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INVITED PAPER*

GENERIC AND SUBTRIBAL RELATIONSHIPS IN NEOTROPICAL CYMBIDIEAE (ORCHIDACEAE) BASED ON *MATK/YCF1* PLASTID DATA

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Abstract. Relationships among all subtribes of Neotropical Cymbidieae (Orchidaceae) were estimated using combined *matK/ycf1* plastid sequence data for 289 taxa. The matrix was analyzed using RAxML. Bootstrap (BS) analyses yield 100% BS support for all subtribes except Stanhopeinae (87%). Generic relationships within subtribes are highly resolved and are generally congruent with those presented in previous studies and as summarized in *Genera Orchidacearum*. Relationships among subtribes are largely unresolved. The Szlachetko generic classification of Maxillariinae is not supported. A new combination is made for *Maxillaria cacaoensis* J.T.Atwood in *Camaridium*.

Key words: Orchidaceae, Cymbidieae, Maxillariinae, *matK, ycf1*, phylogenetics, *Camaridium, Maxillaria cacaoensis, Vargasiella*

Cymbidieae include many of the showiest Neotropical epiphytic orchids and an unparalleled diversity in floral rewards and pollination systems. Many researchers have posed questions such as "How many times and when has male euglossine bee pollination evolved?"(Ramírez *et al*. 2011), or "How many times have oil-reward flowers evolved?" (Reis *et al.* 2000) within this clade, but answering such questions requires a densely sampled and well-supported phylogenetic hypothesis. Although the broad outlines of relationships within Cymbidieae were revealed by the *rbcL/matK* analyses of Freudenstein *et al.* (2004) and summaries of Chase *et al.* (2003), both of these studies were constrained by low taxon sampling and low bootstrap support for many clades. The most recent publication of the *Genera Orchidacearum* series (Pridgeon 2009) provided a concise and authoritative summary of knowledge of this clade that includes 11 subtribes. Phylogenetic trees for Neotropical Cymbidieae published in that volume were based upon our nrITS/*matK*/*ycf1* data sets that were unpublished and included many sequences not deposited in GenBank. In attempting to rework these data for publication, we decided that attempting to align nrITS sequences across the entire tribe was unrealistic due to high levels of sequence divergence, and instead to concentrate our efforts on assembling a larger plastid data set based on two regions (*matK* and *ycf1*) that are among the most variable plastid exon regions and can be aligned with minimal ambiguity across broad taxonomic spans. Although various plastid spacer regions such as *trnL-F* or *atpB-rbcL* are more rapidly evolving (Shaw *et al.* 2005), they (like nrITS) are difficult or impossible to align with confidence across Cymbidieae. In this paper, we present phylogenetic analyses of ca. 280 taxa of Cymbidieae including representatives of 10 subtribes and most genera (excluding many Oncidiinae) utilizing the majority of the *matK* exon and a ca. 1500 base pair (bp) portion of the 3' end of *ycf1*. Phylogenetic relationships within Oncidiinae were addressed in detail by Neubig *et al.* (2012). Relationships within Maxillariinae were studied using nrITS/*matK*/*atpB-rbcL* spacer by Whitten *et al.*(2007), and the *Bifrenaria* clade was analyzed in more detail using nrITS/*trnL-F* by Koehler *et al.* (2002). Zygopetalinae relationships were previously studied using nrITS/*matK*/*trnL-F* (Neubig *et al.*, 2009b; Whitten *et al.*, 2005).

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Methods

Most *matK* sequences were downloaded from GenBank from previous studies of Cymbidieae subtribes. Additional sequences were generated using primers *matK*-19F (CGTTCTGACCATATTGCACTATG) and *matK* 1520R (CGGATAATGTCCAAATACCAAATA) and the amplification and sequencing protocols of Whitten *et al.* (2007). A ca. 1500 bp portion of 3' portion of *ycf1* was amplified and sequenced using the primers and protocols in Neubig *et al.* (2009a). A list of taxa, vouchers, and GenBank numbers is presented in Table 1. Matrices were aligned using Muscle (Edgar, 2004)followed by manual adjustment of gaps to maintain reading frame using Se-Al (Rambaut 1996). The *matK* matrix was trimmed to eliminate a region of ambiguous alignment in the first 100 bp. *Polystachya* was chosen as the outgroup based upon broader sampling (Neubig *et al.* 2009a). Matrices and a list of vouchers are deposited in the Dryad Digital Repository (http://doi.org/10.5061/dryad.2rm60) or are available from the author. The resulting combined matrix consists of 288 ingroup taxa and 1 outgroup (*Polystachya*); the aligned matrix consists of 3618 characters (1605 for *matK*; 2013 for *ycf1*). Gaps are coded as missing data.

The aligned matrix was analyzed using maximum likelihood (ML) as implemented in RAxML-HPC Blackbox version 7.6.3 (Stamatakis, 2006) via the CIPRES Science Gateway computing facility (http://www.phylo.org/index.php/portal/). Analyses were run using default values with 200 fast bootstrap replicates. The resulting bootstrap trees were saved to a treefile, opened in PAUP* (Swofford 2003), and a majority-rule consensus tree was generated to display bootstrap support values. FigTree 1.4.0 (Rambaut 2013) was used to edit and print the best ML tree.

Results and Discussion

The resulting best ML tree is presented in Figures 1-5; bootstrap (BS) values above 75% are annotated on this tree. Overall, the tree agrees well with previous studies based on plastid and nuclear regions (Górniak *et al.* 2010). Subtribe Cymbidiinae is represented by only a single taxon (*Cymbidium*); it is sister to all remaining taxa. All subtribes (as delimited in *Genera Orchidacearum*) received 100% BS support (except for Stanhopeinae), but most relationships among subtribes lack BS support.

Eulophiinae — (Fig. 1). Out of the nine genera recognized in this subtribe, our sampling included the only two Neotropical genera; the majority of species are from the tropics of Africa, Madagascar, Asia, and Australia. Eulophiinae are weakly sister to Catasetinae in the single ML tree.

Catasetinae — (Fig. 1). Recent molecular phylogenetic studies (Batista et al., In press) place the three species of *Cyanaeorchis* Barb.Rodr. in Catasetinae; it is sister to *Grobya* Lindl., and they are sister to all remaining Catasetinae. Our sampling includes five of the seven genera, with *Grobya* and *Mormodes* absent; other phylogenetic studies confirm *Grobya* as monophyletic and a member of Catasetinae (Monteiro *et al.* 2010). Unpublished *ycf1* and *matK* sequences for *Cyanaeorchis arundinae* (Rchb.f.) Barb.Rodr. and unidentified *Grobya* species (Whitten and Batista, unpubl.) confirm these relationships. Oscar Peréz (pers. comm.) also reported finding plastid/nuclear incongruence among sections of *Cycnoches*.

Cyrtopodiinae — (Fig. 1). Our analyses confirm the distinctiveness of this monogeneric subtribe from the vegetatively similar Catasetinae; *Cyrtopodium* is weakly sister to all remaining Cymbidieae, and not to Catasetinae, confirming the relationships found by Pridgeon and Chase (Pridgeon & Chase 1998).

Oncidiinae — (Fig. 1). Our sampling of Oncidiinae was minimal, including placeholder representatives of the major clades within the subtribe; a much more extensive sampling based on *matK/ycf1* plus other regions was presented by Neubig *et al.* (2012). Oncidiinae are in a highly supported clade that includes subtribes Eriopsidinae, Zygopetalinae, Stanhopeinae, Coeliopsidinae, and Maxillariinae but relationships within this clade are poorly supported.

Eriopsidinae — (Fig. 2). Dressler (1981) included *Eriopsis* in Cyrtopodiinae on the basis of floral traits and pollinarium structure but later regarded it as *incertae sedis* (Dressler 1993). Szlachetko (1995) created a subtribe to accommodate this anomalous genus; our trees confirm its uniqueness relative to other subtribes.

TABLE 1. List of taxa sequenced with GenBank numbers and voucher information.

Taxon	***matK***	***ycf1***	**Voucher:Herbarium**
Acineta chrysantha (C. Morren) Lindl.	KF660253	KF660372	Whitten 91360 (FLAS)
Acineta superba (Kunth) Rchb.f.	KF660254	KF660523	Whitten 3378 (FLAS)
Aetheorhyncha andreettae (Jenny) Dressler	AY869932	KF660386	Dressler 6360 (FLAS)
Aganisia fimbriata Rchb.f.	AY870006	KF660404	Breuer s.n. (M)
Aganisia pulchella Lindl.	AY870007	KF660403	Breuer s.n. (M)
Anguloa hohenlohii C. Morren	AF239429	KF660512	Whitten 3023 (FLAS)
Anguloa uniflora Ruiz & Pav.	KF660255	KF660364	Whitten 3263 (FLAS)
Batemannia lepida Rchb.f.	AY869990	KF660323	Gerlach 92-3900 (M)
Benzingia cornuta (Garay) Dressler	AY869927	KF660450	Whitten 1818 (FLAS)
Benzingia estradae (Dodson) Dodson	AY869930	KF660398	Gerlach 96-4287 (M)
Benzingia hajekii (D.E.Benn. & Christenson) Dressler	AY869929	KF660377	Whitten 1751 (FLAS)
Benzingia reichenbachiana (Schltr.) Dressler	AF239421	KF660363	Whitten 1747 (FLAS)
Bifrenaria inodora Lindl.	DQ210744	KF660365	Whitten 0097 (FLAS)
Bifrenaria tetragona (Lindl.) Schltr.	DQ210751	KF660529	Whitten 0506 (FLAS)
Bifrenaria tyrianthina (Lodd. ex Loudon) Rchb.f.	DQ210752	KF660379	Whitten 0507 (FLAS)
Braemia vittata (Lindl.) Jenny	AF239476	KF660338	Chase 84748 (FLAS)
Brasiliorchis gracilis (Lodd.) R. B. Singer, S. Koehler & Carnevali	DQ210811	KF660426	Whitten 2303 (FLAS)
Brasiliorchis schunkeana (Campacci & Kautsky) R. B. Singer, S. Koehler & Carnevali	DQ210799	KF660421	Whitten 1992 (FLAS)
Brassia aurantiaca (Lindl.) M.W.Chase	AF239492	FJ563573	Williams s.n. (FLAS)
Brassia jipijapensis Dodson & N.H.Williams	FJ564762	FJ563258	Whitten 1829 (FLAS)
Camaridium bradeorum Schltr.	DQ210963	KF660468	Whitten 2639 (FLAS)
Camaridium carinatum (Barb.Rodr.) Hoehne	DQ210828	KF660431	Whitten 2337 (FLAS)
Camaridium ctenostachys (Rchb.f.) Schltr.	DQ210967	KF660471	Whitten 2647 (FLAS)
Camaridium cucullatum (Lindl.) M.A Blanco	DQ210753	KF660354	Whitten 2547 (FLAS)
Camaridium dendrobioides Schltr.	DQ210952	KF660463	Whitten 2627 (FLAS)
Camaridium horichii (Senghas) M.A. Blanco	DQ210937	KF660461	Whitten 2602 (FLAS)
Camaridium nutantiflorum Schltr.	DQ210964	KF660469	Whitten 2643 (FLAS)
Camaridium ochroleucum Lindl.	DQ210626	KF660312	Gerlach 2003-3648 (M)
Camaridium paleatum (Rchb.f.) M.A.Blanco	DQ210907	KF660458	Whitten 2561 (FLAS)
Camaridium scalariforme (J.T.Atwood) M.A.Blanco	DQ210957	KF660466	Whitten 2633 (FLAS)
Camaridium vestitum (Sw.) Lindl.	DQ209866	KF660304	Atwood & Whitten 5070 (SEL)
Catasetum expansum Rchb.f.	KF660256	KF660525	Whitten 3543 (FLAS)
Chaubardia klugii (C.Schweinf.) Garay	AY869973	KF660378	Whitten 1853 (FLAS)
Chaubardia surinamensis Rchb.f.	AY869974	KF660309	Gerlach 2001-2159 (M)
Chaubardiella pubescens Ackerman	AY869944	KF660416	Whitten 1620 (FLAS)
Chaubardiella subquadrata (Schltr.) Garay	AY869945	KF660407	Whitten s.n. (FLAS)
Chaubardiella tigrina (Garay & Dunst.) Garay	AY869946	KF660311	Gerlach 1651 (M)
Chondrorhyncha hirtzii Dodson	AY869916	KF660389	Whitten 1637 (FLAS)
Chondrorhyncha hirtzii Dodson	AY869913	KF660406	Maduro & Olmos 217 (FLAS)
Chondrorhyncha rosea Lindl.	AY869914	KF660385	Whitten 1760 (FLAS)

TABLE 1. Continues.

Taxon	***matK***	***ycf1***	**Voucher:Herbarium**
Chondroscaphe amabilis (Schltr.) Senghas & G.Gerlach	AY869966	KF660391	Whitten 1855 (FLAS)
Chondroscaphe bicolor (Rolfe) Dressler	AY869971	KF660390	Dressler ex Hoffman s.n. (FLAS)
Chondroscaphe eburnea (Dressler) Dressler	AY869915	KF660408	Dressler 6361 (FLAS)
Chondroscaphe flaveola (Linden & Rchb.f.) Senghas & G.Gerlach	AY869969	KF660320	Gerlach 93-3342 (M)
Christensonella ferdinandiana (Barb.Rodr.) Szlach., Mytnik, Górniak & Smiszek	DQ210670	KF660353	Koehler 109 (UEC)
Christensonella nardoides (Kraenzl.) Szlach., Mytnik, Górniak & Smiszek	DQ210890	KF660452	Whitten 2502 (FLAS)
Christensonella pacholskii (Christenson) S.Koehler	DQ210851	KF660437	Whitten 2393 (FLAS)
Cirrhaea fuscolutea Lindl.	KF660257	KF660508	Whitten 2976 (FLAS)
Cirrhaea seidelii Pabst	KF660258	KF660333	Gerlach s.n. (M)
Cischweinfia pusilla (C.Schweinf.) Dressler & N.H.Williams	FJ565130	FJ563799	Whitten 3300 FLAS
Clowesia dodsoniana E.Aguirre	KF660259	KF660524	Whitten 3542 (FLAS)
Cochleanthes flabelliformis (Sw.) R.E.Schult. & Garay	AY869965	KF660513	Whitten 99113 (FLAS)
Coeliopsis hyacinthosma Rchb.f.	AF239440	KF660337	Whitten 93153 (FLAS)
Comparettia falcata Poepp. & Endl.	FJ563869	FJ563283	Williams N084 (FLAS)
Comparettia macroplectron Rchb.f. & Triana	FJ565135	FJ563804	Whitten 3425 (FLAS)
Coryanthes elegantium Linden & Rchb.f.	KF660260	KF660318	Whitten 87267 (FLAS)
Coryanthes macrantha (Hook.) Hook.	KF660261	KF660319	Gerlach O-21458 (M)
Coryanthes verrucolineata G.Gerlach	KF660262	KF660317	Gerlach 96-4284 (M)
Cryptarrhena guatemalensis Schltr.	AY869983	KF660476	Pupulin & Campos 2957 (USJ)
Cryptarrhena lunata R.Br.	AY869982	KF660405	Whitten 98000 (FLAS)
Cryptocentrum beckendorfii Carnevali	KF660263	KF660307	Beckendorf s.n. (CICY)
Cryptocentrum peruvianum (Cogn.) C.Schweinf.	DQ210820	KF660430	Whitten 2322 (FLAS)
Cryptocentrum roseans (Schltr.) A.D.Hawkes	DQ210903	KF660457	Whitten 2554 (FLAS)
Cycnoches cooperi Rolfe	KF660264	KF660526	Whitten 3591 (FLAS)
Cycnoches lehmannii Rchb.f.	KF660265	KF660328	Whitten 87011 (FLAS)
Cycnoches manoelae P.Castro & Campacci	KF660266	KF660310	Gerlach 05-1231 (M)
Cycnoches pachydactylon Schltr.	KF660267	KF660316	Gerlach 00-3414 (M)
Cymbidium devonianum Paxton	KF660268	KF660325	Chase 87030 (K)
Cyrtidiorchis alata (Ruiz & Pav.) Rauschert	DQ210627	KF660321	Gerlach 94-4005 (M)
Cyrtidiorchis alata (Ruiz & Pav.) Rauschert	DQ211044	KF660505	Whitten 2932 (FLAS)
Cyrtochilum serratum (Lindl.) Kraenzl.	FJ563842	FJ562462	Chase O-032 (K)
Cyrtopodium andersonii (Lamb. ex Andrews) R.Br.	KF660269	KF660329	Kew no voucher
Cyrtopodium flavum (Nees) Link & Otto ex Rchb.	KF660270	KF660522	Whitten 3377 (FLAS)
Cyrtopodium longibulbosum Dodson & G.A.Romero	KF660271	KF660453	Whitten 2504 (QCA)
Daiotyla albicans (Rolfe) Dressler	AY869917	KF660396	Whitten 1932 (FLAS)
Dichaea eligulata Folsom	EU123625	EU123747	Pupulin 1094 (USJ-L)
Dichaea fragrantissima Folsom	EU123628	EU123750	Pupulin 4601 (USJ-L)
Dichaea panamensis Lindl.	EU123650	EU123772	Whitten 2556 (FLAS)
Dichaea trulla Rchb.f.	EU123671	EU123792	Whitten 2475 (FLAS)

Table 1. Continues.

Taxon	***matK***	***ycf1***	**Voucher:Herbarium**
Dipteranthus grandiflorus (Lindl.) Pabst	AF350587	FJ563191	Chase O-103 (K)
Dressleria dilecta (Rchb.f.) Dodson	AF239507	EU490731	Whitten F1046 (SEL)
Dressleria fragrans Dodson	KF660272	KF660327	Dodson 8855 (SEL)
Dressleria helleri Dodson	KF660273	KF660326	Hills 87145 (FLAS)
Embreea herrenhusana (Jenny) Jenny	KF660275	KF660314	Gerlach 04-2526 (M)
Embreea rodigasiana (Claes ex Cogn.) Dodson	KF660276	KF660313	Gerlach 05-2172 (M)
Eriopsis biloba Lindl.	DQ210866	EU490743	Whitten 3327 (FLAS)
Eriopsis biloba Lindl.	DQ210866	KF660441	Whitten 2439 (FLAS)
Eriopsis biloba Lindl.	DQ461806	KF660515	Whitten 3153 (QCA)
Erycina pusilla (L.) N.H.Williams & M.W.Chase	FJ565025.	FJ563690	Whitten 1771 FLAS
Eulophia guineensis Lindl.	AF239509	EU490745	Whitten 99029 (FLAS)
Eulophia petersii (Rchb.f.) Rchb.f.	KF660274	KF660332	Chase 22361 (K)
Fernandezia cuencae (Rchb.f.) M.W.Chase	FJ565079	KF660454	Whitten 2537 (FLAS)
Fernandezia sanguinea (Lindl.) Garay & Dunst.	FJ565009	FJ563674	Whitten 1700 FLAS
Fernandezia tica Mora-Ret. & García Castro	FJ564944	FJ563591	Dressler & Atwood s.n. FLAS
Galeandra devoniana M.R.Schomb. ex Lindl.	KF660278	KF660330	Pupulin 1133 (JBL)
Galeottia burkei (Rchb.f.) Dressler & Christenson	AY869987	KF660400	Maguire & Politi 28175 (AMES)
Galeottia ciliata (Morel) Dressler & Christenson	AY869989	KF660401	Breuer s.n. (M)
Galeottia colombiana (Garay) Dressler & Christenson	AY869986	KF660397	Gerlach 93-3396 (M)
Gongora amparoana Schltr.	AF239481	KF660367	Whitten 91036 (FLAS)
Gongora armeniaca (Lindl.) Rchb.f.	AF239482	KF660334	Hills 86143 (FLAS)
Gongora armeniaca (Lindl.) Rchb.f.	AF239482	KF660374	Whitten F1636 (FLAS)
Gongora escobariana Whitten	KF660279	KF660347	Whitten 95023 (FLAS)
Gongora hirtzii Dodson & N.H.Williams	KF660280	KF660349	Whitten 93109 (FLAS)
Gongora ilense Whitten & Jenny	AF239480	KF660509	Whitten 2982 (FLAS)
Gongora portentosa Linden & Rchb.f.	AF239485	KF660341	Bennett 5258 (FLAS)
Gongora portentosa Linden & Rchb.f.	KF660281	KF660350	Bennett 5279 (FLAS)
Gongora seideliana Rchb.f.	KF660282	KF660348	Whitten F-1635 (FLAS)
Gongora sphaerica Jenny	KF660283	KF660331	Whitten 2003 (FLAS)
Gongora tridentata Whitten	AF239483	KF660373	Whitten 1083 (FLAS)
Grandiphyllum robustissimum (Rchb.f.) Docha Neto	FJ563959	FJ563597	Whitten 1777 FLAS
Guanchezia maguirei (C.Schweinf.) G.A.Romero & G.Carnevali	KF660284	KF660410	Maguire & Politi 27931 (AMES)
Heterotaxis crassifolia Lindl.	DQ210897	KF660455	Whitten 2544 (FLAS)
Heterotaxis equitans (Schltr.) Ojeda & Carnevali	DQ210877	KF660448	Whitten 2483 (FLAS)
Heterotaxis maleolens (Schltr.) Ojeda & Carnevali	DQ209972	KF660486	Whitten 2764 (FLAS)
Heterotaxis santanae (Carnevali & I.Ramírez) Ojeda & Carnevali	DQ209973	KF660487	Whitten 2765 (FLAS)
Heterotaxis valenzuelana (A.Rich.) Ojeda & Carnevali	DQ210950	KF660510	Whitten 2620 (FLAS)
Heterotaxis violaceopunctata (Rchb.f.) F.Barros	DQ210807	KF660424	Whitten 2294 (FLAS)
Hintonella mexicana Ames	FJ564940	FJ562874	Whitten W513 (FLAS)
Horichia dressleri Jenny	AF239458	KF660340	Whitten 93151 (FLAS)

TABLE 1. Continues.

Taxon	***matK***	***ycf1***	**Voucher:Herbarium**
Houlletia brocklehurstiana Lindl.	KF660285	KF660335	Gerlach s.n. (M)
Houlletia odoratissima Linden ex Lindl. & Paxton	KF660286	KF660315	Gerlach 97-3285 (M)
Houlletia sanderi Rolfe	AF239467	KF660376	Whitten 93079 (FLAS)
Houlletia tigrina Linden ex Lindl.	AF239466	KF660375	Whitten 91354 (FLAS)
Huntleya wallisii (Rchb.f.) Rolfe	EU123674	EU123796	Whitten 88026 (FLAS)
Hylaeorchis petiolaris (Schltr.) Carnevali & G.A.Romero	DQ211020	KF660352	Whitten 2874 (FLAS)
Inti bicallosa (Rchb.f.) M.A.Blanco	DQ209946	KF660417	Whitten 1677 (FLAS)
Inti bicallosa (Rchb.f.) M.A.Blanco	DQ210960	KF660467	Whitten 2636 (FLAS)
Inti chartacifolia (Ames & C.Schweinf.) M.A.Blanco	DQ209942	EU490750	Whitten 1597 (FLAS)
Inti chartacifolia (Ames & C.Schweinf.) M.A.Blanco	DQ211000	KF660485	Whitten 2752 (FLAS)
Ixyophora viridisepala (Senghas) Dressler	AY869942	KF660418	Whitten 1749 (FLAS)
Kefersteinia excentrica Dressler & Mora-Ret.	AY869934	KF660507	Dressler 6236 (FLAS)
Kefersteinia maculosa Dressler	AY869938	KF660422	Whitten 1997 (FLAS)
Kefersteinia microcharis Schltr.	AY869937	KF660308	Pupulin 252 (USJ)
Kefersteinia trullata Dressler	AY869936	KF660423	Whitten 1998 (FLAS)
Kegeliella atropilosa L.O.Williams & A.H.Heller	AF239459	KF660342	Whitten 93101 (FLAS)
Kegeliella kupperi Mansf.	AF263666	KF660339	Whitten F167 (FLAS)
Koellensteinia graminea (Lindl.) Rchb.f.	AY870003	KF660429	Chase 159 (K)
Lacaena spectabilis (Klotzsch) Rchb.f.	KF660287	KF660346	Whitten F-184 (FLAS)
Lockhartia amoena Endres & Rchb.f.	FJ564686	FJ563116	Blanco 1803 (FLAS)
Lueckelia breviloba (Summerh.) Jenny	KF660288	KF660382	Gerlach 96-6072 (M)
Lueddemannia pescatorei (Lindl.) Linden & Rchb.f.	AF239472	KF660488	Gerlach 2003-1482(M)
Lycaste aromatica (Graham) Lindl.	AF263669	KF660322	Freudenstein s.n.
Lycomormium fiskei H.R.Sweet	AF239441	KF660528	Whitten 91340 (FLAS)
Mapinguari auyantepuiensis (Foldats) Carnevali & R.B.Singer	DQ210830	KF660432	Whitten 2347 (FLAS)
Mapinguari longipetiolatus (Ames & C.Schweinf.) Carnevali & R.B.Singer	DQ210747	KF660305	Atwood & Whitten 5075 (SEL)
Maxillaria acostae Schltr.	DQ210965	KF660470	Whitten 2644 (FLAS)
Maxillaria angustissima Ames, F.T.Hubb. & C.Schweinf.	DQ210993	KF660479	Whitten 2735 (FLAS)
Maxillaria augustae-victoriae F.Lehm.&Kraenzl.	DQ211026	KF660500	Whitten 2893 (FLAS)
Maxillaria brachybulbon Schltr.	DQ210773	KF660414	Whitten 1583 (FLAS)
Maxillaria buchtienii Schltr.	DQ211047	KF660506	Whitten 2940 (FLAS)
Maxillaria cacaoensis J.T.Atwood	KC747493	KC747494	Whitten 3362 (FLAS)
Maxillaria calantha Schltr.	DQ210900	KF660456	Whitten 2550 (FLAS)
Maxillaria canarina D.E.Benn. & Christenson	KF660289	KF660518	Whitten 3256 (FLAS)
Maxillaria chionantha J.T.Atwood	DQ210969	KF660472	Whitten 2649 (FLAS)
Maxillaria confusa Ames & C.Schweinf.	DQ210994	KF660480	Whitten 2736 (FLAS)
Maxillaria dalessandroi Dodson	DQ211024	KF660499	Whitten 2889 (FLAS)
Maxillaria dillonii D.E.Benn. & Christenson	KF660290	KF660496	Whitten 2878 (FLAS)
Maxillaria ecuadorensis Schltr.	DQ210989	KF660478	Whitten 2724 (FLAS)
Maxillaria elegantula Rolfe	DQ210921	KF660460	Whitten 2576 (FLAS)

TABLE 1. Continues.

Taxon	*matK*	*ycf1*	Voucher:Herbarium
Maxillaria exaltata (Kraenzl.) C.Schweinf.	DQ210818	KF660428	Whitten 2317 (FLAS)
Maxillaria gentryi Dodson	DQ210975	KF660475	Whitten 2656 (FLAS)
Maxillaria grayi Dodson	KF660291	KF660497	Whitten 2879 (FLAS)
Maxillaria guadalupensis Cogn.	DQ210775	KF660415	Whitten 1593 (FLAS)
Maxillaria guadalupensis Cogn.	KF660292	KF660445	Whitten 2468 (FLAS)
Maxillaria hennisiana Schltr.	DQ210918	KF660459	Whitten 2572 (FLAS)
Maxillaria litensis Dodson	KF660293	KF660498	Whitten 2888 (FLAS)
Maxillaria longipes Lindl.	DQ210999	KF660484	Whitten 2751 (FLAS)
Maxillaria longissima Lindl.	DQ210996	KF660482	Whitten 2745 (FLAS)
Maxillaria lueri Dodson	DQ210954	KF660464	Whitten 2629 (FLAS)
Maxillaria meridensis Lindl.	DQ210870	KF660443	Whitten 2451 (FLAS)
Maxillaria ochroleuca Lodd. ex Lindl.	DQ210844	KF660435	Whitten 2378 (FLAS)
Maxillaria platypetala Ruiz & Pav.	DQ211033	KF660502	Whitten 2909 (FLAS)
Maxillaria porrecta Lindl.	DQ210948	KF660462	Whitten 2617 (FLAS)
Maxillaria pulla Linden & Rchb.f.	DQ210872	KF660444	Whitten 2459 (FLAS)
Maxillaria silvana Campacci	DQ210997	KF660483	Whitten 2747 (FLAS)
Maxillaria sp. nov.	KF660294	KF660520	Whitten 3337 (FLAS)
Maxillaria splendens Poepp. & Endl.	FJ565112	FJ563781	Whitten 2949 FLAS
Maxillaria triloris E.Morren	DQ209887	KF660411	Blanco 1640 (USJ)
Maxillaria triloris E.Morren	DQ211038	KF660503	Whitten 2917 (FLAS)
Maxillariella arbuscula (Lindl.) M.A.Blanco & Carnevali	DQ211013	KF660491	Whitten 2810 (FLAS)
Maxillariella elatior (Rchb.f.) M.A.Blanco & Carnevali	DQ210797	KF660420	Whitten 1986 (FLAS)
Maxillariella oreocharis (Schltr.) M.A.Blanco & Carnevali	DQ210971	KF660473	Whitten 2652 (FLAS)
Maxillariella ponerantha (Rchb.f.) M.A.Blanco & Carnevali	DQ210973	KF660474	Whitten 2654 (FLAS)
Maxillariella procurrens (Lindl.) M.A.Blanco & Carnevali	DQ210854	KF660438	Whitten 2397 (FLAS)
Maxillariella variabilis (Bateman ex Lindl.) M.A.Blanco & Carnevali	DQ210995	KF660481	Whitten 2737 (FLAS)
Miltonia regnellii Rchb.f.	AF239491	FJ563571	Chase 86059 (K)
Mormolyca peruviana C.Schweinf.	DQ210885	KF660451	Whitten 2497 (FLAS)
Mormolyca polyphylla Garay & Wirth	DQ211009	KF660489	Whitten 2789 (FLAS)
Mormolyca richii (Dodson) M.A.Blanco	DQ210836	KF660434	Whitten 2362 (FLAS)
Mormolyca ringens (Lindl.) Gentil	DQ210680	KF660493	Whitten 2857 (FLAS)
Mormolyca schlimii (Linden & Rchb.f.) M.A.Blanco	DQ210847	KF660436	Whitten 2386 (FLAS)
Neogardneria murrayana (Gardner ex Hook.) Schltr. ex Garay	AY869997	KF660402	Gerlach s.n. (M)
Neomoorea wallisii (Rchb.f.) Schltr.	DQ210743	EU490754	Whitten 3010 (FLAS)
Nitidobulbon nasutum (Rchb. f.) I.Ojeda & Carnevali	DQ210756	KF660419	Whitten 1869 (FLAS)
Nitidobulbon proboscideum (Rchb. f.) I.Ojeda & Carnevali	DQ209857	KF660303	Atwood & Whitten 5056 (SEL)
Notyliopsis beatricis P.Ortiz	FJ565086	FJ563753	Whitten 2674 FLAS
Oeceoclades maculata (Lindl.) Lindl.	KF660295	KF660519	Whitten 3333 (FLAS)
Oncidium cirrhosum (Lindl.) Beer	FJ563845	FJ562480	Chase 86235 (K)
Oncidium sphacelatum Lindl.	FJ563863	FJ563267	Whitten 3467 (FLAS

Table 1. Continues.

Taxon	***matK***	***ycf1***	**Voucher:Herbarium**
Oncidium weinmannianum (Königer) M.W. Chase & N.H. Williams	FJ565036	FJ563701	Whitten 2328 FLAS
Ornithidium aggregatum Rchb.f.	DQ210880	KF660449	Whitten 2488 (FLAS)
Ornithidium canarense (J.T.Atwood) M.A.Blanco & Ojeda	DQ209959	KF660440	Whitten 2437 (FLAS)
Ornithidium coccineum (Jacq.) Salisb. ex R.Br.	DQ209875	KF660494	Whitten 2860 (FLAS)
Ornithidium donaldeedodii Ackerman & Whitten	KF660296	KF660527	Forbes s.n. (UC)
Ornithidium fulgens Rchb.f.	DQ209968	KF660465	Whitten 2630 (FLAS)
Ornithidium giganteum Lindl.	DQ210817	KF660427	Whitten 2316 (FLAS)
Ornithidium multicaule (Poepp. & Endl.) Rchb.f.	DQ211032	KF660501	Whitten 2905 (FLAS)
Ornithidium serrulatum Lindl.	DQ211010	KF660490	Whitten 2800 (FLAS)
Ornithidium sophronitis Rchb.f.	DQ210809	KF660425	Whitten 2296 (FLAS)
Ornithocephalus dalstroemii (Dodson) Toscano & Dressler	FJ564705	FJ563134	Blanco 2980 FLAS
Ornithocephalus dalstroemii (Dodson) Toscano & Dressler	FJ564705	FJ563761	Blanco 2980 FLAS
Ornithocephalus inflexus Lindl.	DQ315891	FJ563120	Blanco 2545 (FLAS)
Otoglossum globuliferum (Kunth) N.H.Williams & M.W.Chase	FJ564700	FJ563129	Blanco 2856 (FLAS)
Otoglossum globuliferum (Kunth) N.H.Williams & M.W.Chase	FJ564700	FJ563129	Blanco 2856 FLAS
Otostylis lepida (Linden & Rchb.f.) Schltr.	AY870009	KF660399	Gerlach 94-968 (M)
Otostylis paludosa (Cogn.) Schltr.	KF660297	KF660517	Whitten 3250 (FLAS)
Paphinia clausula Dressler	KF660298	EU490758	Whitten 3600 (FLAS)
Paphinia neudeckeri Jenny	AF239471	KF660371	Whitten 88041 (FLAS)
Peristeria elata Hook.	AF239442	EU490761	Whitten 90158 (FLAS)
Pescatoria cerina (Lindl. & Paxton) Rchb.f.	AY869952	KF660384	Whitten s.n. (FLAS)
Pescatoria coronaria Rchb.f.	AY869954	KF660368	Whitten 1758 (FLAS)
Pescatoria lamellosa Rchb.f.	AY869953	KF660369	Whitten 1755 (FLAS)
Pescatoria lawrenceana (Rchb.f.) Dressler	AF350662	KF660393	Whitten 1636 (FLAS)
Pescatoria lehmannii Rchb.f.	AF239422	KF660492	Whitten 2848 (FLAS)
Pescatoria pulvinaris (Rchb.f.) Dressler	AY869950	KF660388	Whitten 1748 (FLAS)
Pityphyllum huancabambae (Kraenzl.) Whitten	DQ209957	KF660439	Whitten 2402 (FLAS)
Pityphyllum laricinum (Kraenzl.) Schltr.	DQ209961	KF660446	Whitten 2473 (FLAS)
Pityphyllum saragurense (Dodson) Whitten	DQ461805	KF660514	Whitten 3084 (QCA)
Polycycnis gratiosa Endres & Rchb.f.	AF239469	EU490769	Whitten 93178 (FLAS)
Polycycnis gratiosa Endres & Rchb.f.	AF239469	EU490769	Whitten 93178 (FLAS)
Polyotidium huebneri (Mansf.) Garay	FJ563960	FJ563598	Romero 3124 AMES
Polystachya cultriformis (Thouars) Lindl. ex Spreng.	DQ091312	KF660306	Carlsward 213 (SEL)
Promenaea stapelioides (Link & Otto) Lindl.	AY870002	EU123797	Whitten 94102 (FLAS)
Promenaea xanthina (Lindl.) Lindl.	AY870000	KF660366	Whitten 1860 (FLAS)
Psychopsiella limminghei (E.Morren ex Lindl.) Lückel & Braem	FJ565152	FJ563820	Whitten 3561 FLAS
Psychopsis sanderae (Rolfe) Lückel & Braem	FJ564712	FJ563158	Chase 86126 (K)
Rhetinantha acuminata (Lindl.) M.A.Blanco	DQ210981	KF660477	Whitten 2698 (FLAS)
Rhetinantha notylioglossa (Rchb.f.) M.A.Blanco	DQ210645	KF660351	Koehler 0033 (UEC)

TABLE 1. Continues.

Taxon	***matK***	***ycf1***	**Voucher:Herbarium**
Rossioglossum krameri (Rchb. f.) M.W. Chase & N.H. Williams	FJ563847	FJ562488	Chase 83166 (K)
Rudolfiella floribunda (Schltr.) Hoehne	AF239433	EU490776	Whitten 97020 (FLAS)
Rudolfiella sp.	FJ564977	FJ563642	Whitten 1618 FLAS
Sauvetrea chicana (Dodson) M.A.Blanco	DQ461813	KF660516	Whitten 3187 (QCA)
Sauvetrea chicana (Dodson) M.A.Blanco	KF660299	KF660521	Whitten 3338 (FLAS)
Sauvetrea laevilabris (Lindl.) M.A.Blanco	DQ210832	KF660433	Whitten 2358 (FLAS)
Schlimmia alpina Rchb.f. & Warsz.	KF660300	KF660345	Bennett 5130 (MOL)
Schlimmia stevensonii Dodson	AF239463	KF660343	Whitten 94107 (FLAS)
Scuticaria hadwenii (Lindl.) Planch.	AF239424	KF660370	Whitten 97109 (FLAS)
Scuticaria salesiana Dressler	DQ210875	KF660447	Whitten 2478 (FLAS)
Sievekingia herrenhusana Jenny	AF239453	KF660336	Whitten 93010 (FLAS)
Soterosanthus shepheardii (Rolfe) Jenny	AF239457	EU490784.	Dodson 18580-3 (FLAS)
Stanhopea anfracta Rolfe	AF239450	KF660511	Whitten 3022 (FLAS)
Stanhopea annulata Mansf.	AF239444	EU490786	Whitten 87242 (FLAS)
Stanhopea cirrhata Lindl.	AF239464	KF660360	Whitten F1296 (FLAS)
Stanhopea confusa G.Gerlach & Beeche	AF239449	KF660359	Whitten 94006 (FLAS)
Stanhopea ecornuta Lem.	AF239445	KF660362	Whitten 90026 (FLAS)
Stanhopea pulla Rchb.f.	AF239451	KF660361	Whitten 93117 (FLAS)
Stanhopea tigrina Bateman ex Lindl.	FJ564736	FJ563222	Whitten 3585 FLAS
Stenia bismarckii Dodson & D.E.Benn.	AY869920	KF660392	Whitten 1698 (FLAS)
Stenia calceolaris (Garay) Dodson & D.E.Benn.	AY869919	KF660394	Whitten 1699 (FLAS)
Stenotyla lankesteriana (Pupulin) Dressler	AY869962	KF660383	Dressler 6363 (FLAS)
Stenotyla lendyana (Rchb.f.) Dressler	AY869963	KF660381	Dressler 6228 (FLAS)
Stenotyla picta (Rchb.f.) Dressler	AY869961	KF660395	Dressler 6235 (FLAS)
Sudamerlycaste ciliata (Ruiz & Pav.) Archila	KF660301	KF660495	Whitten 2877 (FLAS)
Telipogon hystrix (Dodson) N.H.Williams & Dressler	DQ315899	FJ563601	Whitten 1824 (FLAS)
Telipogon parvulus C.Schweinf.	DQ315909	FJ563574	Whitten 99259 (FLAS)
Telipogon pogonostalix Rchb.f.	AF239488	FJ562506	Chase O-123 (K)
Tolumnia gundlachii (C.Wright ex Griseb.) N.H.Williams & Ackerman	FJ565132	FJ563801	Whitten 3358 FLAS
Tolumnia pulchella (Hook.) Raf.	FJ564820	FJ563411	Whitten 3499 (FLAS)
Trevoria zahlbruckneriana (Schltr.) Garay	KF660302	KF660324	Dodson 17309 (MO)
Trichocentrum jonesianum (Rchb.f.) M.W.Chase & N.H.Williams	AF350653	FJ562496	Chase 86118 (K)
Trichocentrum luridum (Lindl.) M.W.Chase & N.H.Williams	FJ564957	FJ563449	Carnevali 6243 (CICY)
Trichoceros antennifer (Humb. & Bonpl.) Kunth	FJ564953	FJ563612	Whitten 1803 (FLAS)
Trigonidium acuminatum Bateman ex Lindl.	DQ210640	KF660358	Koehler 363 (UEC)
Trigonidium acuminatum Bateman ex Lindl.	DQ210867	KF660442	Whitten 2442 (FLAS)
Trigonidium egertonianum Bateman ex Lindl.	DQ210714	KF660356	Koehler 317 (UEC)
Trigonidium egertonianum Bateman ex Lindl.	DQ210730	KF660357	Koehler 361 (UEC)
Trigonidium insigne Rchb.f. ex Benth. & Hook.f.	DQ211041	KF660504	Whitten 2926 (FLAS)

TABLE 1. Continues.

Taxon	matK	ycf1	Voucher:Herbarium
Trigonidium turbinatum Rchb.f.	DQ210713	KF660355	Koehler 315 (UEC)
Trizeuxis falcata Lindl.	FJ563850	FJ563198	Chase O-129 (K)
Vasqueziella boliviana Dodson	AF239473	KF660344	Vasquez s.n. (FLAS)
Warczewiczella discolor (Lindl.) Rchb.f.	AY869959	KF660412	Whitten 1859 (FLAS)
Warczewiczella marginata Rchb.f.	AY869958	EU490794	Whitten s.n. (FLAS)
Warczewiczella wailesiana (Lindl.) E.Morren	AY869960	KF660387	Gerlach 93-3314 (M)
Warrea warreana (Lodd. ex Lindl.) C.Schweinf.	AF239417	EU123798	Whitten 1752 (FLAS)
Xylobium leontoglossum (Rchb.f.) Benth. ex Rolfe	DQ209970	KF660413	Whitten 2683 (FLAS)
Xylobium pallidiflorum (Hook.) G.Nicholson	AF239434	EU490795	Whitten 1876 (FLAS)
Xylobium zarumense Dodson	AF239435	KF660380	Whitten 1881 (FLAS)
Zygopetalum maxillare Lodd.	AY869996	FJ562864	Whitten 94103 (FLAS)
Zygosepalum tatei (Ames & C.Schweinf.) Garay & Dunst.	AY869994	KF660409	Maguire & Politi 27494 (AMES)

Zygopetalinae — (Fig. 2). Our results are largely congruent with our previous study (Whitten *et al.* 2005) based on *matK*/*trnL-F*/ITS data, although there is less support for many genera. The non-monophyly of *Warczewiczella* is unusual, and might be due to mislabeled DNA samples; resampling with new collections is needed. Relationships within *Dichaea* were clarified by Neubig *et al.* (2009b). Subtribe Vargasiellinae consists of one genus with two poorly collected species, one from the tepuis of Venezuela and the other from eastern Peru. We were unable to obtain DNA of these taxa. Dressler (1993) included *Vargasiella* C.Schweinf. in Zygopetalinae but suggested it might warrant subtribal status. Romero-González and Carnevali (1993) validated the subtribal name and suggested that it should remain in its own subtribe pending better specimens and molecular data. Recent collections and DNA sequences of *Vargasiella peruviana* C.Schweinf. place it with high support in Zygopetalinae in an unresolved clade with *Warrea warreana* (Lodd. ex Lindl.) C.Schweinf. and *Warreopsis* spp. (Szlachetko *et al.*, in press; M. Kolanowska, pers. comm.). *Vargasiella* is sister to *Warrea* but with weak support. These data confirm Dressler's intuition (Dressler 1993) regarding its subtribal position; therefore, Vargasiellinae should not be recognized.

Coeliopsidinae — (Fig. 3). Our sampling included one species of each of the three genera comprising this small subtribe. The subtribe is highly supported but weakly sister to Stanhopeinae in agreement with Whitten *et al.* (2000).

Stanhopeinae — (Fig. 3). Although the circumscription of generic boundaries within this subtribe are highly congruent with morphology-based classifications, this subtribe has the lowest BS support (87%). The odd monotypic *Braemia vittata* (Lindl.) Jenny is sister to all other genera. These data are highly congruent with the trees of Whitten *et al.* (2000), but the placement of *Sievekingia* requires more study. In the Whitten *et al.* (2000) analyses based upon *matK/trnL-F*/ nrITS, *Sievekingia* is strongly sister to *Coryanthes*. In the plastid *matK/ycf1* trees, the single sample of *Sievekingia* is sister to the multiflowered clade of *Stanhopea* (creating a paraphyletic *Stanhopea*). More extensive sampling with nuclear and plastid regions is needed to resolve this, because it appears to be one of the few instances of conflict between nrITS and plastid trees in Cymbidieae. One possible source of error within the *Stanhopea/Coryanthes/Sievekingia* clade is from missing data in *ycf1* for *Coryanthes*; the 3720F primer did not amplify for *Coryanthes*; consequently, about half of the *ycf1* sequence data are missing for *Coryanthes* species.

Maxillariinae — (Figs. 4, 5). Relationships within Maxillariinae were addressed in greater detail by Whitten *et al.* (2007), Blanco *et al.* (2007; 2008), and Blanco (2013) based upon a larger taxon sampling of *matK*/nrITS1&2/*atpB-rbcL* spacer. Our sampling with *matK/ycf1* was smaller (119 taxa vs. over 600),

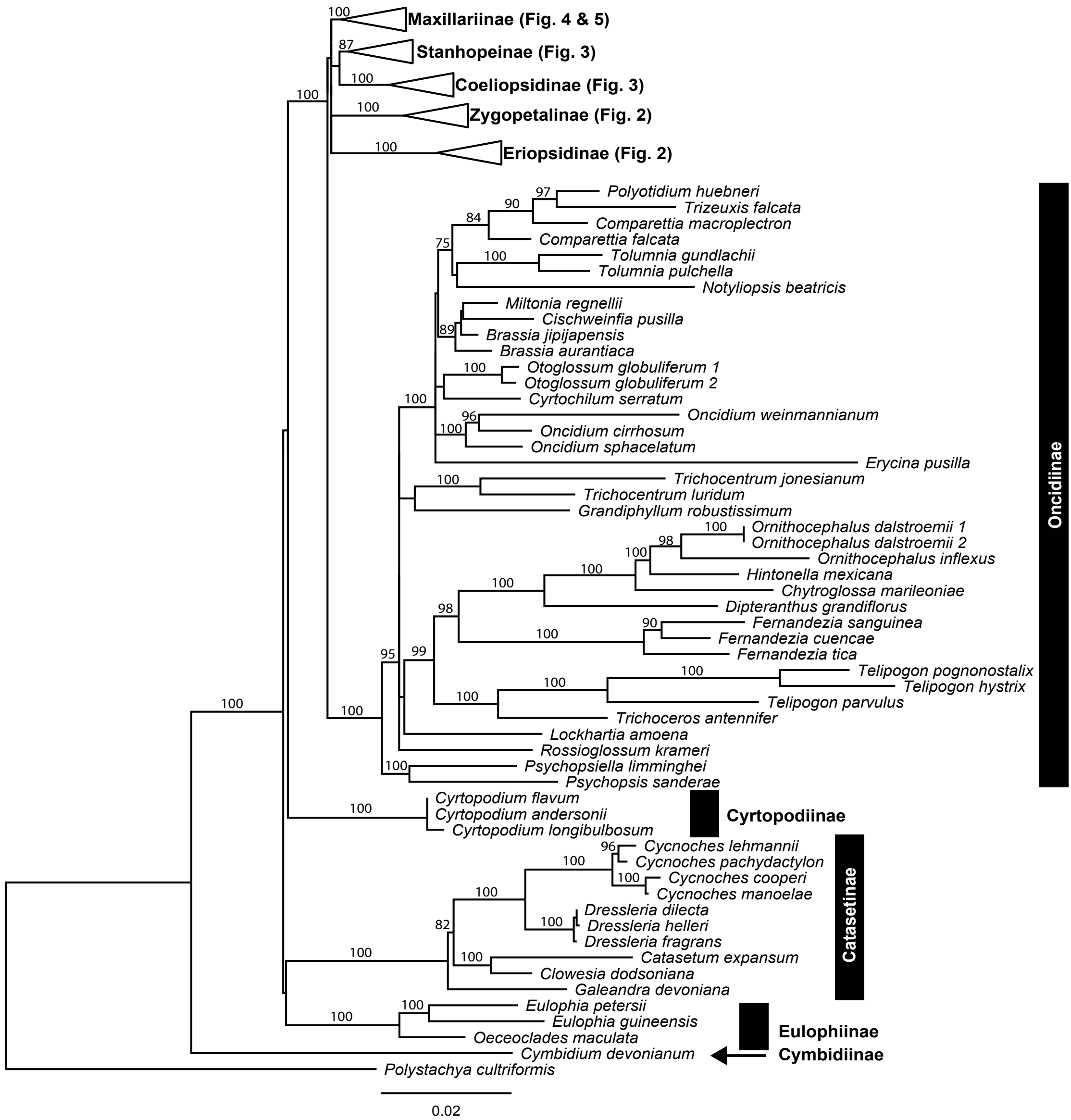

FIGURE 1. Best ML tree with bootstrap values added, showing Cymbidiinae, Eulophiinae, Catasetinae, Cyrtopodiinae, and Oncidiinae.

but the two data sets recovered the same major clades, supporting the generic concepts presented by Blanco *et al*. (2007). Our sampling included two individuals of several species; in each pair, there are nucleotide differences separating the two, indicating that *ycf1*/*matK* is often capable of resolving not only closely related species but also intraspecific variation.

Several taxa not present in the 2007 sampling were added to this study. These include *Cryptocentrum beckendorfii* Carnevali *and Maxillaria cacaoensis* J.T.Atwood. *Cryptocentrum beckendorfii*, an anomalous species with large pseudobulbs, is placed within *Cryptocentrum* with 100% BS support (Fig. 5). *Maxillaria cacaoensis* was hypothesized by Atwood to be a member of the *Camaridium cucullatum* (Lindl.) M.A.Blanco clade (=*Psittacoglossum* La Llave & Lex., but DNA samples of this rare taxon became available only recently. *Maxillaria*

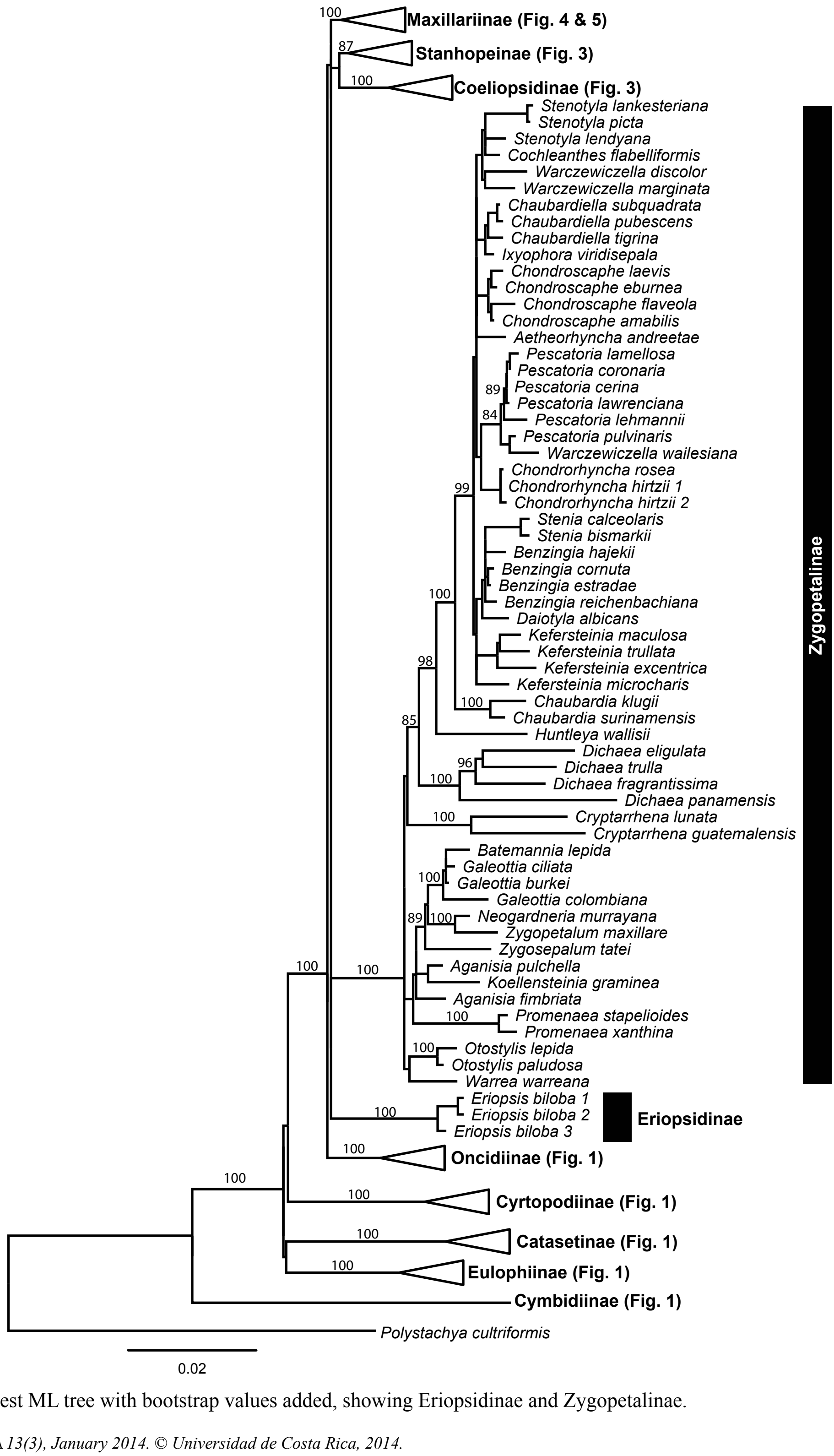

FIGURE 2. Best ML tree with bootstrap values added, showing Eriopsidinae and Zygopetalinae.

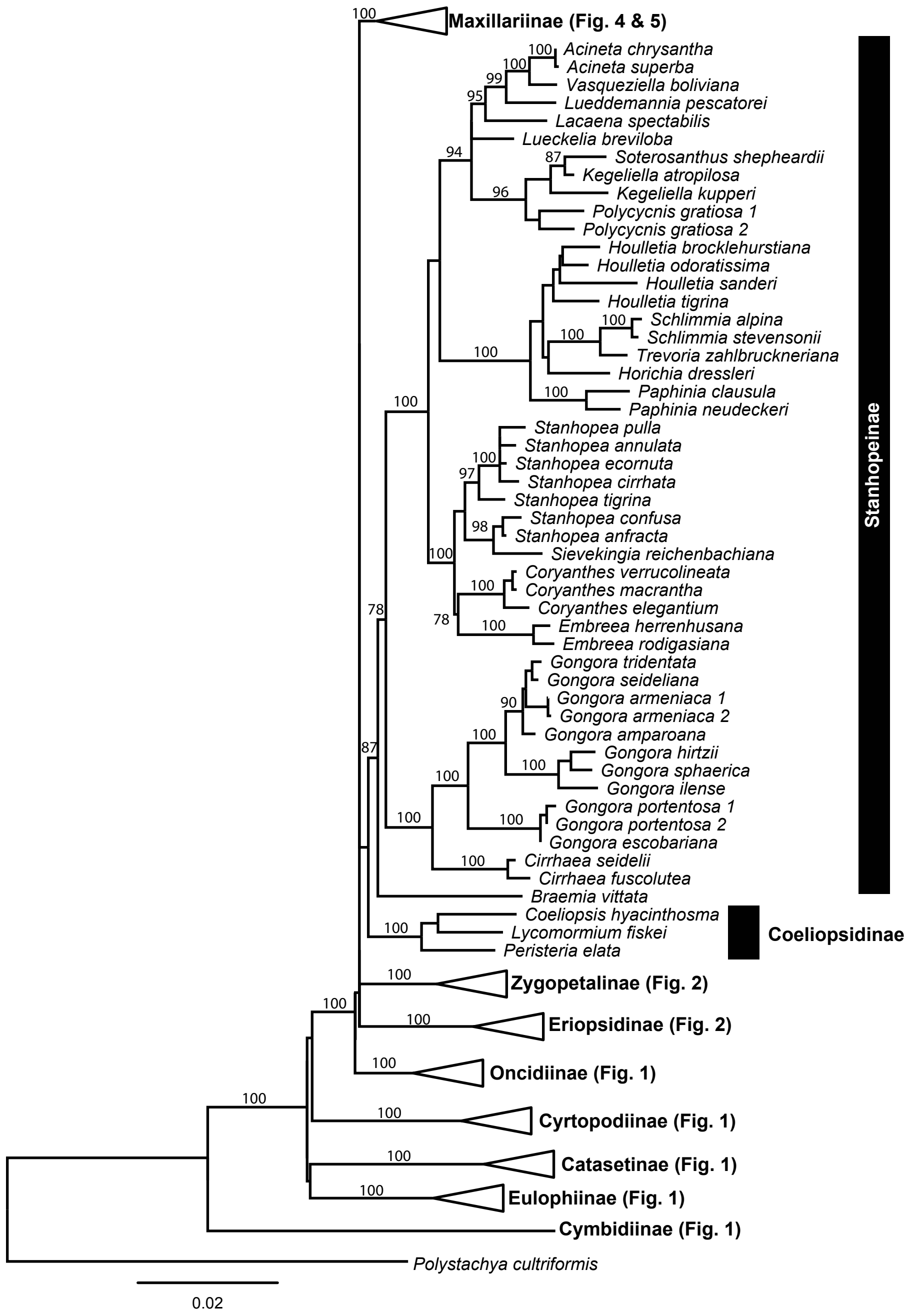

FIGURE 3. Best ML tree with bootstrap values added, showing Coeliopsidinae and Stanhopeinae.

cacaoensis is sister to *C. cucullatum* in our *ycf1/ matK* trees (Fig. 5), and requires a new combination in *Camaridium*. It was erroneously transferred to *Mapinguari* Carnevali & R.B.Singer by Szlachetko *et al.* (2012). Morphologically, it resembles a dwarf *C. cucullatum*, and the capsule has apical dehiscence, a trait shared by all *Camaridium* species for which we have observed mature fruits. Based upon these molecular and morphological data, we transfer this species to *Camaridium*.

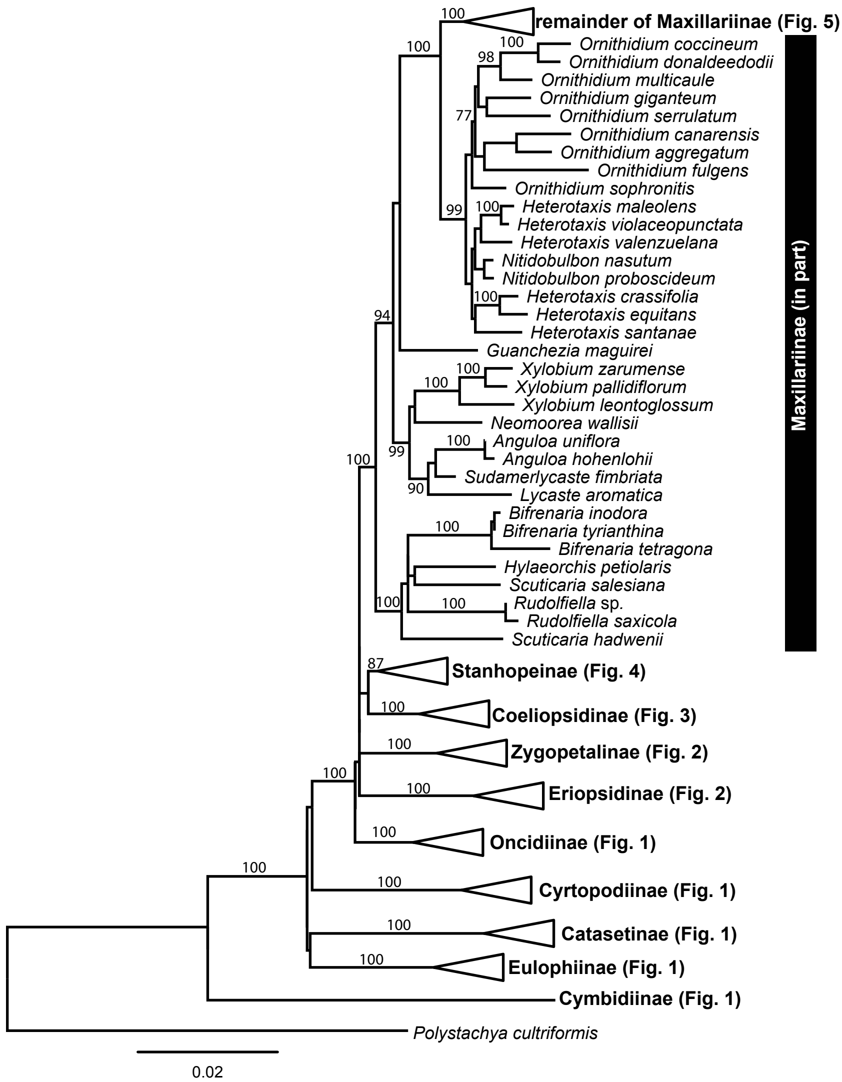

FIGURE 4. Best ML tree with bootstrap values added, showing basal portion of Maxillariinae.

Camaridium cacaoense (J.T.Atwood) Whitten, ***comb. nov.***

Basionym: *Maxillaria cacaoensis* J.T.Atwood, Selbyana 19(2):254. 1999 (1998, pub. 1999).

Mapinguari cacaoense (J.T.Atwood) Szlach. & Sitko, Biodiv. Res. Conservation 25:30. 2012, ***syn. nov.***

The Whitten *et al.* (2007) and Blanco *et al.* (2007) classifications of Maxillariinae were based upon analyses of nrITS/*matK*+*trnK*/*atpB*-*rbcL* spacer for over 600 individuals. An alternative classification was published by Szlachetko *et al.* (2012). The Szlachetko classification was based on analyses of a 249-taxon nrITS matrix that is largely congruent (though less resolved) than the Whitten *et al.* trees. The resulting Szlachetko classification accepts most of the genera proposed by Blanco *et al.* (2007) but splits many of them to increase the number of genera from 17 to 37.

A detailed, genus-by-genus critique of the Szlachetko *et al.* (2012) classification falls outside the scope of this paper, but we reject the generic concepts presented in their paper. Szlachetko and coworkers reject monophyly as a criterion for generic rank; therefore, many of their genera are paraphyletic

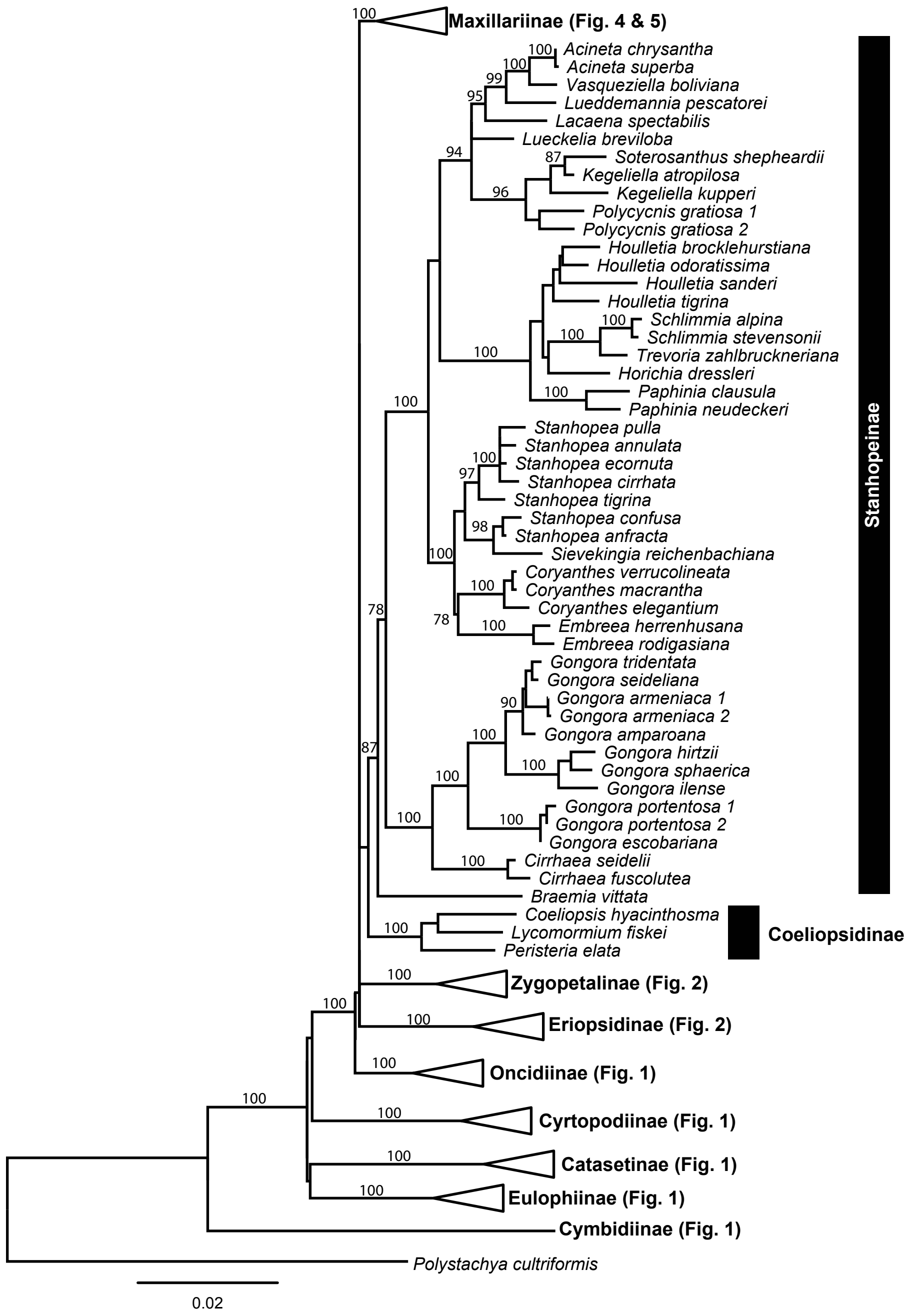

FIGURE 5. Best ML tree with bootstrap values added, showing remainder of Maxillariinae.

or polyphyletic as plotted onto any molecular or morphological tree and are based on idiosyncratically selected morphological characters (floral and/or vegetative), often without molecular data or with contradicting molecular evidence.

Many of their new genera consist of one or two morphologically odd species embedded within larger genera [e.g., *Marsupiaria* Hoehne = *Heterotaxis valenzuelana* (A.Rich.) Ojeda & Carnevali; *Vazquezella* Szlach. & Sitko = *Heterotaxis* *equitans* (Schltr.) Ojeda & Carnevali; *Chrysocycnis* Linden & Rchb.f., *Anthosiphon* Schltr., *Hoehnella* Szlach. & Sitko = *Rhetinantha witseniodes* (Schltr.) M.A.Blanco; *Pseudocymbidium* Szlach. & Sitko = *Maxillaria lueri* Dodson]. Other genera are composed of 15 or more species that are monophyletic but are embedded within other genera (e.g. *Calawaya* Szlach. & Sitko, embedded in *Maxillaria* Ruiz & Pav.). *Camaridium* Lindl. is split into at least eight genera. Some segregates (*e.g.*, *Chaseopsis* Szlach. & Sitko) are based solely upon morphological traits and include species that were not included in either molecular study [*e.g.*, *Camaridium burgeri* (J.T.Atwood) M.A.Blanco]. Their circumscription of *Chaseopsis* omits taxa that are sister to the generitype in the molecular trees but lack the defining essential "generic" characters (*e.g., Maxillaria flava* Ames, F.T.Hubb. & C.Schweinf. = *Camaridium ramonense* (Schltr.) M.A.Blanco; *Maxillaria lankesteri* Ames = *Camaridium aurantiacum* (Schltr.) M.A.Blanco). The Szlachetko *et al.* classification produces genera that are easily suited to production of dichotomous keys, because any morphologically anomalous species are automatically placed into another genus. Because there is no objective basis for selecting "critical" characters that define genera, their classification is without merit.

Conclusions

The *matK*/*ycf1* data produce trees that are highly congruent with the classification presented in volume 5 *Genera Orchidacearum*. Most subtribes have high bootstrap support, and generic relationships are congruent with previous molecular studies. In comparison to plastid intron/spacer regions (*e.g., trnL-F*, *atpB-rbcL*), these coding regions can be aligned with much more confidence across larger taxonomic groups (*e.g.*, tribes), especially if they are aligned using amino acid translations. This combination also appears capable of providing species-level discrimination in some genera, although more detailed sampling is needed to evaluate this fully. In terms of sequencing ease and cost effectiveness vs. phylogenetic resolution, the combination of *matK*/*ycf1*/nrITS may prove efficient within Orchidaceae. Nevertheless, these plastid trees fail to provide resolution and support of relationships among subtribes.

Givnish *et al.* (2013) recently utilized complete plastomes to estimate phylogenetic relationships among 39 orchid taxa. Although only a few subtribes of Cymbidieae were represented in their data set, subtribal relationships were still unresolved. Their results imply that the addition of more plastid genes with the objective of resolving these nodes may be futile and that these relationships will only be resolved by the addition of nuclear data sets. Clearly, much more data are needed before we fully understand the patterns of evolution within Cymbidieae.

We hope to add more representatives of Cymbidiinae, Eulophiinae, and Catasetinae. Catasetinae might provide an excellent system for study of the evolution of diverse floral reward systems; it includes five genera that are all androeuglossophilous fragrance-reward flowers (*Catasetum*, *Cycnoches*, *Clowesia*, *Dressleria*, *Mormodes*); these five genera are sister to *Galeandra*, with nectar deceit flowers, to *Grobya*, with oil-reward flowers (Pansarin et al., 2009), and to *Cyanaeorchis*, with unknown pollinators.

Previous attempts to utilize molecular clock methods to estimate the age of subtribes within Cymbidieae (Ramírez *et al.* 2011) utilized more limited taxon sampling that was biased towards androeuglossophilous taxa. Our more complete sampling of generic relationships based on more sequence data might warrant reexamination of these age estimates.

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