, & Romowicz are simply diminutive and/or brightly colored taxa embedded within *Cyrtorchilum* (Dalström, 2001), probably reflecting a shift in pollinators, although there are few observations of pollination.



*Cyrt. macranthum*

*Cyrt. macranthum*



C



*Cyrt. macranthum*



*Cyrtorchilum edwardii*

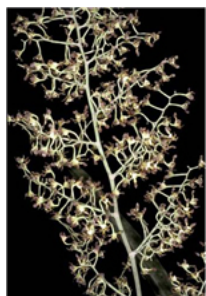


*Cyrtorchilum ioplocon*

*Cyrtorchilum ixioides*



*Cyrt. leopoldianum*



*Cyrt. sp.* inflorescence



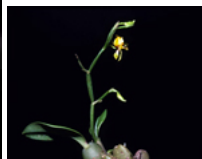
*Cyrt. (Dasyglossum)*  
sp.



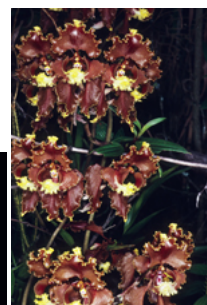
*Cyrtorchilum*  
*ventilabrum*



*Cyrtorchilum aureum*



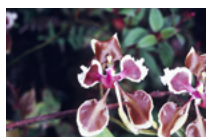
*Cyrtorchilum meirax*



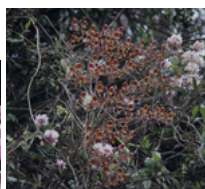
*Cyrt. lamelligerum*



*Cyrt. halteratum*



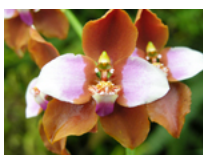
*Cyrt. monachicum*



*Cyrt. sp.*



*Cyrt. sp.*



*Cyrt. sp.*



*Cyrt. sp.*



*Cyrt. sp.*



*Cyrt. gargantua*



*Cyrt. gargantua*

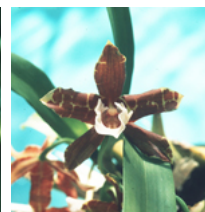


*Cyrt. gargantua*

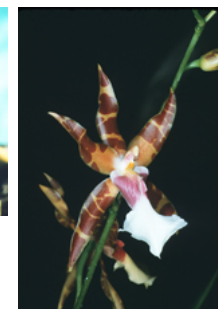
*Miltonia* Lindl. (10 spp.; [Fig. 10](#)) occurs in Argentina, Brazil, Paraguay, and Venezuela and is sister to a clade that includes *Systeloglossum*, *Oliveriana*, *Cischweinfia*, *Aspasia*, and *Brassia*. Some *Miltonia* species (e.g., *M. regnellii* Rchb.f. and *M. spectabilis* Lindl.) have a short column and a broad, flat lip with a simple, reduced callus, but floral morphology varies a great deal among the species. *Miltonia clowesii* (Lindl.) Lindl. has typical *Oncidium*-like oil-bee flowers, whereas *M. candida* Lindl. and *M. russelliana* (Lindl.) Lindl. have the lip partly or completely encircling the column, giving them the appearance of a *Cischweinfia* (suggestive of pollination by nectar-foraging bees). They also have the clinandrial and column arms found in many species of *Cischweinfia* (see below). *Miltonia flavescens* (Lindl.) Lindl. on the other hand resembles a species of *Brassia* in its floral traits, with a similar bilobed lip callus forming a nectar-cavity-like chamber on the lip base and elongate, spidery tepals. The above-mentioned species with the author combination "(Lindl.) Lindl." are due to Lindley considering these to be species of *Cyrtorchilum* or *Odontoglossum* when he first described them, again an indication of the floral diversity present in a small set of species that forms a clade in our analyses. Like *M. clowesii*, *M. phymatochila* (Lindl.) N.H. Williams & M.W. Chase also has typical oncidoid oil-bee flowers with a large complex callus and tabula infrastigmatica. The latter species was transferred from *Oncidium* to *Miltonia* by Williams, et al. (2001b) and subsequently transferred to a monotypic genus, *Phymatochilum*, by Christenson (2005), who cited it as an aberrant member of *Miltonia* (a virtual "round peg in a square hole"; E. A. Christenson, pers. comm.), but in our view it is no more or less aberrant than the other species with unusual floral traits found in *Miltonia*.



*Miltonia sp.*

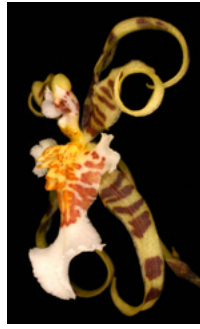


*Miltonia candida*





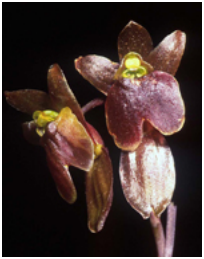
*Miltonia clowesii*



*Miltonia phymatochila*

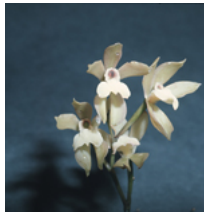
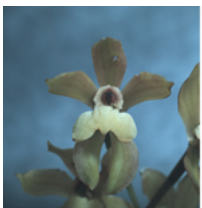
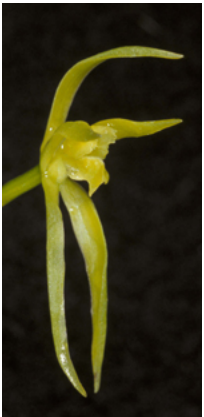
Sister to *Miltonia* is a clade of the following three genera with relatively small flowers that have a prominent clinandrial hood on the column and strongly ancipitous pseudobulbs:

***Systeloglossum*** Schltr. (5 spp.; [Fig. 10](#)) has small, purple or yellow-green flowers with a prominent column foot and a simple hinged lip; pollination is presumably by nectar-foraging insects. Szlachetko (2006) created the monotypic *Diadeniopsis* Szlach. for *Systeloglossum bennettii* (Garay) Dressler & N.H. Williams. His emphasis on and interpretation of gynostemial structure mistakenly placed it in the twig epiphyte clade as a relative of *Comparettia*.



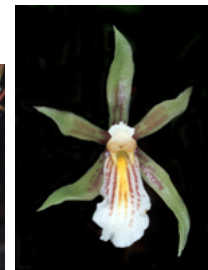
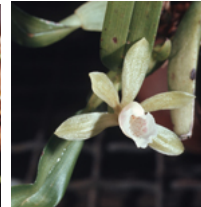
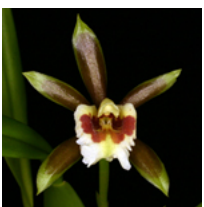
*Systeloglossum bennettii*    *Systeloglossum* sp.

***Oliveriana*** Rchb.f. (6 spp.; [Fig. 10](#)) is a high-elevation, Andean genus with relatively flat, open flowers, and Chase (2009b) suggested the flowers are pollinated by hummingbirds on the basis of pollinarium morphology (two widely spaced pollinia with a wedge-shaped viscidium and a bilobed stigma, which are otherwise features found in hummingbird-pollinated Oncidiinae species). Plants are scandent, in contrast to the mostly caespitose habit of other genera in this clade.



*Oliveriana brevilabia*    *Oliveriana egregia*    *Oliveriana egregia*

***Cischweinfia*** Dressler & N.H. Williams (11 spp.; [Fig. 10](#)) grows in middle-elevation forests (to 1,500 m) from Costa Rica to Bolivia. Flowers have a tubular lip enfolding the column and are reportedly pollinated by nectar-seeking euglossine bees (Williams, 1982). *Cischweinfia pygmaea* (Pupulin, J. Valle, & G. Merino) M.W. Chase has diminutive plants with small flowers and a simple lip. It was originally described as an *Ada* Lindl., but molecular data from this study clarified its generic placement (Chase & Whitten, 2011).



*Cis. popowiana*    *Cis. pusilla*    *Cis. pusilla*    *Cis. rostrata*    *Cis. parva*    *Cis. platychila*





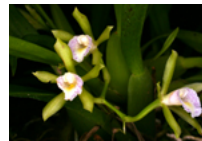
*Cis. dasyandra*



*Cis. dasyandra*



*Cis. dasyandra*



*Cis. dasyandra*



*Cis. dasyandra*

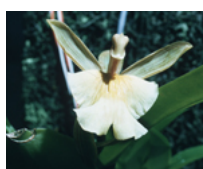
*Aspasia* Lindl. (7 spp.; [Fig. 10](#)) ranges from Central America, northern South America and the Andes to coastal Brazil. It is vegetatively similar to *Brassia*, but the flowers have a flat lip partially adnate to a relatively long column and bent at a right angle, forming a false nectary. Several species are pollinated by euglossine bees, although there may be a mixture of nectar deceit and fragrance reward involved, depending upon the species (Zimmerman & Aide, 1987). *Aspasia* represents the only known occurrence of male euglossine pollination in this clade (*Miltonia* to *Brassia*, [Fig. 10](#)).



*Aspasia epidendroides*



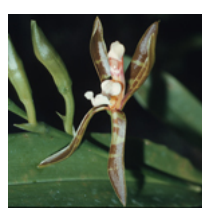
*Asp. epidendroides*



*Aspasia principissa*



*Aspasia principissa*



*Aspasia psittacina*



*Aspasia psittacina*



*Aspasia lunata*

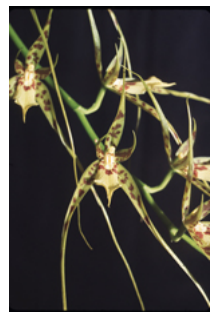


*Aspasia lunata*

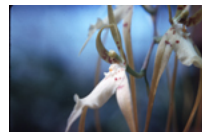


*Aspasia lunata*

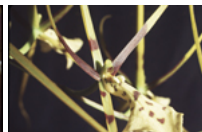
*Brassia* R.Br. (approximately 74 spp.; Figs. 2Q,R; [Fig. 10](#)) includes *Ada* Lindl., *Brachtia* Rchb.f., and *Mesospinidium* Rchb.f. These genera have been difficult to separate on the basis of floral and vegetative characters. Chase (2009b) treated these separately, but he indicated this to be unsatisfactory. *Brachtia* (7 spp., Andean) is sister to *Brassia* s.s. (approximately 35 spp., Mexico through Central America, Caribbean, to tropical South America). The two genera are vegetatively similar and basic pollinarium and floral structures are similar. They share a simple lip with a pair of small basal keels. They differ mainly in the relative size of the flowers and floral bracts; *Brachtia* (Fig. 2R) has relatively small flowers with large bracts partially enclosing the flowers. These two genera are sister to *Ada* (approximately 35 spp.) and *Mesospinidium* (approximately 7 spp.), both ranging from Central America south through the Andes to Bolivia. *Ada* originally was monotypic and composed of a single hummingbird-pollinated species with bright orange to red flowers (Fig. 2Q), but Williams (1972a) realized that it was morphologically similar to a clade of *Brassia* (the "glumaceous" *Brassias*), and he transferred this group into *Ada*, greatly enlarging the genus. *Ada* is not monophyletic, with *Ada allenii* (L.O. Williams ex C. Schweinf.) N.H. Williams sister to *Mesospinidium* and remaining *Ada*. Florally, *Mesospinidium* are small versions of *Ada*. Given the shared suite of floral morphologies and habits and the aberrant phylogenetic position of *Ada allenii*, lumping them all into *Brassia* seems the simplest solution.



*Brassia caudata*



*Brassia caudata*



*Brassia gireoudiana*



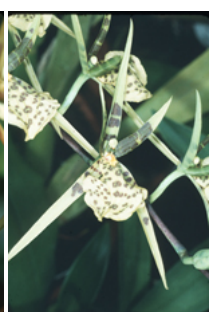
*Brassia gireoudiana*



*Brassia arcuigera*



*Brassia arcuigera*



*Brassia maculata*



*Brassia jipijapaensis*



*Brassia (Ada) allenii*



*Brassia (Ada) allenii*



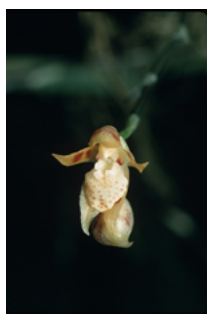
*Brassia (Ada) elegantula*



*Brassia (Ada) chlorops*



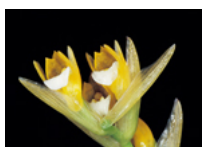
*Brassia (Ada)*  
*aurantiaca*



*Brassia (Mesospinidium)*  
*incantans*



*Brassia (Brachtia)*  
*andina*



*Brassia (Brachtia)*  
*andina*

The sister relationship between the following two morphologically divergent genera was unsuspected prior to molecular studies. These genera are remarkably different in size, habit, and floral morphology.

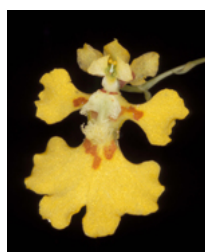
***Erycina*** Lindl. (10 spp.; Fig. 1U; Fig. 10), as broadly defined by Williams et al. (2001a), includes *Psygmorchis* Dodson & Dressler and monotypic *Stacyella* Szlach. [= *Erycina crista-galli* (Rchb. f.) N.H. Williams & M.W. Chase]. All three genera have bright yellow oil reward/deceit flowers and were at one time considered members of *Oncidium*. Although these three genera could be maintained, we favor lumping them to emphasize their similar floral morphology and modified habit (absence of an apical leaf on pseudobulbs, if pseudobulbs are present). Dodson (2003) reported the pollination of *Ery. glossomystax* by *Epicharis rustica* Friese, an oil-collecting bee closely related to the large genus *Centris*.



*Erycina echinata*



*Ery. (Psygmorchis)*  
*pusilla*



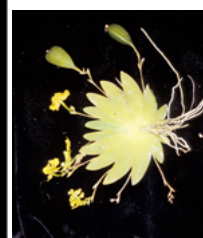
*Ery. (Psygmorchis)*  
*glossomystax*



*Ery. (Psygmorchis)*  
*zamorensis*



*Erycina* plant



*Erycina* plant

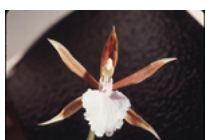


Comparison of *E.*  
*pumilio* and *E. crista-*  
*galli*

***Rhynchostele*** Rchb.f. (13 spp.; Fig. 10) as circumscribed here is primarily Mexican and includes *Amparoa* Schltr. and *Mesoglossum* Halb.; *Cymbiglossum* Halb. and *Lemboglossum* Halb. are later synonyms of *Rhynchostele*. Lumping of these genera is also supported by anatomical similarities (Rojas Leal, 1993). Most of these species were treated as members of *Odontoglossum* until split out by Halbinger, first as *Cymbiglossum* and later as *Lemboglossum*. Morphological analyses by Soto and coworkers (Soto, Salazar, & Rojas Leal, 1993) revealed a close relationship between these species and the much reduced *Rhynchostele pygmaea* Rchb.f. They transferred all these taxa into *Rhynchostele*, a move that is supported by our molecular data.



*Rhynchostele rossii*



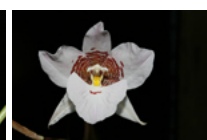
*Rhynchostele stellata*



*Rhynchostele maculata*



*Rhynchostele*  
*candidula*

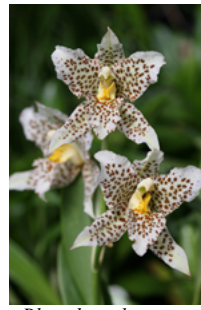


*Rhynchostele*  
*cervantesii*

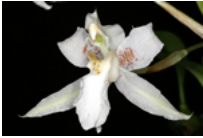




*Rhynchosele cordata*



*Rhynchosele aptera*



*Rhynchosele galleotiana*



*Rhynchosele madrensis*



*Rhynchosele majalis*

*Gomesa* R.Br. (approximately 125 spp.; Figs. 1P,Q,R; Fig. 11) as circumscribed here is relatively broad and includes at least 23 other generic concepts (Chase, 2009b; Chase, et al., 2009a) with a great diversity of floral morphology and size. *Gomesa* has a center of distribution in Brazil, especially the Mata Atl ntica, where these species largely replace *Oncidium* (the genus in which most of them were once included), but it extends to northern Argentina and Amazonian Peru. Nearly all species have fused lateral sepals, a trait that makes them easy to recognize in spite of their floral diversity. In contrast, *Oncidium* is largely absent from Brazil (*O. baueri* is the sole representative), and their lateral sepals are usually free. The two genera rarely produce hybrids in horticulture.

Based on the enormous floral diversity within *Gomesa*, Brazilian and French workers have proposed a number of segregates (Docha Neto, Baptista & Campacci, 2006), but several of these are not monophyletic (e.g., *Alatiglossum* Baptista, *Carenidium* Baptista, *Coppensia* Dumort.). Several recent segregates are monotypic: *Campaccia venusta* (Drapiez) Baptista, P.A. Harding, & V.P. Castro; *Hardingia paranaensis* (Kraenzl.) Docha Neto & Baptista (not included in our analyses); and *Nitidocidium gracile* (Lindl.) F. Barros & V.T. Rodriguez. To make matters worse, Szlachetko and colleagues also segregated a number of genera from this same set of species, often using the same type species but including different sets of species than the Brazilian workers (e.g., *Concocidium* Romowicz & Szlach. and *Carenidium*, both based on *Oncidium concolor* Hook.). Also, Szlachetko (2006) segregated three species of *Oncidium* as the genus *Rhinocerotidium* Szlach. (*O. longicornu* Mutel, *O. macronyx* Rchb.f., *O. rhinoceros* Rchb.f.; most workers lump these into a single species). He based the genus mostly upon the large, horn-like lip callus, but the lip callus is perhaps the most variable floral feature within Oncidiinae. These species are closely related to *G. varicosa* (Lindl.) M.W. Chase & N.H. Williams, a species with a relatively large lip and small callus.



*Gomesa* sp.



*Gomesa* sp.



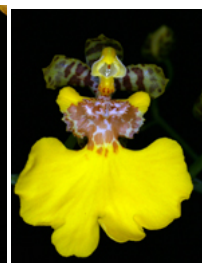
*Gomesa longipes*



*Gomesa longipes*



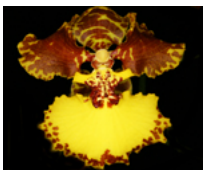
*Gomesa longipes* rear



*Gomesa flexuosa*



*Gomesa zappii*



*Gomesa gardneri*



*Gomesa imperatoris*



*Gomesa barbata*



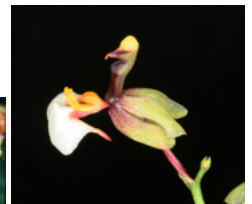
*Gomesa concolor*



*Gomesa concolor*



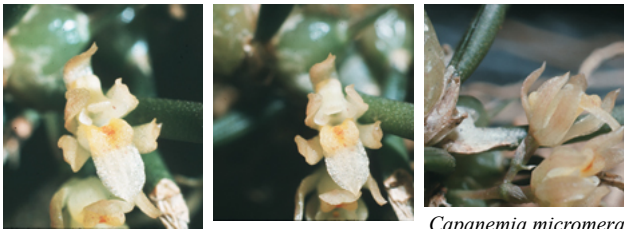
*Gomesa ranifera*



*G. (Ornithophora) radicans*

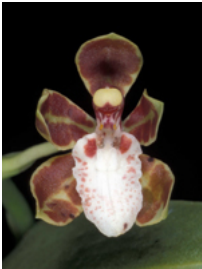
*Capanemia* Barb. Rodr. (7 spp.; Fig. 11) is represented in our analyses by only a single species, *Capanemia superflua* (Rchb.f.) Garay that is sister to *Solenidium*. Recent studies have reduced the number of species in the genus, but molecular data are needed to confirm the monophyly of the seven recognized species (Buzatto, et al., 2011; Buzatto, Singer & van den Berg, 2010). The genus is centered in southeastern Brazil, extending to Argentina and Uruguay. Florally, the genus is similar to unrelated *Leochilus*, but most species do not produce nectar, except *C. therezae* Barb. Rodr. (Buzatto, et al., in press). Singer and Cocucci (1999) reported visits by halictid bees and vespid wasps. *Sanderella* also falls here (C. van den Berg, pers. comm.). Morphologically, *Sanderella* Kuntze is similar to *Capanemia* (the oldest name) and *Sanderella* should probably be combined with *Capanemia*. Its exact status cannot be determined until *Sanderella* and more species of *Capanemia* are sampled.





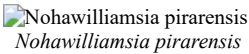
*Capanemia micromera* *Capanemia micromera* *Capanemia micromera*

*Solenidium* Lindl. (3 spp.; Fig. 11) is an Amazonian genus and is similar florally to its sister, *Capanemia*, bearing small flowers with prominent column wings and an upturned tip of the anther cap; more detailed studies of both may support their combination.



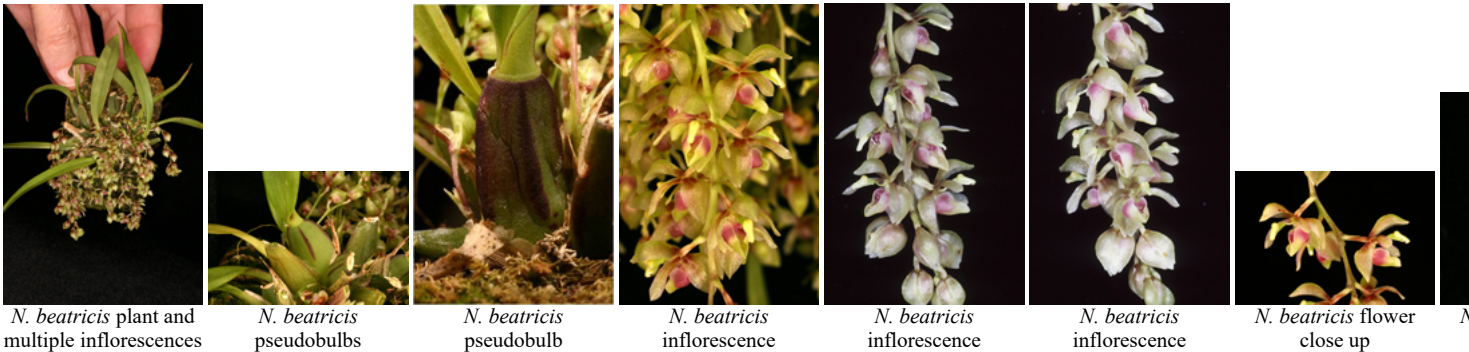
*Solenidium portillae*

*Nohawilliamsia* M.W. Chase & Whitten (1 sp.; Fig. 1V, Fig. 11) was created to accommodate this single odd species with no close or clear relatives based on our analyses thus far. It was formerly known as *Oncidium pirarense* Rchb.f. (syn. *O. orthostates* Ridl.) from southern Venezuela, Guyana, Suriname, and Brazil (Chase, 2009a; Chase, et al., 2009a; Whitten, 2009). Although the flowers are similar to many yellow flowered species of *Oncidium*, they lack a tabula infrastigmatica. The leaves have a minutely dentate margin, and plantlets (keikis) are produced on old inflorescences and on top of old pseudobulbs; all of these traits are unusual within Oncidiinae.



*Nohawilliamsia pirarense*

*Notyliopsis* P. Ortiz (1 spp.; Fig. 11) from the wet Colombian Chocó has diminutive flowers that superficially resemble those of *Notylia* Lindl., but the pseudobulbs are reminiscent of *Zelenkoa*.



*N. beatricis* plant and multiple inflorescences *N. beatricis* pseudobulbs *N. beatricis* pseudobulb *N. beatricis* inflorescence *N. beatricis* inflorescence *N. beatricis* inflorescence *N. beatricis* flower close up

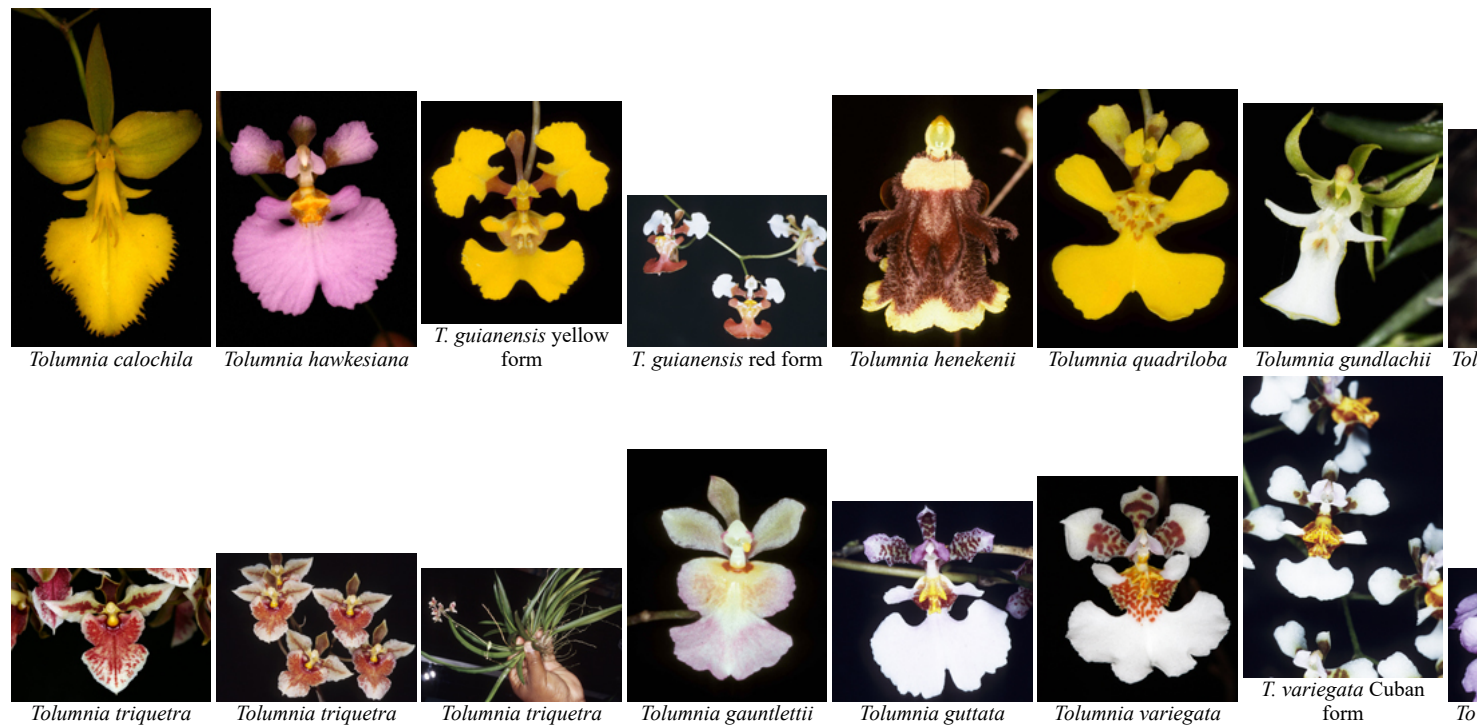
*Zelenkoa* M.W. Chase & N.H. Williams (1 sp.; Fig. 1W; Fig. 11) was long considered an oddity when it was included in *Oncidium* (often in its own monotypic section), but molecular data revealed its distinctiveness. Like *Nohawilliamsia*, it also has bright yellow flowers that lack a tabula infrastigmatica. Often epiphytic on cacti in dry coastal forests of Ecuador and Peru, the plants have mottled ovoid pseudobulbs that resemble those of *Notyliopsis*, which is also a member of this grade relative to *Tolumnia* and other twig epiphytes.



*Zelenkoa onusta*

*Tolumnia* Raf. (approximately 40 spp.; Figs. 1X,Y, 2D; Fig. 11) has long been recognized as a distinct group ("equitant" oncidiums) based on their psymoid fan of succulent leaves and usual absence of pseudobulbs. There is extensive polyploidy within the genus (Braem, 1986) resulting in some conflict between nuclear and plastid phylogenetic trees. Most species have oil-bee flowers that do not secrete oil; pollination by *Centris* bees is reported for several species (Ackerman, Meléndez-Ackerman, & Salguero Faria, 1997; Nierenberg, 1972). *Tolumnia guibertiana* (A. Rich.) Braem (endemic to western Cuba) is completely dependent on oil-gathering female bees (*Centris poecila* Lepeletier) for fruit production (Vale, Rojas, & Alvarez, 2011). *Tolumnia henekenii* (R.H.Schomb. ex Lindl.) Nir has a furry, insect-like lip and is reportedly pseudocopulatory (Dod, 1976). Braem and Garay have published or resurrected several (often monotypic) segregates based on floral oddities; these include

*Olgasis* Raf., *Antillanorchis* (Wright ex Griesb.) Garay, *Hispaniella* Braem, *Jamaiciella* Braem, *Braasiella* Braem, Lockel, & Russmann, and *Gudrunia* Braem. Recognition of all these segregates would require at least a dozen genera to be carved from *Tolumnia* to maintain monophyly. We feel this is unwarranted. *Tolumnia* is sister to all others in the remainder of the tree (twig epiphytes), but this relationship is only weakly supported. In contrast to most twig epiphytes, *Tolumnia* species often occur on the larger axes of trees and live for many years, rather than being restricted to terminal twigs with extremely rapid life cycles, but they also have seeds with pronounced hooks or knob-like extensions (Chase, 1988).

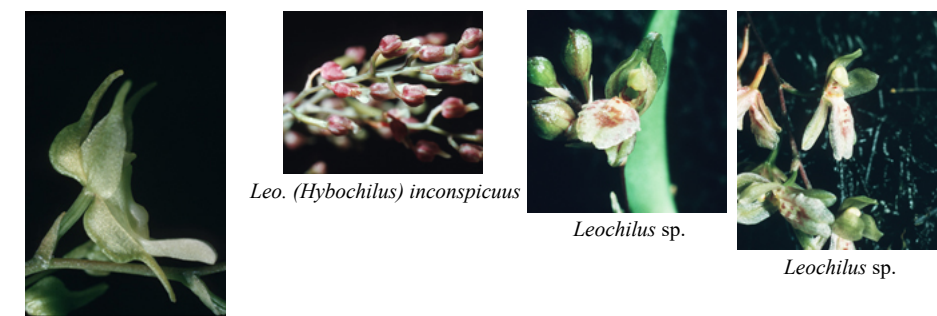


**The twig epiphytes**--The clade comprising the remainder of the tree (*Plectrophora* H.Focke to *Notylia* Lindl., Fig. 12) has been informally referred to as the "twig epiphyte" clade. Chase (1988) first discussed the morphological and life history features that unite these taxa. Twig epiphytes often grow on the smallest branches ( $\leq 2.5$  cm) in exposed, high-light zones, have rapid life cycles (often reaching maturity in one season), produce hooks or projections on the seed testa (mostly likely for rapid uptake of water), exhibit psygmoid (paedomorphic) habits, and velamen (root epidermis) cells much longer than wide with evenly spaced secondary thickenings. Not all taxa in this clade are extreme twig epiphytes restricted to terminal twig habitats, but the majority display many of these features. Twig epiphytes occur in other clades of Oncidiinae (e.g., *Erycina*, Fig. 10), as well as in other subtribes [e.g., *Dendrophylax porrectus* (Rchb. f.) Carlswald & Whitten, Angraecinae]. None of the genera of the twig epiphyte clade (all genera in Fig. 12) secrete oil or mimic oil flowers. Instead, they attract either nectar-seeking animals or are pollinated by fragrance-collecting male euglossine bees. *Suarezia* Dodson (1 sp.) was not sampled, but it is presumed to be a member of this clade on the basis of its morphology.

*Plectrophora* H.Focke (9 spp.; Fig. 12) are diminutive plants with relatively large flowers with a funnel-shaped lip and a sepaline spur without nectar horns. The presence of nectar has not been confirmed, but the flowers likely are pollinated by long-tongued insects seeking nectar.



*Leochilus* Knowles & Westc. (12 spp.; Fig. 12) are true twig epiphytes, occurring only on small branches and twigs. The small flowers of most species have a simple lip with a shallow nectar cavity at the base. Chase (1986a) reported pollination of two species by nectar-foraging, short-tongued *Stelopolybia* wasps and *Lasioglossum* bees. Three other monotypic genera are now included in *Leochilus* on the basis of their position in phylogenetic studies: *Goniochilus* Chase, *Hybochilus* Schltr., and *Papperitzia* Rchb.f. The floral structure of the first two is similar to that of the other species of *Leochilus*, but that of *Papperitzia* is highly divergent. In spite of this, the single species of *Papperitzia* was originally included in *Leochilus*.



***Pterostemma*** Kraenzl. (2 spp.; [Fig. 12](#)) are diminutive Andean twig epiphytes with tiny flowers that are probably bee-pollinated. Their habits are monopodial tufted plants or psymoid fans 1-2 cm in size. The flowers have a dorsal anther with a long stipe and long, forward-sweeping column arms. Both sequence data and morphology confirmed a close relationship of *Hirtzia* Dodson to *Pterostemma*, so the two were lumped (Chase, Williams, & Whitten, 2009b).



*Pter. benzingii*



*Pter. benzingii* plant

***Ionopsis*** Kunth (3 spp.; [Fig. 12](#)) ranges widely throughout the Neotropics. The white to pink flowers have a simple lip with a short sepalar spur without any obvious reward and are probably pollinated by nectar-seeking bees.

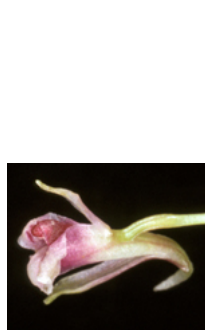


*Ionopsis satyrioides*



*Ionopsis utricularioides*

***Comparettia*** Poepp. & Endl. (approximately 60 spp.; Fig. 2W; [Fig. 12](#)) is broadly circumscribed here to include all species with a sepalar nectar spur(s) furnished by a horn or pair of horns on the column base that secrete nectar. Generic segregates lumped here include *Chaenanthus* Lindl., *Diadenium* Poepp. & Endl., *Neokoehleria* Schltr., *Pfisteria* Senghas, *Scelochiloides* Dodson & M.W. Chase, *Scelochilopsis* Dodson & M.W. Chase, *Scelochilus* Klotzsch, and *Stigmatorthos* M.W. Chase & D.E. Bennett. As more species in this clade were discovered in recent years, generic limits have become more obscure, and amalgamation of all taxa with nectar horns into a single genus seems the best solution. *Scelochilus* appears not to be monophyletic. There is variation in vegetative habit within this clade from psymoid fans to caespitose plants with bifacial leaves and pseudobulbs. Some species can begin flowering as juvenile psymoid plants before transformation into adult plants with pseudobulbs, and damage can cause a reversal to the psymoid seedling habit. Pollination by hummingbirds (*Amazilia* sp., *Chlorostilbon maugaeus*) is documented for *C. falcata* (Dodson, 1965; Salguero-Faria & Ackerman, 1999). Pollination by butterflies and long-tongued bees seems likely for some taxa.



*Comp. (Diadenium) micrantha*



*Comp. (Scelochilus) heterophylla*



*Comp. macroplectron*



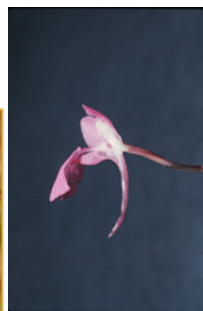
*Comp. (Scelochilus) tungurahuae*



*Comp. (Scelochilus) williamsii*



*Comp. speciosa*



*Comp. falcata*

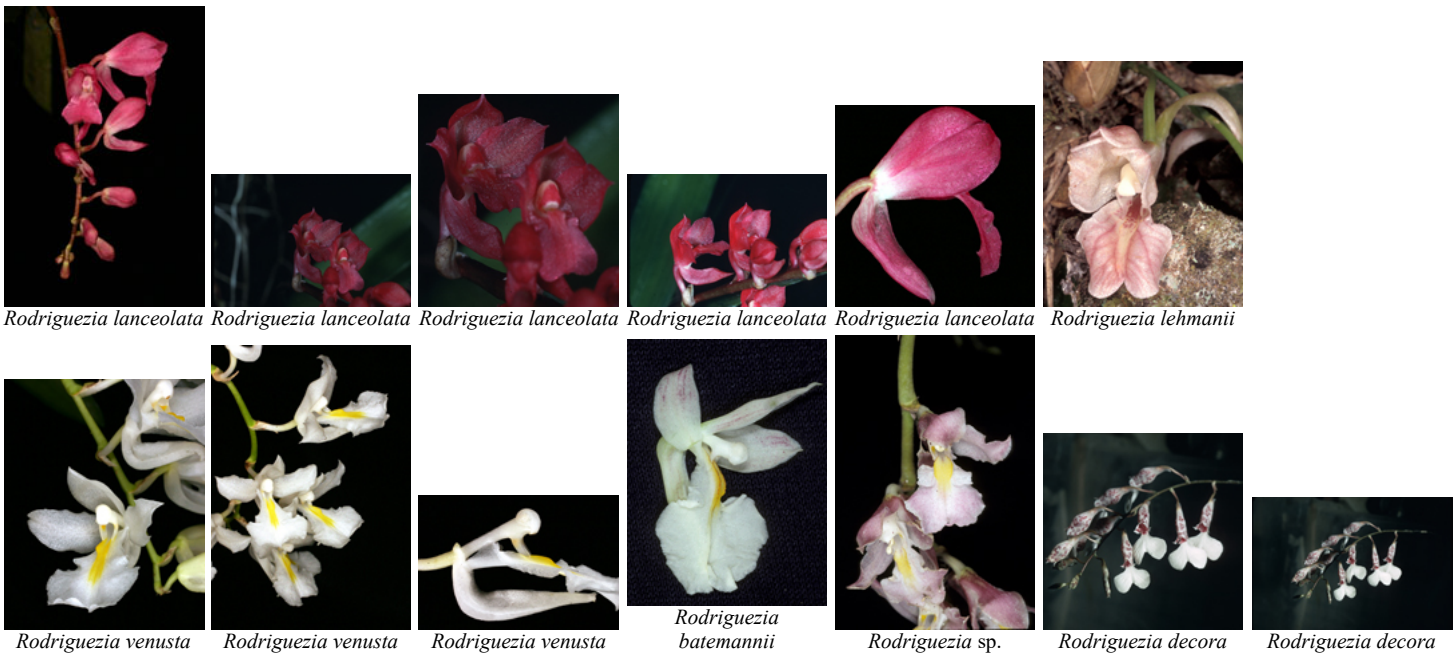
***Polyotidium*** Garay (1 sp.; [Fig. 12](#)) is reported only from Ecuador, Venezuela, Brazil, and the Orinoco drainage of Colombia. The 5 mm, fleshy, bright orange flowers have a simple lip and a dorsal anther, suggestive of hummingbird pollination. Its phylogenetic position is unresolved within a strongly supported terminal clade that includes *Rodriguezia*, *Sutrina*, *Macroclinium*, and *Notylia*.

***Sutrina*** Lindl. (2 spp.; [Fig. 12](#)) consists of poorly known species from Amazonian Peru and Bolivia. The yellow-green flowers have simple, linear tepals and lip that do not open widely, forming a tube-like structure. Nothing is known of pollination, but morphology suggests pollination by nectar-foraging insects.

***Rodriguezia*** Ruiz & Pav. (approximately 48 spp.; Fig. 2X; [Fig. 12](#)) ranges from Mexico south to Argentina, with one species (*R. lanceolata*) found on many islands in the Caribbean. The flowers are relatively large, brightly colored, and showy for members of the twig epiphyte clade. The lip is often relatively large and flat, and the lateral sepals are fused along one or both lateral margins to form a curved nectar spur. A projection from the column base secretes nectar into this spur. Reported pollinators include hummingbirds, butterflies, and nectar-foraging bees (Dodson, 1965). There are two strongly supported clades within *Rodriguezia*, and Chase (2009b) noted the

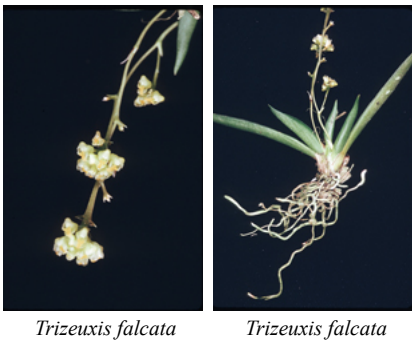


non-monophyletic placement of *R. decora* Rchb.f. in nrITS trees published in *Genera Orchidacearum*. This unusual Brazilian species was not included our sampling, but it may warrant generic status. It has long, wiry rhizomes between sympodia and lacks the spur found in other species.



**Schunkea** Senghas (1 sp.; [Fig. 12](#)) is known only from southeastern Brazil; the small cream colored flowers have an open lip and an unusual pair of downward-pointing arms on the column apex. Nothing is known of pollination. Its placement within this clade is unresolved, and Chase (2009b) hypothesized that it might be related to the monotypic *Suarezia* from eastern Ecuador. *Suarezia* was not included in our sampling.

**Trizeuxis** Lindl. (1 sp.; [Fig. 12](#)) is wide ranging from Costa Rica south to Peru and also in eastern Brazil. Its flowers are perhaps the smallest of any Oncidiinae, only 2-3 mm across, yet they are outcrossing and often found growing on twigs of cultivated *Citrus* L. and *Psidium* L. Pollinators are unknown, but presumed to be small nectar-foraging insects.



**Seegeriella** Senghas (2 spp.; [Fig. 12](#)) is restricted to Argentina and Brazil. Like *Trizeuxis*, the yellow-green flowers are diminutive with a simple lip and sepals that do not open widely. Pollinators are presumed to be nectar-seeking insects.

The remaining four genera are all pollinated by fragrance-collecting male euglossine bees, and all but *Warmingia* have a narrow, slit-like stigma, pollinaria with a button-like viscidium and a long, narrow stipe, and pollinia that are dorsiventrally flattened and thin to match the opening of the slit-like stigmatic cavity. The narrow pollinia and stigmatic slit probably act to reduce self-pollination. When first removed by a bee, the pollinia are too wide to fit easily into the narrow stigmatic slit (W.M. Whitten, pers. obs.). The stigma widens after pollinarium removal. Several minutes to hours of drying are required to shrink the pollinia before they will slip into the stigma, during which time the bee is likely to have flown to another plant.

**Macradenia** R. Br. (10 spp.; [Fig. 12](#)) ranges from Mexico south throughout most of lowland South America. The pendent, unbranched inflorescence bears numerous flowers that attract fragrance-collecting male euglossine bees. The anther is terminal and beaked, and the column and lip are twisted, giving the flower a distinct asymmetry unique within Oncidiinae. This asymmetry may be related to pollinarium deposition on the side of the bee's head or eye.



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*Warmingia* Rchb.f. (3 spp.; [Fig. 12](#)) has an oddly disjunct distribution, including Costa Rica, southern Ecuador, and Brazil. Pollination has not been reported, but their floral fragrance is similar to some *Macroclinium* and is produced abundantly during the morning, suggestive of pollination by male euglossine bees.

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*Macroclinium* Barb. Rodr. (approximately 40 spp.; Fig. 2Z; [Fig. 12](#)) ranges throughout much of the Neotropics from Mexico south to Peru and Brazil. The plants are diminutive twig epiphytes, and are often found on cultivated *Citrus* L. and *Psidium* L. The flowers are similar in morphology and function to its sister genus *Notylia*, but the two differ in inflorescence and vegetative habit. *Macroclinium* species often are monopodial, with small psymoid fans usually lacking pseudobulbs. The inflorescence is pendent, pseudo-umbellate, with clusters of numerous delicate flowers with narrow sepals, petals, and lip. In spite of their small size, the fragrant flowers attract relatively large male euglossine bees. Pollinaria are deposited on the face (frons) of the bee during fragrance collection.



*Macroclinium dalstroemii*



*Macroclinium* sp.



*Macroclinium* sp.

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*Notylia* Lindl. (approximately 60 spp.; [Fig. 12](#)) also range throughout much of the Neotropics, similar to its sister, *Macroclinium*. In contrast to the paedomorphic fans of *Macroclinium*, plants of *Notylia* mature to bear spherical or cylindrical and relatively slender pseudobulbs and relatively large conduplicate leaves. The flowers are similar to those of *Macroclinium*, but are presented evenly spaced on a pendent, usually unbranched raceme. Pollination is also by male euglossine bees, with pollinarium deposition on the frons.



*Notylia* sp.



*Notylia latilabia*



*Notylia* sp.

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## Conclusions

This study presents well supported and highly resolved phylogenetic hypotheses of relationships of all major clades within Oncidiinae based on dense taxon sampling. The deeper topology of this tree strongly reflects the emphasis on plastid data. Additional nuclear data sets such as *Xdh* (Głowiak, Paun & Chase, 2010) would be useful to increase support for the topology and improve the resolution of the spine of the tree. Our translation of this tree into a generic classification results in the first classification of Oncidiinae in which the genera are demonstrably monophyletic. Comparison of our trees with previous classifications reveals that most of the taxonomic disputes involve clades that contain large numbers of species with yellow "oncidoid" floral morphology. We hypothesize that widespread mimicry involving Malpighiaceae, Oncidiinae and perhaps *Calceolaria* (Calceolariaceae) has resulted in extensive homoplasy in gross floral features within Oncidiinae. Previous non-cladistic classifications of Oncidiinae were based largely on floral characters, and the homoplasy in oil flower-related floral traits resulted in non-monophyletic generic concepts. Clades with other pollination syndromes (e.g., nectar reward/deceit or male euglossine fragrance rewards) generally display fewer taxonomic disagreements. The generic scheme presented here paves the way for monographic work and studies of character evolution. Orchid taxonomists may still disagree on which clades to recognize at generic level (e.g., *Trichocentrum*), but the phylogenetic hypotheses from this study will be useful for framing such debates.

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Assembling  
the Tree of  
Life:  
Orchidaceae

# ONCIDIINAE (ORCHIDACEAE)



This study expands our previous work on subtribes [Maxillariinae](#), [Oncidiinae](#), [Zygopetalinae](#), and Stanhopeinae.

Phylogenetic trees for tribe Maxillarieae (= synonym Cymbidieae) and subtribes Maxillariinae, Oncidiinae, and Zygopetalinae are available here along with a non-phylogenetic visualization of the genera of Orchidaceae arranged by subtribe. The generic visualization is presented with **Freeplane** software, which has specific hardware and software requirements. **Freeplane** has worked on all of the Windows machines we have tried it on running Windows 7 with Internet Explorer and Firefox, on Macintosh running Safari and Chrome, but not with Internet Explorer (Apple stopped supporting Internet Explorer some time ago), and on Linux machines running Ubuntu. **Freeplane** is available free for download from the [Freeplane](#) web site. If it does not run on your computer, please let me know, stating the browser and operating system you are using. **The links to the subfamilies do not work on some mac's. I am trying to fix these things.**

This is a taxonomically, not phylogenetically, arranged visualization of all the genera of the Orchidaceae, following *Genera Orchidacearum*, published by Oxford University Press [except for tribe Vandeae (subtribes Adrorhizinae, Aeridinae, Agrostophyllinae, Angraecinae, and Polystachyinae) and tribe Dendrobieae (*Bulbophyllum*, *Dendrobium*), which is now out.]. For the present, I follow Dressler(1993) in listing the genera of tribes Vandeae and Dendrobieae and their subtribes. If you click on the red arrow to the left or right of the generic name, it should (slowly, it takes a few seconds for the window to open) show a photo of a representative species of that genus, or a link to a specimen, at least for most Oncidiinae, most Maxillariinae, most Stanhopeinae, all Coeliopsidinae, some Zygopetalinae, as well as scattered genera from other groups.

*Genera Orchidacearum* uses tribe Cymbidieae to include Maxillarieae and they make a good case for it - it was already used in the key to tribes.

**[FreePlane Visualization of Genera of Orchidaceae](#)**. This does not incorporate the latest treatment of Vandeae from *Genera Orchidacearum* 6.

This will take you to the **Freeplane** depiction of the family, where you can click to expand any group. It takes a few seconds for the image to download, be patient. Some of the links to photos do not work right now, and I am trying to correct the broken links.

The vanilloids, apostasioids, and cypripedioids are shown in [vanilloids, apostasioids, and cypripedioids](#).



The basal epidendroids are shown in [basal epidendroids](#).

The orchidoids are shown in [orchidoids](#). This does not load properly, but if you go to the FreePlane Visualization of Genera of Orchidaceae, the subfamily is there.

The higher epidendroids are shown in [higher epidendroids](#).

And the unplaced tribes are shown in [unplaced tribes](#).

The current thinking on phylogenetics of subtribe Maxillariinae is best shown on the web site **MAXILLARIINAE** and the best phylogenetics of subtribe Oncidiinae are given in the cladograms listed at the bottom of this page.

**MAXILLARIEAE** - phylogenetic chart and discussion. Click on the PHYLOGENETICS link and scroll down and see our discussion of PHYLOGENETICS OF SUBTRIBE MAXILLARIINAE.

**ONCIDIINAE** - phylogenetic chart and discussion. This is actually a part of the Maxillarieae page, so don't let the top header confuse you. This was developed before the current web site and is somewhat out of date now. See the cladograms listed at the bottom of this page for the latest results.

**ZYGOPETALINAE** - phylogenetic chart and discussion. This is actually a part of the Maxillarieae page, so don't let the top header confuse you. This was developed before the current web site and is somewhat out of date now.

More links to phylogenetic works will be added as they are ready.

**FreePlane Visualization of Genera of Orchidaceae**. - This does not incorporate the latest treatment of Vandaeae from *Genera Orchidacearum* 6. This is a taxonomically, not phylogenetically, arranged visualization of all the genera of the Orchidaceae, following *Genera Orchidacearum*, published by Oxford University Press: *Genera Orchidacearum* 6 came out in May 2014. For the present, I follow *Genera Orchidacearum* 6 in listing the genera of tribes Vandaeae and Dendrobieae and their subtribes. If you click on the red arrow to the left or right of the generic name, it should (slowly, it takes a few seconds for the window to open) show a representative species of that genus, or a link to a specimen, at least for most Oncidiinae, most Maxillariinae, most Stanhopeinae, all Coeliopsidinae, some Zygopetalinae, as well as scattered genera from other groups. Some of the links to photos do not work. I am trying to figure out the problem.

The following cladograms are taken from our publication. [Fig 3](#), [Fig 4](#), [Fig 5](#), [Fig 6](#), [Fig 7](#), [Fig 8](#), [Fig 9](#), [Fig 10](#), [Fig 11](#), [Fig 12](#).

Figure 3. Comparison of ML bootstrap consensus (BS) trees resulting from analyses of separate (plastid vs. nrITS) data sets for the 7-region data set for 122 taxa. Asterisks indicate 95-100% BS support.

Figure 4. Single ML tree resulting from analysis of combined (plastid + nrITS) 7-region data set for 122 taxa. Asterisks indicate 95-100% BS support.

Figures 5-12. Single ML tree resulting from analysis of combined 5-region data set for 736 individuals.

[Table 1 \(genera accepted here\).](#)

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Assembling  
the Tree of  
Life:  
Orchidaceae

# ONCIDIINAE (ORCHIDACEAE)



This study expands our previous work on subtribes [Maxillariinae](#), [Oncidiinae](#), [Zygopetalinae](#), and Stanhopeinae.

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Assembling  
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# ONCIDIINAE (ORCHIDACEAE)

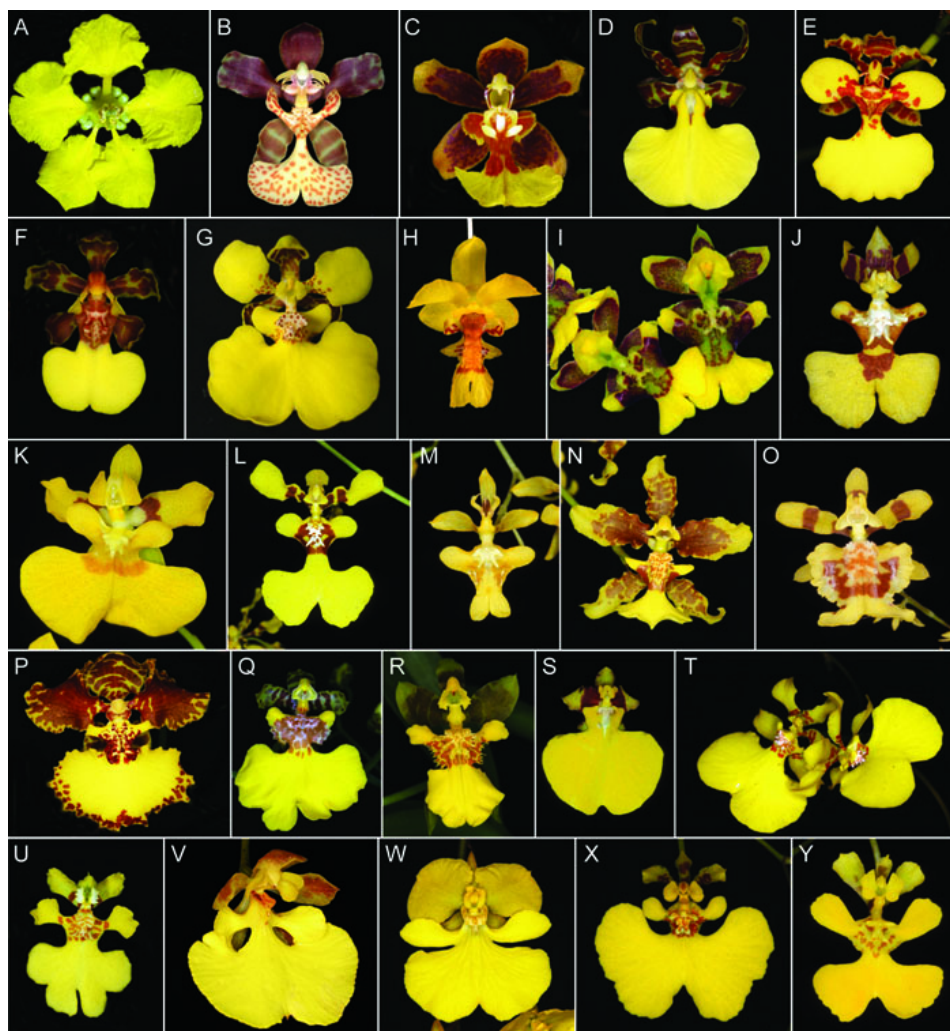


This study expands our previous work on subtribes [Maxillariinae](#), [Oncidiinae](#), [Zygopetalinae](#), and Stanhopeinae.

## INTRODUCTION TO ONCIDIINAE

This page is under construction and will eventually contain photos of a large number of species of Oncidiinae, but until then check out the [LINKS](#) to find other sites with photos and information on Oncidiinae, or visit this site's [HOME](#) page to see a number of photos of species of Oncidiinae.

Our highly trained staff of orchidologists. Left to right: Robert L. Dressler (now located at the Lankester Botanical Garden in Costa Rica), Norris H. Williams (seated), and W. Mark Whitten. Photo by Lotte Skov.



Representatives of major clades of core Oncidiinae- part 1.

Figure 1. Various genera and species of Oncidiinae displaying hypothetical mimicry of yellow Malpighiaceae flowers.

A) *Malpighia* sp.; B) *Psychopsiella limminghei*; C) *Grandiphyllum auriculatum*; D) *Trichocentrum nanum*; E) *Trichocentrum cebolleta*; F) *Trichocentrum ascendens*; G) *Rossiglossum ampliatus*; H) *Lockhartia leptocaula*; I) *Fernandezia ecuadorensis*; J) *Vitekorchis excavata*; K) *Oncidium cultratum*; L) *Oncidium obryzatum*; M) *Oncidium* sp.; N) *Oncidium sphacelatum*; O) *Oncidium heteranthum*; P) *Gomesa gardneri*; Q) *Gomesa insignis*; R) *Gomesa longipes*; S) *Otoglossum harlingii*; T) *Otoglossum scansor*; U) *Erycina pusilla*; V) *Nohawilliamsia orthostates*; W) *Zelenkoa onusta*; X) *Tolumnia urophylla*; Y) *Tolumnia quadriloba*.

Photos by W. Mark Whitten.



Representatives of major clades of core Oncidiinae- part 2.

Figure 2. Oncidiinae displaying various pollination syndromes.

Row 1 A-E: Hypothetical purple Malpighiaceae mimics. A) *Malpighia glabra*; B) *Oncidium sotoanum*; C) *Cyrtorchilum edwardii*; D) *Tolumnia hawkesiana*; E) *Cyrtorchilum ioplocon*;

Rows 2 (all) and 3 K-O, Oncidiinae that secrete oil from localized elaiophores: F) *Lockhartia longifolia*; G-H) *Cyrtorchilum serratum* (arrow denotes elaiophore); I-J) *Oncidium cheiroporum* (arrow denotes elaiophore); K) *Ornithocephalus cochleariformis*; L) *Ornithocephalus dalstroemii*; M) *Ornithocephalus dressleri*; N) *Phymatidium falcifolium*; O) *Oncidium* sp.; (*Sigmatostalix* clade);

Row 4 P-S, putative hummingbird-pollinated species: P) *Fernandezia subbiflora*; Q) *Brassia aurantiaca*; R) *Brassia andina*; S) *Oncidium* (*Cochlioda*) *beyrodtioides*;

Row 4 T-U, pseudocopulatory species: T) *Tolumnia henekenii*; U) *Trichoceros antennifer*;

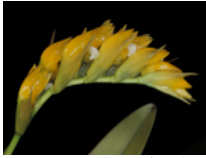
Row 5 V-Y, species pollinated by nectar-foraging insects: V) *Trichocentrum longicalcaratum*; W) *Comparettia macroplectron*; X) *Rodriguezia* sp.; Y) *Trichopilia rostrata*;

Row 5,Z: floral fragrance reward flower pollinated by male euglossine bees: Z) *Macroclinium dalstroemii*.

Photo E courtesy Guido Deburghgraeve; all others by Mark Whitten.



*Brassia aurantiaca*



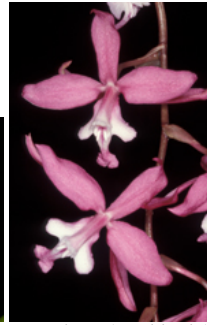
*Brassia (Brachtia) andina*



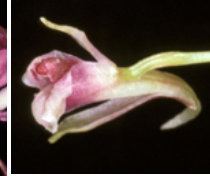
*Brassia* sp.



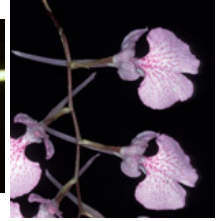
*Cischweinfia popowiana*



*Oncidium (Cochlioda) beyrodtioides*



*Comparettia (Diadenium) micrantha*



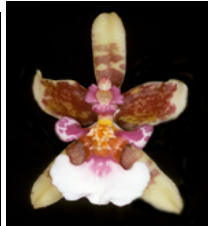
*Comparettia macroplectron*



*Comparettia (Scelochilus) tungurahuae*



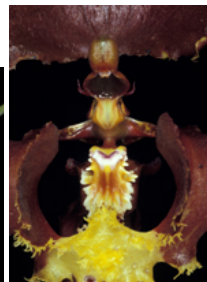
*Cuitlauzina pendula*  
pink form



*Cyrtorchiloides riopalenqueana*



*Cyrtorchilum* aff.  
*ixioides*



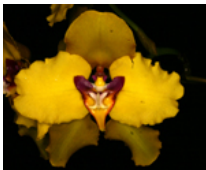
*Cyrtorchilum annulare*  
detail



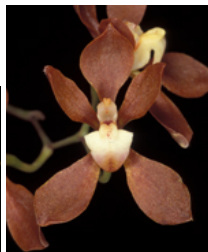
*Cyrtorchilum edwardii*



*Cyrtorchilum ioplocon*



*Cyrtorchilum macranthum*



*Cyrtorchilum (Dasyglossum) sp.*



*Cyrtorchilum leopoldianum*



*Cyrtorchilum macranthum*



*Cyrtorchilum* sp.





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# ONCIDIINAE (ORCHIDACEAE)



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## DATABASES

The \*.nex files can be downloaded for you to examine on your computer. These files are available for viewing by downloading them (search for Oncidiinae) from the [Dryad digital repository](#) site (or just click on the file name below, but the files you download from here will not be aligned) and will work only on a late model computer with lots of RAM. If you are using a MAC, then you can examine the matrices using color fonts, but you need to first extract or expand the [Colorfonts.sea.bin](#) file and then put it in your **SYSTEM** folder in the **FONTS** folder on your MAC. You need the latest version of PAUP\* (- available from [Sinaeur Associates](#) - ) to examine or run these files, but this is the only good way for you to see our data matrices. We assume you know something about cladistics and molecular systematics, as well as how to execute a NEXUS file and run PAUP\* analyses.

The file [Oncid7gene.nex](#) is a combined large data matrix of 736 samples (representing approximately 600 species) and 8,020 characters. This will allow you to generate a cladogram based on nrITS, *trnH-psbA*, *5'ycf1*, *3'ycf1*, and *matK*.

The file [Oncid\\_COMB.nex](#) is a matrix of ITS, *trnH-psbA*, *3'ycf1*, *5'ycf1*, *matK*, *rbcL*, and *psaB* for 122 taxa and 10,023 characters. It is set up so you can analyze for any one region, or all of them combined. This smaller, restricted taxon analysis included several relatively conserved plastid genes (*rbcL*, *psaB*) with the goal of providing increased resolution and support for the spine of the tree.

The file [Colorfonts.sea.bin](#) contains the color font file you will need to really work with the data matrix and see what's going on.

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**FreeMind** is available free for download from the [FreeMind](#) web site. If it does not run on your computer, please let me know, stating the browser and operating system you are using.

Andrew Rambaut's excellent program [Se-AL](#) is a program for creating alignments in color. It is available FREE from the web site, it only runs on MAC's, **but Se-AL will not run on Mac OS X 10.7**. Sorry PC users, but he has no plans to make it available for PC's. There might be programs out there that make color fonts for PC's, but I am not aware of any that are as good as Se-AL. The only program that comes close (as far as I know) is SeaView, a multiplatform, graphical user interface for multiple sequence alignment and molecular phylogeny. [SeaView](#) is available and free for PC's and MAC's, as well as for 32-bit Linux on x86, 64-bit Linux on x86\_64, and Solaris on SPARC. It is not as user friendly as Se-AL, but it does do alignments with [Muscle](#) and [Clustal Omega](#) and the alignments are in color.

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Our highly trained staff of orchidologists at the University of Florida. Left to right: Robert L. Dressler (now at the Lankester Botanical Garden in Costa Rica), Norris H. Williams (seated), and W. Mark Whitten. Photo by Lotte Skov.



**KURT M. NEUBIG** received his PhD (December 2012) in the University of Florida's Department of Biology studying the systematics of the *Sobralia* alliance, where he tested the monophyly of the genera, with special reference to the evolution of flower size and pollination syndromes. His other studies, both past and present, include: the systematics of the genus *Dichaea* (Orchidaceae), the biogeography and phylogenetics of *Teagueia* (Orchidaceae), the phylogenetics and population genetics of the *Mikania micrantha* complex (Asteraceae), the phylogenetics of tribe Hibisceae (Malvaceae), polyploidy and reticulate evolution in *Kosteletzkya* (Malvaceae), the evolution of the phytochrome gene in bryophytes, and sex-linkage in *Ceratodon purpureus*.

**W. MARK WHITTEN** has extensive field and lab experience in orchid systematics, pollination biology, orchid chemical ecology, and molecular systematics. He supervised DNA aliquot distribution, voucher databasing, PCR and sequencing troubleshooting, GenBank data entry, and matrix construction.

**NORRIS H. WILLIAMS** (FLS) has an extensive background in orchid biology, including orchid anatomy, palynology, pollination biology, chemical ecology, and molecular systematics. He has developed extensive contacts throughout Central and South America during the past 40+ years and has been interested in the Oncidiinae for over 40 years. He has recruited students from Mexico to Brazil and has active collaborations in Mexico, Costa Rica, Panama, Colombia, Ecuador, Peru, and Brazil.

**MARIO A. BLANCO** was a PhD student in the University of Florida's Department of Biology (graduated August 2011), where he just finished a monographic revision of the genus *Lockhartia*. He is interested in various aspects of orchid biology, including taxonomy, pollination biology, and functional morphology. He is particularly interested in subtribes Maxillariinae, Oncidiinae, and Pleurothallidinae.

**LORENA ENDARA** was a PhD student (May 2013) in the University of Florida's Department of Biology working on speciation patterns of *Scaphosepalum* (Orchidaceae: Pleurothallidinae). Her main interest is to understand the evolutionary and environmental factors that have led to the high orchid diversity present in the

Neotropics and for this purpose she has explored diverse fields of systematics of several pleurothallid genera. She is an active contributor to the conservation status assessments of Ecuadorian orchids and conservation policies that protect orchids.

**[GORDON BURLEIGH](#)** is an Assistant Professor in the Department of Biology at UF and is responsible for the computer analyses of the Oncidiinae.

**[KATIA SILVERA](#)** is a former graduate student at UF. She received her MS degree from UF in 2003, and her PhD in the Department of Biochemistry & Molecular Biology at the University of Nevada, Reno. She works on the evolution of Crassulacean Acid Metabolism in orchids, with emphasis on Oncidiinae. She is currently a Postdoctoral Fellow at the Smithsonian Tropical Research Institute, and a Postdoctoral Scholar with the Center for Conservation Biology at UCR.

**[JOHN C. CUSHMAN](#)** is a Professor in the Department of Biochemistry & Molecular Biology at the University of Nevada, Reno and is a leading authority on CAM metabolism. His research interests include functional genomics of crassulacean acid metabolism (CAM); mechanisms of the evolutionary origins of CAM in tropical orchids; functional genomic studies of resurrection plants for improving abiotic stress tolerance in crops; and the development of alternative, low water use input biofuel feedstocks that do not compete with food and feed.

**[MARK W. CHASE](#)** (FLS) is Director of the Molecular Systematics Section, Jodrell Laboratory, Royal Botanic Gardens, Kew and is the leader of many major collaborations in angiosperm molecular systematics. He was instrumental in developing large-scale collaborative phylogenetic projects and has extensive experience in orchid systematics. Most orchid molecular phylogenetic workers have collaborated with Mark, and his lab at Kew has played a leading role in training orchid biologists.

Together, the group represents a diverse, world-wide assembly of some of the most active and productive researchers on Orchidaceae.

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## LINKS TO INTERESTING AND USEFUL SITES

Adapted in part from Darin Penneys [Melastomataceae](#) WebSite and used with his permission. The links all worked when this page was designed. See date at bottom of page.

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### Phylogenetics

[TreeBASE](#) - TreeBASE is a centralized location for a vast scope of phylogenetic information.

[PAUP\\*](#) - PAUP\* is the most commonly used phylogenetic analysis program. The MAC version is a necessity for anyone seriously interested in molecular systematics.

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### Herbaria and Collections

[Types at the Smithsonian Institution](#) - Search the Smithsonian (US) collection of thousands of type specimens.

[New York Botanical Garden](#) - Search the entire collection at the New York Botanical Garden (NY).

[Types at NYBG](#) - Type specimens at the New York Botanical Garden (NY).

[Harvard](#) - Types, general specimens, and other databases at the Harvard University Herbaria (HUH).

[Types at the University of Florida](#) - Type specimens at the University of Florida herbarium (FLAS).

[Paris](#) - Search the Museum National d'Histoire Naturelle (P).

[Instituto Nacional de Biodiversidad \(INBio\), Costa Rica](#) - A directory of genera, species, and collection label data for Orchidaceae in the collection at the Instituto Nacional de Biodiversidad (INBio), Costa Rica.

[Missouri Botanical Garden - TROPICOS](#) - The source for tropical specimens.

[Royal Botanic Garden Edinburgh - Databases](#) - Another good source of specimens.

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**DNA - find gene sequences, chromosome numbers, or see how PCR and cycle sequencing work**



[NCBI](#) - Search GenBank for DNA sequences of anything.

[IPCN](#) - Index to Plant Chromosome Numbers.

[DNA Learning Center](#) - This takes you to a great site devoted to public genetics education. An operating unit of Cold Spring Harbor Laboratory, it offers news and information about resources, workshops, and programs. Good animation to show how PCR and cycle sequencing work. Essential to understanding molecular systematics. Works on PC's and MAC's, but you need to download the animations.

[Sinauer Associates](#) - The source for PAUP\* by Swofford and other interesting things.

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### **Taxonomic resources**

[Kew Orchid Checklist](#) - The Kew Orchid Checklist of all currently recognized genera and species [Royal Botanic Gardens, Kew (2004)] is used as our reference. The current link is to the entire live, database-driven monocot checklist.

[IPNI](#) - The ultimate in plant names and bibliographic references.

[Kew Databases](#) - This is an important resource for conducting literature searches. This is what we used to call Kew Record. It now takes you to a more extensive database. Here you can search across Kew's three major bibliographic databases in one go.

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### **Floristics**

Just a few links to get you to some interesting pages.

[Flora Mesoamericana](#) - THE major floristic work for Central America. In Spanish and English.

[Biological Diversity of the Guianas](#) - Covers the three countries in northeastern South America.

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### **Orchid Related Web Sites**

This part could go on and on and on, so only a few preliminary links are given here. This should get you started in finding orchid web pages.

[Epidendra](#) - Lankester Gardens, Epidendra Site. Lankester Botanical Gardens in Costa Rica maintains this web site, which is an excellent source of information on Neotropical orchid species as well as having links to a number of interesting sites.

[Lankester Gardens](#) - Lankester Botanical Gardens in Costa Rica is an outstanding botanical garden, well worth a visit if you are in Costa Rica. The site is in both English and Spanish.

[Selby Gardens](#) - The Marie Selby Botanical Gardens in Sarasota Florida - great to visit, large display collection of orchids.

[Fairchild Tropical Botanic Garden](#) - The Fairchild Tropical Botanic Garden 10901 Old Cutler Road Coral Gables, FL 33156 - great to visit, large display collections of orchids and other tropical plants.

[Orchid Research Newsletter](#) - Newsletter from Kew, covers all aspects of scientific research on orchids.

[Ecuagenera](#) - Ecuagenera, the largest nursery for orchids in Ecuador. The site contains a tremendous amount of information on orchids.

[The Orchid Mall](#) - A set of links to a number of orchid related pages, many commercial ones. We have no relation to any of these vendors or web pages, but thought this link might be useful.

[American Orchid Society](#) - The major organization devoted to all aspects of orchids.

[The Sobralia Pages](#) - Not Oncidiinae, but devoted to another very interesting group of orchids, and has some good links. We have some molecular data on this group (*Sobralia* and its relatives) and should have it available soon.

[The Stanhopea Pages](#) - Another good page for interesting genera.

[Phylogenetics of Maxillariinae \(Orchidaceae\)](#) A link to one of our earlier projects.

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**All links were working on 28 June 2013.**

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This study expands our previous work on subtribes [Maxillariinae](#), [Oncidiinae](#), [Zygopetalinae](#), and Stanhopeinae.

In recent years, orchid systematists have made great progress in clarifying evolutionary relationships among orchid genera, based largely upon cladistic analyses of both molecular and morphological/anatomical data sets. A well-supported outline of tribal and subtribal relationships is quickly emerging, limited primarily by the rate that rare taxa can be collected and analyzed. As such broad scale studies progress, it is becoming clear that one of the most daunting remaining tasks will be the phylogenetic revision of very large, species rich genera (e.g., *Bulbophyllum*, *Epidendrum*, *Maxillaria*, *Pleurothallis*). An even greater problem is that few taxonomists have the years of intensive study and breadth of knowledge to work with these large taxa. For example, few taxonomists are able to accurately identify a randomly-chosen *Pleurothallis* or *Maxillaria* species. Existing keys and subgeneric classifications are incomplete and are based upon admittedly artificial classifications.

## ABSTRACT

Phylogenetic relationships within the orchid subtribe Oncidiinae *sensu* Chase were inferred using maximum likelihood analyses of single and multilocus DNA sequence data sets. Analyses included both nrITS DNA and plastid regions (*matK* exon, *trnH-psbA* intergenic spacer, and two portions of *ycf1* exon) for 738 individuals representing approximately 600 species plus 7 outgroup taxa. Based on the well resolved and highly supported results (bootstrap consensus), we recognize 61 genera in Oncidiinae. Mimicry of oil-secreting Malpighiaceae and other floral syndromes evolved in parallel across the subtribe, and many clades exhibit extensive variation in pollination-related traits. Because previous classifications heavily emphasized these floral features, many genera in earlier classifications were non-monophyletic. Our classification based on monophyly will facilitate focused monographs and clarifies the evolution of morphological and biochemical traits of interest within this highly diverse subtribe.

## ACKNOWLEDGMENTS

The authors thank the curators of the herbaria of la Pontificia Universidad Católica de Quito (QCA), la Universidad de Panamá (PMA), and la Universidad de Costa Rica (USJ), as well as el Ministerio del Ambiente del Ecuador and el Autoridad Nacional del Ambiente de Panama for facilitating our research and issuing permits. We are especially grateful to the Portilla family and their staff at Ecuagenera Ltd. (Ecuador), to Andrés Maduro and staff at Finca Dracula (Panama), to researchers and staff at Jardín Botánico Lankester (Costa Rica), the Marie Selby Botanical Gardens (Sarasota, Florida, USA), the Atlanta Botanical Garden (Atlanta, Georgia, USA), Steve Beckendorf (Berkeley, CA, USA), Harry and Andy Phillips (Encinitas, California), and Günter Gerlach (Munich Botanical Garden, Munich, Germany) for allowing us generous access to their orchid collections. Delsy Trujillo contributed Peruvian specimens. Samantha Koehler, Universidade Federal de São Paulo, SP, Brazil and Aparacida de Faria, Universidade Estadual de Maringá, PR, Brazil contributed data for



Brazilian taxa. Robert L. Dressler and Calaway H. Dodson helped to initiate this project and provided access to specimens, taxonomic advice, and assistance with field work, and Stig Dalström provided invaluable determinations of many specimens and stimulating discussions, although they do not necessarily agree with our conclusions. DNA sequencing was performed by the ICBR core facility at the University of Florida. This work was supported by NSF grants DEB-9815821 to NHW, DEB-9509071 to WMW, DEB-0234064 to NHW and WMW, and IOB-0543659 to JCC, NHW, and WMW, by grants from the American Orchid Society Fund for Education and Research, the Florida Museum of Natural History, and the Royal Botanic Gardens, Kew. Additional funding was provided by Furniss Foundation graduate student fellowships from the American Orchid Society to Mario A. Blanco and Lorena Endara and by a Kew Latin American Research Fellowship to Mario A. Blanco to study specimens in European herbaria.

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I thank Steve Beckendorf of Berkeley, California for the use of the photos of *Onc. lepturum*, *Onc. karwinskii*, *Rhynchostele aptera*, *Rhyn. candidula*, *Rhyn. cervantesii*, *Rhyn. madrensis*, *Rhyn. majalis*, and *Rhyn. rossii*. Steve has a very good Flickr site with many interesting photographs of [Oncidiinae](#).

Mark Whitten supplied many of the photographs used here, too many to mention individually, and I thank him profusely. Thanks also to James D. Ackerman (UPRRP) for providing the photograph of *Cyrtochilum meirax*; Kurt Neubig who also supplied many photographs used here; Mario Blanco and Günter Gerlach for most of the photographs of *Lockhartia*; and special thanks to Samantha Koehler for providing many photographs of *Gomesa* species.

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I especially thank Kent D. Perkins, Senior Biologist and Collection Manager, FLAS, Florida Museum of Natural History, University of Florida, for help with setting up this web site. His knowledge, helpfulness, good cheer, and friendship have been invaluable. He is mostly responsible for the images in the Phylogenetics section, especially the images for the herbarium specimens. Also, Sarah Fazenbaker, of the FLMNH Office of Museum Technology, was extremely helpful in helping me get the code right.

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Key Words: elaiophores - euglossine pollination - hummingbird pollination - *matK* - mimicry - Neotropics - oil-collecting bees - nrITS - *trnH-psbA* - *ycf1*

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