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Generic recircumscriptions of Oncidiinae (Orchidaceae: Cymbidieae) based on maximum likelihood analysis of combined DNA datasets

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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 nuclear ribosomal internal transcribed spacer DNA and plastid regions (*matK* exon, *trnH-psbA* intergenic spacer and two portions of *ycf1* exon) for 736 individuals representing approximately 590 species plus seven outgroup taxa. Based on the well resolved and highly supported results, 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 recognized were not 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. © 2011 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2012, **168**, 117–146.

ADDITIONAL KEYWORDS: elaiophores – euglossine pollination – hummingbird pollination – *matK* – mimicry – Neotropics – oil-collecting bees – nrITS – *trnH-psbA* – *ycf1*.

INTRODUCTION

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 almost 4000 m a.s.l. in the Andes; several species of *Brassia* R.Br., *Miltoniopsis* God.-Leb. and *Oncidium* Sw. are important ornamental crops. Oncidiinae are members of a Neotropical clade that includes Coeliopsidinae, Maxillariinae, Stanhopeinae and Zygopetalinae; these five subtribes are each clearly monophyletic and collectively are sister to Eriopsidinae, although relationships among the five subtribes still lack strong bootstrap support; for an example, see the molecular trees presented in Cribb (2009).

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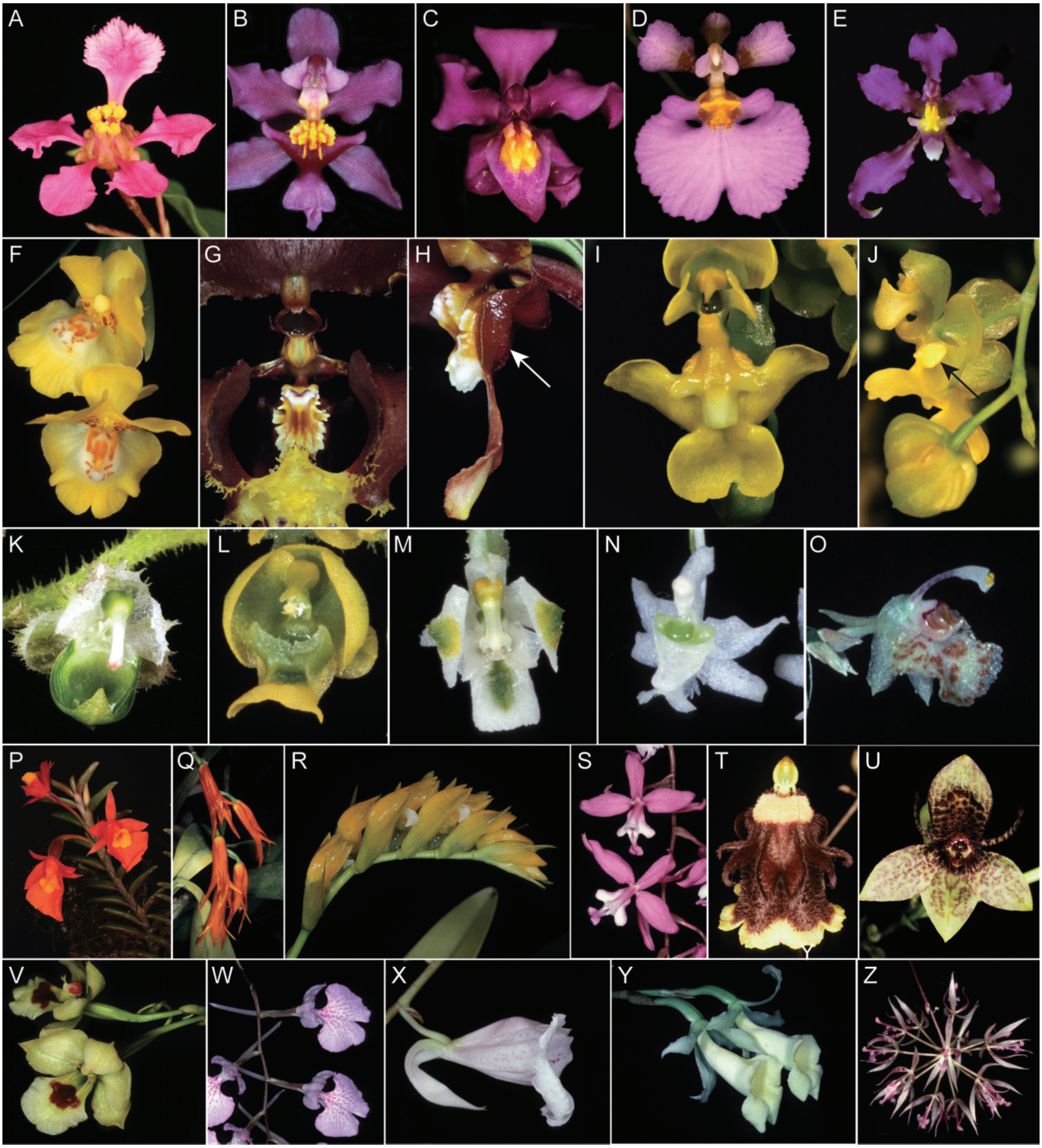
Previous classifications of Oncidiinae were intuitively based mainly on floral morphology and, to a lesser extent, chromosome number, and all were produced without cladistic methodology (Garay & Stacy, 1974; Dressler, 1993; Senghas, 1997). Recent molecular studies have helped resolve and define Oncidiinae and circumscribe many genera (Chase & Palmer, 1987; Williams *et al*., 2001a; Williams, Chase & Whitten, 2001b; Sandoval-Zapotitla *et al*., 2010). Subtribes Ornithocephalinae and Telipogoninae, long held separate on the basis of their four pollinia (versus 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* Dressler, 1993) are likely to be paraphyletic to Maxillarieae, and the two might be regarded as a single tribe (Cymbidieae *sensu* Chase *et al*., 2003). In the current circumscription, Oncidiinae include taxa with both two and four pollinia. Largely in accordance with the generic concepts of Chase (2009b), the subtribe includes 61 genera and approximately 1600 species. Before 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).

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, although deceit flowers are the most common pollination strategy (Chase, 2009b). Chromosome numbers range from the lowest known in orchids ($2n = 10$) 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 pseudobulbs of 1 kg 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 considered to have arisen repeatedly (Silvera *et al*., 2009, 2010a, b). Understanding the evolution of this range of form and function 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 a lack of reliable phylogenetic hypotheses. Our goal is to use combined plastid and nuclear ribosomal internal transcribed spacer (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.

Pollination and floral mimicry in Oncidiinae

Historically, many of the difficulties with generic circumscription in Oncidiinae are probably the result of homoplasy and mimicry in flower shape and colour. Generic boundaries have long been contentious in both the botanical and horticultural communities (Garay, 1963; Braem, 2010). As in most orchid groups, generic concepts have traditionally 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. 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 is usually 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 considered to serve a role in sexual selection by female euglossines (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; Figure 1 (Reis *et al*., 2000; Silvera, 2002; Sigrist & Sazima, 2004; Damon & Cruz-López, 2006; Reis *et al*., 2007; Carmona-Díaz & García-Franco, 2009; Vale *et al*., 2011). These oil flowers attract a variety of female bees of various sizes of several different genera in tribes Centridini, Tapinostapidini and Tetrapediini, of family Apidae (formerly assigned to a separate family, Anthophoridae, and still occasionally referred to as 'anthophorid' bees). The female bees collect oil from specialized glands (elaiophores) on the flowers and use the oils as provisions and/or waterproofing for larval cells (Cane *et al*., 1983; Roubik, 1989; Melo & Gaglianone, 2005). Numerous species of Oncidiinae that are putative mimics of malpighs exhibit a suite of characters that include bright yellow or purple flowers, elaiophores consisting of epidermal pads on lateral lobes of the lip or pads of trichomes on the lip callus and a tabula infrastigmatica (i.e. a fleshy ridge

Figure 1. Various genera of Oncidiinae displaying putative mimicry of yellow Malpighiaceae and/or *Calceolaria* flowers. A, *Malpighia* sp. (model). B, *Psychopsiella limminghei* (Morren ex Lindl.) Lückel & Braem. C, *Grandiphyllum auriculatum* (Vell.) Docha Neto. D, *Trichocentrum splendidum* (A.Rich. ex Duch.) M.W.Chase & N.H.Williams. E, *Trichocentrum cebolleta* (Jacq.) M.W.Chase & N.H.Williams. F, *Trichocentrum ascendens* (Lindl.) M.W.Chase & N.H.Williams. G, *Rossioglossum ampliatum* (Lindl.) M.W.Chase & N.H.Williams. H, *Lockhartia lepticaula* D.E.Benn. & Christenson. I, *Fernandezia ecuadorensis* (Dodson) M.W.Chase. J, *Vitekorchis excavata* (Lindl.) Romowicz & Szlach. K, *Oncidium cultratum* Lindl. L, *Oncidium obryzatum* Rchb.f. M, *Oncidium* sp. N, *Oncidium sphacelatum* Lindl. O, *Oncidium heteranthum* Poepp. & Endl. P, *Gomesa gardneri* (Lindl.) M.W.Chase & N.H.Williams. Q, *Gomesa insignis* (Rolfe) M.W.Chase & N.H.Williams. R, *Gomesa longipes* (Lindl. & Paxt.) M.W.Chase & N.H.Williams. S, *Otoglossum harlingii* (Stacy) N.H.Williams & M.W.Chase. T, *Otoglossum scansor* (Rchb.f.) Carnevali & I.Ramírez. U, *Erycina pusilla* (L.) N.H.Williams & M.W.Chase. V, *Nohawilliamsia pirarense* (Rchb.f.) M.W.Chase & Whitten. W, *Zelenkoa onusta* (Lindl.) M.W.Chase & N.H.Williams. X, *Tolumnia urophylla* (Lodd. ex Lindl.) Braem. Y, *Tolumnia quadriloba* (C.Schweinf.) Braem. Photographs by W. Mark Whitten.



at the base of the column that is grasped by the mandibles of the bee, freeing their front and middle legs to collect oil). Many Oncidiinae also possess prominent elaiophores (Fig. 2F–J): *Oncidium cheirophorum* Rchb.f., *Oncidium sotoanum* R.Jiménez & Hágsater, *Trichocentrum cavendishianum* (Bateman) M.W.Chase & N.H.Williams and various species of *Gomesa* R.Br. (Stpiczynska, Davies & Gregg, 2007; Stpiczynska & Davies, 2008; Aliscioni *et al*., 2009; Davies & Stpiczynska, 2009; Pansarin, Castro & Sazima, 2009). 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 (Fig. 2F–O).

Figure 2. Oncidiinae displaying various pollination syndromes. Row 1 (A–E) Putative mimics of purple Malpighiaceae. A, *Malpighia glabra* L. (model). B, *Oncidium sotoanum* R.Jiménez & Hágsater. C, *Cyrtochilum edwardii* (Rchb.f.) Kraenzl. D, *Tolumnia hawkesiana* (Moir) Braem. E, *Cyrtochilum ioplocon* (Rchb.f.) Dalström. Rows 2 and 3 (F–O) Oncidiinae that secrete oil from localized elaiophores. F, *Lockhartia longifolia* (Lindl.) Schltr. G, H, *Cyrtochilum serratum* (Lindl.) Kraenzl. (arrow denotes elaiophore). I–J, *Oncidium cheirophorum* Rchb.f. (arrow denotes elaiophore). K, *Ornithocephalus cochleariformis* C.Schweinf. L. *Ornithocephalus dalstroemii* (Dodson) Toscano & Dressler. M, *Ornithocephalus dressleri* (Toscano) Toscano & Dressler. N, *Phymatidium falcifolium* Lindl. O, *Oncidium* sp. (*Sigmatostalix* clade). Row 4 (P–S) Putative hummingbird-pollinated species. P, *Fernandezia subbiflora* Ruiz & Pav. Q, *Brassia aurantiaca* (Lindl.) M.W.Chase. R, *Brassia andina* (Rchb.f.) M.W.Chase. S, *Oncidium beyrodtioides* M.W.Chase & N.H.Williams. Row 4 (T–U) Pseudocopulatory species. T, *Tolumnia henekenii* (R.H.Schomb. ex Lindl.) Nir. U, *Trichoceros antennifer* Kunth. Row 5 (V–Y) Species pollinated by nectar-foraging insects. V, *Trichocentrum longicalcaratum* Rolfe. W, *Comparettia macroplectron* Rchb.f. & Triana. X, *Rodriguezia* sp. Y, *Trichopilia rostrata* Rchb.f. Row 5 (Z) Floral fragrance reward flower pollinated by male euglossine bees. Z, *Macroclinium dalstroemii* Dodson. Photograph (E) courtesy Guido Deburghgraeve; all others by W. Mark Whitten.

Some oil-secreting taxa with relatively small, greenish white flowers (e.g. *Ornithocephalus* Hook., *Phymatidium* Lindl.; Fig. 2K–O) attract a subset of oil-foraging bees with smaller body sizes and do not appear to be involved in mimicry. Perhaps a larger percentage of Oncidiinae possess flowers with similar malpigh-mimicking colour (bee-ultraviolet-green; Powell, 2008), morphology and tabula infrastigmatica, although they lack clearly demonstrable elaiophores. These species represent oil deceit flowers that lure oil-collecting bees but fail to produce a legitimate reward (Fig. 1).

The floral morphology of Oncidiinae is probably the result of a complex mixture of Batesian and Müllerian mimicry (Roy & Widmer, 1999). Using spectral reflectance analyses, Powell (2008) demonstrated that many Oncidiinae with yellow flowers closely match the colour of yellow malpigh flowers [*Byrsonima crassifolia* (L.) Kunth] and thus satisfy one of the criteria for Batesian mimicry. By mapping these traits onto an Oncidiinae phylogenetic tree, he estimated at least 14 independent origins of putative malpigh mimicry within Oncidiinae. Carmona-Díaz & García-Franco (2009) demonstrated that the rewardless *Trichocentrum cosymbephorum* (C.Morren) R.Jiménez & 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. Further, Sazima & Sazima (1988) showed that some eglandular Malpighiaceae (lacking sepalar elaiophores) are possible mimics of glandular forms. There are probably complex mimicry relationships between Malpighiaceae species, oil-producing Oncidiinae and oil-deceit Oncidiinae. We also suspect that some Oncidiinae mimic oil-producing *Calceolaria* L. (Calceolariaceae) because they occur at high elevations where malpighs are absent or rare and *Calceolaria* spp. are common. For example, *Otoglossum harlingii* (Stacy) N.H.Williams & M.W.Chase (Fig. 1S) bears a striking visual similarity to sympatric species of *Calceolaria*. 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 the 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.

MATERIAL AND METHODS

Taxon sampling

Specimens were obtained from wild-collected or cultivated plants (see Supporting information, Appendix S1); most taxon names follow the generic concepts of Chase (2009b), except for genera we have now lumped (e.g. *Brachtia* Rchb.f., *Ada* Lindl. and *Mesospinidium* Rchb.f. into *Brassia*; *Pachyphyllum* Kunth and *Raycadenco* Dodson into *Fernandezia* Ruiz & Pav.) or split (*Psychopsiella* Lückel & Braem from *Psychopsis* Raf.). Sampling of Oncidiinae included 736 accessions from a total of 590 ingroup species. We included seven outgroup taxa from other subtribes of Cymbidieae (Cameron *et al.*, 1999; Cameron, 2004). We were unable to obtain DNA of the following rare, minor genera: *Caluera* Dodson & Determann (three species), *Centroglossa* Barb.Rodr. (five species), *Cypholoron* Dodson & Dressler (two species), *Dunstervillea* Garay (one species), *Platyrhiza* Barb.Rodr. (one species), *Quekettia* Lindl. (five species), *Rauhiella* Pabst & Braga (three species), *Sanderella* Kuntze (two species), *Suarezia* Dodson (one species) and *Thysanoglossa* Porto & Brade (two species).

Extraction, 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 2 × buffer and 2 μL of either β-mercaptoethanol or proteinase-K (25 micrograms/mL; Promega, Inc.). Some total DNAs were then cleaned with QIAquick PCR (Qiagen) purification columns to remove inhibitory secondary compounds. Amplifications were performed using an Eppendorf Mastercycler EP Gradient S thermocycler and Sigma brand reagents in 25-μL volumes with reaction components for ITS: 0.5–1.0 μL of template DNA (approximately 10–100 ng), 11 μL of water, 6.5 μL of 5 M betaine, 2.5 μL of 10 × buffer, 3 μL of $MgCl_2$ (25 mM), 0.5 μL of 10 mM dNTPs, 0.5 μL each of 10 μM primers and 0.5 units of Taq DNA polymerase. For the plastid regions, the reaction components used were: 0.5–1.0 μL of template DNA (approximately 10–100 ng), 16–18 μL of water, 2.5 μL of 10 × buffer, 2–3 μL of $MgCl_2$ (25 mM), 0.5 μL of 10 mM dNTPs, 0.5 μL each of 10 μM primers and 0.5 units (0.2 μL) of Taq polymerase.

The thermocycler programmes used to amplify each region comprised:

nrITS (ITS 1 + 5.8S rDNA + ITS 2): This region was amplified with a touchdown protocol using the parameters 94 °C for 2 min; 15 × (94 °C for 1 min; 76 °C for 1 min, reducing 1 °C per cycle; 72 °C for 1 min); 21 × (94 °C for 1 min; 59 °C for 1 min; 72 °C for 1 min); 72 °C for 3 min with the primers 17SE and 26SE *sensu* 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 approximately 1800 bp in length. This region was amplified with the parameters 94 °C for 3 min; 33 × (94 °C for 45 s; 60 °C for 45 s; 72 °C for 2 min); 72 °C for 3 min, with primers –19F (Molvray, Kores & Chase, 2000) and trnK2R (Johnson & Soltis, 1994). Internal sequencing primers were *matK* intF (TGAGCGAACA-CATTTCTATGG) and *matK* intR (ATAAGGT-TGAAACCAAAAGTG). Some samples were amplified using the primers 56F and 1520R (Whitten, Williams & Chase, 2000) that yielded a shorter, although almost complete, sequence of the *matK* exon (missing the 3′ spacer).

psaB: This region was amplified with the parameters 94 °C for 3 min; 33 × (94 °C for 30 s; 55 °C for 30 s; 72 °C for 2 min); 72 °C for 4 min, using the primers NY159 and NY160 *sensu* Cameron (2004).

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

trnH-psbA: This region was amplified with the parameters 94 °C for 3 min; 33 × (94 °C for 1 min; 58 °C for 1 min; 72 °C for 1 min 20 s); 72 °C for 6 min, with the primers F and R *sensu* Xu *et al*. (2000).

ycf1: We sequenced two noncontiguous portions of *ycf1* (Neubig *et al*., 2009) including approximately 1200 bp from the 5′ end and approximately 1500 bp from the 3′ end. Both were amplified using a ‘touchdown’ protocol with the parameters 94 °C for 3 min; 8 × (94 °C for 30 s; 60–51 °C for 1 min; 72 °C for 3 min); 30 × (94 °C for 30 s; 50 °C for 1 min; 72 °C for 3 min); 72 °C for 3 min. Primers for the 5′ portion are 1F (ATGATTTTTAAATCTTTTCTACTAG) and 1200R (TTGTGACATTTCATTGCGTAAAGCCTT). Primers for the 3′ portion are 3720F (TACGTATGTAATGAAC-GAATGG) and 5500R (GCTGTTATTGGCATCAAAC-CAATAGCG). Additional internal sequencing primers are intF (GATCTGGACCAATGCACATATT) and intR (TTTGATTGGGATGATCCAAGG).

PCR products were cleaned with Microclean™ (The Gel Company) in accordance with manufacturer's instructions. Purified PCR products were then cycle-sequenced using the parameters 96 °C for 10 s; 25 × (96 °C for 10 s; 50 °C for 5 s; 60 °C for 4 min). The cycle sequencing mix consisted of 3 μL of water, 1 μL of fluorescent Big Dye dideoxy terminator, 2 μL of Better Buffer™ (The Gel Company), 1 μL of template and 0.5 μL of primer. Cycle sequencing products were cleaned using ExoSAP™ (USB Corporation) in accordance with the manufacturer's instructions. Purified cycle sequencing products were directly sequenced on an ABI 377, 3100 or 3130 automated sequencer accordance with the manufacturer's instructions (Applied Biosystems). Electropherograms were edited and assembled using SEQUENCHER, version 4.9 (GeneCodes). All sequences were deposited in GenBank (see Supporting information, Appendix S1).

Data analysis

We constructed two data matrices. The first included seven DNA regions (nrITS, *trnH-psbA*, 3′*ycf1*, 5′*ycf1*, *matK*, *rbcL* and *psbA*) for 122 taxa. This smaller restricted data set included several relatively conserved plastid genes (*rbcL*, *psbA*) with the goal of providing increased resolution and support for the deeper nodes of the tree. The outgroup for this data set was *Eulophia graminea* Lindl. The second matrix included five DNA regions (nrITS, *trnH-psbA*, 5′*ycf1*, 3′*ycf1* and *matK*) for 736 taxa. Outgroup taxa were *Eriopsis biloba* Lindl., *Eulophia graminea*, *Cyrtidiorchis stumpflei* (Garay) Rauschert, a species of *Rudolfiella* Hoehne, *Stanhopea jenishiana* F.Kramer ex Rchb.f., and *Stanhopea tigrina* Bateman ex Lindl. The *trnH-psbA* matrix contained many gaps of dubious alignment, and we excluded 1259 positions out of 2027 aligned positions (62%). Data matrices are available from W. Mark Whitten (whitten@flmnh.ufl.edu) and at: ftp://ftp.flmnh.ufl.edu/Public/oncids/

Maximum likelihood (ML) phylogenetic analyses were performed on both data sets using RaxML, version 7.0.4 (Stamatakis, 2006). For each data set, 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 (GTR; Tavare, 1986) model of evolution with among-site rate variation modeled using the 'CAT' discrete rate categories option. For 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 and for region-specific branch lengths. To find the optimal tree for each data set, we performed five runs of the ML heuristic searches and 200 nonparametric bootstrap replicates to assess clade support in the tree (Felsenstein, 1985).

RESULTS

Seven-locus data set (Figs 3, 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. Based on visual inspection of the trees, there appears to be nuclear versus plastid conflict in the relationships of *Psychopsis*, *Psychopsiella* and *Trichopilia* Lindl. *Psychopsis* and *Psychopsiella* are strongly supported as sister in the nrITS tree, although *Psychopsis* is strongly supported as sister to *Psychopsiella* and *Trichopilia* in the plastid tree. *Vitekorchis* Romowicz & Szlach. is isolated in both nuclear and plastid tree. 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* Raf. is strongly supported as sister to *Erycina* Lindl. + *Rhynchostele* Rchb.f. in nrITS results, although plastid data place *Tolumnia* as a well-supported member of a derived clade (including *Nohawilliamsia* M.W.Chase & Whitten to *Comparettia* Poepp. & Endl.). The combined plastid + nrITS seven-region analysis (122 taxa; Fig. 4) is largely consistent with the analysis of the larger five-locus data (736 taxa; Figs 5–12), although the addition of *rbcL* and *psbA* 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 group (e.g. most *Erycina*; Fig. 10). In a few cases, samples from putatively the same species do not fall together (e.g. *Erycina pusilla* (L.) N.H.Williams & M.W.Chase, Fig. 10; *Cyrtochilum cimiciferum* (Rchb.f.) Dalström, Fig. 9). Some of these may be the result of errors in determinations but, usually, these represent taxonomically confusing groups with poorly-defined species boundaries.

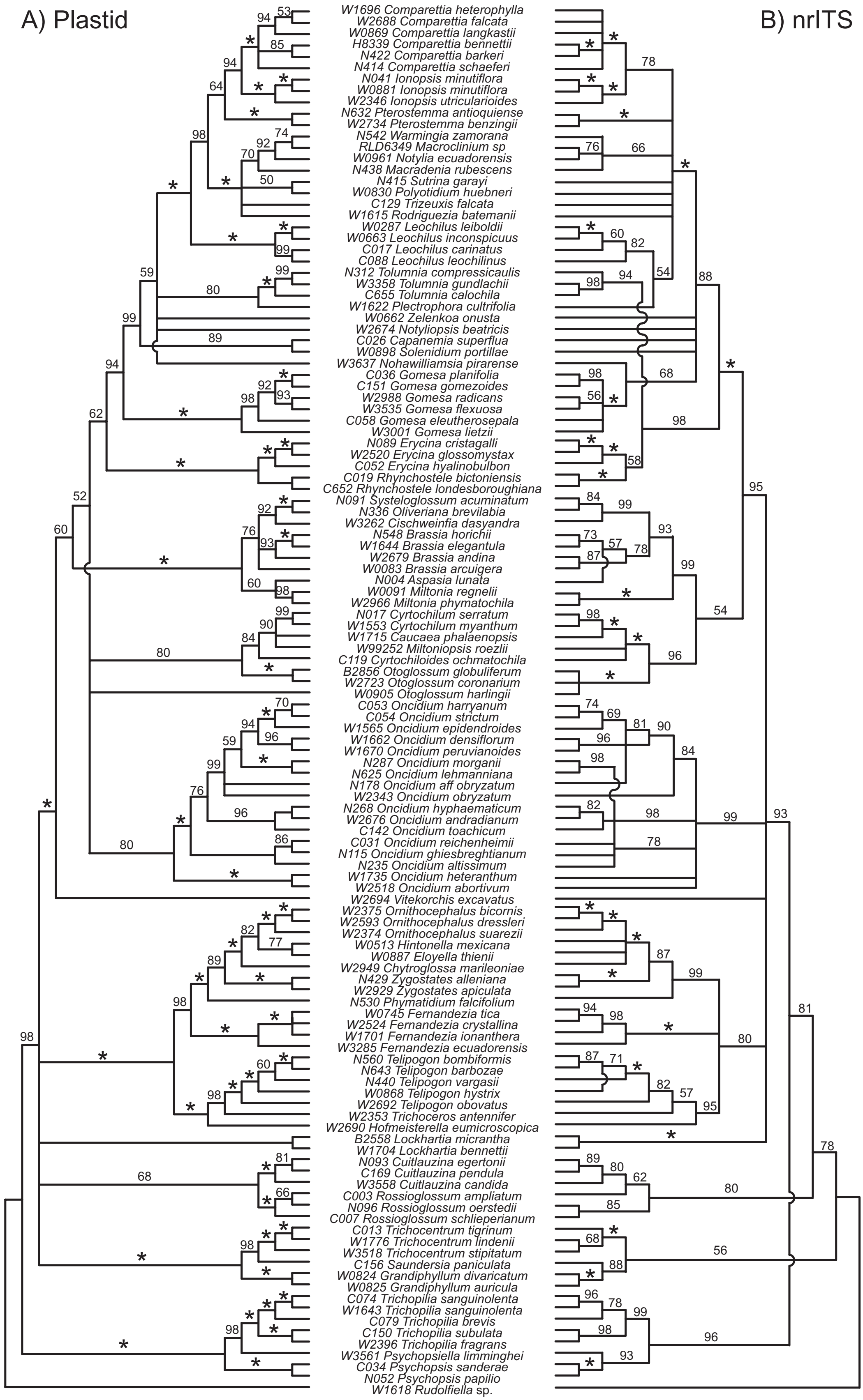
DISCUSSION

We recognize 61 clades in this tree (Figs 5–12) at generic level (Table 1). All of the clades that we recognize at generic level are strongly supported, and there is also strong support for almost all supra-generic nodes in the tree. Monotypic genera include *Zelenkoa* M.W.Chase & N.H.Williams, *Notyliopsis* P.Ortiz 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* Senghas, *Trizeuxis* Lindl., *Seegeriella* Senghas and *Warmingia* Rchb.f. Genera are discussed in order of appearance in the cladogram (Figs 5–12). More detailed information for each genus is provided in Chase (2009b).

***Psychopsis* Raf.** (five 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 unpublished nrITS trees to avoid creation of a monotypic genus, although analysis of the combined data sets place *Psychopsiella* sister to *Trichopilia* Lindl. Chromosome numbers also differ: $2n = 38$ for *Psychopsis* (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* by *Heliconius* butterflies but his observations have not been replicated.

***Psychopsiella* Lückel & Braem** (one sp.; Figs 1B, 5) is monotypic and vegetatively resembles a dwarf *Psychopsis*, although it lacks the elongate dorsal sepal and petals of the latter. It is restricted to Brazil and has been reported from Venezuela, near Caracas, although 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.; Figs 2Y, 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* Lindl. and *Sobralia* Ruiz & Pav.


A) Plastid
B) nrITS
W1696 Comparettia heterophylla
W2688 Comparettia falcata
W0869 Comparettia langkastii
H8339 Comparettia bennettii
N422 Comparettia barkeri
N414 Comparettia schaeferi
N041 Ionopsis minutiflora
W0881 Ionopsis minutiflora
W2346 Ionopsis utricularioides
N632 Pterostemma antioquiense
W2734 Pterostemma benzingii
N542 Warmingia zamorana
RLD6349 Macroclinium sp
W0961 Notylia ecuadorensis
N438 Macradenia rubescens
N415 Sutrina garayi
W0830 Polyotidium huebneri
C129 Trizeuxis falcata
W1615 Rodriguezia batemanii
W0287 Leochilus leiboldii
W0663 Leochilus inconspicuus
C017 Leochilus carinatus
C088 Leochilus leochilinus
N312 Tolumnia compressicaulis
W3358 Tolumnia gundlachii
C655 Tolumnia calochila
W1622 Plectrophora cultrifolia
W0662 Zelenkoa onusta
W2674 Notyliopsis beatricis
C026 Capanemia superflua
W0898 Solenidium portillae
W3637 Nohawilliamsia pirarense
C036 Gomesa planifolia
C151 Gomesa gomezoides
W2988 Gomesa radicans
W3535 Gomesa flexuosa
C058 Gomesa eleutherosepala
W3001 Gomesa lietzii
N089 Erycina cristagalli
W2520 Erycina glossomystax
C052 Erycina hyalinobulbon
C019 Rhynchostele bictoniensis
C652 Rhynchostele londesboroughiana
N091 Systeloglossum acuminatum
N336 Oliveriana brevilabia
W3262 Cischweinfia dasyandra
N548 Brassia horichii
W1644 Brassia elegantula
W2679 Brassia andina
W0083 Brassia arcuigera
N004 Aspasia lunata
W0091 Miltonia regnelii
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N017 Cyrtochilum serratum
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W1715 Caucaea phalaenopsis
W99252 Miltoniopsis roezlii
C119 Cyrtochiloides ochmatochila
B2856 Otoglossum globuliferum
W2723 Otoglossum coronarium
W0905 Otoglossum harlingii
C053 Oncidium harryanum
C054 Oncidium strictum
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W1662 Oncidium densiflorum
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N530 Phymatidium falcifolium
W0745 Fernandezia tica
W2524 Fernandezia crystallina
W1701 Fernandezia ionanthera
W3285 Fernandezia ecuadorensis
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N643 Telipogon barbozae
N440 Telipogon vargasii
W0868 Telipogon hystrix
W2692 Telipogon obovatus
W2353 Trichoceros antennifer
W2690 Hofmeisterella eumicroscopica
B2558 Lockhartia micrantha
W1704 Lockhartia bennettii
N093 Cuitlauzina egertonii
C169 Cuitlauzina pendula
W3558 Cuitlauzina candida
C003 Rossioglossum ampliatum
N096 Rossioglossum oerstedii
C007 Rossioglossum schlieperianum
C013 Trichocentrum tigrinum
W1776 Trichocentrum lindenii
W3518 Trichocentrum stipitatum
C156 Saundersia paniculata
W0824 Grandiphyllum divaricatum
W0825 Grandiphyllum auricula
C074 Trichopilia sanguinolenta
W1643 Trichopilia sanguinolenta
C079 Trichopilia brevis
C150 Trichopilia subulata
W2396 Trichopilia fragrans
W3561 Psychopsiella limminghei
C034 Psychopsis sanderae
N052 Psychopsis papilio
W1618 Rudolfiella sp.

Figure 3. Comparison of maximum likelihood bootstrap (BS) consensus trees resulting from analyses of the separate [(A) plastid versus (B) nuclear ribosomal internal transcribed spacer (nrITS)] data sets for the seven-region data set for 122 taxa. Asterisks indicate 100% BS support.

have similar gullet flowers, and they also are visited by nectar-seeking euglossine bees. Vegetatively, plants of *Trichopilia* are similar to *Psychopsis* and *Psychopsiella*. We include *Helcia* Lindl., *Leucohyle* Klotzch and *Neoescobaria* Garay, which are embedded within *Trichopilia*. These differ primarily in the lack of lip/column fusion and have previously been recognized as members of *Trichopilia*.

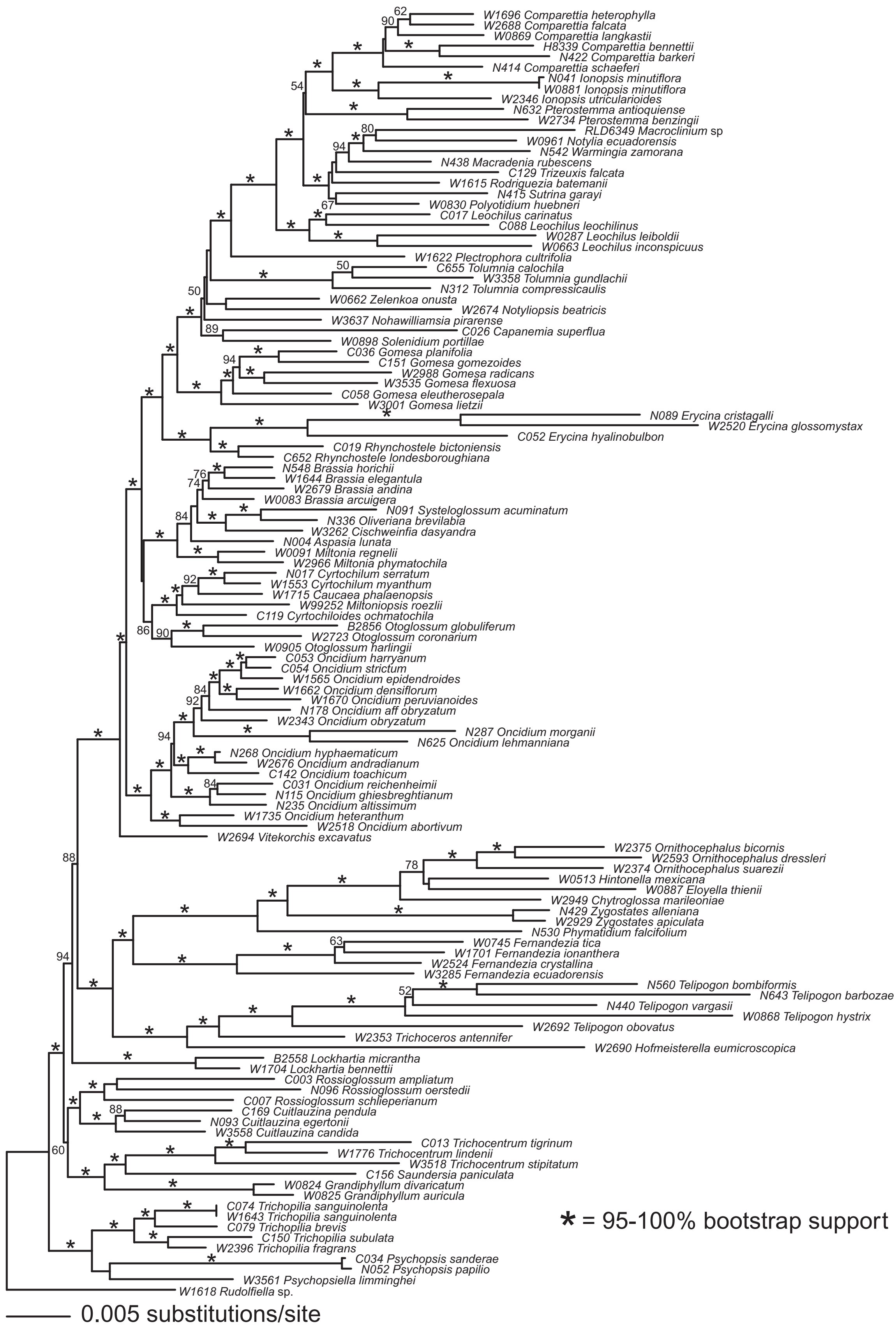
Rossioglossum **(Schltr.) Garay & G.C.Kenn.** (ten spp.; Fig. 5), as circumscribed here, includes *Ticoglossum* Lucas Rodr. ex Halb. and *Chelyorchis* Dressler & N.H.Williams. This genus also includes considerable floral diversity, suggestive of pollination by a variety of bees, although pollination data are mostly lacking. *Rossioglossum ampliatum* (Lindl.) M.W.Chase & N.H.Williams (Fig. 1G) has numerous bright yellow (bee-ultraviolet-green; Powell, 2008) *Oncidium*-like flowers that are malpigh mimics, whereas other *Rossioglossum* [e.g. *R. insleayi* (Baker ex Lindl.) Garay & G.C.Kenn. and *Rossioglossum grande* (Lindl.) Garay & G.C.Kenn.] 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 & 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*, as a result of its floral distinctiveness within this clade, would result in a paraphyletic *Rossioglossum*. The genus ranges mostly from Mexico to Central America, with *Chelyorchis pardoi* 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.** (ten spp.; Fig. 5), as circumscribed here, includes *Dignathe* Lindl., *Osmoglossum* (Schltr.) Schltr. and *Palumbina* Rchb.f and 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. All four genera were segregated by various workers from *Odontoglossum*. *Cuitlauzina pendula* Lex. has a tabula infrastigmatica, although its pollinator is unknown; its colour (white or pink) makes it unlikely to be an oil-bee flower. Despite their gross floral disparity, they share a prominent clinandrial hood and similar pollinarium morphology (Sosa *et al*., 2001).

Grandiphyllum **Docha Neto** (ten spp.; Figs 1C, 5) ('Brazilian mule-ears') 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, although they lack the complex tubularized pollinarium stipe (Chase, 1986b) typical of *Oncidium s.s.*, *Grandiphyllum* and *Saundersia* Rchb.f. could be lumped into *Trichocentrum*, although doing so would create a genus that is even more difficult to diagnose morphologically.

Saundersia **Rchb.f.** (two 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.** (70 spp.; Figs 1D, E, F, 2V, 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 *Trichocentrum 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- or resin-rewarding species: *Trichocentrum 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. At least one species, *Trichocentrum tigrinum* Linden & Rchb.f., has a strong fragrance and attracts fragrance-collecting male euglossines (van der Pijl & Dodson, 1966). Most *Trichocentrum s.s.* with spurs might be deceit flowers, attracting nectar-foraging euglossine or other long-tongued bees. Chromosome number varies greatly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RLD6349 Macroclinium sp
W0961 Notylia ecuadorensis
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C129 Trizeuxis falcata
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C036 Gomesa planifolia
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W2966 Miltonia phymatochila
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N625 Oncidium lehmanniana
N268 Oncidium hyphaematicum
W2676 Oncidium andradianum
C142 Oncidium toachicum
C031 Oncidium reichenheimii
N115 Oncidium ghiesbreghtianum
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W1735 Oncidium heteranthum
W2518 Oncidium abortivum
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W1701 Fernandezia ionanthera
W2524 Fernandezia crystallina
W3285 Fernandezia ecuadorensis
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N440 Telipogon vargasii
W0868 Telipogon hystrix
W2692 Telipogon obovatus
W2353 Trichoceros antennifer
W2690 Hofmeisterella eumicroscopica
B2558 Lockhartia micrantha
W1704 Lockhartia bennettii
C003 Rossioglossum ampliatum
N096 Rossioglossum oerstedii
C007 Rossioglossum schlieperianum
C169 Cuitlauzina pendula
N093 Cuitlauzina egertonii
W3558 Cuitlauzina candida
C013 Trichocentrum tigrinum
W1776 Trichocentrum lindenii
W3518 Trichocentrum stipitatum
C156 Saundersia paniculata
W0824 Grandiphyllum divaricatum
W0825 Grandiphyllum auricula
C074 Trichopilia sanguinolenta
W1643 Trichopilia sanguinolenta
C079 Trichopilia brevis
C150 Trichopilia subulata
W2396 Trichopilia fragrans
C034 Psychopsis sanderae
N052 Psychopsis papilio
W3561 Psychopsiella limminghei
W1618 Rudolfiella sp.
* = 95-100% bootstrap support
0.005 substitutions/site

Figure 4. Single maximum likelihood tree resulting from analysis of the combined [plastid + nuclear ribosomal internal transcribed spacer (nrITS)] seven-region data set for 122 taxa. Asterisks indicate 100% bootstrap support (BS); values above lines are BS percentages.

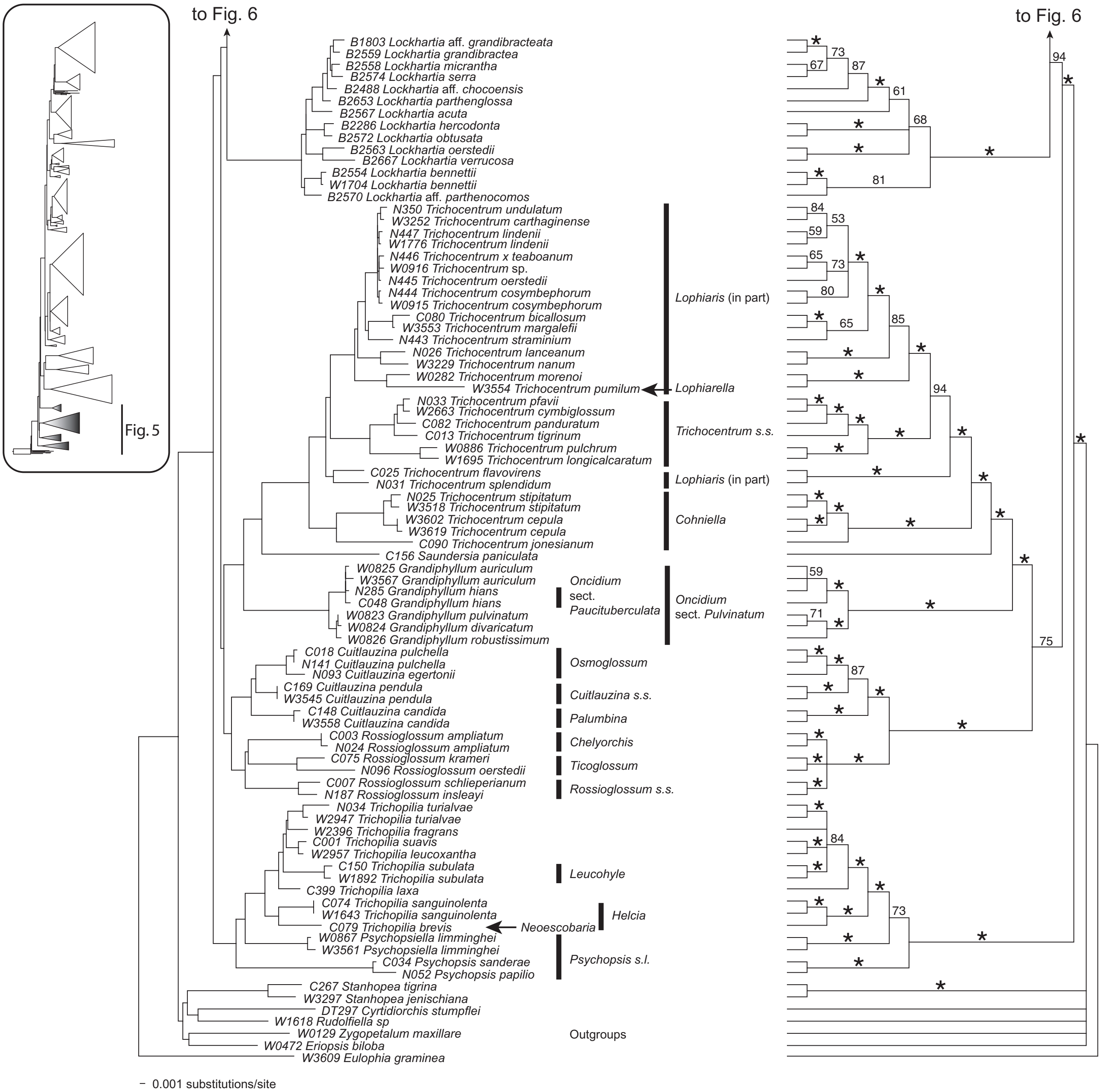

Figure 5. Portion (outgroups to *Lockhartia*) of single maximum likelihood tree resulting from analysis of the combined five-region data set for 736 individuals. The tree on the right side of the figure displays bootstrap (BS) support > 50%; asterisks indicate 95–100% BS support. Generic segregates that we do not recognize and have lumped are indicated in the trees to the right of the accepted names.

within this clade, forming a continuum from $2n = 24–72$ that does not correlate well with subclades. Chase & Olmstead (1988) hypothesized that the range of numbers is the result of chromosomal condensation and does not involve polyploidy. Some reports (Braem, 1993; Christenson, 1999; Fernandez-Concha *et al*., 2010) have favoured a narrow circumscription of *Trichocentrum* (restricted to those species

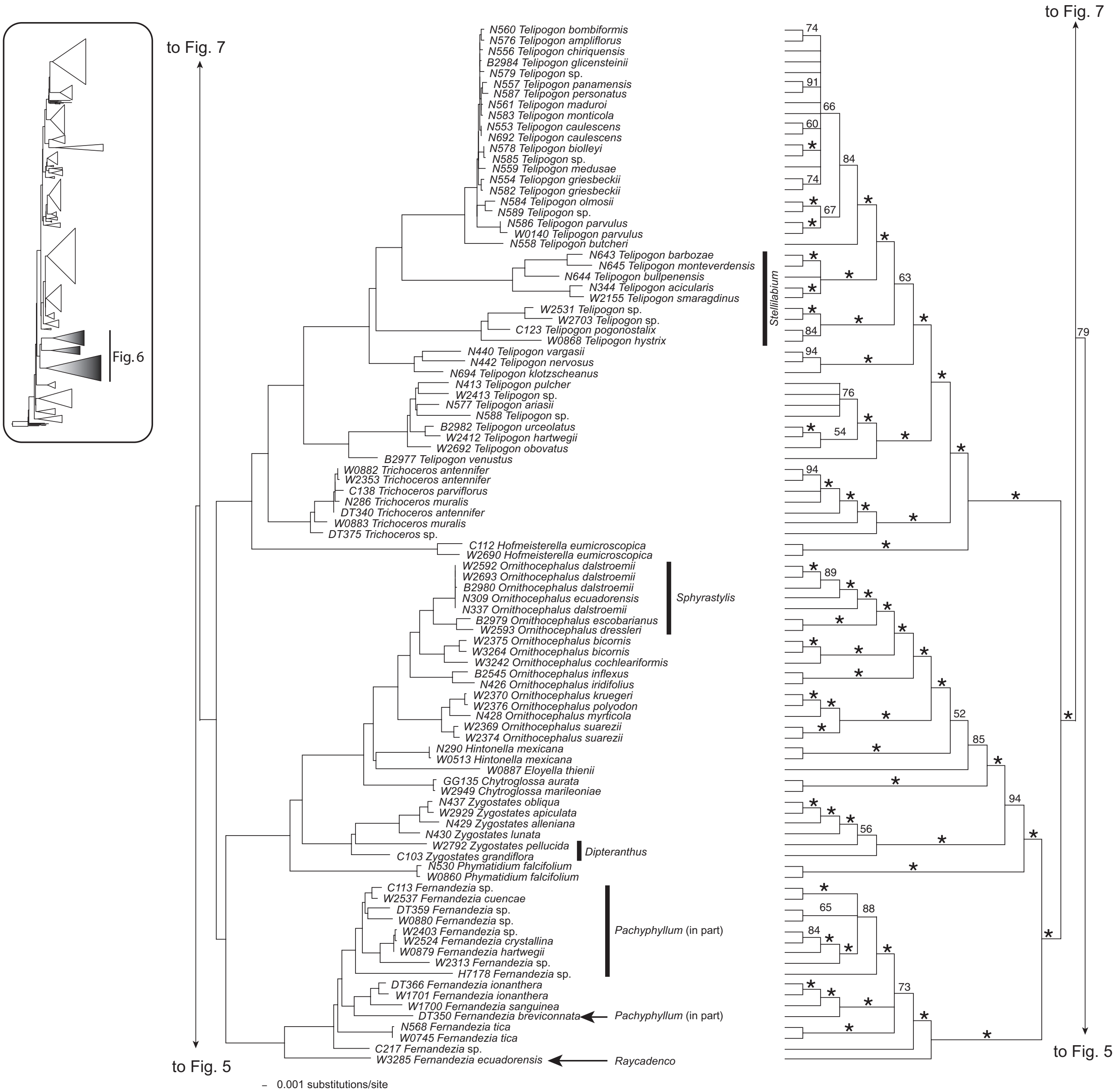

Figure 6. Continuation (*Fernandezia* to *Telipogon*) of single maximum likelihood tree resulting from analysis of the combined five-region data set for 736 individuals. The tree on the right side of the figure displays bootstrap (BS) support > 50%; asterisks indicate 95–100% BS support. Generic segregates that we do not recognize and have lumped are indicated in the trees to the right of the accepted names.

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*) is included in *Lophiaris*, although *Lophiarella* should also include *Trichocentrum flavovirens* (L.O.Williams) M.W.Chase & N.H.Williams and *T. splendidum* (A.Rich. ex Duch.) M.W.Chase & N.H.Williams if it 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, 5) has confused orchidologists for decades and has been placed in a number of suprageneric taxa. The genus

Figure 7. Continuation (*Vitekorchis* to *Oncidium*) of single maximum likelihood tree resulting from analysis of the combined five-region data set for 736 individuals. The tree on the right side of the figure displays bootstrap (BS) support > 50%; asterisks indicate 95–100% BS support. Generic segregates that we do not recognize and have lumped are indicated in the trees to the right of the accepted names.

ranges throughout much of the Neotropics. The flowers are mostly bright yellow and bear oil-secreting trichomes, similar to many Oncidiinae, although they lack a tabula infrastigmatica. The pollinaria have elongate caudicles that partially replace a stipe (similar to *Pachyphyllum* Kunth), and all but one species have a 'braided' vegetative habit with pseudomonopodial stems lacking pseudobulbs and

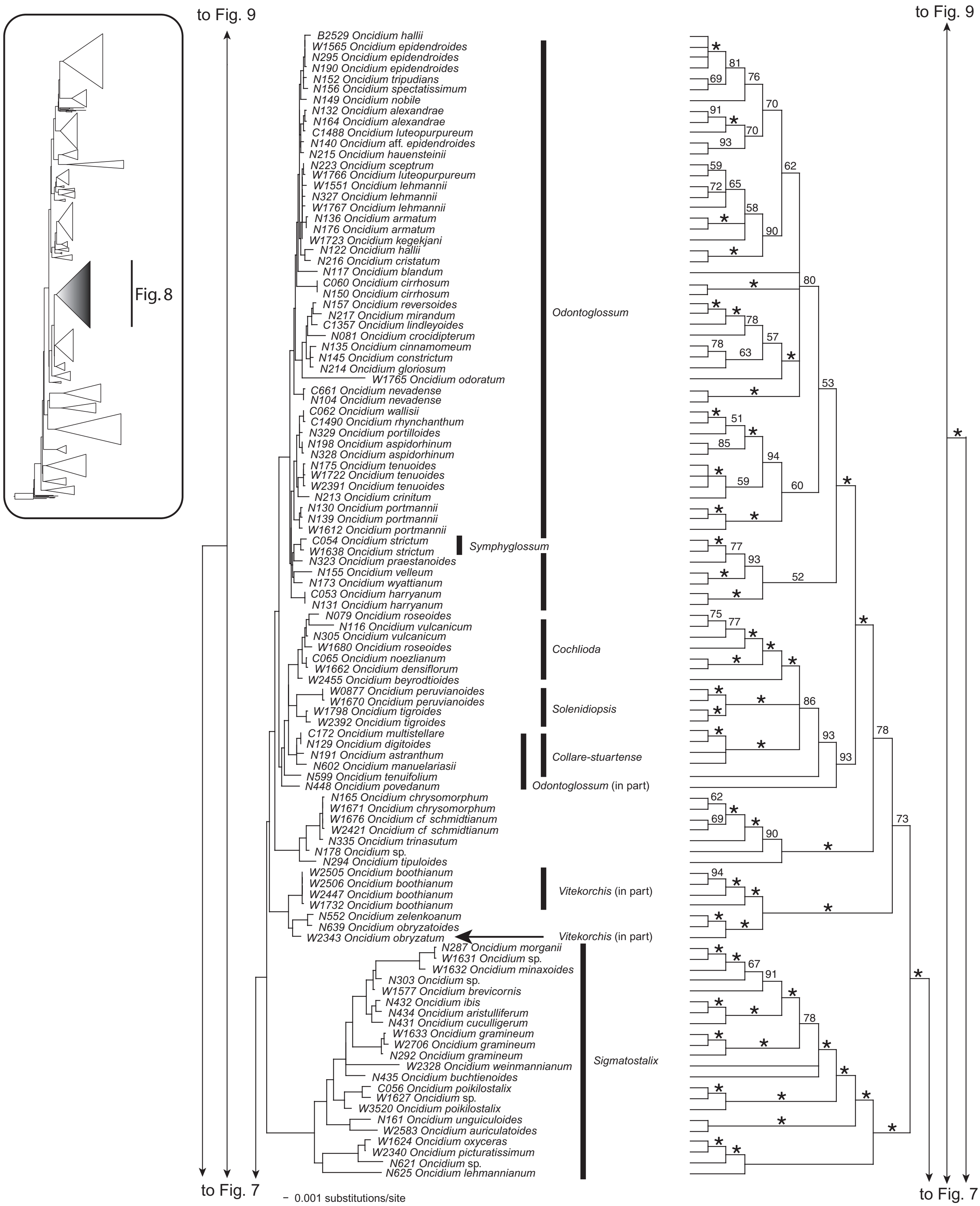

Figure 8. Continuation (*Oncidium*) of single maximum likelihood tree resulting from analysis of the combined five-region data set for 736 individuals. The tree on the right side of the figure displays bootstrap (BS) support > 50%; asterisks indicate 95–100% BS support. Generic segregates that we do not recognize and have lumped are indicated in the trees to the right of the accepted names.

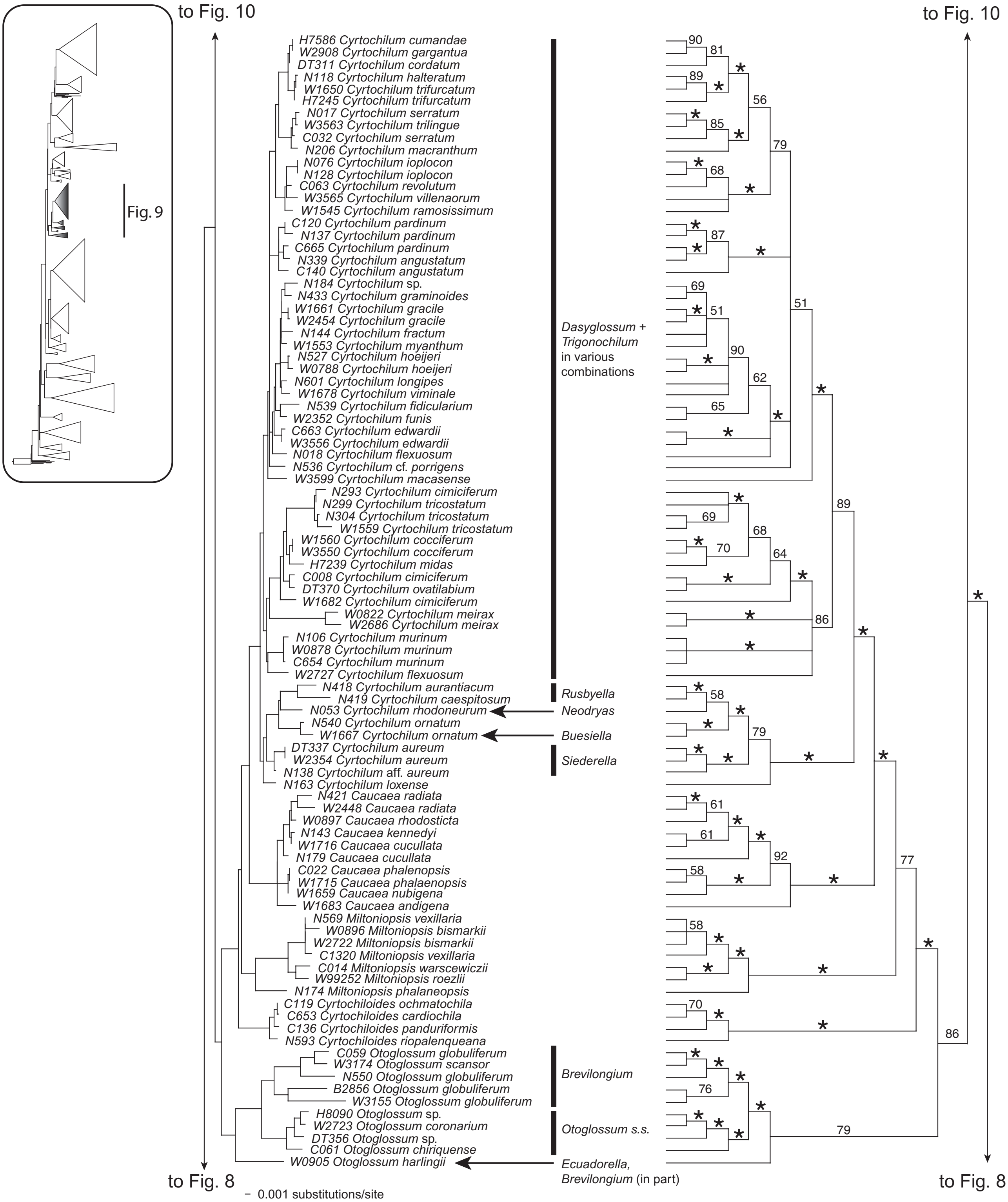

Figure 9. Continuation (*Otoglossum* to *Cyrtochilum*) of single maximum likelihood tree resulting from analysis of the combined five-region data set for 736 individuals. The tree on the right side of the figure displays bootstrap (BS) support > 50%; asterisks indicate 95–100% BS support. Generic segregates that we do not recognize and have lumped are indicated in the trees to the right of the accepted names.

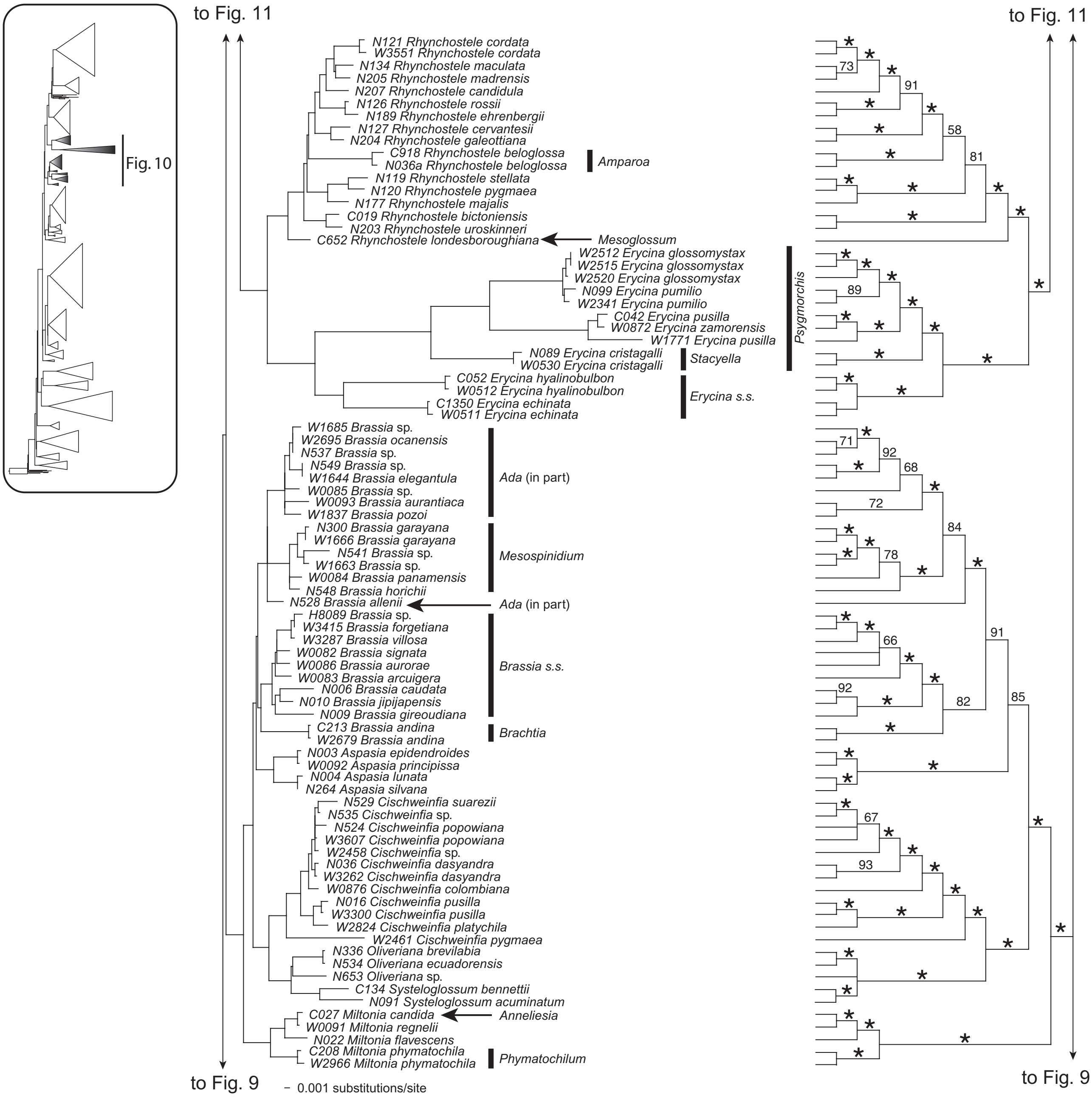

Figure 10. Continuation (*Miltonia* to *Rhynchostele*) of single maximum likelihood tree resulting from analysis of the combined five-region data set for 736 individuals. The tree on the right side of the figure displays bootstrap (BS) support > 50%; asterisks indicate 95–100% BS support. Generic segregates that we do not recognize and have lumped are indicated in the trees to the right of the accepted names.

tightly overlapping, unifacial, non-articulate leaves. The capsules have apical dehiscence instead of lateral. These unusual features led some workers to place *Lockhartia* in a separate subtribe, Lockhartiinae Schltr., although the molecular data strongly support its position within Oncidiinae. The unusual vegetative features are best explained as paedomorphic traits common to many seedlings of Oncidiinae (Chase, 1986b). One species (*Lockhartia genegeorgei* D.E.Benn. & Christenson) has prominent pseudobulbs with articulated, bifacial leaves; the lack of paedomorphic 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

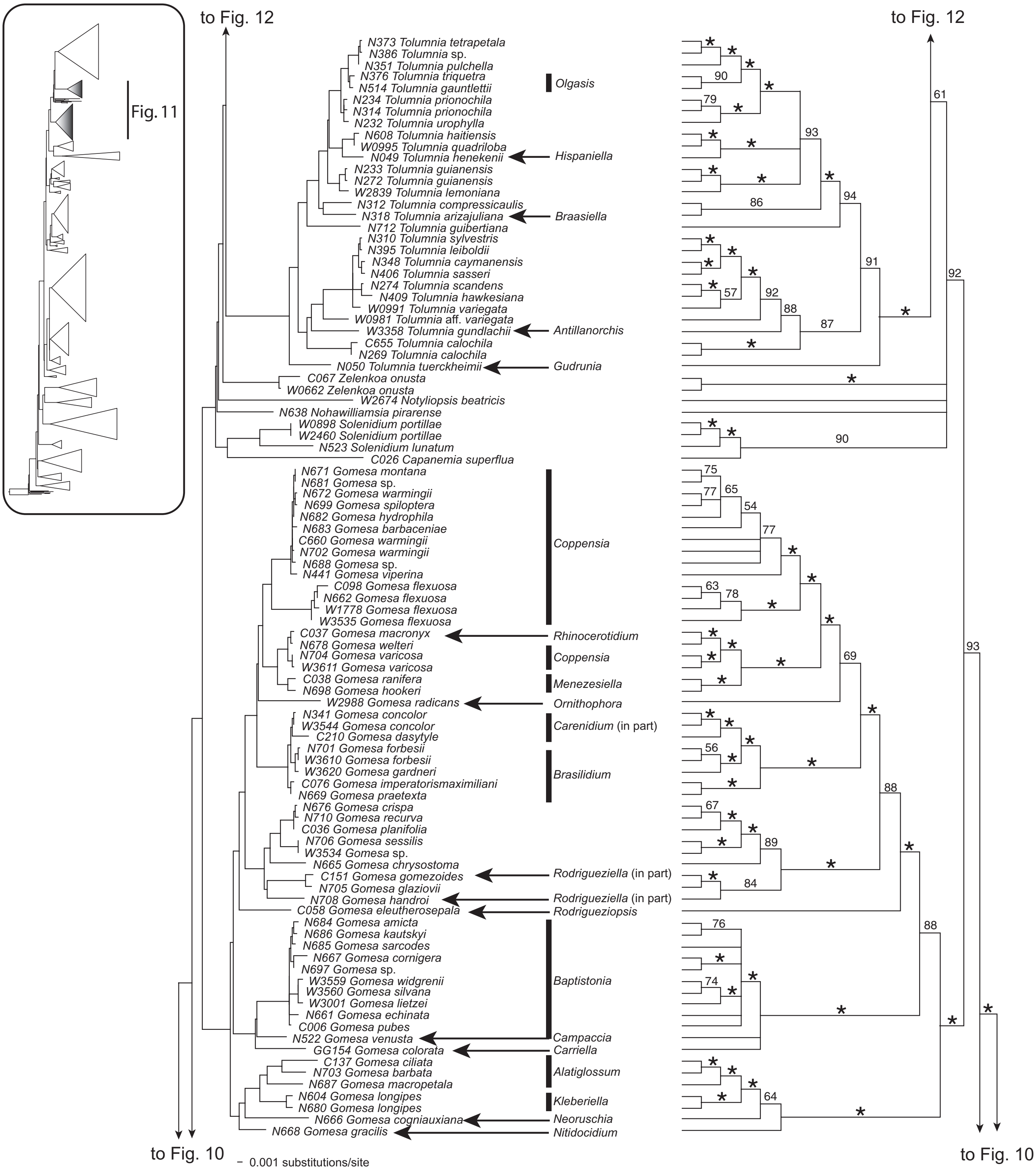

Figure 11. Continuation (*Gomesa* to *Tolumnia*) of single maximum likelihood tree resulting from analysis of the combined five-region data set for 736 individuals. The tree on the right side of the figure displays bootstrap (BS) support > 50%; asterisks indicate 95–100% BS support. Generic segregates that we do not recognize and have lumped are indicated in the trees to the right of the accepted names.

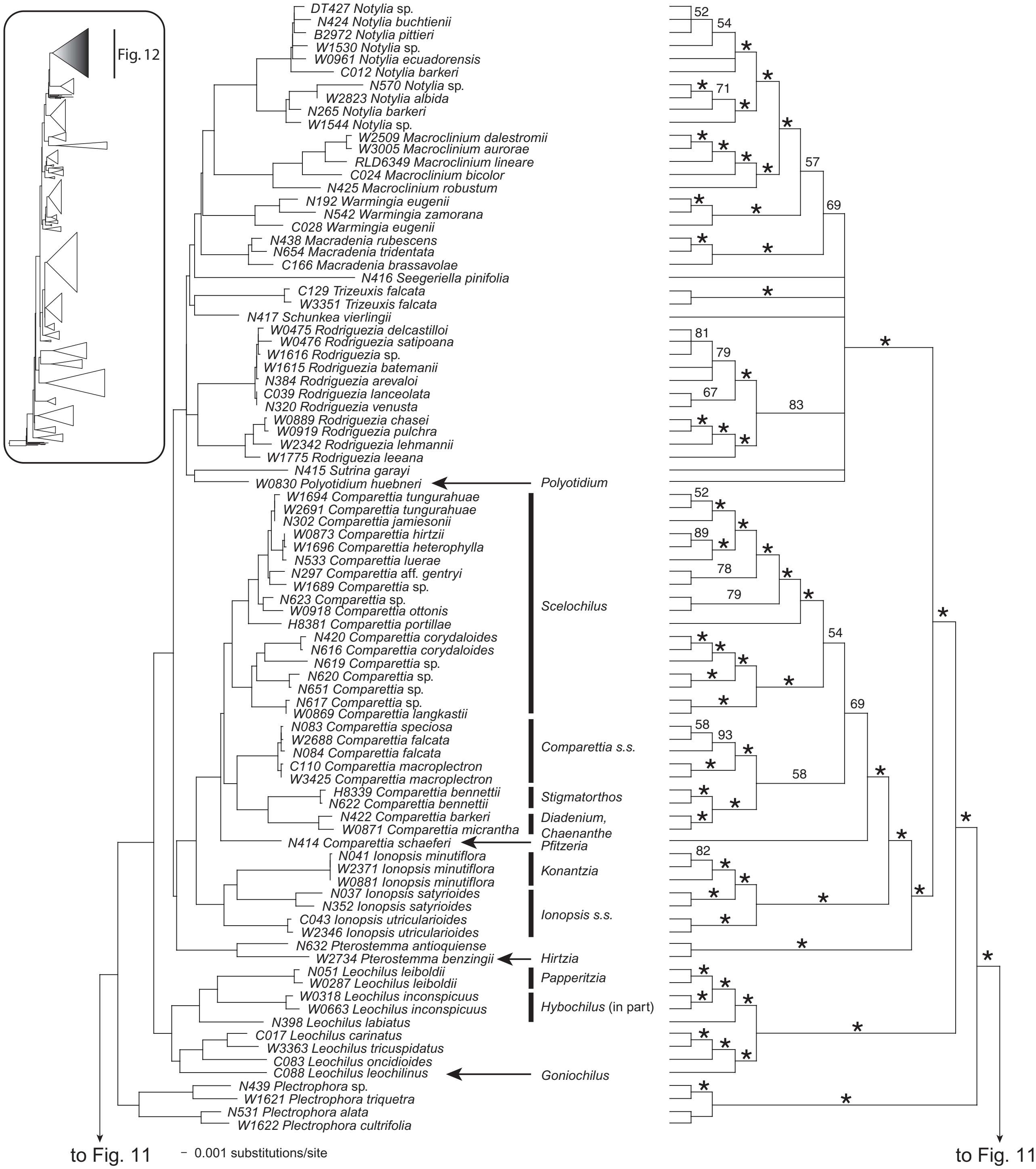

Figure 12. Continuation (*Plectrophora* to *Notylia*) of single maximum likelihood tree resulting from analysis of the combined five-region data set for 736 individuals. The tree on the right side of the figure displays bootstrap (BS) support > 50%; asterisks indicate 95–100% BS support. Generic segregates that we do not recognize and have lumped are indicated in the trees to the right of the accepted names.

Table 1. Genera of Oncidiinae recognized in the present study

Genera recognized in this paper	Figure number (of Fig. 5–12) where genus occurs in tree
Aspasia Lindl.	10
Brassia R.Br.	10
Caluera Dodson & Determann	Not sampled
Capanemia Barb.Rodr.	11
Caucaea Schltr.	9
Chytroglossa Rchb.f.	6
Cischweinfia Dressler & N.H.Williams	10
Comparettia Poepp. & Endl.	12
Cuitlauzina La Llave & Lex.	5
Cyrtochiloides N.H. Williams & M.W.Chase	9
Cyrtochilum Kunth	9
Eloyella P.Ortiz	6
Erycina Lindl.	10
Fernandezia Lindl.	6
Gomesa R.Br.	11
Grandiphyllum Docha Neto	5
Hintonella Ames	6
Hofmeisterella Rchb.f.	6
Ionopsis Kunth	12
Leochilus Knowles & Westc.	12
Lockhartia Hook.	5
Macradenia R.Br.	12
Macroclinium Barb.Rodr.	12
Miltonia Lindl.	10
Miltoniopsis God.-Leb.	9
Nohawilliamsia M.W.Chase & Whitten	11
Notylia Lindl.	12
Notyliopsis P.Ortiz	11
Oliveriana Rchb.f.	10
Oncidium Sw.	7,8
Ornithocephalus Hook.	6
Otoglossum (Schltr.) Garay & Dunst.	9
Phymatidium Lindl.	6
Platyrhiza Barb.Rodr.	Not sampled
Plectrophora H.Focke	12
Polyotidium Garay	12
Psychopsiella Lückel & Braem	5
Psychopsis Raf.	5
Pterostemma Kraenzl.	12
Rauhiella Pabst & Braga	Not sampled
Rhynchostele Rchb.f.	10
Rodriguezia Ruiz & Pav.	12
Rossioglossum (Schltr.) Garay & G.C.Kenn.	5
Saundersia Rchb.f.	5
Schunkea Senghas	12
Seegeriella Senghas	12
Solenidium Lindl.	11
Suarezia Dodson	Not sampled
Sutrina Lindl.	Not sampled
Systeloglossum Schltr.	10
Telipogon Kunth	6
Thysanoglossa Porto & Brade	Not sampled
Tolumnia Raf.	11
Trichocentrum Poepp. & Endl.	5
Trichoceros Kunth	6
Trichopilia Lindl.	5
Trizeuxis Lindl.	12
Vitekorchis Romowicz & Szlach.	7
Warmingia Rchb.f.	12
Zelenkoa M.W. Chase & N.H.Williams	11
Zygostates Lindl.	6

for inclusion in our analyses, although we feel its segregation into a monotypic genus is unwarranted. It may be a natural intergeneric hybrid between *Lockhartia* (probably *Lockhartia lepticaula* D.E.Benn. & Christenson) and a species of *Oncidium* or *Vitekorchis*; the elongate, nonbifid pollinarium stipe of *L. genegeorgei* is very different from that of other *Lockhartia* spp.

The following seven genera include taxa formerly placed in the monopopodial subtribes Pachyphyllinae (pollinia with two long stipes/caudicles) and Ornithocephalinae (four pollinia).

***Fernandezia* Lindl.** (approximately 50 spp.; Figs 1I, 2P, 6) has recently been re-circumscribed to include both *Pachyphyllum* and *Raycadenco* (Chase & Whitten, 2011). The monotypic *Raycadenco* has yellow and brown flowers with a tabula infrastigmatica typical of many oil-bee pollinated species of *Oncidium*, although the plants are monopodial (and therefore lack pseudobulbs), a habit shared with others in this clade. *Raycadenco* is sister to *Fernandezia* and *Pachyphyllum*. These latter two genera were previously distinguished on the basis of flower size and colour. *Pachyphyllum* has tiny white 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 them 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* just because it has oil-bee flowers when we disregard different pollination syndromes in other genera (e.g. *Cyrtochilum* Kunth, *Gomesa* R.Br., *Oncidium*, etc.).

The genera that we sampled comprising the former Ornithocephalinae are monophyletic in our trees, although several are represented by only a single sample (Figs 2K–N, 6): ***Phymatidium* Lindl.** (ten spp.), ***Zygostates* Lindl.** (20 spp.), ***Chytroglossa* Rchb.f.** (three spp.), ***Eloyella* P.Ortiz** (seven spp.), ***Hintonella* Ames** (one sp.) and ***Ornithocephalus* Hook.** (50 spp.). These genera possess tiny green to white or yellow flowers that secrete oil via labellar elaiophores and are pollinated by smaller genera of oil-collecting bees (Buchmann, 1987). Toscano de Brito & 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.** (five spp.), ***Caluera* Dodson & Determann** (three spp.), ***Rauhiella* Pabst & Braga** (three spp.), ***Platyrhiza* Barb.Rodr.** (one sp.) and ***Thysanoglossa* Porto & Brade** (two 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. His results also confirm the monophyly and inclusion in this clade of the other four genera. Although we do not recognize *Centroglossa* in this treatment, several of the species still need to be transferred to *Zygostates*.

Hofmeisterella **Rchb.f.** (one sp.; Fig. 6), ***Trichoceros*** **Kunth** (nine spp.; Figs 2U, 6) and ***Telipogon*** **Kunth** (170 spp.; Fig. 6) include species formerly placed in subtribe Telipogoninae on the basis of four pollinia (versus two in Oncidiinae) and pseudocopulatory flowers with furry columns and lip calli that are pollinated by male tachinid flies. 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 biphyletic 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).

Vitekorchis **Romowicz & Szlach.** (six spp.; Figs 1J, 7) is an Andean genus that is sister to *Oncidium* in our trees but without strong bootstrap 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* (*Oncidium boothianum* Rchb.f., *Oncidium iricolor* Rchb.f., *Oncidium obryzatum* Rchb.f.)

Oncidium **Sw.** (520 spp.; Figs 1K–O, 2I, J, O, S, 7, 8), as circumscribed broadly here, includes many previously recognized genera, including *Odontoglossum* Kunth, *Sigmatostalix* Rchb.f., *Cochlioda* Lindl., *Symphyglossum* Schltr., *Mexicoa* Garay, *Miltonioides* Brieger & Lückel and *Solenidiopsis* Senghas, and a number of recent, minor segregates such as *Chamaeleorchis* Senghas & Lückel, *Collare-stuartense* Senghas & Bockemühl 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 (*Oncidium 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* Lindl. and *Odontoglossum* Kunth, although such angles form a continuum and use of this single-character to define genera resulted in highly artificial classifications, as shown by Dressler & 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 reflect evolutionary shifts in pollinators. The traditional emphasis on floral features has resulted in many polyphyletic genera. Almost 50 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*, although this course seems to be inevitable, since the information gained from experiments in hybridization and from cytological studies strongly points in that direction’. We feel that it is better to use vegetative features in combination with a few floral traits to define broader genera. The molecular analyses demonstrate the high levels of homoplasy in pollinator-related traits. Most members of *Oncidium s.s.* are characterized by flowers 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 (Fig. 2I, J). *Cochlioda* and *Symphyglossum* represent adaptations for hummingbird pollination, with bright red/pink/purple tubular flowers (Fig. 2S). The lumping of *Sigmatostalix* within *Oncidium* seems initially inappropriate, although 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. 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 to diagnose using floral or vegetative traits.

A few species of *Oncidium* (e.g. *Oncidium echinops* Königer, *Oncidium heteranthum* Poepp. & Endl.; Fig. 7) produce branched inflorescences with terminal normal flowers on the branches, although the proximal flowers are abortive and sterile, consisting of only a cluster of yellow tepals that function as osmophores (W. M. Whitten, pers. observ.). In other species (*Oncidium pentadactylon* Lindl.), abortive flowers are terminal, with all other proximal flowers being normal. Szlachetko, Mytnik-Ejsmont & Romowicz (2006) described *Heteranthocidium* to accommodate these species, although 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. *Oncidium boothianum*, *Oncidium exalatum* Hágsater, *Oncidium fuscans* Rchb.f., *Oncidium pollardii* Dodson & Hágsater). All heteranthous species sampled here form a clade of 16 accessions (*Oncidium retusum* Lindl. to *Oncidium heterodactylum* Kraenzl., Fig. 7), although not all the species in this clade bear dimorphic flowers consistently (*O. retusum*, *Oncidium cultratum* Lindl., *Oncidium 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.** (15 spp.; Fig. 1S, T, 9) was originally regarded as a subgenus of *Odontoglossum* by Schlechter, although 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* sections *Serpentia* (Kraenzl.) Garay, *Brevilongium* Christenson and *Ecuadorella* Dodson & G.A.Romero. Before molecular data, a close relationship between *Otoglossum s.s* and *Oncidium* section *Serpentia* was totally unsuspected. *Otoglossum s.s.* bear many-flowered inflorescences arising laterally from pseudobulbs widely spaced on woody rhizomes (Jenny, 2010), whereas *Oncidium* section *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 that same as in *Otoglossum s.s.* The molecular data strongly support *Oncidium* section *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 & Romero created the 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 *Cyrtochilum*, to which *Otoglossum* is close).

Cyrtochiloides **N.H.Williams & M.W.Chase** (four spp.; Figs 1J, 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 *Cyrtochilum*; both have ovoid pseudobulbs rounded in cross-section (not angled) with two to six leaf-bearing subtending sheaths.

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

Caucaea **Schltr.** (five to 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*. Despite the floral similarity to *Oncidium*, they are not closely-related. *Caucaea* is sister to *Cyrtochilum*, 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.

Cyrtochilum **Kunth** (120 spp.; Figs 2C, E, G, H, 9) is restricted to the high Andes of Colombia and Venezuela south to Peru, with a single species, *Cyrtochilum meirax* (Rchb.f.) Dalström, occurring in the Caribbean (Dalström, 2001). Many species have long (3–4 m), vining inflorescences and large showy flowers (some with prominent elaiophores; Fig. 2G, H), although a few species have diminutive plants and flowers. Vegetatively, *Cyrtochilum* are distinguished by dull pseudobulbs that are round or ovoid in cross section with two to four apical leaves and two to six leaf-bearing sheaths and relatively thick roots; in contrast, *Oncidium* spp. have glossy, ancipitous (two-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 sank both *Odontoglossum* and *Cyrtochilum* into *Oncidium*, and Kraenzlin resurrected the genus in 1922. *Dasyglossum* Königer & Schildhauer and *Trigonochilum* Königer & Schildhauer were created to accommodate some of the smaller flowered *Cyrtochilum* spp., although 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, Górniak & Romowicz are simply diminutive and/or brightly coloured taxa embedded within *Cyrtochilum* (Dalström, 2001), probably reflecting a shift in pollinators, although there are few observations of pollination.

***Miltonia* Lindl.** (ten spp.; Fig. 10) occurs in Argentina, Brazil, Paraguay and Venezuela and is sister to a clade that includes *Systeloglossum* Schltr., *Oliveriana* Rchb.f., *Cischweinfia* Dressler & N.H.Williams, *Aspasia* Lindl. and *Brassia*. Some *Miltonia* species (e.g. *Miltonia regnellii* Rchb.f and *Miltonia spectabilis* Lindl.) have a short column and a broad, flat lip with a simple, reduced callus, although the floral morphology varies a great deal among the species. *Miltonia clowesii* (Lindl.) Lindl. has typical *Oncidium*-like oil-bee flowers, whereas *Miltonia candida* Lindl. and *Miltonia 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 abovementioned species with the author combination '(Lindl.) Lindl.' are the result of Lindley considering these to be species of *Cyrtochilum* 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 oncidioid 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* Christenson (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*.

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.** (five spp.; Fig. 10) has small, yellow–green or brownish–purple 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 bennetii* (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*.

***Oliveriana* Rchb.f.** (six 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 species of Oncidiinae). Plants are scandent, in contrast to the mostly caespitose habit of other genera in this clade.

***Cischweinfia* Dressler & N.H.Williams** (11 spp.; Fig. 10) grows in middle-elevation forests (up to 1500 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*, although the molecular data from this study clarified its generic placement (Chase & Whitten, 2011).

***Aspasia* Lindl.** (seven spp.; Fig. 10) ranges from Central America, northern South America and the Andes to coastal Brazil. It is vegetatively similar to *Brassia*, although 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 fragrance-reward male euglossine pollination in this clade (*Miltonia* to *Brassia*, Fig. 10).

***Brassia* R.Br.** (74 spp.; Figs 2Q, R, 10) includes *Brachtia*, *Ada* and *Mesospinidium*. Chase (2009b) treated these separately but indicated this to be unsatisfactory. These genera have been difficult to separate on the basis of floral and vegetative characters. *Brachtia* (seven spp., Andean) is sister to *Brassia s.s.* (*c.* 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 seven spp.), both ranging from Central America south through the Andes to Bolivia. *Ada* was originally monotypic and composed of a single hummingbird-pollinated species with bright orange to red flowers (Fig. 2Q), although Williams (1972) realized that it was morphologically similar to a clade of *Brassia* (the 'glumaceous' brassias). 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 aberrant phylogenetic position of *Ada allenii*, lumping them all into *Brassia* seems the simplest solution.

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.** (ten spp.; Figs 1U, 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 (Pérez-Hérnandez *et al*., 2011) and were at one time considered members of *Oncidium*. Although these three genera could be maintained, we favour lumping them to emphasize their similar floral morphology and modified habit (absence of an apical leaf on pseudobulbs, if pseudobulbs are present).

***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, 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.

***Gomesa* R.Br.** (125 spp.; Figs 1P–R, 11) as circumscribed here is relatively broad and includes at least 23 other generic concepts (Chase *et al*., 2009a; Chase, 2009b) with a great diversity of floral morphology and size. *Gomesa* has a centre of distribution in Brazil, especially the Mata Atlântica, where these species largely replace *Oncidium* (the genus in which most of them were once included), although it extends to northern Argentina and Amazonian Peru. Almost all species have fused lateral sepals, a trait that makes them easy to recognize despite their floral diversity. By 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), although 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. (*Oncidium longicornu* Mutel, *Oncidium macronyx* Rchb.f and *Oncidium rhinoceros* Rchb.f.; most workers lump these into a single species). He based the genus mostly upon the large, horn-like lip callus, although the 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.

***Capanemia* Barb. Rodr.** (seven spp.; Fig. 11) is represented in our analyses by only a single species, *Capanemia superflua* (Rchb.f.) Garay that is sister to *Solenidium* Lindl. Recent studies have reduced the number of species in the genus, although molecular data are needed to confirm whether the seven recognized species form a monophyletic group (Buzatto, Singer & van den Berg, 2010; Buzatto *et al*., 2011). The genus is centred in south-eastern Brazil, extending to Argentina and Uruguay. Florally, the genus is similar to unrelated *Leochilus* Knowles & Westc., although most species do not produce nectar, except

C. therezae Barb. Rodr. (Buzatto *et al*., 2011). Singer & Cocucci (1999) reported visits by halictid bees and vespid wasps. *Sanderella* also falls here (C. van den Berg, pers. comm.). Morphologically, *Sanderella* is similar to *Capanemia* (the oldest name) and should probably be combined with it. The exact status of *Sanderella* cannot be determined until it and more species of *Capanemia* are sampled.

***Solenidium* Lindl.** (three spp.; Fig. 11) is an Amazonian genus 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.

***Nohawilliamsia* M.W.Chase & Whitten** (one sp.; Figs 1V, 11) was created to accommodate a single odd species with no close or clear relatives based on our analyses thus far. It was formerly known as *Oncidium pirarense* Rchb.f. (synonym *Oncidium orthostates* Ridl.) from southern Venezuela, Guyana, Suriname and Brazil (Whitten, 2009; Chase, 2009a; Chase *et al*., 2009a). Although the flowers are similar to many yellow 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 these traits are unusual within Oncidiinae.

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

***Zelenkoa* M.W.Chase & N.H.Williams** (one sp.; Figs 1W, 11) was long considered an oddity when it was included in *Oncidium* (often in its own monotypic section), although molecular data revealed its distinctiveness. Like *Nohawilliamsia*, it 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.

***Tolumnia* Raf**. (40 spp.; Figs 1X, Y, 2D, 11) has long been recognized as a distinct group ('equitant' oncidiums) based on their psygmoid 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 (N. Williams, unpubl. data). Most species have oil-bee flowers that do not secrete oil; pollination by *Centris* bees is reported for several species (Nierenberg, 1972; Ackerman, Meléndez-Ackerman & Salguero Faria, 1997; Vale *et al*., 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, Lückel & 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), although this relationship is only weakly supported. In contrast to most twig epiphytes, *Tolumnia* spp. occur on the larger axes of trees and live for many years, rather than being restricted to terminal twigs with extremely rapid life cycles, although 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*; 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 (most likely for attachment to small twigs and rapid uptake of water) and 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, although the majority display many of these features. Twig epiphytes occur in other clades of Oncidiinae (e.g. *Erycina*; Fig. 10), and in other subtribes (e.g. *Dendrophylax porrectus* (Rchb.f.) Carlsward & Whitten, Angraecinae). None of the genera of the twig epiphyte clade (all genera in Fig. 12) is known to secrete oil or mimic oil flowers. Instead, they attract either nectar-seeking animals or are pollinated by fragrance-collecting male euglossine bees. ***Suarezia* Dodson** (one sp.) was not sampled, although it is presumed to be a member of this clade on the basis of its morphology.

***Plectrophora* H.Focke** (nine spp.; Fig. 12) is a genus of 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, although the flowers are probably pollinated by long-tongued insects seeking nectar.

***Leochilus* Knowles & Westc.** (12 spp.; Fig. 12) is a genus of 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*, although that of *Papperitzia* is highly divergent. Despite this, the single species of *Papperitzia* was originally included in *Leochilus*.

***Pterostemma* Kraenzl.** (two spp.; Fig. 12) is a genus of diminutive, extreme 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 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).

***Ionopsis* Kunth** (three 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.

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

***Polyotidium* Garay** (one 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* Ruiz & Pav., *Macroclinium* Barb. Rodr. and *Notylia*.

***Sutrina* Lindl.** (two 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, although morphology suggests pollination by nectar-foraging insects.

***Rodriguezia* Ruiz & Pav.** (48 spp.; Figs 2X, 12) ranges from Mexico south to Argentina, with one species (*Rodriguezia lanceolata* Ruiz & Pav.) found on many islands in the Caribbean. The flowers are relatively large, brightly coloured 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 *Rodriguezia decora* Rchb.f. in nrITS trees published in *Genera Orchidacearum*. This unusual Brazilian species was not included our sampling, although it may warrant generic status. It has long, wiry rhizomes between sympodia and lacks the spur found in other species.

***Schunkea* Senghas** (one sp.; Fig. 12) is known only from south-eastern Brazil; the small cream 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. The latter was not included in our sampling.

***Trizeuxis* Lindl.** (one 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, although presumed to be small nectar-foraging insects.

***Seegeriella* Senghas** (two 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* Rchb.f. 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 stigmatic slit, and the stigma is too narrow (W. M. Whitten, pers. observ.). 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**. (ten 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 head or eye of the bee.

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

***Macroclinium* Barb. Rodr.** (40 spp.; Figs 2Z, 12) ranges throughout much of the Neotropics from Mexico south to Peru and Brazil. The plants are diminutive extreme twig epiphytes, and are often found on cultivated *Citrus* and *Psidium*. The flowers are similar in morphology and function to its sister genus *Notylia*, although the two differ in inflorescence and vegetative habit. *Macroclinium* species are often monopodial, with small psygmoid fans generally lacking pseudobulbs. The inflorescence is pendent, pseudo-umbellate, with clusters of numerous delicate flowers with narrow sepals, petals and lip. Despite 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 (Dodson, 1967).

***Notylia* Lindl.** (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 a pseudobulb and relatively large conduplicate leaves. The flowers are similar to those of *Macroclinium*, although they are presented evenly spaced on a pendent, usually unbranched raceme. Pollination is also by fragrance-collecting male euglossine bees, with pollinarium deposition on the labrum or frons of the bee (Warford, 1992; Singer & Koehler, 2003; Pérez-Hérnandez *et al*., 2011).

CONCLUSION

The present 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* (Górniak, Paun & Chase, 2010) would be useful to increase support for the topology and improve 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 ‘oncidioid’ 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 noncladistic classifications of Oncidiinae were largely based 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. within *Trichocentrum s.l.*), although the phylogenetic hypotheses from the present study will be useful for framing such debates.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. List of voucher specimens and GenBank numbers. The DNA numbers correspond to individuals sequenced in Figs 3–12.

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