

## GENERIC RELATIONSHIPS OF ZYGOPETALINAE (ORCHIDACEAE: CYMBIDIEAE): COMBINED MOLECULAR EVIDENCE

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**ABSTRACT.** The phylogenetic relationships of the orchid subtribe Zygopetalinae were evaluated using parsimony analyses of combined DNA sequence data of nuclear ITS 1 and 2 (including the 5.8s region and portions of the flanking 18s and 26s regions) and of the plastid *trnL* intron plus the *trnL-F* intergenic spacer and the plastid *matK*. Analyses of the three separate data sets produced highly congruent and moderately supported patterns, so these were combined in a single analysis. Combined analysis of 104 ingroup and two outgroup taxa produced highly resolved cladograms. Zygopetalinae comprises a *Zygopetalum* grade or clade (pseudobulbs prominent; leaves usually plicate, revolute); a *Huntleya* grade (pseudobulbs reduced or lacking; leaves conduplicate), including *Dichaea*, *Huntleya*, *Chaubardia*, and the *Chondrorhyncha* complex, plus *Cryptarrhena* that is weakly supported as sister to the *Huntleya* clade; and a *Warrea* grade. *Chondrorhyncha s.l.* is polyphyletic and six genera are here segregated as monophyletic taxa (see Key words).

**RESUMEN.** Se evaluaron las relaciones filogenéticas de la subtribu Zygopetalinae mediante análisis de parsimonia de datos combinados de secuencias de ADN de ITS nuclear 1 y 2 (incluyendo la región 5.8s y partes de las regiones adyacentes 18s y 26s), del intrón del plastidio *trnL*, del espaciador intergénico *trnL-F* y del *matK* del plastidio. El análisis de los tres juegos de datos separados mostró patrones muy congruentes y moderadamente sustentados, de modo que éstos fueron combinados en un solo análisis. El análisis combinado de 104 taxa internos y 2 externos produjo cladogramas de alta resolución. Zygopetalinae abarca un grado o clado de *Zygopetalum* (pseudobulbos prominentes; hojas a menudo plicadas, revolutas); un clado de *Huntleya* (pseudobulbos reducidos o ausentes; hojas conduplicadas), que incluye *Dichaea*, *Huntleya*, *Chaubardia*, y el complejo de *Chondrorhyncha*, además de *Cryptarrhena*, débilmente sustentada como grupo hermano del clado de *Huntleya*; y un grado de *Warrea*. *Chondrorhyncha s.l.* es polifilética; por ello, aquí se segregan 6 géneros como taxa monofiléticos (ver palabras clave).

**KEY WORDS / PALABRAS CLAVE:** *Aetheorhyncha*; Cymbidieae; *Daiotyla*; *Echinorhyncha*; *Euryblema*; *Ixyophora*; Orchidaceae; *Stenotyla*, Zygopetalinae.

The subtribe Zygopetalinae comprises about 418 species (Royal Botanic Gardens, Kew, 2003) of Neotropical orchids with diverse vegetative and floral morphologies. Zygopetalinae possess four superposed pollinia; in most taxa, the pollinia are flattened and the stigma is transversely narrow and slit-like. Traditionally, Zygopetalinae have been placed in tribe Maxillarieae; however, as molecular data indicate that Maxillarieae sensu Whitten *et al.* (2000) is sister to a paraphyletic grade of cymbidioid taxa, Chase *et al.* (2003) lumped Maxillarieae together with Cymbidiinae, Eulophiinae, Bromheadiinae, and Catasetinae to create a broader and monophyletic Cymbidieae. Regardless of taxonomic rank, the generic relationships within Cymbidieae are becoming clarified by molecular systematic studies.

Several classifications of Maxillarieae were produced in the past decade: Senghas and Dietrich (1992), Dressler (1993), Szlachetko (1995), Whitten *et al.* (2000), and Chase *et al.* (2003). The three earlier classifications (based on morphology) disagree on circumscriptions of Zygopetalinae; Dressler (1993) proposed a broad Zygopetalinae containing several informal alliances, whereas Szlachetko (1995) divided these taxa among six subtribes. The combined molecular analysis of Maxillarieae (Whitten *et al.* 2000) indicated high bootstrap support for a monophyletic Zygopetalinae and supported the inclusion of two morphologically anomalous genera within Zygopetalinae: *Cryptarrhena* (4 species) and *Dichaea* (ca. 111 species). Zygopetalinae sensu Dressler (1993) has been further divided by various authors, formally or informally, into groups based upon several characters, especially: 1) the presence/absence, size, and number of internodes of pseudobulbs; 2) the number of flowers per inflorescence; and 3) leaf veneration (revolute or conduplicate).

We examine relationships within Zygopetalinae using cladistic and Bayesian analyses of combined molecular data sets of internal transcribed spacers 1 and 2 (nuclear ribosomal DNA; hereafter referred to as ITS), of the plastid *trnL* intron and *trnL-F* spacer (hereafter referred to as *trnL-F*), and of the plastid gene *matK*. Our sampling of taxa is more complete for the *Huntleya* clade (one flower/inflorescence; pseudobulbs small or lacking; conduplicate leaves), and our discussion will focus on this clade.

#### MATERIALS AND METHODS

Species examined, voucher information, and GenBank accession numbers are listed in Table 1. *Maxillaria* and

*Rudolfiella* (Maxillariinae) were used as outgroups based on the combined analyses of Maxillarieae (Whitten *et al.* 2000). Protocols for extraction, amplification, primers used, and sequencing are presented in Whitten *et al.* (2000). Sequences were aligned manually using Se-Al (Rambaut 1996). The aligned data matrices are available from the authors (WMW) and as a PopSet in GenBank. All cladistic analyses were performed using PAUP\* version 4.0b (Swofford 1999). Bayesian analyses were performed using MrBayes 3.0 (Huelsenbeck & Ronquist 2003). The data matrix consisted of 105 individuals (two outgroups; 99 species plus six duplicates).

*Search strategies* — Each matrix (ITS, *trnL-F*, *matK*, and the combined ITS/*trnL-F/matK*) was subjected to 1000 replicates of random taxon entry additions, MULTREES on, using sub-tree pruning and re-grafting (SPR) swapping, but saving only five trees per replicate to minimize time spent swapping on suboptimal islands. The resulting shortest trees were swapped to completion or until 20 000 trees were saved. Confidence limits for trees were assessed by performing 1000 replicates of bootstrapping (Felsenstein 1985) using equal weighting, SPR swapping, MULTREES on, and holding only five trees per replicate. We assessed congruence of the separate data sets by visual inspection of the individual bootstrap consensus trees. We considered the bootstrap trees to be incongruent only if they displayed “hard” (*i.e.*, highly supported) incongruence, rather than “soft” (poorly supported) incongruence (Seelanan *et al.* 1997, Wiens 1998). We use the following descriptions for categories of bootstrap support: weak, 50-74%; moderate, 75-84%; strong 85-100%. We consider percentages less than 50% to be unsupported because such groups do not occur in the majority of the trees. Bayesian analyses were performed on the combined data set only using MrBayes 3.0 (Huelsenbeck & Ronquist 2003). The parameters for the Bayesian analysis were as follows: lset nst=2; rates=gamma; set autoclose=yes; mcmc ngen=2,000,000; printfreq=100; samplefreq=10; nchains=4; savebrlens=yes; mcmc; sumt; burnin=200,000 contype=halfcompat. The first 10000 trees were omitted and the majority rule consensus tree was obtained in PAUP\* from the remaining trees.

#### RESULTS

Table 2 presents the number of included aligned positions in the matrix, the number of variable sites, the number and percentage of phylogenetically informative

sites, the percentage of sites that are variable, the number of trees, number of steps, consistency index (CI) excluding uninformative characters, and retention index (RI) for each separate and combined analysis. Alignment was unambiguous for *matK* and was not problematic for ITS and *trnL-F*. The *trnL-F* alignment contained indels up to 50 bases long, but these were usually easily aligned and often were autoapomorphic.

*matK*—The *matK* matrix was the least variable of the three and yielded the least resolution. The trimmed amplified region ranges from 1314 to 1323 base pairs (bp); the aligned length is 1341 bp and contains four indels ranging in length from three to nine bp (not scored as characters). Two indels are autapomorphic; one indel of nine bp occurs in two of the three sampled species of *Huntleya*, and another nine-base indel occurs in four of the eight taxa of the *Bollea/Pescatorea* clade. The matrix contains 154 potentially parsimony-informative characters. Heuristic search (Fitch criterion) yielded 2115 trees (L=472, CI=0.53 excluding uninformative characters here and below, RI=0.81). The few clades with high bootstrap support (Fig. 1) are usually genera or clades within genera.

*trnL-F*—Fifteen accessions from ten taxa repeatedly yielded double bands or heterogeneous PCR products that produced mixed sequences (suggestive of multiple copies of this region) and were excluded from the *trnL-F* analyses. The excluded taxa were: *Ackermania estradae*, *Chaubardiella pubescens*, *Chaubardiella tigrina*, *Chondrorhyncha andreettae*, *Chondrorhyncha* aff. *rosea*, *Chondroscape flaveola*, *Koellensteinia boliviensis*, *Otostylis lepida*, *Neogardneria murrayana*, and *Stenia bismarkii*. Five additional samples (*Batemannia lepida*, *Galeottia burkei* – two accessions, *G. ciliata*, and *G. colombiana*) yielded clean sequences, with several deletions and many mutations not present in congeners, resulting in the placement of these five taxa on a relatively long branch (ca. 65 steps) relative to their congeners in the shortest trees. This long branch is suggestive of possible paralogy within the *trnL-F* region; future studies will include cloning of *trnL-F* PCR products to clarify problems due to multiple copies.

The amplified *trnL-F* region ranges in length from 968 (*Promenaeta stapelioides*) to 1154 (*Warczewiczella discolor*) base pairs (bp). The aligned *trnL-F* matrix is 1358 bp long, and includes 829 bases of the *trnL* intron, the 3' *trnL* exon (51 bp), 439 bp of the intergenic spacer, and 25 bp of the 5' end of *trnF*. Two indels (26 bp of

intron and 9 bp of spacer) were judged unalignable and were excluded from the analysis. Heuristic search (Fitch criterion) yielded 9310 trees (L=443, CI=0.64, RI=0.87). In the bootstrap consensus (Fig. 2), *Warrea warreana* is weakly supported as sister to all other taxa, and the *Zygopetalum* grade (as defined in the combined analysis, Figs 4-5) + *Cryptarrhena* form an unresolved polytomy basal to *Dichaea* + *Huntleya* clade. Within the *Huntleya* grade, *Huntleya* and *Chaubardia* are successively basal to a moderately supported (83% BS) clade of all remaining *Huntleya* clade. Relationships within this core *Huntleya* grade are poorly resolved and many clades are weakly supported.

ITS rDNA—The aligned ITS rDNA matrix is 838 bp in length: 110 bp of the 18S region, ITS 1 (235 bp), the 5.8S gene (164 bp), ITS 2 (267 bp), and 62 bp of the 26S region. The heuristic search (Fitch criterion) yielded 857 equally parsimonious trees of 949 steps (CI=0.54, RI=0.86).

The ITS bootstrap consensus (Fig. 3) is the most highly resolved of the three data sets and is highly congruent with the plastid data set. The *Zygopetalum* grade (as defined in the combined analysis, Figs 4-5) + *Cryptarrhena* again form a basal polytomy, but many clades are highly supported: *Koellensteinia* + *Otostylis* + *Paradisanthus*; *Zygopetalum* + *Neogardneria* + *Pabstia*; *Galeottia* + *Batemannia*; and *Warrea* + *Warreopsis*. However, support for the *Huntleya* clade + *Dichaea* is weak (64% BS). Within the strongly supported *Huntleya* clade (90% BS), *Huntleya* and *Chaubardia* are strongly supported as basal to the core *Huntleya* clade (*Chondrorhyncha caquetae* to *Cochleanthes flabelliformis*). Many clades within this core *Huntleya* clade are moderately to strongly supported, including monophyletic *Chondroscape* (100% BS) and *Kefersteinia* (99% BS). However, many genera are not supported as monophyletic, e.g., *Chondrorhyncha*, *Cochleanthes*, *Stenia*, *Bollea*, and *Pescatorea*. In the latter two genera, the lack of support for monophyly is due to low sequence divergence. In other genera (e.g., *Chondrorhyncha*), sequence divergence is high and the species form several highly divergent and well supported clades.

*Combined analysis*—Comparison of bootstrap consensus trees for analyses of both data sets revealed no hard incongruence, i.e., clades that are highly supported in one analysis that conflict with different and highly supported clades in the others (Williams *et al.* 2001). We therefore performed a combined analysis of both data

sets. The equally weighted analysis produced 10000+ trees of 1887 steps (CI=0.54, RI=0.85); swapping to completion on these trees yielded the same set of trees. A randomly chosen single tree (with bootstrap values added) is presented in Figs. 4 & 5. The large number of equally parsimonious trees in the combined analysis is probably due to the inclusion of the *trnL-F* data set; analysis of the *matK* + ITS data (not shown) produced only 240 shortest trees.

We also performed a Bayesian analysis of the combined data set using MrBayes 3.0. The resulting tree (not shown) has the same topology as the one shown from the parsimony analysis (Fig. 4 & 5), and Bayesian posterior probabilities higher than 95% are shown on the tree together with bootstrap values.

In the combined analysis, Zygopetalinae are highly supported as monophyletic (see Table 2, Figs.4-5). The prominently pseudobulbed taxa (*Zygopetalum* grade) form a clade in the strict consensus of all shortest trees but without bootstrap or Bayesian support and most nodes within this group are weakly supported. Well-supported clades include *Neogardneria* + *Zygopetalum* + *Pabstia* and *Galeottia* + *Zygosepalum* + *Batemannia*. *Cryptarrhena* (with two species) is strongly supported as monophyletic but is isolated on a long branch basal (without bootstrap support) to *Dichaea* and the *Huntleya* clade. *Dichaea*, *Huntleya*, and *Chaubardia* are highly supported as monophyletic on long branches; they are successively basal with strong support to the remaining taxa of the *Huntleya* clade comprising the *Chondrorhyncha* complex.

In the *Chondrorhyncha* complex (Fig. 4), only a few traditionally recognized genera are strongly supported as monophyletic; these include *Chaubardiella*, *Chondroscape*, *Dodsonia*, *Kefersteinia*, and *Warczewiczella*. Most notably, *Chondrorhyncha* (as currently circumscribed) is polyphyletic, with its members falling into eight highly supported clades, including *Stenia* + *Dodsonia*, *Ackermania* + *Benzingia* + *Chondrorhyncha reichenbachiana*, and *Bollea* + *Pescatorea*. However, the combined data set does not resolve deeper nodes within the *Chondrorhyncha* complex.

## DISCUSSION

Previous classifications divide Zygopetalinae *s.l.* into several groups, recognized either formally as separate subtribes (Huntleyinae, Zygopetalinae, Warreinae,

Dichaeinae; Szlachetko 1995) or as informal clades (Dressler 1993). Several grades are recognizable in our analyses: *Huntleya* grade (including *Dichaea* and *Cryptarrhena*; pseudobulbs absent or very small, leaves duplicate); *Zygopetalum* grade (pseudobulbs conspicuous, leaves usually convolute); and the *Warrea* grade (pseudobulbs of several internodes, leaves plicate). *Dichaea* and *Cryptarrhena* were often placed in their own subtribes due to their morphological divergence from other Zygopetalinae (Dressler 1993, Szlachetko 1995), but data from *rbcL* (Cameron *et al.* 1999) and *matK*, *trnL-F*, and ITS (Whitten *et al.* 2000, present study) strongly support their inclusion in Zygopetalinae in spite of their placement on relatively long branches.

The inclusion of these anomalous genera results in a subtribe difficult to define with morphological synapomorphies. Potential morphological characters defining the subtribe are the (usual) presence of four superposed flattened pollinia, usually a transverse slit-like stigma (but *Dichaea* has a rounded stigma and variable pollinia), and a column provided with an infrastigmatic keel (*Chondrorhyncha* spp. hereafter treated as the genera *Daiotyta*, *Kefersteinia*, and *Warreopsis*), a tooth (*Kefersteinia*) often basal (*Cryptarrhena*, *Pescatorea*, *Warczewiczella*) or a ligule (*Dichaea*). Additional synapomorphies are the violet color (not purple) present in the flowers of many genera (*Acacallis*, *Cochleanthes*, *Dichaea*, *Koellensteinia*, *Otostylis*, *Pabstia*, *Warczewiczella*, *Zygopetalum*, *Zygosepalum*), a color rarely found in other groups of Neotropical Orchidaceae, and the obvious tendency of the group to occupy shady, sub-optimal niches in the forest canopies (associated with transformations in the epidermis in *Benzingia* and many species of *Dichaea*).

Perhaps the two characters are somewhat correlated, the lilac color having a special significance in attracting pollinators in subdued light. Within the *Huntleya* grade, perhaps the more useful synapomorphy is the presence of two apical bracts on the peduncle, a character widespread among all the genera with the exception of the many-flowered *Cryptarrhena*. These bracts differ greatly between them in shape and size. The more basal, adaxial bract, which envelops the pedicel and ovary, as well as the inner bract, is usually large and cucullate. The apical bract is smaller, ligulate, and projects beneath the flower abaxial to the lip. Members of the closely related Lycastinae and Maxillariinae also possess four pollinia, but the pollinia are usually globose or slightly flattened, and the stigmas are oval

and not slit-like.

Dressler (1993), who included *Vargasiella* in Zygotetralinae, mentioned possible placement in its own subtribe; Romero and Carnevali (1993) validated the subtribe Vargasiellinae, which was also recognized by Szlachetko (1995). We were unable to obtain extractable material of this genus for inclusion in this study and its placement remains uncertain.

Our sampling within the *Huntleya* grade is more complete, especially for Central American taxa, and some conclusions and taxonomic transfers are justified by the analyses. The discussion is arranged by the genera recognized in Figs. 4 & 5, although *Hoehneella* is not in the figure (see discussion below).

*Cryptarrhena* — This genus (two species) is morphologically anomalous within the subtribe and is isolated on a very long branch. Its placement within the subtribe in the combined cladogram is unresolved, but it is sister to the *Huntleya* clade in many of the shortest trees. The spicate, pendent inflorescences have numerous, small flowers, whereas most of the *Huntleya* clade have single-flowered inflorescences. *Cryptarrhena lunata* has fleshy, strongly keeled leaves and lacks pseudobulbs, whereas *C. guatemalensis* has thinner leaves and small pseudobulbs. Nevertheless, several characters link *Cryptarrhena* to other genera of Zygotetralinae. The anchor-shaped lip is similar to that of *Dichaea*, and the column bears a conspicuous clinandrium (hood) similar to those of *Huntleya* and *Chaubardia*, and a distinct basal tooth. Within the subtribe, many-flowered inflorescences are also present in *Galeottia*, *Warrea*, *Warreopsis*, and *Zygotetralum*, among others.

*Chaubardia* — Florally, *Chaubardia* (three species) is very similar to *Huntleya*; both possess flat, open flowers with rhomboid lips bearing a conspicuously toothed callus. The columns of both genera possess lateral wings and often a hooded clinandrium, but the sepals and petals are narrower than those of *Huntleya*. *Chaubardia* is characterized by small, inconspicuous pseudobulbs at the base of fan-shaped growths, whereas *Huntleya* species lack pseudobulbs. The molecular data strongly support monophyly of *Chaubardia* and its separation from *Huntleya*.

*Hoehneella* — We were unable to obtain extractable material of this small genus of 1 or 2 species. Morphologically, it is similar to *Huntleya* and

*Chaubardia*. According to Senghas and Gerlach (1992-1993), the plants possess small pseudobulbs similar to those of *Chaubardia* and its viscidium is transversely elliptic and lacks a stipe. [Type: *H. gehrtiana* (Hoehne) Ruschi]

*Huntleya* — This is a distinctive and easily recognized genus with about 13 species. The plants lack pseudobulbs, and some species possess elongate rhizomes separating the fan-shaped growths. The flowers are large, star-shaped, and flat with relatively broad sepals and petals and are probably fragrance-reward flowers pollinated by male euglossine bees.

*Dichaea* — *Dichaea* is the largest and most distinctive genus in the subtribe (about 111 species) and is widely distributed from Mexico to Brazil. It is characterized by long, many-leaved, pseudomonopodial stems that are pendent in many species. Solitary flowers bearing an anchor-shaped lip are produced successively along the leafy stems, and all species are probably pollinated by fragrance-collecting male euglossine bees (although autogamous forms occur). The genus is monophyletic and the representatives of *Dichaea* are on a relatively long branch and are remarkable for the high levels of sequence divergence among the species; the branch lengths within *Dichaea* are greater than the lengths among most genera within the subtribe. These data indicate that sequencing of ITS and plastid regions has great potential for resolving species relationships within this moderately large genus. Conversely, the low levels of sequence divergence within many genera (e.g., *Kefersteinia*, *Bollea*, *Pescatorea*) indicate that sequencing these regions for additional taxa will not help to clarify relationships within these genera.

The remaining taxa within the *Huntleya* clade (Fig. 4) include many species that have been included in *Chondrorhyncha*. Generic delimitation within this clade has been difficult and many species have complex nomenclatural histories as orchidologists have shifted them from one genus to another. This taxonomic confusion probably reflects repeated evolutionary changes in pollination mechanisms that produced homoplasious floral morphologies. Many species in this clade produce gullet flowers that appear to be nectar-deceit flowers for long-tongued visitors, probably nectar-foraging euglossine bees (Ackerman 1983). The funnel-shaped lips do not produce a true spur, but do have a notch on either side of the base of the lip that permits passage of a bee's tongue. The lateral sepals are swept back and revolute, forming a tubular false spur

enclosing the notch on either side of the lip. We have not observed nectar production in any species with this morphology, and we conclude they are nectar deceit flowers. Earlier workers have placed many species with this deceit morphology in *Chondrorhyncha* or *Cochleanthes*. Our molecular cladograms indicate that species with this deceit morphology are scattered among various clades with other floral mechanisms, and therefore genera based on gross floral morphology are polyphyletic. The lack of resolution in the deeper nodes of Fig. 4 does not allow a clear reconstruction of the evolution of floral traits within this clade. Nevertheless, there are numerous well-supported clades that warrant generic recognition and conflict strongly with existing generic delimitations. In order to recognize these monophyletic clades at the generic level several generic transfers and nomenclatural changes are necessary.

*Chondrorhyncha* (*sensu stricto*) — *Chondrorhyncha* as traditionally defined is polyphyletic. The only feature defining *Chondrorhyncha* in the traditional sense is the relatively simple rostellum and viscidium, probably the ancestral condition for much of the complex. We have not yet sampled authentic material of the type species, *C. rosea* Lindl. Our Colombian sample, sent as that species, may be closer to *C. caquetae* Fowlie, but both are close to the type species, and several other South American species resemble both *C. rosea* and *C. hirtzii* in the form of the callus. Although species currently placed in *Chondrorhyncha* are scattered in at least eight clades throughout the cladogram, the type species (*C. rosea*) falls in a small highly supported clade with *C. aff. hirtzii* and *C. hirtzii*. Consequently, this clade is recognized as *Chondrorhyncha s.s.*; its members are restricted to northern South America and are characterized by a lip with a 2-toothed callus that narrows distally and by an ovate viscidium without a distinct stipe. Based on morphology, unsampled species that likely fall in this clade include *C. fosterae* Dodson, *C. macronyx* Kraenzl., *C. suarezii* Dodson, and *C. velastiguii* Dodson.

*Chondroscaphe* (Dressler) Senghas & G. Gerlach — *Chondroscaphe* (about 14 species) is characterized by distinctive “para-rostellar lobules” that sometimes clasp the viscidium and the well developed stipe. The lips have a narrow basal callus, plus a second callus-like thickening or pad of trichomes distal to the basal callus. Most species also have narrow leaves and large flowers with highly fimbriate lips. First described as a section of *Chondrorhyncha*, the fimbriate members of the *C. flaveola* complex were given generic status by Senghas

and Gerlach (1993b; type: *Zygopetalum flaveolum* Linden & Rchb.f.). The *C. bicolor* group is congeneric with the *C. flaveola* complex; however, more material of this complex is needed to clarify species limits. The description of *C. bicolor* is vague, and the type specimen is poorly preserved (Dressler 2001). *Chondrorhyncha* and *Chondroscaphe* are compared in Table 3.

***Daiotyla* Dressler, gen. nov.**

*Chondrorhynchae* Lindley similis, sed labelli callo crasso et bilobato differt.

Type species: *Chondrorhyncha albicans* Rolfe, Bull. Misc. Inform. Kew 40: 195. 1898.

Etymology: From the Greek terms *daio* (divide) and *tyla* (knot or callus).

*Daiotyla* differs from *Chondrorhyncha* mainly in the thick, 2-parted basal callus that reaches to about the middle of the lip. The pollinarium is similar to that of *Chondrorhyncha*. Our molecular data place it as sister to *Stenia*, but the lip shape is quite unlike that of *Stenia*. The vegetative habit is similar to that of *Stenia*, but it is also similar to that of most species of *Chondrorhyncha s.s.* and to other genera with medium-sized plants. The genus consists of three described species and at least one species waiting for description. Drawings and photographs of *D. crassa* and *D. albicans* are given by Dressler (1983b: 222-223) and Pupulin (2003: 469-470).

***Daiotyla albicans* (Rolfe) Dressler, comb. nov.**

Basionym: *Chondrorhyncha albicans* Rolfe, Kew Bull. 140: 195. 1898.

***Daiotyla crassa* (Dressler) Dressler, comb. nov.**

Basionym: *Chondrorhyncha crassa* Dressler, Die Orchidee 34: 222. 1983.

***Daiotyla maculata* (Garay) Dressler, comb. nov.**

Basionym: *Chondrorhyncha maculata* Garay, Orquideologia 4: 21. 1969.

*Stenia* — A highly supported clade contains five species of *Stenia* plus *Dodsonia*. All species possess rigid pouched or longitudinally folded lips and prominent stipes. Although *Dodsonia* is not embedded within *Stenia*, the molecular data do not support its segregation from *Stenia*; the sister relationship depicted in Fig. 4 collapses in the strict consensus of shortest trees. We have not sampled *Dodsonia falcata* Ackerman, but no morphological characters warrant either species' separation from *Stenia*, and we transfer the species of *Dodsonia* to *Stenia* below. Though *Stenia* is monophyletic, the structure of the pollinaria is

extraordinarily variable within the genus (Fig. 6).

There are two published species of *Dodsonia* (*D. saccata*, the type, and *D. falcata* Ackerman). Both were known only from the type collections until cultivated material of *Dodsonia* was identified recently in horticultural collections (Neudecker & Gerlach 2000, Whitten, unpublished). The cultivated material is intermediate in floral morphology between the types of the two species, leading Neudecker and Gerlach (2000) to conclude that *Dodsonia* may consist of a single variable species. With the recent description of *Stenia glatzii* (see Neudecker & Gerlach 2000, for excellent photographs and drawings) that is intermediate in morphology between *Dodsonia* and other species of *Stenia*, there seems little justification for maintaining *Dodsonia* as a distinct genus. *Dodsonia saccata* was originally described as a *Stenia*, but a new combination is required for *D. falcata*. The genus as redefined now contains about 12 species.

***Stenia falcata* (Ackerman) Dressler, *comb. nov.***

Basionym: *Dodsonia falcata* Ackerman, Selbyana 5: 118. 1979.

*Benzingia* —A highly supported clade of six species comprises *Ackermania*, *Benzingia*, and *Chondrorhyncha reichenbachiana*. These taxa are diverse in floral morphology, but *C. reichenbachiana* and *Ackermania* possess striking vegetative similarities. *Chondrorhyncha reichenbachiana* has resupinate flowers with a gullet shaped lip and reflexed, rolled lateral sepals that form a false spur, similar to other species of the *Chondrorhyncha* complex (e.g., *Cochleanthes lipscombiae*, Ackerman 1983). Its callus is laminar, somewhat bilobed and irregularly toothed, somewhat like that of the species of *Chondrorhyncha* moved below to *Euryblema*. Flowers of *Ackermania* and *Benzingia* lack the false spurs, possess saccate lips, and may be either resupinate or non-resupinate, depending upon the species. These floral differences are suggestive of different pollination systems and/or pollinarium deposition sites (nectar deceit in *C. reichenbachiana*; probably male euglossine fragrance reward in the other genera). These floral differences contradict the seemingly close relationships indicated by the molecular data. Vegetatively, most members of this clade are strikingly similar; most possess narrow, fan shaped growths with leaves that are a distinctive glaucous gray-green and pendent. The upper epidermal leaf cells are papillose, giving the leaf surface a pebbly or sparkling appearance; in all other genera of Fig. 4,

the upper epidermal cells are smooth. These vegetative synapomorphies support the molecular data, and indicate that pollination systems and floral morphologies might be evolutionarily labile. Similar patterns of agreement between molecular and vegetative characters (but not floral traits) are seen in several clades of Oncidiinae (Williams, Chase, and Whitten, in prep.) which also display mixtures of deceit and reward pollination systems.

The molecular data indicate that *Ackermania*, *Benzingia*, and *Chondrorhyncha reichenbachiana* should be treated as a single genus. A fungal genus bears the name *Ackermannia* Pat., differing by only one letter. The priority of these two names is currently awaiting clarification by the IAPT, but the controversy is moot for our purposes here. *Benzingia* Dodson has priority over *Ackermania*; therefore, we transfer all species of this clade into *Benzingia*.

Type: *Benzingia hirtzii* Dodson ex Dodson, Lindleyana 10(2): 74. 1995.

***Benzingia caudata* (Ackerman) Dressler, *comb. nov.***

Basionym: *Chondrorhyncha caudata* Ackerman, Selbyana 5: 299. 1981.

***Benzingia cornuta* (Garay) Dressler, *comb. nov.***

Basionym: *Chondrorhyncha cornuta* Garay, Orquideología 5: 20. 1970.

*Benzingia estradae* (Dodson) Dodson ex Dodson, Lindleyana 10(2): 74. 1995.

Basionym: *Chondrorhyncha estradae* Dodson, Icon. Pl. Trop. 1: t. 22. 1980.

Dodson and Romero (1995) transferred this species to *Benzingia*, but it is unlike the type species, *B. hirtzii*. *Benzingia hirtzii* resembles *Chaubardiella* in the non-resupinate flowers and the form of the viscidium. *Benzingia estradae* has pendent, rather than nonresupinate flowers, which, however, may function in much the same way.

***Benzingia hajekii* (D.E. Benn. & Christenson) Dressler, *comb. nov.***

Basionym: *Ackermania hajekii* D.E. Benn. & Christenson, Icon. Orchid. Peruv. t. 602. 2001.

***Benzingia jarae* (D.E. Benn. & Christenson) Dressler, *comb. nov.***

Basionym: *Ackermania jarae* D.E. Benn. & Christenson, Brittonia 47: 182. 1995

***Benzingia palorae* (Dodson & Hirtz) Dressler, *comb. nov.***

Basionym: *Stenia palorae* Dodson & Hirtz, Icon. Pl. Tropic. ser. II 6: 583. 1989.

***Benzingia reichenbachiana* (Schltr.) Dressler, *comb. nov.***

Basionym: *Chondrorhyncha reichenbachiana* Schltr., Repert. Spec. Nov. Regni Veg. 17: 15. 1921.

***Euryblema* Dressler, gen. nov.**

*Warczewiczellae* Rchb.f. *similis*, sed *labelli callo laminiformi, sepalis petalisque anatonis differt*.

Type species: *Cochleanthes anaton* Dressler, Die Orchidee 34(4): 160. 1983.

Etymology: From the Greek *eurys*, broad, and *blema*, blanket or cover, referring to callus shape.

First described as a *Cochleanthes* because of the short, rounded chin and the shield-like viscidium, and then transferred to *Chondrorhyncha* by Senghas (1990), *C. anaton* does not fit either group well, and it together with *C. andreae* Ortiz, make a distinctive group with high bootstrap support. Vegetatively both are easily recognized by their red spotted leaf sheaths (or stem base). *Euryblema* resembles *Warczewiczella* in the short, blunt chin and in the broad, shield-like viscidium/stipec. The callus, however, is broad and laminar, covering about the basal half of the lip. The name *Euryblema* refers to this "broad apron". Further, the sepals and petals of both species curve upwards, and both have the leaf sheaths marked with red. The genus consists of two described species. We have not been able to obtain material of *Cochleanthes thienii* Dodson, which is possibly congeneric with these two species.

***Euryblema anatonum* (Dressler) Dressler, comb. nov.**

Basionym: *Cochleanthes anaton* Dressler, Die Orchidee 34: 160. 1983.

Dressler (1983a) illustrates this species.

***Euryblema andreae* (Ortiz) Dressler, comb. nov.**

Basionym: *Chondrorhyncha andreae* Ortiz, Orquideología 19(4): 13. 1994.

Possibly congeneric: *Cochleanthes thienii* Dodson, Icon. Pl. Trop. t. 026. 1980.

*Kefersteinia* Rchb.f. —This is a group (more than sixty described species) of small plants with small flowers. Its most distinctive synapomorphies are a very thin inflorescence axis and a ventral keel on the column. The basal callus and the ventral keel of the column position the pollinator so that the pollinia are attached to the base of an antenna of a male euglossine bee; this pollinarium deposition site is unique among euglossine-pollinated orchids. Szlachetko (2003) elevated *Kefersteinia* sect. *Umbonatae* Senghas & Gerlach to generic level as *Senghasia*, and distinguished it from sect. *Kefersteinia* on the presence or absence of a large umbonate lip callus. Our sampling includes four taxa

in sect. *Umbonatae* (*K. excentrica*, *K. guacamayoana*, *K. trullata*, and *K. maculosa*) and two species from sect. *Kefersteinia* (*K. expansa* and *K. microcharis*). Our results indicate that these sections are not monophyletic. At present, we choose not to recognize *Senghasia* because it would unnecessarily split a monophyletic, morphologically distinctive genus into two groups that are unlikely to be monophyletic.

***Echinorhyncha* Dressler, gen. nov.**

*Warczewiczellae* Rchb.f. *similis*, sed *appendicibus echinatis sub columna differt*.

Type species: *Chondrorhyncha litensis* Dodson, Icon. Pl. Trop., ser. 2, 5: pl. 417. 1989.

Etymology: From the Greek *echinos*, sea urchin or hedgehog, and *rhynchos*, beak, referring to the appendages under the column.

This clade consists of four or five species that resemble *Warczewiczella*, but the column bears two or more bristly, sea urchin-like appendages on the underside. The stipec is pandurate or narrowed basally. Drawings of *E. ecuadorensis* and *E. litensis* are given in Dodson (1989, plates 415 and 417, cited below).

***Echinorhyncha antonii* (Ortiz) Dressler, comb. nov.**

Basionym: *Chondrorhyncha antonii* Ortiz, Orquideología 19: 14. 1994.

***Echinorhyncha ecuadorensis* (Dodson) Dressler, comb. nov.**

Basionym: *Chondrorhyncha ecuadorensis* Dodson, Icon. Pl. Tropic. ser. 2, 5: 415. 1989.

***Echinorhyncha litensis* (Dodson) Dressler, comb. nov.**

Basionym: *Chondrorhyncha litensis* Dodson, Icon. Pl. Tropic. ser. 2, 5: 417. 1989.

***Echinorhyncha vollesii* (Gerlach, Neudecker & Seeger) Dressler, comb. nov.**

Basionym: *Chondrorhyncha vollesii* Gerlach, Neudecker & Seeger, Die Orchidee 40(4): 131. 1989.

***Aetheorhyncha* Dressler, gen. nov.**

*Chondroscaphi* (Dressler) Senghas & G. Gerlach *similis*, sed *secundo callo distali deficienti, labello carina basali ornato, viscidio triangulari differt*.

Type species: *Chondrorhyncha andreetae* Jenny, Die Orchidee 40(3): 92. 1989.

Etymology: From the Greek *aethes*, strange or different, and *rhynchos*, snout or muzzle.

*Chondrorhyncha andreetae* Jenny is weakly supported as sister to the group here treated as *Ixyophora*, but

does not fit any other group now known, though superficially similar to *Chondroscape*. The lip has a strong median keel basal to the two-lobed callus, the blade of the lip is pubescent, and the viscidium is truncate and subtriangular. The term *rhynchos* (snout or muzzle) is intended more to suggest a relationship to *Chondrorhyncha* than to describe a specific feature of the flower. The genus consists of a single known species. Drawings are given by Jenny (1989: 93).

***Aetheorhyncha andreetae* (Jenny) Dressler, *comb. nov.***

Basionym: *Chondrorhyncha andreetae* Jenny, Die Orchidee 40(3): 92. 1989.

***Ixyophora* Dressler, *gen. nov.***

*Warczewiczellae* Rchb.f. *similis*, sed *stipite prope viscidium panduriformi vel angusto differt.*

Type species: *Chondrorhyncha viridisepala* Senghas, Die Orchidee 40(5): 181, f. 1989.

Etymology: From the Greek *ixys*, waist, and *phoreus*, bearer or carrier, referring to the narrow “waist” of the stipe.

Superficially similar to *Warczewiczella*, these species are distinctive in the form of the stipe that is narrowed between the viscidium and the pollinaria. These species form a group sister to *Chaubardiella* (Fig. 4). Senghas (1989: 180) gives a drawing of *I. viridisepala* and Senghas and Gerlach (1991: 283) illustrate *I. aurantiaca*.

***Ixyophora aurantiaca* (Senghas & Gerlach) Dressler, *comb. nov.***

Basionym: *Chondrorhyncha aurantiaca* Senghas & Gerlach, Die Orchidee 42: 282. 1991.

***Ixyophora carinata* (Ortiz) Dressler, *comb. nov.***

Basionym: *Chondrorhyncha carinata* Ortiz, Orquideología 19(2): 18. 1994.

***Ixyophora viridisepala* (Senghas) Dressler, *comb. nov.***

Basionym: *Chondrorhyncha viridisepala* Senghas, Die Orchidee 40: 181. 1989.

*Chaubardiella* Garay — This uniform group (about eight species) has nonresupinate flowers and deeply concave lips; the viscidia are placed on the legs of its pollinators. The combined analysis forms a strongly supported group (Fig. 4).

*Pescatorea* (16 spp.) and *Bollea* (12 spp.) have long been regarded as sister taxa. As traditionally defined, these genera differ primarily in the relative width of the column (much broader in *Bollea*), but possess

similar floral shapes and are known to form natural “intergeneric” hybrids. In our sampling, the four species of *Pescatorea* are intercalated among the three representatives of *Bollea* on short branches; together, the clade is well supported. Given these relatively trivial morphological distinctions and the lack of molecular support for maintaining them as separate genera, we conclude they should be treated as a single genus. Both genera were described in the same publication, giving neither name clear priority. Since *Bollea* contains fewer species than *Pescatorea*, we choose *Pescatorea* as the generic name for this clade to minimize the number of nomenclatural transfers. The name *Pescatorea* is adopted here and the original *Pescatoria* is considered a typographical or orthographical error, the generic name being derived from the personal name Pescatore. The name *Pescatoria* was not an intentional latinization, as the author himself adopted the alternative spelling in successive publications. The correction does not affect the first syllable of the name or the first letter of the name. The generic name *Pescatorea* is formed with the addition of the letter “a” to the customary spelling of the personal name, as recommended by the International Code of Botanical Nomenclature (ICBN).

*Pescatorea* Rchb.f., Bot. Zeitung (Berlin) 10: 667. 1852. [as *Pescatoria*, orth. var.]

Type species: *Pescatorea cerina* (Lindl. & Paxton) Rchb.f., Bot. Zeitung (Berlin) 10: 667. 1852.

***Pescatorea coelestis* (Rchb.f.) Dressler, *comb. nov.***

Basionym: *Bollea coelestis* Rchb.f., Gard. Chron. ser. 2, 5: 756. 1876.

***Pescatorea ecuadorana* (Dodson) Dressler, *comb. nov.***

Basionym: *Bollea ecuadorana* Dodson, Selbyana 7: 354. 1984.

***Pescatorea hemixantha* (Rchb.f.) Dressler, *comb. nov.***

Basionym: *Bollea hemixantha* Rchb.f., Gard. Chron. ser. 3, 4: 206. 1888.

***Pescatorea hirtzii* (Waldvogel) Dressler, *comb. nov.***

Basionym: *Bollea hirtzii* Waldvogel, Die Orchidee 33(4): 143. 1982

***Pescatorea lalindei* (Linden) Dressler, *comb. nov.***

Basionym: *Batemannia lalindei* Linden, Numer. List 90. 1873.

***Pescatorea lawrenceana* (Rchb.f.) Dressler, *comb. nov.***

Basionym: *Bollea lawrenceana* Rchb.f., Gard. Chron. ser. 2, 15: 462. 1881.

***Pescatorea pulvinaris* (Rchb.f.) Dressler, *comb. nov.***

Basionym: *Bollea pulvinaris* Rchb.f., Linnaea 41: 107. 1877.

***Pescatorea violacea* (Lindl.) Dressler, *comb. nov.***

Basionym: *Huntleya violacea* Lindl., Sert. Orchid.

t. 26. 1838.

***Pescatorea whitei* (Rolfe) Dressler, comb. nov.**

Basionym: *Zygopetalum whitei* Rolfe, Gard. Chron. ser. 3, 7: 354. 1890.

*Warczewiczella* — These species have been lumped with *Cochleanthes* by some workers (Schultes & Garay 1959), but the molecular data strongly support the separation of *Warczewiczella* from *Cochleanthes* as proposed by Fowlie (1969) together with some more recently described species, but excluding *W. picta* (here placed in *Stenotyla*). As defined here, the genus consists of 10-12 species. This clade consists of plants with relatively large flowers with a lip enfolding the base of the column and with a thick, sulcate basal callus composed of several or many ridges. The stipe is shield-shaped. The lateral sepals are variable and are rolled and backswept to form false spurs in some taxa (e.g., *W. amazonica*). The clade is well supported in the combined tree with the exception of *W. wailesiana*, which is on a relatively long branch that is unsupported as sister to the other *Warczewiczella* species in the strict consensus of the shortest trees. Morphologically, it agrees closely with other species in this clade, so we include it in this genus even though it lacks strong molecular support. The molecular data do not unite it with any other clade, and we wish to avoid creation of monotypic genera lacking strong molecular or morphological support.

Type species: *Warczewiczella discolor* (Lindl.) Rchb. f., Bot. Zeit. Berlin 10: 636. 1852.

= *Warrea discolor* Lindl., J. Hort. Soc. London 4: 265. 1849.

***Warczewiczella guianensis* (Lafontaine, Gerlach & Senghas) Dressler, comb. nov.**

Basionym: *Cochleanthes guianensis* Lafontaine, Gerlach & Senghas, Die Orchidee 42: 285. 1991.

***Warczewiczella lobata* (Garay) Dressler, comb. nov.**

Basionym: *Cochleanthes lobata* Garay, Orquideología 4: 21. 1969.

***Warczewiczella palatina* (Senghas) Dressler, comb. nov.**

Basionym: *Cochleanthes palatina* Senghas, Die Orchidee 41: 96. 1990.

***Stenotyla* Dressler, gen. nov.**

*Chondrorhyncha* Lindley similis, sed mento brevi, labelli callo basali, angusto, et pseudobulbis manifeste evolutis differt.

Type species: *Chondrorhyncha lendyana* Rchb.f. Gard. Chron., n.s. 26: 103. 1886.

Etymology: From the Greek *stenos* (narrow) and *tylo* (callus), describing the shape of the lip callus.

The three species of this group possess a vegetative similarity to *Chondrorhyncha*, but with small, distinct pseudobulbs concealed in the leaf bases. Members of this genus are clearly distinguished by the very narrow 2- or 4-toothed basal callus, the short chin and the presence of pseudobulbs. Pupulin (2000: 22) illustrates *S. lankesteriana*.

***Stenotyla lankesteriana* (Pupulin) Dressler, comb. nov.**

Basionym: *Chondrorhyncha lankesteriana* Pupulin, Lindleyana 15: 21. 2000.

***Stenotyla lendyana* (Rchb.f.) Dressler, comb. nov.**

Basionym: *Chondrorhyncha lendyana* Rchb.f., Gard. Chron. n.s. 26: 103. 1886.

***Stenotyla picta* (Rchb.f.) Dressler, comb. nov.**

Basionym: *Warczewiczella picta* Rchb.f., Gard. Chron. n.s. 20: 8. 1883.

*Chondrorhyncha helleri* L.O. Williams is closely allied to *S. lendyana*, but the material available is not sufficient to show whether or not it is distinct. *Chondrorhyncha estrellensis* Ames, if distinct, would also be included in *Stenotyla*.

*Cochleanthes* — With the recognition of *Warczewiczella*, *Cochleanthes* now consists of only two species: the type, *C. flabelliformis*, and *C. aromatica*. The lip does not enfold the base of the column, and the column is distinctly keeled.

Although our sampling within the pseudobulbous *Zygopetalum* grade (Fig. 5) is sparse, the cladograms reveal several inconsistencies with current generic concepts. *Koellensteinia* is polyphyletic, and the three representative species are scattered within a clade containing *Acacallis*, *Otostylis*, *Paradisanthus*, and *Zygosepalum*. *Zygopetalum* is also polyphyletic; *Z. maxillare* is sister to a clade containing *Neogardneria murrayana*, *Pabstia*, and several other *Zygopetalum* species. Finally, a strongly supported (100% bs) clade contains *Galeottia*, *Batemannia*, and *Zygosepalum labiosum*. Three of the *Galeottia* species plus *Batemannia lepida* are on a very long branch relative to the other members of this clade. As noted above, this long branch is due to unusual (possibly paralogous)

*trnL-F* sequences, and relationships within this clade should be viewed with suspicion until problems with *trnL-F* are resolved or until sequence data from other regions are included.

Key to the Genera of the *Chondrorhyncha* complex

- 1a Plants pendent, leaves lax, minutely papillose, gray-green ..... *Benzingia* (most species)
- 1b Plants erect, leaves not papillose or gray-green ..... 2
- 2a Flowers nonresupinate ..... 3
- 2b Flowers resupinate or pendent ..... 4
- 3a Column foot 0.5-1.5 mm; viscidium curling on removal; apex of lip acute, entire ..... *Chaubardiella*
- 3b Column foot about 2 mm; viscidium apparently not curling; apex of lip rounded, erose ..... *Benzingia hirtzii*
- 4a Lip deeply pouched ..... 5
- 4b Lip open or infundibuliform, but not deeply concave ..... 6
- 5a Lip usually pinched in or closed distally; callus generally sharply many toothed; plants erect; pollinarium with a prominent stipe ..... *Stenia*
- 5b Lip open distally; plants usually pendent; callus shallowly or few toothed; pollinarium with a small stipe ..... *Benzingia*
- 6a Callus basal ..... 7
- 6b Callus near or reaching middle of lip ..... 10
- 7a Column with distinct wings near middle; with pseudobulbs (often small) ..... *Chaubardia*
- 7b Column without wings near middle or wings only apical; usually without pseudobulbs ..... 8
- 8a Callus narrow, with 2 or 4 teeth ..... *Stenotyla*
- 8b Callus wide, with 6-20+ ridges or teeth ..... 9
- 9a Each ridge of callus ending in an acuminate bristle; leaves large (25-30 x 3-5 cm), flowers large (6-10 cm diameter) ..... *Huntleya*
- 9b Ridges of callus rounded, without bristles; leaves small (about 10 x 2 cm), flowers small (about 3 cm diameter) ..... *Hoehneella*
- 10a Column with a ventral keel; viscidium curling upon removal; inflorescence axis thin; callus usually bilobed; flowers small (2-3 cm diameter) ..... *Kefersteinia*
- 10b Column usually without a ventral keel; viscidium not curling; inflorescence axis thick; callus variable; flowers large (6-10 cm diameter) ..... 11
- 11a Lip margins basally turned upward surrounding column, flowers more or less gullet shaped ..... *Warczewiczella*
- 11b Lip more or less flat, margins not surrounding column, flowers more or less patent ..... 12
- 12a Column distinctly keeled beneath ..... *Cochleanthes*
- 12b Column flat or concave beneath ..... 13
- 13a Callus of raised, rounded keels, together more or less semicircular ..... *Pescatorea*
- 13b Callus flattened or 2-lobed, not semicircular ..... 14
- 14a Callus wide and laminar, with many irregular teeth, \_ to 2/3 length of lip, 1/3 to 5/6 width of lip; stipe broad and shield shaped ..... *Euryblema*
- 14b Callus bilobed and fleshy, narrower or triangular, with few teeth; stipe narrow or narrowed near viscidium ..... 15
- 15a Lip with a second thickening distal to the bilobed callus; pollinarium with a distinct stipe; lip often fimbriate ..... *Chondroscaphe*
- 15b Lip without a second thickening; pollinarium with a small or indistinct stipe; lip not fimbriate ..... 16
- 16a Lip acuminate ..... *Benzingia*
- 16b Lip truncate, rounded or retuse ..... 17
- 17a Callus wide, bilobed, thick and fleshy ..... *Daiotyla*
- 17b Callus of 2 or various teeth, widest basally and narrowing distally, not thick and fleshy ..... 18
- 18a Column with 2 or more globose, trichome covered appendages beneath; stipe broad or shield-like ..... *Echinorhyncha*

- 18b Column without globose, setose appendages beneath; stipe variable .....19  
 19a Lip with a prominent keel below the 2-lobed callus; lip blade pilose; viscidium triangular, truncate .....  
 .....*Aetheorhyncha*  
 19b Lip without a basal keel; callus various; lip blade glabrous; viscidium ovate or subpandurate ( $\pm$  elliptic).....20  
 20a Viscidium ovate, without conspicuous stipe .....*Chondrorhyncha*  
 20b Viscidium subpandurate; stipe distinct .....*Ixyophora*

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Table 1. List of taxa examined, GenBank numbers, and voucher specimens.

Taxon	Collector	Voucher location	GenBank numbers ITS	GenBank numbers <i>matK</i>	GenBank numbers <i>trnL-F</i>
<i>Acacallis cyanea</i> Lindl.	Whitten 93107	FLAS	AY870104	AY870005	AY869907
<i>Acacallis fimbriata</i> (Rchb. f.) Schltr.	Breuer & Gerlach s.n.	M	AY870105	AY870006	AY869908
<i>Ackermania caudata</i> (Ackerman) Dodson & R. Escobar	Whitten 1750	FLAS	AY870027	AY869928	AY869842
<i>Ackermania cornuta</i> (Garay) Dodson & R. Escobar	Whitten 1818	FLAS	AY870026	AY869930	AY869841
<i>Ackermania hajekii</i> D.E.Benn. & Christenson	Whitten 1751	FLAS	AY870028	AY869929	AY869843

<i>Aganisia pulchella</i> Lindl.	Breuer & Gerlach s.n.	M	AY870106	AY870007	AY869909
<i>Batemannia colleyi</i> Bateman ex Lindl.	Chase 84746	K	AF239343	AF239439	AF239535
<i>Batemannia lepida</i> Rchb.f.	Gerlach 92/3900	M	AY870089	AY869990	n.a.
<i>Benzingia estradae</i> (Dodson) Dodson ex Dodson	Gerlach 96/4287	M	AY870029	AY869930	AY869844
<i>Benzingia hirtzii</i> Dodson ex Dodson	Hirtz 7178	QCNE	AY870030	AY869931	n.a.
<i>Bollea ecuadorana</i> Dodson	Whitten 1861	FLAS	AY870050	AY869951	AY869863
<i>Bollea lawrenciana</i> Rchb.f.	Whitten 1636	FLAS	AY870048	AY869949	AY869861
<i>Bollea pulvinaris</i> Rchb.f.	Whitten 1748	FLAS	AY870049	AY869950	AY869862
<i>Chaubardia heteroclita</i> (Poepp. & Endl.) Dodson & D.E. Benn.	Whitten 1761	FLAS	AF239323	AF239419	AF239515
<i>Chaubardia klugii</i> (C. Schweinf.) Garay	Whitten 1853	FLAS	AY870072	AY869973	AY869885
<i>Chaubardia surinamensis</i> Rchb.f.	Gerlach 01/2159	M	AY870073	AY869974	AY869886
<i>Chaubardiella pacuarensis</i> Jenny	Whitten 94094	FLAS	AY870046	AY869947	AY869859
<i>Chaubardiella pubescens</i> Ackerman	Whitten 1620	FLAS	AY870043	AY869944	AY869856
<i>Chaubardiella subquadrata</i> (Schltr.) Garay	Whitten s.n.	FLAS	AY870044	AY869945	AY869857
<i>Chaubardiella tigrina</i> (Garay & Dunst.) Garay	Gerlach 1651	M	AY870045	AY869946	AY869858
<i>Chondrorhyncha</i> aff. <i>carinata</i> P. Ortiz	Whitten 2773	FLAS	AY870040	AY869941	AY869853
<i>Chondrorhyncha albicans</i> Rolfe	Whitten 1932	FLAS	AY870016	AY869917	AY869831
<i>Chondrorhyncha andreae</i> P. Ortiz	Whitten 1849	FLAS	AY870047	AY869948	AY869860
<i>Chondrorhyncha andreetae</i> Jenny	Dressler 6360	M	AY870031	AY869932	n.a.
<i>Chondrorhyncha</i> aff. <i>hirtzii</i> Dodson	Maduro & Olmos 217	FLAS	AY870012	AY869913	n.a.
<i>Chondrorhyncha crassa</i> Dressler	Dressler s. n.	FLAS	AY870017	AY869918	AY869832
<i>Chondrorhyncha hirtzii</i> Dodson	Whitten 1637	FLAS	AY870015	AY869916	AY869830
<i>Chondrorhyncha lankesteriana</i> Pupulin	Dressler 6363	FLAS	AY869832	AY869962	AY869874
<i>Chondrorhyncha lendyana</i> Rchb.f.	Dressler 6228	FLAS	AY870062	AY869963	AY869875
<i>Chondrorhyncha litensis</i> Dodson	Whitten 99319	FLAS	AY870039	AY869940	AY869852
<i>Chondrorhyncha picta</i> (Rchb.f.) Senghas	Dressler 6235	FLAS	AY870060	AY869961	AY869873
<i>Chondrorhyncha reichenbachiana</i> Schltr.	Whitten 1747	FLAS	AF239325	AF239421	AF239517
<i>Chondrorhyncha rosea</i> Lindl.	Whitten 1760	FLAS	AY870013	AY869914	n.a.
<i>Chondrorhyncha viridisejala</i> Senghas #1	Whitten 1749	FLAS	AY870041	AY869942	AY869854
<i>Chondrorhyncha viridisejala</i> Senghas #2	Gerlach 98/2798	M	AY870042	AY869943	AY869855
<i>Chondroscaphe</i> aff. <i>chestertonii</i> (Rchb.f.) Senghas & G. Gerlach	Whitten 99308	FLAS	AY870069	AY869970	AY869882
<i>Chondroscaphe amabilis</i> (Schltr.) Senghas & G. Gerlach	Whitten 1855	FLAS	AY870065	AY869966	AY869878
<i>Chondroscaphe atrilinguis</i> Dressler	Dressler 6289	FLAS	AY870071	AY869972	AY869884
<i>Chondroscaphe</i> cf. <i>laevis</i> Dressler	Dressler 6357	FLAS	AY870067	AY869968	AY869880
<i>Chondroscaphe eburnea</i> (Dressler) Dressler	Dressler 6361		AY870014	AY869915	AY869829
<i>Chondroscaphe escobariana</i> (Dodson & Neudecker) C. Rungius ex C. Rungius	Whitten 1850	FLAS	AY870066	AY869967	AY869879
<i>Chondroscaphe flaveola</i> (Linden & Rchb.f. ex Rchb.f.) Senghas & G. Gerlach	Gerlach 93/3342	M	AY870068	AY869969	AY869881
<i>Chondroscaphe laevis</i> Dressler	Hoffmann s.n.	FLAS	AY870067	AY869968	AY869883
<i>Cochleanthes anatona</i> Dressler	Whitten 1754	FLAS	AY870032	AY869933	AY869845
<i>Cochleanthes aromatica</i> (Rchb.f.) R.E. Schultes & Garay	Whitten 1759	FLAS	AY870063	AY869964	AY869876
<i>Cochleanthes flabelliformis</i> (Sw.) R.E. Schultes & Garay	Whitten 99113	FLAS	AY870064	AY869965	AY869877
<i>Cochleanthes guianensis</i> A. Lafontaine, G. Gerlach & K. Senghas	Gerlach 93/3271	M	AY870055	AY869956	AY869868

<i>Cochleanthes guianensis</i> A. Lafontaine, G. Gerlach & K. Senghas	Gerlach 93/3272	M	AY870056	AY869957	AY869869
<i>Cochleanthes wailesiana</i> (Lindl.) R.E. Schult. & Garay	Gerlach 93/3314	M	AY870059	AY869960	AY869872
<i>Cryptarrhena guatemalensis</i> Schltr.	F. Pupulin & J.A. Campos 2957	USJ	AY870082	AY869983	AY869895
<i>Cryptarrhena lunata</i> R. Br. #1	Whitten 98000	FLAS	AY870081	AY869982	AY869894
<i>Cryptarrhena lunata</i> R. Br. #2	Chase 307	K	AF239324	AF239420	AF239516
<i>Dichaea campanulata</i> C. Schweinf.	Whitten 1851	FLAS	AY870079	AY869980	AY869892
<i>Dichaea panamensis</i> Lindl.	Whitten 1724	FLAS	AY870080	AY869981	AY869893
<i>Dichaea aff. morrisii</i> Fawc. & Rendle	Pupulin 1189	FLAS	AY870078	AY869979	AY869891
<i>Dichaea squarrosa</i> Lindl.	Higgins 1021	FLAS	AY869891	AY869978	AY869890
<i>Dodsonia saccata</i> (Garay) Ackerman #1	Whitten 1697	FLAS	AY870024	AY869925	AY869839
<i>Dodsonia saccata</i> (Garay) Ackerman #2	Neudecker & Gerlach s.n.	M	AY870025	AY869926	AY869840
<i>Galeottia burkei</i> (Rchb.f.) Dressler & Christenson #1	Gerlach 97/3370	M	AY870086	AY869987	n.a.
<i>Galeottia burkei</i> (Rchb.f.) Dressler & Christenson #2	Maguire & Politi 28175	AMES	AY870087	AY869988	n.a.
<i>Galeottia ciliata</i> (Morel) Dressler & Christenson	Breuer s.n.	unvouchered	AY870088	AY869989	n.a.
<i>Galeottia colombiana</i> (Garay) Dressler & Christenson	Gerlach 93/3396	M	AY870085	AY869986	n.a.
<i>Galeottia fimbriata</i> Linden & Rchb.f.	Whitten 2774	FLAS	AY870091	AY869992	AY869896
<i>Galeottia grandiflora</i> A. Rich.	Chase 89013	K	AY870092	AY869993	AY869897
<i>Huntleya gustavii</i> (Rchb.f.) Schltr.	Whitten 1864	FLAS	AY870076	AY869977	AY869889
<i>Huntleya wallisii</i> (Rchb.f.) Rolfe #1	Whitten 88026	FLAS	AY870074	AY869975	AY869887
<i>Huntleya wallisii</i> (Rchb.f.) Rolfe #2	Whitten 1858	FLAS	AY870075	AY869976	AY869888
<i>Kefersteinia excentrica</i> Dressler & Mora-Retana	Dressler 6236	FLAS	AY870033	AY869934	AY869846
<i>Kefersteinia expansa</i> (Rchb.f.) Schltr.	Whitten 1996	FLAS	AY870038	AY869939	AY869851
<i>Kefersteinia guacamayoana</i> Dodson & Hirtz	Gerlach 93/3382	M	AY870034	AY869935	AY869847
<i>Kefersteinia maculosa</i> Dressler	Whitten 1997	FLAS	AY870037	AY869938	AY869850
<i>Kefersteinia microcharis</i> Schltr.	Pupulin 252	USJ	AY870036	AY869937	AY869849
<i>Kefersteinia trullata</i> Dressler	Whitten 1998	FLAS	AY870035	AY869936	AY869848
<i>Koellensteinia altissima</i> Pabst	Chase 90004	K	AF239327	AF239423	AF239519
<i>Koellensteinia boliviensis</i> (Rolfe) Schltr.	Gerlach 94/99	M	AY870103	AY870004	n.a.
<i>Koellensteinia graminea</i> (Lindl.) Rchb.f.	Chase O-159	K	AY870102	AY870003	AY869906
<i>Maxillaria violaceopunctata</i> Rchb.f.	Whitten 1980	FLAS	AY870109	AY870010	AY869911
<i>Neogardneria murrayana</i> (Gardner ex Hook.) Schltr.	Gerlach s.n.	M	AY870096	AY869997	AY869900
<i>Otostylis lepida</i> (Linden & Rchb.f.) Schltr.	Gerlach 94/968	unvouchered	AY870108	AY870009	n.a.
<i>Pabstia jugosa</i> (Lindl.) Garay	Gerlach 937-894	M	AY870098	AY869999	AY869902
<i>Pabstia viridis</i> (Lindl.) Garay	Gerlach 99/2619	M	AY870090	AY869991	n.a.
<i>Paradisanthus micranthus</i> (Barb. Rodr.) Schltr.	Chase 87056	K	AY870107	AY870008	AY869910
<i>Pescatorea cerina</i> (Lindl. & Paxton) Rchb.f.	Whitten s.n.	FLAS	AY870051	AY869952	AY869864
<i>Pescatorea coronaria</i> Rchb.f.	Whitten 1758	FLAS	AY870053	AY869954	AY869866
<i>Pescatorea lamellosa</i> Rchb.f.	Whitten 1755	FLAS	AY870052	AY869953	AY869865
<i>Pescatorea lehmannii</i> Rchb.f.	Whitten 93041	FLAS	AF239326	AF239422	AF239518
<i>Promenaea ovatiloba</i> (Klinge) Cogn.	Chase O-133	K	AY870100	AY870001	AY869904
<i>Promenaea stapelioides</i> (Link & Otto) Lindl.	Whitten 94102	FLAS	AY870101	AY870002	AY869905
<i>Promenaea xanthina</i> Lindl.	Whitten 1860	FLAS	AY870099	AY870000	AY869903
<i>Rudolfiella saxicola</i> (Schltr.) C. Schweinf.	Whitten 97020	FLAS	AY870110	AY870011	AY869912
<i>Stenia aff. wendiae</i> D.E. Benn. & Christenson	Whitten s.n.	FLAS	AY870023	AY869924	AY869838
<i>Stenia bismarckii</i> Dodson & D.E. Benn.	Whitten 1698	FLAS	AY870019	AY869920	AY869834

<i>Stenia calceolaris</i> (Garay) Dodson & D.E. Benn.	Whitten 1699	FLAS	AY870018	AY869919	AY869833
<i>Stenia glatzii</i> Neudecker & Gerlach	Neudecker s.n.	M	AY870020	AY869921	AY869835
<i>Stenia pallida</i> Lindl.	Whitten 88010	FLAS	AY870021	AY869922	AY869836
<i>Stenia pallida</i> Lindl.	Dressler s.n.	FLAS	AY870022	AY869923	AY869837
<i>Warczewiczella walesiana</i> (Lindl.) Rchb.f. ex E. Morren	Gerlach 93/3314	M	AY870059	AY869960	AY869872
<i>Warczewiczella discolor</i> (Lindl.) Rchb.f.	Whitten 1859	FLAS	AY870058	AY869959	AY869871
<i>Warczewiczella lipscombiae</i> (Rolfe) Fowlie	Gerlach 94/4006	M	AY870054	AY869955	AY869867
<i>Warczewiczella marginata</i> Rchb.f.	Whitten s.n.	FLAS	AY870057	AY869958	AY869870
<i>Warrea warreana</i> (Lodd. ex Lindl.) C. Schweinf.	Whitten 1752	FLAS	AF239321	AF239417	AF239513
<i>Warreopsis colorata</i> (Linden & Rchb.f.) Garay	Gerlach s.n.	unvouchered	AY870083	AY869984	n.a.
<i>Warreopsis pardina</i> (Rchb.f.) Garay	Gerlach s.n.	unvouchered	AY870084	AY869985	n.a.
<i>Zygopetalum intermedium</i> Lodd. ex. Lindl.	Chase 160	FLAS	AY870097	AY869998	AY869901
<i>Zygopetalum maxillare</i> Lodd.	Whitten 94103	FLAS	AY870095	AY869996	AY869899
<i>Zygosepalum labiosum</i> (Rich.) Garay	Gerlach s.n.	M	AY870094	AY869995	AY869898
<i>Zygosepalum tatei</i> (Ames & Schltr.) Garay & Dunst.	Maguire & Politi 27494	AMES	AY870093	AY869994	n.a.

Table 2. Values and statistics from PAUP analyses of separate and combined data matrices.

	<i>matK</i>	<i>trnL-F</i>	ITS 1&2	<i>matK</i> + <i>trnL-F</i> + ITS 1&2
# included positions in matrix	1341	1358	838	3537
# variable sites	262	292	399	953
# potentially phylogenetically informative sites (%)	154 (10%)	146 (10.8%)	289 (34.5%)	589 (16.7%)
% of sites variable	19.5	21.5	47.6	26.9
# of trees (Fitch)	2115	9310	857	10,000+
# of steps	472	443	949	1887
CI	0.53	0.64	0.54	0.54
RI	0.81	0.87	0.86	0.85
Ave. # of changes per variable site (# steps/# var. sites)	1.8	1.5	2.4	2.0

Table 3. A comparison of some features in *Chondroscaphe* and *Chondrorhyncha*.

Character	<i>Chondroscaphe</i>	<i>Chondrorhyncha</i>
Lateral sepals	not reflexed	often reflexed
Lip and petal margin	often fimbriate	entire or undulate
Calli	second thickening distally	single callus
Stipe	distinct, attached to mid-viscidium	slight, attached to edge of viscidium
Pollinia	sublinear, unequal	obovoid, subequal

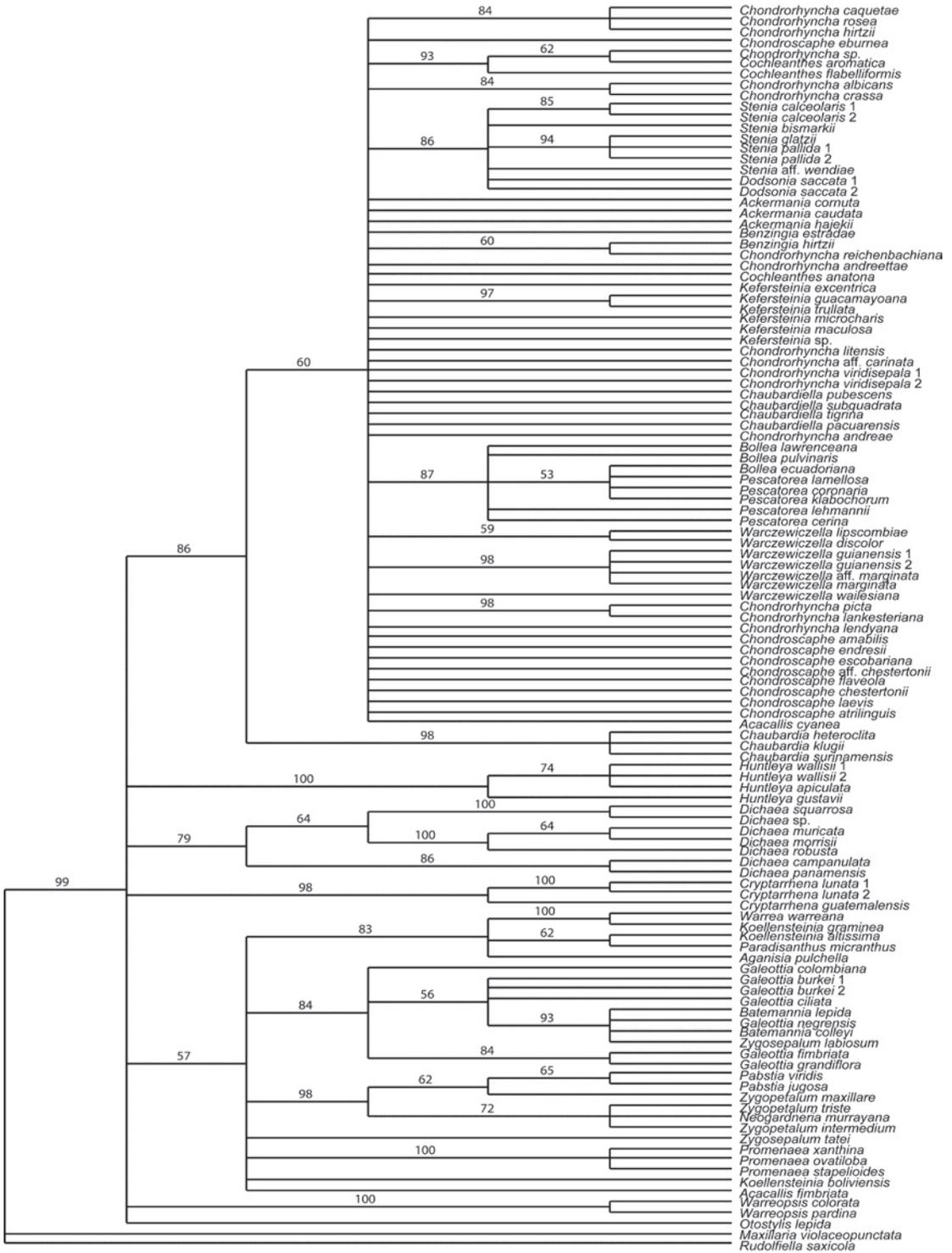


Fig.1. Bootstrap consensus of *matK* data set. Values above branches are bootstrap percentages (1000 replicates).

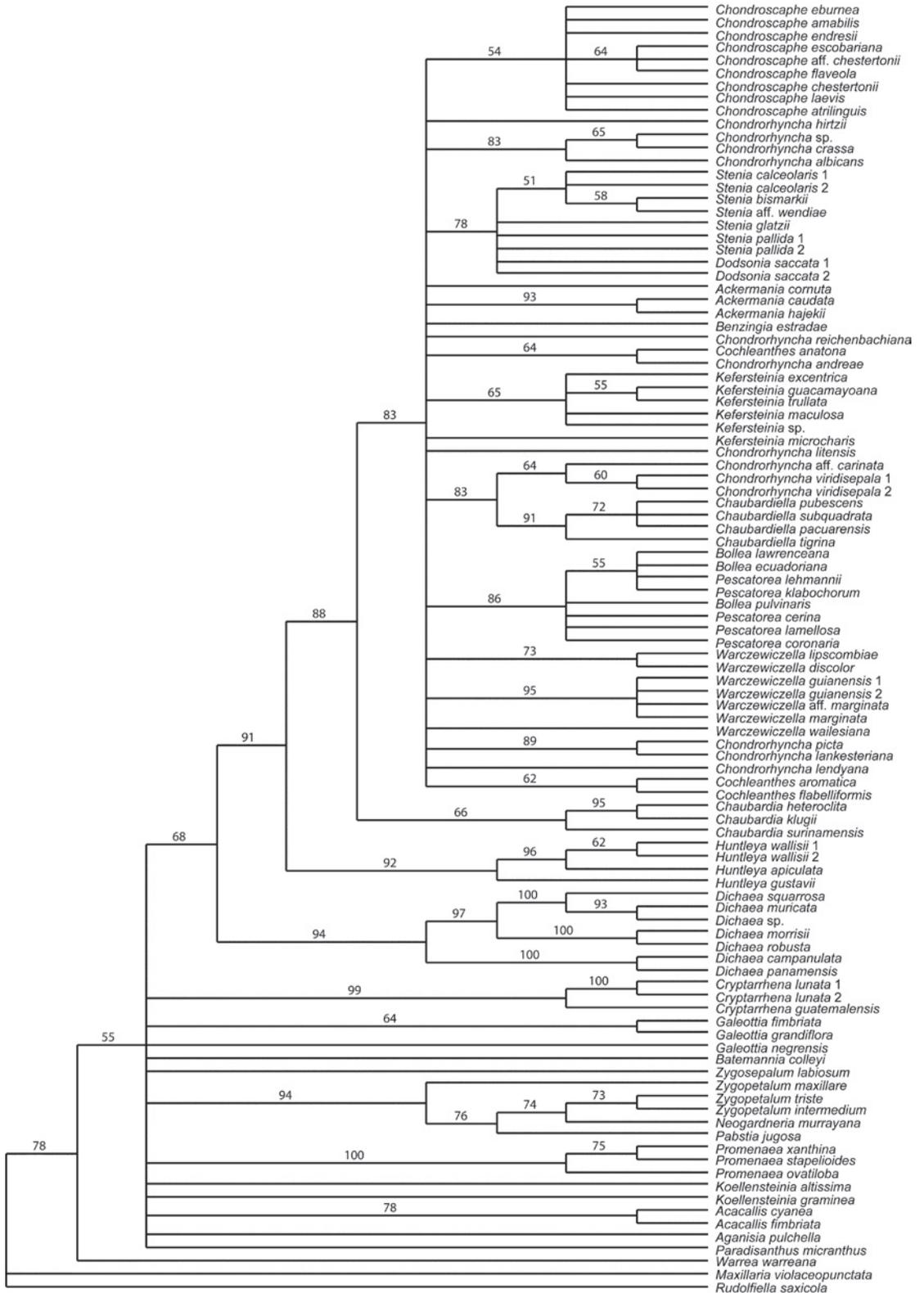


Fig.2. Bootstrap consensus of *trnL-F* data set. Values above branches are bootstrap percentages (1000 replicates).

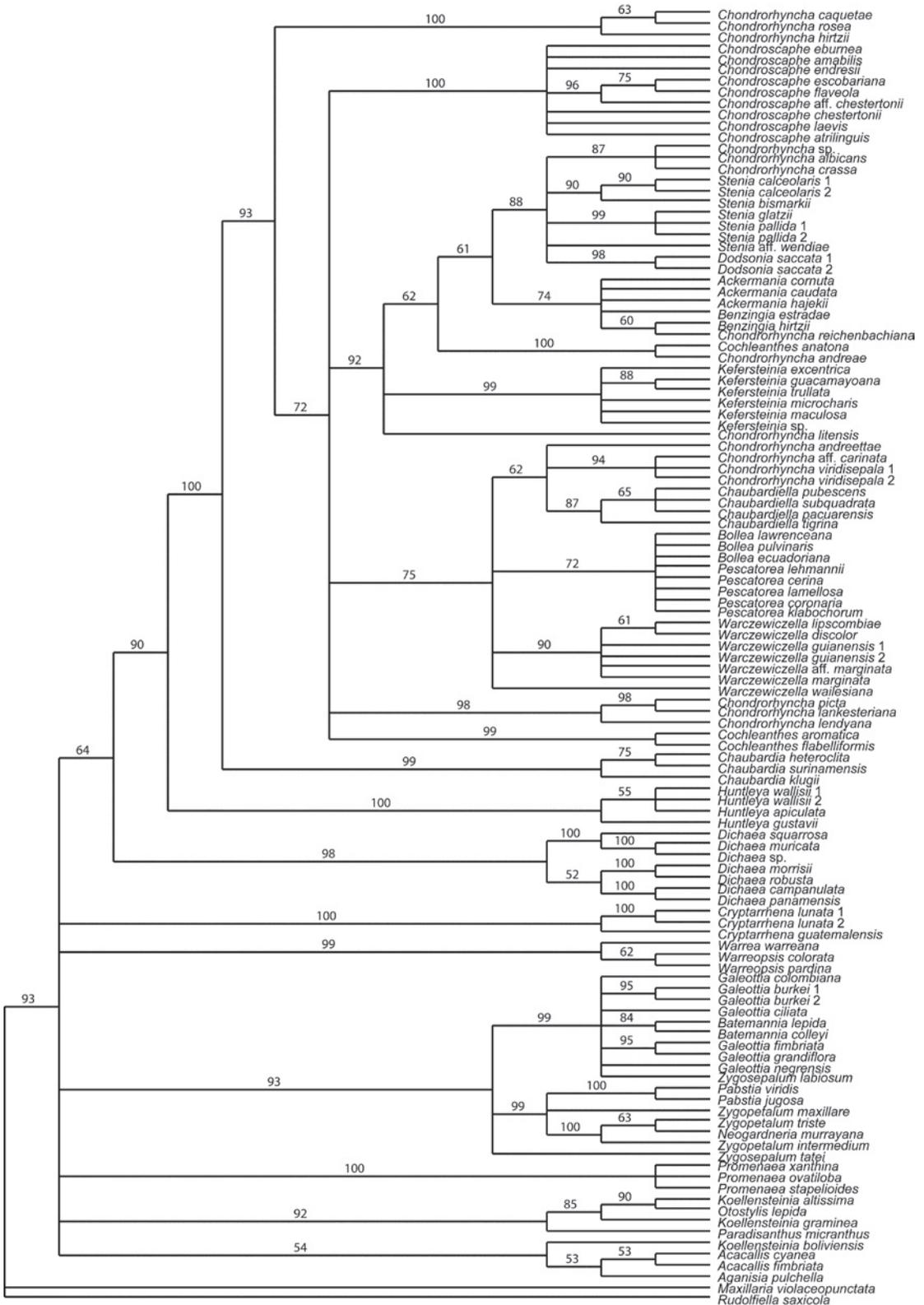


Fig.3. Bootstrap consensus of ITS rDNA data set. Values above branches are bootstrap percentages (1000 replicates).

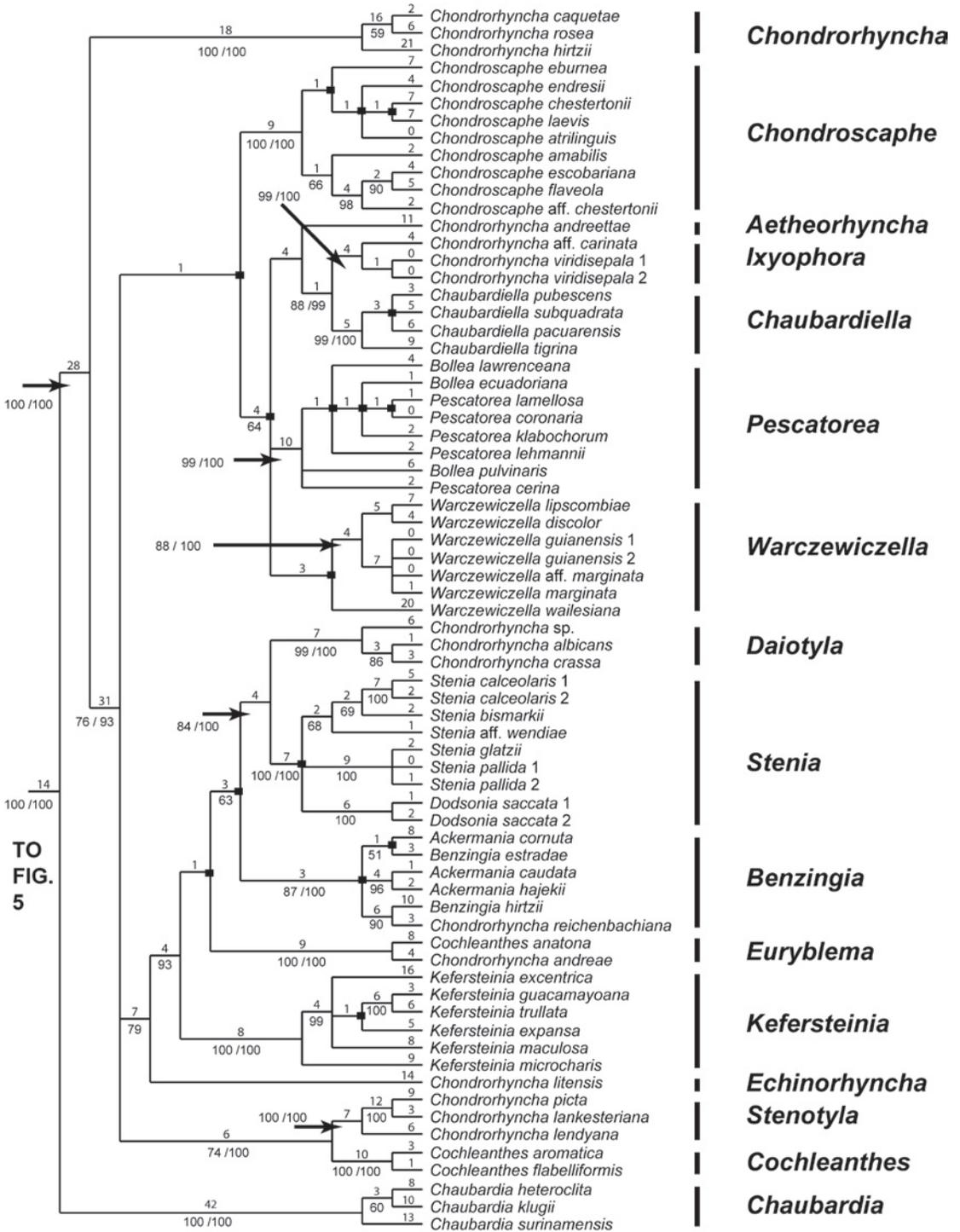


Fig. 4. Randomly-chosen most parsimonious tree resulting from cladistic analyses of combined *matK/trnL-F/ITS* rDNA data set for the mainly pseudobulbless groups of the tree. Values above branches are Fitch lengths; values below branches are bootstrap percentages followed by Bayesian posterior probability values if > 95; an asterisk indicates posterior probability value < 95. Black squares indicate nodes that collapse in the strict consensus tree.

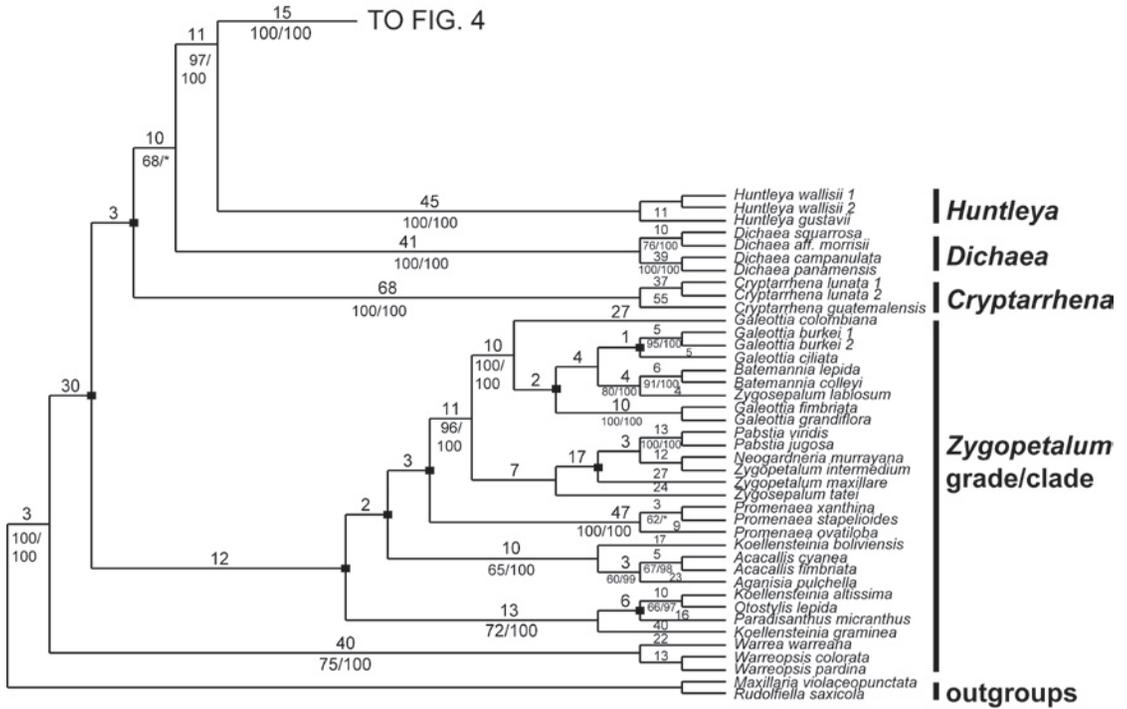


Fig. 5. Continuation of Fig. 4 of single randomly-chosen most parsimonious tree resulting from cladistic analysis of combined *matK/trnL-F/ITS* rDNA data set. Values above branches are Fitch lengths; values below branches are bootstrap percentages followed by Bayesian posterior probability values if > 95; an asterisk indicates posterior probability value <95. Black squares indicate nodes that collapse in the strict consensus tree.

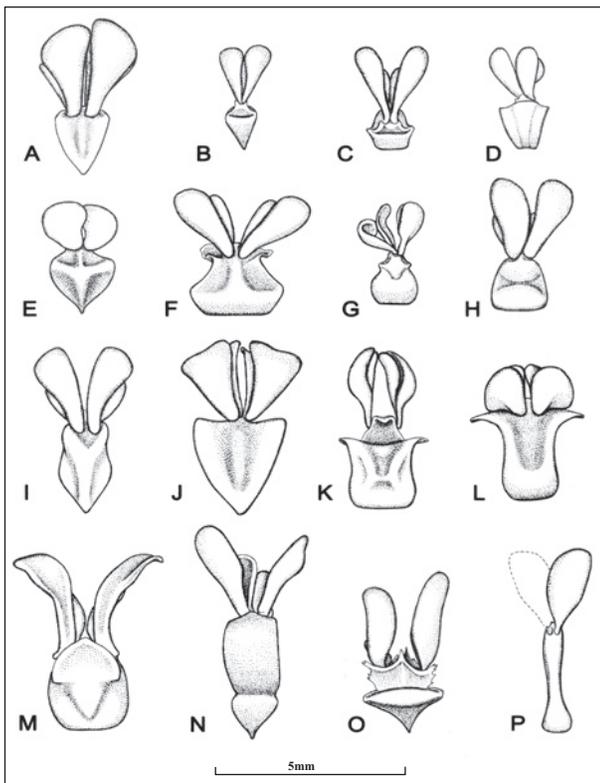


Fig. 6. Pollinaria of genera of Zygopetalinae of the *Huntleya* clade. (a) *Chondrorhyncha* sp. (Ecuador). (b) *Benzingia reichenbachiana*. (c) *Benzingia caudata*. (d) *Daiotyla albicans*. (e) *Cochleanthes flabelliformis*. (f) *Chaubardiella pubescens*. (g) *Kefersteinia deflexipetala*. (h) *Aetheorhyncha andreettae*. (i) *Ixyophora viridisepala*. (j) *Euryblema anatum*. (k) *Warczewiczella discolor*. (l) *Echinorhyncha litensis*. (m) *Chondroscape eburnea*. (n) *Chondroscape genyri*. (o) *Stenia pallida*. (p) *Stenia lilliana*.

a-e, *Chondrorhyncha* type, with triangular to ovate viscidia and short stipes, varying in size; f-g, with viscidia that clasp cylindrical appendages of the pollinator (antennae or legs); h, truncate viscidium with broad stipe; i, triangular viscidium with stipe narrowed basally; j-l, wide, shield-like stipes; m-p, variation within genera with well-developed stipes. Drawings by Stig Dalström.

