



INVITED REVIEW

An updated classification of Orchidaceae

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Since the last classification of Orchidaceae in 2003, there has been major progress in the determination of relationships, and we present here a revised classification including a list of all 736 currently recognized genera. A number of generic changes have occurred in Orchidaceae (Orchidoideae), but the majority of changes have occurred in Epidendroideae. In the latter, almost all of the problematic placements recognized in the previous classification 11 years ago have now been resolved. In Epidendroideae, we have recognized three new tribes (relative to the last classification): Thaieae (monogeneric) for *Thaia*, which was previously considered to be the only taxon *incertae sedis*; Xerorchideae (monogeneric) for *Xerorchis*; and Wulpschlaegelieae for achlorophyllous *Wulpschlaegelia*, which had tentatively been placed in Calypsoeae. Another genus, *Devogelia*, takes the place of *Thaia* as *incertae sedis* in Epidendroideae. Gastrodieae are clearly placed among the tribes in the neottiid grade, with Neottieae sister to the remainder of Epidendroideae. Arethuseae are sister to the rest of the higher Epidendroideae, which is unsurprising given their mostly soft pollinia. Tribal relationships within Epidendroideae have been much clarified by analyses of multiple plastid DNA regions and the low-copy nuclear gene *Xdh*. Four major clades within the remainder of Epidendroideae are recognized: Vandeeae/Podochileae/Collabieae, Cymbidieae, Malaxideae and Epidendreeae, the last now including Calypsoinae (previously recognized as a tribe on its own) and Agrostophyllinae *s.s.* Agrostophyllinae and Collabiinae were unplaced subtribes in the 2003 classification. The former are now split between two subtribes, Agrostophyllinae *s.s.* and Adrorrhizinae, the first now included in Epidendreeae and the second in Vandeeae. Collabiinae, also probably related to Vandeeae, are now elevated to a tribe along with Podochileae. *Malaxis* and relatives are placed in Malaxidinae and included with Dendrobiinae in Malaxideae. The increased resolution and content of larger clades, recognized here as tribes, do not support the ‘phylads’ in Epidendroideae proposed 22 years ago by Dressler. © 2015 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2015, 177, 151–174.

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INTRODUCTION

Orchidaceae are one of the two largest families of flowering plants, and are perhaps second only to

Asteraceae (*The Plant List*, 2014). New species are being described in both families at a rate of roughly 500 per year. We now recognize 736 genera in Orchidaceae, and new orchid genera are being described at a rate of about 13 per year (the average over 10 years prior to 2004; Schuiteman, 2004), but the great

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majority of these are segregates of species from other genera and are not based on newly discovered taxa. There are exceptions to this general pattern, such as *Devogelia* (Schuiteman, 2004) and *Danxiaorchis* (Zhai *et al.*, 2013), the former not obviously morphologically similar to any other genus of Epidendroideae and the latter a member of Calypsoinae, as documented by molecular studies. Since the last classification of Orchidaceae (Chase *et al.*, 2003), nearly 150 new genera have been described, but we do not accept most of these here. Some are related to genera that are polyphyletic, such as *Habenaria* and *Eulophia*, and accepting additional genera in such groups is premature until a well-sampled phylogenetic study has been completed. Other newly described genera are merely the result of splitting of genera demonstrated to be monophyletic, such as *Masdevallia*, *Dendrobium* and *Corybas*; the benefits of splitting are unclear to us, and we have resisted this sort of taxonomic change. It may well be that, in the longer term, recognition of such segregates will prevail, but more discussion is required before a consensus to make such changes is reached. A prominent example in which such splitting of a genus was eventually accepted is that of *Cypripedium*, which had been the sole genus of that subfamily (or even family). Although all segregate genera had been proposed by the turn of the 19th century, the sole use of *Cypripedium* continued until the 1950s, more than 50 years after Rolfe published *Phragmipedium* (Rolfe, 1896).

Many descriptions of new genera now include molecular (DNA) analyses to demonstrate their necessity, whereas, in previous decades, morphology was the generally accepted basis for the description of new taxa. More newly described species are also being published in studies in which DNA evidence for their distinctiveness is included (Zhai *et al.*, 2013; Su *et al.*, 2014; Xu *et al.*, 2014), and both trends should be encouraged, whenever suitable material for DNA work is available. Descriptions of new orchid taxa at whatever rank should include genetic as well as morphological studies. The days in which intuition played a major role in such studies are coming to an end.

Since the publication of the last classification of Orchidaceae in Chase *et al.* (2003) with partial revisions in Pridgeon *et al.* (2005, 2009, 2014), there has been a great deal of progress in understanding the phylogenetics of the largest subfamily, Epidendroideae. Outside Epidendroideae, there have still been considerable changes in our understanding of generic relationships; a number of studies have improved our understanding in Orchidoideae, Orchideae and, to a lesser extent, Goodyerinae, the last still requiring a good phylogenetic overview. Elsewhere, there have been few changes since Chase *et al.* (2003).

Our general philosophy in developing the classification of Orchidaceae has been to minimize the number of tribes in order to make the system as simple as possible. Garay (1972) (based on Schlechter, 1926) recognized five subfamilies, but these were not equivalent to the five here, although four of the five names are the same (differing in Neottioideae versus Vanilloideae). Dressler (1993) also recognized five subfamilies, but he split Spiranthoideae from Orchidoideae and included *Vanilla* and relatives in Epidendroideae. Five is a reasonable number of subfamilies and is easily remembered by everyone, but, in other large families, the number of subfamilies has been greatly increased as a result of molecular studies and a tendency to split in order to maintain some long-recognized subfamilies, making these systems much more difficult for students and non-specialists to use. As a result of the expansion in the number of subfamilies, only some of the larger ones will be taught in plant taxonomy courses, which makes it more difficult for students to learn about the diversity present in these families that is represented by the smaller subfamilies. Students learning plant taxonomy will be more likely to learn about Apostasioideae (two genera) than they will be to hear about Stiffioideae (five genera), Wunderlichioideae (eight genera) or Pertyoideae (five genera) when there are 11 subfamilies of Asteraceae (Panero & Funk, 2002). Thirty-five tribes are used in Asteraceae versus 21 in Orchidaceae. We have tended to reduce well-supported sister tribes to a single tribe. For example, Calypsoeae were found to be sister to Epidendreae in van den Berg *et al.* (2005), Górniak, Paun & Chase (2010) and Freudenstein & Chase (2015), and, following the above-stated principle, we have changed the status of the former to a subtribe of Epidendreae, Calypsoinae. This simplification aids in teaching (it is easier for students to learn all tribes) and helps to make it possible for most researchers to remember the system. From a biological point of view, such an association also helps to understand the biogeography of Epidendreae as a whole. We have applied this same principle to subtribes, and so, for example, have placed *Dilomilis*, *Neocogniauxia* and *Tomzania* in Pleurothallidinae, *Arpophyllum* in Laeliinae and *Coelia* in Calypsoinae. In each of these cases, the group or genus was sister to the larger clade and could have been maintained, perhaps arguing for this on the basis of continuity or morphological homogeneity. At the generic level, the prevailing principle is that of lumping (the broad treatments of *Bulbophyllum*, *Dendrobium* and *Epidendrum* being the most prominent examples), but there have been exceptions (see the discussion below on the status of *Maxillaria*, for example).

We present below, in a rough phylogenetic sequence, a description of the changes in each subfamily, tribe

and subtribe; at the end, in the Appendix, is a list of the genera with the number of species indicated (from the Monocot Checklist, Govaerts, 2014); this also includes authors for all genera. Since the last classification (Chase *et al.*, 2003), there have been no changes in Apostasioideae and Cypripedioideae, and so we begin with Vanilloideae, in which there have been only a few. A 'classification tree' that summarizes what is known about higher level relationships is presented in Figure 1.

VANILLOIDEAE

Here, we split Vanilloideae into two tribes, Pogoniaceae and Vanilleae, in line with Pridgeon *et al.* (2003), rather than into two subtribes as in Chase *et al.* (2003). *Dictyophyllaria dietschiana* (Edwall) Garay has been investigated and found to be embedded in *Vanilla* (Pansarin 2010; Cameron, 2011); this species was originally described in *Vanilla*, and so it can now simply be considered as a member of that genus again. It is unusual in *Vanilla* in not being a climber and having small leaves, but florally it fits well there. *Cleisthes* has long been known not to be monophyletic (Cameron & Chase, 1999; Cameron, 2004, 2006; Pansarin, Salatino & Salatino, 2008), and so Pansarin & de Barros (2009) described *Cleistesiopsis* for the North American clade that does not go with the tropical American species, including the type species, *C. grandiflora* (Aubl.) Schltr. The position of achlorophyllous *Pogoniopsis* has been the subject of some controversy. It had been previously placed near subtribe Pogoniinae by most authors, including Chase *et al.* (2003), but, at that time, no DNA data were available. On morphological grounds, Cameron (2003) suggested a position close to *Triphora* (Triphorinae, Triphoreae, Epidendroideae). However, when fresh material for DNA study became available, Pansarin (2005), using only nuclear ribosomal internal transcribed spacer (nrITS), found that it was instead likely to be a member of Vanilloideae, although the taxon sampling of this study was not sufficiently robust to address this problematic placement. Also problematic was the use of only nrITS, which is difficult to align at deeper taxonomic levels in Orchidaceae, particularly for a highly sequence-divergent group such as Vanilloideae (Cameron, 2009). In a more thoroughly sampled study, Cameron & van den Berg (in press) found that, with 18S rDNA and two mitochondrial DNA regions, the position of *Pogoniopsis* was more likely to be in accord with its morphology, and we thus place it near *Triphora* here.

ORCHIDOIDEAE

In Orchidoideae, no study published thus far has resolved with internal support relationships of the

four tribes recognized in this classification. Thus, we show them as an unresolved trichotomy in Figure 1. Changes at the generic level in Orchidoideae have been numerous, as a result of ongoing phylogenetic studies that have included many more species and, in particular, previously unsampled genera. We have treated here the formerly recognized tribe Chloraeae as a subtribe in Cranichideae because recent phylogenetic studies (Cisternas, Salazar & Verdugo, 2012a) have demonstrated that, with greater sampling of taxa and characters than in Pridgeon *et al.* (2001a), this clade is sister to another group in which Pterostylidinae (including *Achlydosa*; see below) is in turn sister to 'core Cranichideae', which includes Goodyerinae, Galeottiellinae, Manniellinae and Cranichidinae/Spiranthinae. This broader circumscription of Cranichideae is consistent with our philosophy of minimizing the number of tribes and is supported by some morphological characters: fleshy roots either clustered or scattered along a rhizome, leaves usually arranged in a basal rosette and a spiranthoid embryo (Clements, 1999).

Cranichideae

Within Chloraeinae, phylogenetic analyses (Chemisquy & Marrone, 2010; Cisternas *et al.*, 2012b) have shown that *Geoblasta penicillata* Rchb.f. is embedded in *Bipinnula*, into which it has been transferred (Cisternas *et al.*, 2012a). *Gavilea* is monophyletic with the inclusion of the species previously treated as *Chloraea chica* Speg. & Kraenzl. [i.e. *Gavilea chica* (Speg. & Kraenzl.) Chemisquy], as is the recircumscribed *Bipinnula*, but *Chloraea* is grossly polyphyletic and needs considerable attention to establish how it should be handled (Cisternas *et al.*, 2012b). Szlachetko & Margońska (2001) and Szlachetko & Tukałło (2008) resurrected *Bieneria* Rchb.f. and *Ulantha* Hook., and created some new genera mostly based on column and perianth features (*Jouyella* Szlach., *Chileorchis* Szlach. and *Correorchis* Szlach.), but these changes are not a viable alternative and would still leave *Chloraea* non-monophyletic. Until a more appropriate solution is found, we prefer to recognize *Chloraea*, but with the understanding that it is not monophyletic.

In Cranichidinae, several studies (Figueroa *et al.*, 2008; Álvarez-Molina & Cameron, 2009; Salazar *et al.*, 2009) have shown that a pair of species, *Prescottia tubulosa* (Lindl.) L.O. Williams and *Pseudocranichis thysanochila* (B.L. Rob. & Greenm.) Garay, are sister to *Prescottia*. These two morphologically divergent species share an apically lobed labellum with incurved sides, a column with two lateral, receptive stigmatic areas, separated by a sterile central area, and two hairpin-like pollinia, all features not shared with any other genus in the subtribe. For these, Salazar (2009) resurrected *Galeoglossum* A. Rich & Galeotti; a third

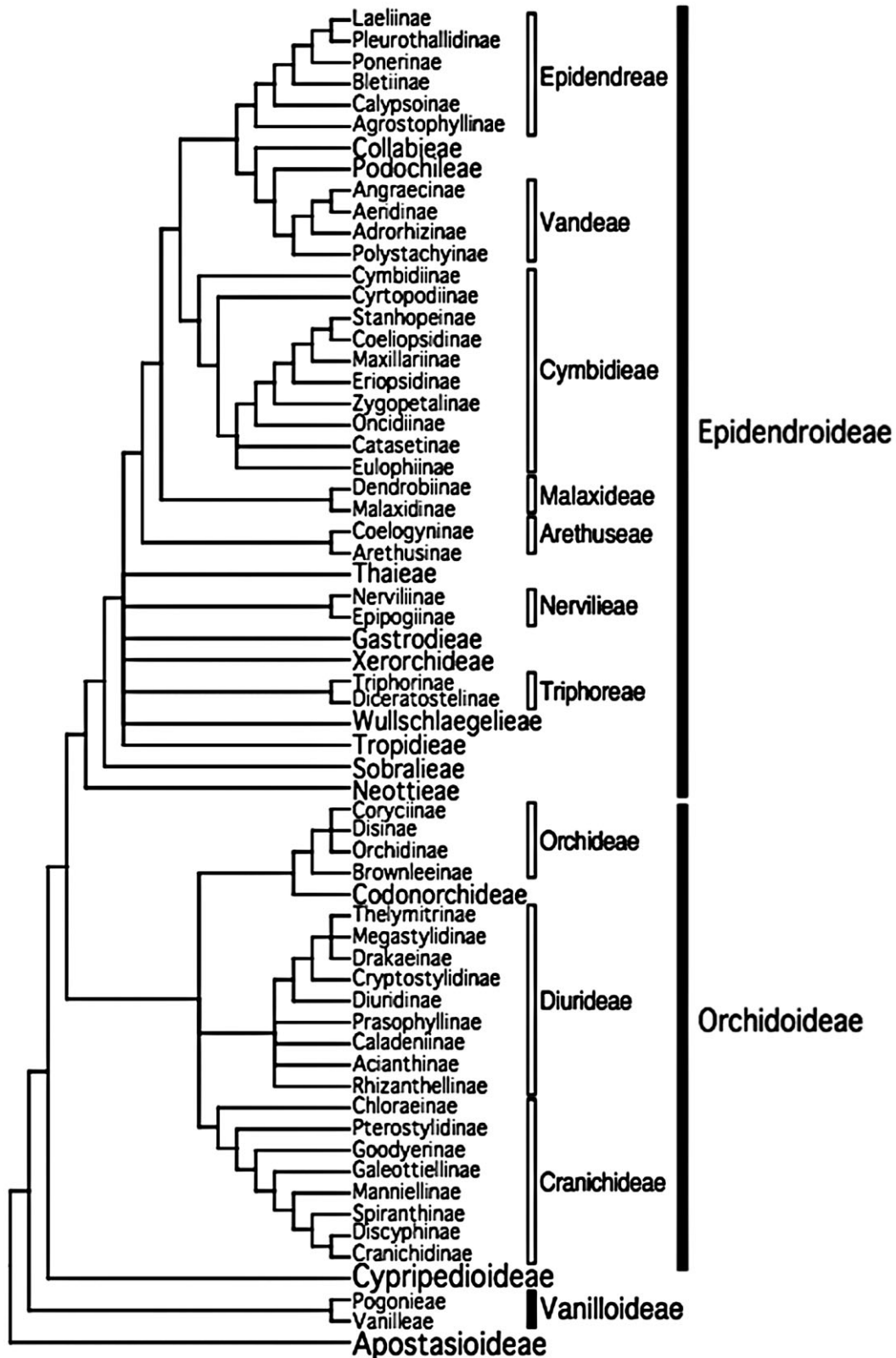


Figure 1. A ‘classification summary’ tree for the subfamilies, tribes and subtribes of Orchidaceae, as circumscribed in this revised classification. This is not based on a phylogenetic analysis *per se*, but rather it is a summary of the published literature, as cited in the text.

species was also added recently (Salazar *et al.*, 2011). Monospecific *Exalaria* Garay & G.A.Romero was shown by Salazar *et al.* (2009) to be nested in *Ponthieva* and included in that genus. In Salazar (2003b), *Nothosteale* was treated as a member of Cranichidinae, but Batista *et al.* (2011) demonstrated that the sole species, *Nothosteale acianthiformis* (Rchb.f. & Warm.) Garay, was a member of Spiranthinae, in which its floral and vegetative morphology generally fitted better, although its non-resupinate flowers are only shared with *Quechua* (see below) in that subtribe. A second species has been described, also from Brazil (Batista *et al.*, 2011).

The situation in Goodyerinae still requires a great deal more study, and the monophyly of several genera as currently circumscribed is unlikely. A new monospecific genus, *Schuitemania*, was described by Ormerod (2002). Although it is not entirely clear that *Schuitemania* is distinct from *Platylophos* A.Rich., it is tentatively recognized here. In addition, Meneguzzo (2012) transferred *Ligeophila* Garay and *Platythelys* to *Aspidogyne* based on inconsistencies in the morphological characters used by Garay when he published these genera. Although it was based solely on morphological evidence, Ormerod (2013) accepted these transfers, and we do also here. In Pterostylidinae, we have included *Achlydosa* (first recognized by Jones *et al.*, 2002), which was shown by Clements, Otero & Miller (2011) not to be related to *Megastylis*, where most authors had included it. A relationship to *Pterostylis* has been shown in several papers, including Cisternas *et al.* (2012b), in which it was well supported as sister to that genus. Jones *et al.* (2002) proposed Achlydosinae for the genus, but this seems unnecessary, given its phylogenetic position. Morphologically, the sole species, *A. glandulosa* (Schltr.) M.A.Clem. & D.L.Jones, has flowers reminiscent of *Pterostylis*, although in detail they differ. It may well be that separate subtribal status would be appropriate, but morphological similarities should be addressed. As pointed out by Cisternas *et al.* (2012b), the floral similarities between *Achlydosa*, Chloraeinae and some members of Diurideae, such as *Megastylis*, probably represent symplesiomorphies for the whole Diurideae/Cranichideae clade and are therefore potentially misleading.

In Spiranthinae, monospecific *Discyphus* (Panama to north-eastern Brazil) is an anomaly. It has a single, sessile, cordate leaf that clasps the base of the inflorescence and lies flat on the substrate, whereas nearly all other members of Spiranthinae have two or more cauline leaves. Florally, *Discyphus* has two separate, cup-shaped stigmas, whereas, in Cranichidinae and other Spiranthinae, there is a single stigmatic surface. Salazar, Berg & Popovkin (2014) found *Discyphus* to be sister to both Cranichidinae and Spiran-

thinae or, alternatively, sister (with bootstrap support < 59%) to Cranichidinae, but there are no obvious morphological similarities supporting such a relationship, thus making it a candidate for a newly recognized subtribe, Discyphinae.

Also in Spiranthinae, another anomalous and poorly known species, most commonly treated as *Cyclopogon glabrescens* (T.Hashim.) Dodson, falls as sister to the pair of *Eurystyles* and *Lankesterella*. Salazar & Jost (2012) described it as a new monospecific genus, *Quechua*. It is unusual in Spiranthinae in having non-resupinate flowers and thick narrow leaves. Another new genus in Spiranthinae is *Sotoa* (Salazar & Ballesteros-Barrera, 2010). The species concerned, originally described as *Deiregyne confusa* Garay, lived up to its species epithet; it had combinations in *Funkiella*, *Spiranthes* and *Schiedeella* before turning up in an isolated position as sister to *Svenkoeltzia*. Solano, Salazar & Jiménez (2011) merged *Microthelys* Garay with *Funkiella*; the species assigned to these genera are mingled in the molecular phylogenetic trees (Salazar, 2003a). A better sampled study of Spiranthinae is nearing completion (G. Salazar *et al.*, unpubl. data), and it is likely that a modest number of additional generic changes in Spiranthinae will be required, although we hope that a modest reduction in the number of genera included will be possible. The numerous finely split genera (at least in terms of morphological distinctions) currently recognized in Spiranthinae were inherited from previous workers, but to the outsider these genera are difficult to recognize. It may well be that some generic condensation would be possible, but starting down this avenue before all relationships are well understood would be unwise. Finally, Borba *et al.* (2014) showed the monospecific *Cotylolabium* to be sister to the remainder of Spiranthinae.

Diurideae

In Diurideae, we have recognized the additional subtribes as delimited in Pridgeon *et al.* (2001a). Relationships of the subtribes are not entirely resolved/supported (Fig. 1), and the most complete analyses are those of Clements *et al.* (2002) and Cameron (2006). We have added two new genera to Caladeniinae, *Ericksonella* and *Pheladenia*, based on the evidence presented in Hopper & Brown (2004). Although Jones *et al.* (2001) recognized a large number of genera segregated from *Caladenia*, we prefer to maintain the broader concept of this large, mostly Australian genus (as per Hopper & Brown, 2004). M. A. Clements (pers. comm.) now agrees with this position as well, although he would go further and include *Cyanicula*, *Elythranthera*, *Ericksonella*, *Glossodia* and *Pheladenia* in *Caladenia*. This, too, seems reasonable, but, for the present, we retain past circumscriptions of *Caladenia*

(as in Hopper & Brown, 2004). *Ericksonella* is a new name for *Glycorchis* D.L.Jones & M.A.Clem. (Jones *et al.*, 2001), for which no type was cited. For the latter, the single species in question (formerly known as *Caladenia saccharata* Rchb.f.) is sister to *Cyanicula* (Jones *et al.*, 2001). Morphologically, this species differs from *Caladenia* in only minor ways. Like *Ericksonella*, *Pheladenia* is monospecific, in this case with the single species *Pheladenia deformis* (R.Br.) D.L.Jones & M.A.Clem., which had been considered to be a member of *Caladenia*, but which falls outside that genus as sister to either *Glossodia/Elythranthera* with nrITS DNA sequences (Jones *et al.*, 2001) or *Caladenia/Cyanicula* with plastid *matK* DNA sequences. Differences in morphology between these species are minor. Expansion of *Caladenia* might be a more appropriate way to treat those species that differ little in morphology from more typical *Caladenia* spp., but which DNA places as sister to other species that have at times also been considered to be members of *Caladenia*.

Orchideae

Diseae were not recognized as a separate tribe in Chase *et al.* (2003) and are not recognized here. This group of genera, mostly from southern Africa, continues to be shown collectively to be paraphyletic to Orchideae (Cameron, 2004, 2006; Waterman *et al.*, 2009), in which tribe we still include them. The number of subtribes that should be recognized for this assemblage of genera is not yet sufficiently clear to be finally determined. The most complete analysis to date, that of Waterman *et al.* (2009), indicated that *Disperis* should continue to be treated as a member of Brownleeinae, although support for its position as sister to *Brownleea* is weak. Within the newly recognized Coryciinae, *Corycium* and *Pterygodium* are not monophyletic, and the relationships of the genera in Coryciinae need a thorough examination. *Pachites* is not related to *Satyrium* or *Huttonaea*, as previously hypothesized on morphological grounds, but instead appears to be sister to Coryciinae plus Orchidinae, including *Huttonaea* (Bytebier *et al.*, 2008), with the last weakly supported as sister to *Disa* (including *Herschelianthe*, *Monadenia* and *Schizodium* as before; Bytebier, Bellstedt & Linder, 2007). We include *Ceratandra*, *Corycium*, *Evotella* and *Pterygodium* in Coryciinae, but it is clear that generic realignments are needed in this subtribe. As a 'holding' classification, we continue to include *Huttonaea* in Disinae, to which we also add *Pachites*, although we know that the evidence supporting this is either weak (the former) or contradicted (the latter) by the study of Waterman *et al.* (2009). It appears that the description of a new subtribe for *Pachites* is likely to be necessary, but we prefer not to do this in this paper.

In subtribe Orchidinae, further phylogenetic work has resulted in a number of changes in the generic circumscription. The limits of *Galearis* and *Platanthera* have been expanded (Bateman *et al.*, 2009; Jin *et al.*, 2014) to include *Amerorchis* Hultén, *Aceratorchis* Schltr. and *Chondradenia* Maxim. ex F.Maek., and *Diphylax* Hook.f and *Smithorchis* Tang & F.T.Wang, respectively. This reduces the number of monospecific genera in this subtribe considerably, but three new monospecific genera have been added: *Hsenhsua* (Jin *et al.*, 2014), *Neolindleya* (Efimov, Lauri & Bateman, 2009) and *Tsaiorchis*. Three Chinese species of *Herminium*, *H. angustilabris* King & Pantl., *H. calceoliforme* W.W.Sm. and *H. carnosolabre* Tang & F.T.Wang, have also been transferred to *Platanthera* (Jin *et al.*, 2014). *Neolindleya* was included in the molecular study of Inda *et al.* (2012) and is related to *Galearis* and *Platanthera*, but it had been omitted from Chase *et al.* (2003) and Pridgeon *et al.* (2001a). *Neolindleya* has recently been included in *Galearis* (Jin *et al.*, 2014). *Tsaiorchis* was considered as a synonym of *Amitostigma* Schltr. in Pridgeon *et al.* (2001a), but falls as sister to *Hemipilia* with weak support in Jin *et al.* (2014), and so we recognize it here. *Hsenhsua* is well supported as sister to the *Herminium* clade (including *Androcorys*, *Herminium* and *Porolabium*, which might well be combined into a single genus, *Herminium s.l.*). *Hemipiliopsis* L.B.Luo & S.C.Chen (Luo & Chen, 2003), which had been thought to be related to *Habenaria* or *Brachycorythis* based on morphology (Luo, Zhu & Kurzweil, 2005; Pridgeon *et al.*, 2014), falls within *Hemipilia* in Jin *et al.* (2014), and so we include it there. *Ponerorchis* and *Neottianthe* are nested within *Amitostigma*, and Jin *et al.* (2014) recognized this whole clade as *Ponerorchis* (the oldest name).

Renz (in Pearce, Cribb & Renz, 2001) established *Bhutanthera* for a small group of diminutive alpine species from Sikkim and Bhutan, some of which had been included in *Habenaria*. It differs from *Habenaria* in the confluent stigma lobes and from *Platanthera* in its globose tubers and trilobed lip. This genus has not been included in phylogenetic analyses and is here only tentatively accepted.

Pedersen, Suksathan & Indhamusika (2002 publ. 2003) established *Sirindhornia* for two unusual new species from northern Thailand. A previously described species also included in *Sirindhornia* had been problematic and was considered a member of *Chusua*, *Habenaria* or *Ponerorchis* by various authors. Chen *et al.* (2009) included it in *Ponerorchis* in the treatment for the *Flora of China*. In Jin *et al.* (2014), *Sirindhornia* is sister to *Ponerorchis* plus *Hemipilia/Tsaiorchis*, but with poor support. It is thus recognized here as a new member of Orchidinae.

Habenaria remains the biggest issue in the phylogenetics of Orchidinae. All studies conducted thus far

indicate that it is paraphyletic to several genera, including *Bonatea*, *Gennaria* and *Pecteilis* (Ponsie *et al.*, 2007; Bateman *et al.*, 2009; Inda, Pimentel & Chase, 2012; Batista *et al.*, 2013). A great deal more study is needed before adjusting the generic limits in this group. As a result of the lack of clarity over the limits of *Habenaria*, we find the recognition of small segregates, such as *Dithrix* (Hook.f.) Schltr. ex Brummitt (Jin *et al.*, 2011, as *Nujiangia* X.H.Jin & D.Z.Li), premature. The only species, *Habenaria griffithii* Hook.f., is unusual in its antenna-like appendages at the base of the column. In Jin *et al.* (2014), it is sister to *Gennaria* with strong support, but the status of *Gennaria* needs to be reconsidered when the phylogenetics of *Habenaria* have been better studied.

The holomycotrophic genus *Silvorchis*, with only one, presumably extinct species from Java, was included in subtribe Epipogiinae in Pridgeon *et al.* (2005). The originally monospecific genus *Vietorchis* Aver. & Averyanova is undoubtedly closely related and probably synonymous. A second species of *Vietorchis* has been described recently (Averyanov *et al.*, 2013), and a new subtribe, Vietorchidinae, to accommodate *Silvorchis* and *Vietorchis* was proposed at the same time. Pending DNA data, we prefer not to adopt this treatment; it seems clear, however, that both genera belong in Orchideae, where, for the time being, we combine them under *Silvorchis* in Orchidinae, based on the column structure, which resembles that of *Brachycorythis*.

EPIDENDROIDEAE

In Epidendroideae, there has been a great deal of change in the generic limits in many tribes/subtribes since Chase *et al.* (2003). Little has changed in the groups with mostly mealy (primitive) pollinia, the formerly recognized Neottioideae. In Triphoreae, we recognize two subtribes in parallel with the treatment in Pridgeon *et al.* (2005), with the addition of heteromycotrophic *Pogoniopsis* (see Vanilloideae above). Likewise, in Nervilieae, we recognize *Nervilia* to be in a separate subtribe from the rest. In both cases, the recognition of subtribes accords with the divergent morphology of *Diceratostele* and *Nervilia*, respectively, from the other genera in these tribes.

Wulschlaegeliae

The position of *Wulschlaegelia* in phylogenetic analyses has varied over time, but its inclusion in Calypsoeae (Chase *et al.*, 2003; Zhai *et al.*, 2013; see below) seems unlikely on morphological grounds. Two recent analyses that we consider to be more reliable (Górniak *et al.*, 2010; Freudenstein & Chase, 2015) place it among the neottioids near the base of Epidendroideae, and we tentatively reinstate *Wulschlaegeliae* here.

Gastrodieae

Neoclemensia Carr has been reduced to synonymy with *Gastrodia* (Wood *et al.*, 2011).

Thaieae

The only genus listed as *incertae sedis* in Chase *et al.* (2003) was Asian *Thaia*, but, in Pridgeon *et al.* (2005), it was tentatively placed in Neottieae. *Thaia* was originally described from Thailand as holomycotrophic (Seidenfaden, 1975), but, when it was rediscovered (Schuiteman *et al.*, 2009), it was found to be leaf-bearing and green, and therefore probably autotrophic. In analyses of multiple DNA loci, *Thaia* was found to be sister to a large clade comprising the epidendroid genera with well-developed pollinia (Xiang *et al.*, 2012) and, because of its phylogenetic placement and divergent morphological traits, it was described as a new tribe, a rank that we follow here.

Arethuseae

Chase *et al.* (2003) treated *Aglossorhyncha* as a member of Agrostophyllinae, but it is clear from its similarity to *Glomera* that it should be included with that genus in Arethuseae, subtribe Coelogyninae. *Glomera* should include *Glossorhyncha* Ridl., *Ischnocentrum* Schltr. and *Sepalosiphon* Schltr. (Schuiteman & de Vogel, 2003; Pridgeon *et al.*, 2005). The position of *Arundina* in this tribe seems clear, but in which of the two subtribes it should be included varies. The best-sampled analysis in terms of data, Freudenstein & Chase (2015), also provides a mixed result depending on the type of analysis (maximum likelihood versus parsimony). Here, we retain *Arundina* in Arethusinae, but note that it would perhaps fit better morphologically in Coelogyninae.

No further work or nomenclatural changes have been made to Coelogyninae since the study of Gravendeel *et al.* (2001), but it was clear from that work that substantial changes to the circumscription of *Coelogyne* and related genera are needed. *Pleione* is sister to a clade with two major subclades, each including species of *Coelogyne* interspersed with representatives of *Bracisepalum*, *Chelonistele*, *Dendrochilum*, *Entomophobia*, *Geesinkorchis*, *Glomera*, *Nabaluaia*, *Neogyna*, *Otochilus*, *Panisea* and *Pholidota*. The easiest solution is simply one large genus, a change in keeping with the broad treatments of *Bulbophyllum*, *Dendrobium* and *Epidendrum*. There is also evidence that distinctive genera, such as *Dendrochilum* and *Pholidota*, are not monophyletic, and so even treating these as subgenera or sections of *Coelogyne s.l.* would not be adequate. Much more study is required here before new combinations should be made.

Collabieae

Dressler (1993) recognized three genera, *Chrysoglossum*, *Collabium* and *Diglyphosa*, as members of Collabiinae, placing them in his category of ‘misfits and leftovers’. He admitted that several other genera with eight pollinia shared their habit with these that have only two pollinia, but he thought a subtribe with the combination of two or eight (but not four or six) pollinia was too much, and he kept these in Blettiinae (Arethuseae). On the basis of results in Goldman *et al.* (2001), Chase *et al.* (2003) first recognized an expanded circumscription of Collabiinae but, because of a lack of resolution, did not assign them a place in Epidendroideae. With the genera now included, we fill in the missing steps and have genera with two, four and eight pollinia. Here, on the basis of results in Górniak *et al.* (2010), we recognize the group as a tribe due to their position as sister to a clade including Vandae and Podochileae. Relative to Chase *et al.* (2003), we include *Aulostylis* Schltr. in *Calanthe* and *Mischobulbum* Schltr. in *Tainia* (both as in Pridgeon *et al.*, 2005) and transfer *Risleya* from Malaxidinae on the basis of Xiang *et al.* (2014). The floral features of mycoheterotrophic *Risleya* appear to be similar to those of *Malaxis*, but it has pollinia with a viscidium and an elongate rostellum, both of which fit better in Collabieae. Also in Xiang *et al.* (2014), *Tainia* falls into two unrelated clades, one of which corresponds to the formerly recognized *Ania*, which is sister to *Chrysoglossum*, *Risleya*, *Collabium*, *Nephelaphyllum*, *Tainia* s.s. and *Hancockia*, and so *Ania* is reinstated here.

The limits of *Calanthe* have been disputed and, in Xiang *et al.* (2014), this is made clearer. *Calanthe delavayi* Finet has been problematic; on the basis of its floral morphology, it was treated as a member of *Phaius* in Pridgeon *et al.* (2005), but it is a member of *Calanthe*. *Cephalantheropsis* is sister to *Calanthe clavata* Lindl. and *Calanthe densiflora* Lindl., apart from most other species of *Calanthe*, to which *Gastrochis* is sister. Finally, *Calanthe* subgenus *Preptanthe* is sister to the rest of this clade. Here, the authors suggest that an expansion of *Calanthe* to include *Cephalantheropsis*, *Gastrochis* and *Phaius* would be most appropriate, given the shared features of these plants and problem with the placement of species such as *Calanthe (Phaius) delavayi*. *Eriodes* was confirmed by Xiang *et al.* (2014) to be a member of Collabieae, despite its deviating morphology (it is an epiphyte, whereas most members of Collabieae are terrestrial). In Chase *et al.* (2003), *Pilophyllum* was simply omitted from the classification because of an oversight.

Malaxideae

Another of the unplaced subtribes in Chase *et al.* (2003) was Dendrobiinae, but it has a clear relation-

ship to Malaxideae in Górniak *et al.* (2010) based on the low-copy nuclear gene *Xdh* and in Xiang *et al.* (2012) who analysed plastid DNA. Here, we shift tribes and subtribes somewhat and recognize these two as Malaxideae, composed of two subtribes Dendrobiinae and Malaxidinae. The taxonomy of Dendrobiinae has been hugely simplified on the basis of Schuiteman (2011), Schuiteman & Adams (2011) and Xiang *et al.* (2013). Those that had been treated as several genera were condensed into one, *Dendrobium* s.l. (Pridgeon *et al.*, 2014). Likewise, *Bulbophyllum* was condensed into a single genus (Pridgeon *et al.*, 2014; Vermeulen, Schuiteman & de Vogel, 2014). A similar treatment might solve the difficulties of the third group with ‘naked’ pollinia: *Malaxis*, *Liparis* and relatives. Neither *Malaxis* nor *Liparis* in their broad sense has been shown to be monophyletic (Cameron, 2005; Lin & Yan, 2013), and a suggested taxonomy in Pridgeon *et al.* (2005) presents another option other than combining all of them into a single genus. The latter solution has yet to be well evaluated, but most authors seem to prefer it (Radins *et al.*, 2014), although not all necessary combinations have been made to make this a viable taxonomic arrangement. Monospecific *Crossoliparis* and *Tamayorkis* are morphologically distinctive New World taxa, and molecular phylogenetic analyses (Radins *et al.*, 2014; G. Salazar *et al.*, unpubl. data) support their recognition.

Cymbidieae

In Cymbidieae, the changes in generic circumscription have been immense. We will go over these briefly, but the treatments in Pridgeon *et al.* (2009) should be consulted for more information. Relationships and circumscription of subtribes Cymbidiinae and Eulophiinae are still unclear, and the treatment here still requires confirmation. Cymbidiinae (Batista *et al.*, 2014) should include at least *Acriopsis*, *Thecopus* and *Thecostele*, in addition to those genera included here in Chase *et al.* (2003). *Porphyroglottis*, from Peninsular Malaysia, Borneo and Sumatra, is included here, but only tentatively; in habit, it resembles Neotropical *Cyrtopodium* (Cyrtopodiinae). In Eulophiinae, we include *Claderia*, which was omitted by oversight from Chase *et al.* (2003), and *Imerinaea*, which had previously been considered to be related to *Polystachya* (Polystachyinae; Vandae; Dressler, 1993). *Graphorkis* was moved here from Cymbidiinae (Batista *et al.*, 2013). In Batista *et al.* (2014), *Dipodium* fell in a weakly supported position as sister to the rest of Cymbidieae, but recognizing a new subtribe for it (and potentially some of the other genera, such as *Claderia* and *Imerinaea*) is premature. Unpublished results (R. Bone, S. Buerki & M. Chase, unpubl. data) place *Geodorum* in the *Eulophia*/

Oeceoclades clade, and so more changes in circumscription of *Eulophia* are anticipated (see below).

Paralophia is added as a newly described genus, segregated from *Eulophia* (Hermans & Cribb, 2005), but so far this hypothesis has not been evaluated phylogenetically. Martos *et al.* (2014) demonstrated that *Eulophia* species from South Africa comprise two unrelated clades; *Oeceoclades* and *Acrolophia* are successively sister to one of these, the clade containing the type species of *Eulophia*. The other clade of *Eulophia* had previously been recognized as *Orthochilus* Hoschst. ex A.Rich. Here, the study of Martos *et al.* (2014) is considered to be inconclusive because of the inclusion of only some of the African taxa comprising Eulophiinae. Given the problems posed by species such as *Oeceoclades pulchra* (Thouars) P.J.Cribb & M.A.Clem. [= *Eulophia pulchra* (Thouars) Lindl.], we argue for a more considered and well-sampled analysis prior to making taxonomic decisions about generic delimitation. For example, the study of Batista *et al.* (2014), which included more 'outgroup' taxa, found *Geodorum* to be more closely related to *Eulophia s.s.* than *Oeceoclades*, which, if true, could swing the argument more strongly in favour of recognizing *Orthochilus*. In addition, the two clades of *Eulophia* identified in Martos *et al.* (2014) differ only in the following trivial characters: inflorescence usually lax with the petals and sepals dissimilar in size and colour in *Eulophia s.s.* versus inflorescence usually dense and often apically clustered with petals and sepals similar in size, shape and colour in *Orthochilus*. Also, there is an issue with *Eulophia callichroma* Rchb.f., which falls in different positions with nrITS and plastid DNA in Martos *et al.* (2014).

In Catasetinae, there were two changes. One was the addition of *Cyanaeorchis*, which previously had been placed in Eulophiinae (Chase *et al.*, 2003; Pridgeon *et al.*, 2005) in the absence of DNA sequence data; *Cyanaeorchis* is sister to *Grobya*. Second, *Cyrtopodium* has been removed from Catasetinae and placed in its own subtribe, Cyrtopodiinae, as in Pridgeon *et al.* (2005). *Cyrtopodium* continues to occupy an isolated position in Cymbidiaceae, perhaps as sister to a clade of the rest of the subtribes, except Cymbidiinae (Freudenstein *et al.*, 2004; Batista *et al.*, 2014). Alternatively, in the analysis of *matK/ycf1* plastid sequence data of Whitten, Neubig & Williams (2014), which included a broad sample of New World Cymbidiaceae, Cyrtopodiinae were found to be sister to all Cymbidiaceae, excluding Cymbidiinae, Eulophiinae and Catasetinae.

In Maxillariinae, a molecular phylogenetic analysis found that many often recognized genera (Chase *et al.*, 2003), such as *Anthosiphon* Schltr., *Chrysocycnis* Linden & Rchb.f., *Cryptocentrum* Benth., *Cyrtidiorchis* Rauschert, *Mormolyca* Fenzl and *Pityphyllum* Schltr.,

were embedded within *Maxillaria* (Whitten *et al.*, 2007). These authors discussed the two options for solving the phylogenetic problems: splitting *Maxillaria* or lumping the above genera into an enlarged *Maxillaria*. They decided to split, stating that *Maxillaria s.l.* would be morphologically undiagnosable. Many of us disagree with this decision and prefer the broader version of *Maxillaria*. Although we agree that some highly peculiar species, such as those in *Chrysocycnis* and *Cyrtidiorchis*, pose difficulties in identifying a completely uniform set of morphological synapomorphies for *Maxillaria s.l.*, there is nonetheless a suite of characters that permits the placement of most of the species into mega-*Maxillaria*: a column foot with a hinged lip (with few exceptions), single-flowered inflorescences and conduplicate leaves. For the specialist, these newly recognized/described genera make sense, but for the vast majority of users this taxonomic scheme is extremely challenging. The circumscriptions provided in Blanco *et al.* (2007) notwithstanding, we recognize here *Maxillaria s.l.* including the following previously widely recognized, newly described or resurrected genera: *Brasiliorchis* R.B.Singer, S.Koehler & Carnevali, *Camaridium* Lindl., *Christensonella* Szlach., Mytnik, Górniak & Smiszek, *Cryptocentrum*, *Cyrtidiorchis*, *Heterotaxis* Lindl., *Hylaeorchis* Carnevali & G.A.Romero, *Inti* M.A.Blanco, *Mapinguari* Carnevali & R.B.Singer, *Maxillariella* M.A.Blanco & Carnevali, *Mormolyca*, *Nitidobulbon* Ojeda, Carnevali & G.A.Romero, *Ornithidium* Salisb. ex R.Br., *Pityphyllum*, *Rhetinantha* M.A.Blanco, *Sauvettrea* Szlach. and *Trigonidium* Lindl.

The only other change in Maxillariinae is the recognition of *Sudamerlycaste* for the clade of former *Lycaste* that is sister to *Anguloa*. This group of species was also described by Ryan & Oakeley (2003) as *Ida* A.Ryan & Oakeley, but it had been preceded by *Sudamerlycaste*; it was treated by Pridgeon *et al.* (2009) as *Ida* because, at that time, it was thought that *Sudamerlycaste* was invalid. A minor question concerning relationships within Maxillariinae is the position of *Horvatia*, for which placement in DNA phylogenetic studies is still lacking. *Guanchezia* was included in the analysis of Whitten *et al.* (2014) and falls in a poorly supported and isolated position in Maxillariinae.

Oncidiinae have also changed a great deal since the classification of Chase *et al.* (2003), but only three new genera have been added: *Grandiphyllum*, *Psychopsiella* and *Vitekorchis*. The change has involved the condensation of many genera, from 90 in Chase *et al.* (2003) to 65 here. Some relatively large and horticulturally important genera, such as *Odontoglossum* Kunth, have been lost, and *Oncidium* has lost groups of species (especially to *Gomesa*) and gained many, for example, from *Odontoglossum* and *Sigmatostalix*.

These changes have not been well received in some quarters (Hamilton, 2011), and further changes in a few genera, such as *Brassia* and *Fernandezia*, were recognized in Pridgeon *et al.* (2014), as well as the merging of *Santanderella* P. Ortiz with *Notyliopsis*. *Pachyphyllum* Kunth and *Raycadenco* Dodson are now included in *Fernandezia* Ruiz & Pav. The only distinctions among these genera were floral features associated with pollination syndromes, and Neubig *et al.* (2012) demonstrated that the species of *Fernandezia* and *Pachyphyllum* are intermingled, with *Raycadenco* being sister to this clade. The massive taxonomic reshuffling of generic limits was attributable to the evident plasticity of floral morphology in Oncidiinae, in particular the parallel evolution of oil-bee pollination in many independent clades (Papadopoulos *et al.*, 2013) and shifts away from this pollination syndrome to other pollinators in clades otherwise largely characterized by the morphological characters associated with oil-bee pollination (Neubig *et al.*, 2012). Readers who require more detailed information should refer to Chase *et al.* (2008), Chase (2009), Chase, Williams & Whitten (2009) and Neubig *et al.* (2012).

Although Stanhopeinae have remained constant, Zygopetalinae have undergone a series of recircumscriptions, resulting in the loss of *Bollea* Rchb.f., *Dodsonia* Ackerman and *Hirtzia* Dodson, and the description/resurrection of seven genera and loss of species in still-recognized genera, such as *Chondrorhyncha*, which fell from 30 to just seven species (Whitten *et al.*, 2005). As with the case of *Maxillaria* above, it could be argued that fewer, larger genera would have been a more useful treatment, but this would have required more study and the addition of many more data in order to obtain better supported results. *Vargasiella* (formerly often in its own subtribe; Pridgeon *et al.*, 2009) was investigated by Szlachetko *et al.* (2014) and was found to fall in a clade with *Warrea* and *Warreopsis*, and so we keep *Vargasiella* in Zygopetalinae as in Chase *et al.* (2003), not in its own subtribe as in Pridgeon *et al.* (2009).

Epidendreae

In Epidendreae, *Chysis* and *Coelia* had been included as unplaced-to-subtribe under Epidendreae (Chase *et al.*, 2003). Chysinae (with only *Chysis*) and Coeliinae (with only *Coelia*) were included in Pridgeon *et al.* (2005) under Epidendreae, but only as a tentative treatment. van den Berg *et al.* (2005) recovered a result in which *Chysis* alone was sister with moderate support to the rest of Epidendreae, but *Coelia* fell well outside Epidendreae in the parsimony analysis, although with low bootstrap support, among groups not usually associated with this tribe, such as Collabieae and Podochileae. In van den Berg *et al.* (2009), *Coelia* and *Chysis* were well supported as successive

sisters to the rest of Epidendreae, but the sampling of outgroups in this study was too limited to give this result much significance. Górnjak *et al.* (2010) and Givnish *et al.* (2013) found *Coelia* and *Chysis* as successive sister taxa to the rest of Epidendreae, although this too was weakly supported. In Freudenstein & Chase (2015) (an analysis of eight DNA regions focusing on Epidendroideae), *Coelia* falls as sister to Calypsoeae with high bootstrap support in both maximum likelihood and parsimony analyses, and we include it there. *Chysis*, however, falls with moderate support as sister to Bletiinae and, as none of the other studies strongly refutes this placement, we treat it as a member of Bletiinae, which is otherwise unchanged.

Ponerinae have the same generic composition as in Chase *et al.* (2003), with the exception of the resurrection of *Nemaconia* (Soto Arenas, Salazar & van den Berg, 2007). The species included in *Nemaconia* were previously referred to *Ponera*, but van den Berg *et al.* (2005, 2009) showed that *Ponera* as recently circumscribed was not monophyletic, a situation rectified by the recognition of *Nemaconia*.

In Pleurothallidinae, most of the upheaval caused by the application of molecular data had been included in Chase *et al.* (2003). A new genus recognized by Pridgeon, Solano & Chase (2001b), *Anthereon* Pridgeon & M.W.Chase, is a synonym of the earlier *Pabstiella*, a name missed by these authors. Circumscription of *Pabstiella* has been much enlarged by various authors (e.g. de Fraga & Kollmann, 2010; Kollmann, 2010; Chiron, Sanson & Ximenes Bolsanello, 2011) relative to the circumscription of *Anthereon sensu* Pridgeon *et al.*, (2001b), which was just six species. *Draconanthes* is also newly accepted here as well as being included in Pridgeon *et al.* (2005). *Kraenzlinella* is also newly accepted as a member of Pleurothallidinae (as reviewed in Pridgeon *et al.*, 2005). Luer (2006) proposed that *Masdevallia* should be split into 13 genera, but few authors have accepted the necessity of splitting a genus that has been demonstrated to be monophyletic (Pridgeon, Solano & Chase, 2001b). We also do not accept this here. Karremans (2014) proposed a new genus, *Lankesteriana* Karremans, for a group of species related to *Anathallis barbulata* (Lindl.) Pridgeon & M.W.Chase because, in an nrITS analysis, they fell closer to other genera than to the rest of *Anathallis*, but support for this result was poor (none of the relevant nodes separating the species ascribed to *Lankesteriana* from the rest of *Anathallis* received the required 0.95 Bayesian posterior probability). We decided not to recognize this genus until there has been a more conclusive result. Finally, Chiron, Guiard & van den Berg (2012) discovered that two species (one first described in *Phloeophila* Hoehne & Schltr., the other then unnamed) formed a small isolated clade

within Pleurothallidinae, and Chiron (2012) named this *Sansonia*. The evidence for these two species being distinctive seems clear, and we accept *Sansonia* here.

In Laeliinae, *Cattleyella* van den Berg & M.W.Chase was proposed for what appeared to be a divergent species of *Cattleya*, *C. araguaiensis* Pabst, which fell outside the core group of *Cattleya* (van den Berg & Chase, 2003), but it now appears that this is a hybrid between *Cattleya* and *Brassavola* (*C. van den Berg*, unpubl. data), which is morphologically better treated in a subgenus of *Cattleya*. A number of genera recognized in Chase *et al.* (2003) were included in *Epidendrum* in Pridgeon *et al.* (2005); these include *Lanium* (Lindl.) Benth., *Nanodes* Lindl. and *Oerstedella* Rehb.f. New genera for parts of *Epidendrum*, such as *Takulumena* Szlach., have also been proposed. It could be argued that it would be better to split a large genus such as *Epidendrum* into many smaller, more morphologically homogeneous genera, but the authors of the treatment in Pridgeon *et al.* (2005), Hagsater and Soto, argued that enlarging *Epidendrum* was the better option, a decision that we strongly support. Withner (1998) erected *Euchile* (Dressler & G.E.Pollard) Withner for three species of *Prosthechea* from Mexico, but these are sister to the rest of *Prosthechea* and differ in only minor ways (in having a midtooth on the column that is not ligulate). We now consider them as members of a broad concept of *Prosthechea* (Higgins, 1997, publ. 1998). *Nageliella* L.O.Williams was transferred to *Domingoa* and *Pinelia* Lindl. to *Homalopetalum* by Soto Arenas *et al.* (2007). *Platyglottis* L.O.Williams and *Hexisea* Lindl. have been included in *Scaphyglottis* by Dressler, Whitten & Williams (2004). *Renata* Ruschi was included in *Pseudolaelia* by Barros (1994) but, until molecular data supported its inclusion there, it was maintained by Chase *et al.* (2003). Pridgeon *et al.* (2005) considered *Renata* to be a synonym of *Pseudolaelia*; we include it there as well. *Schomburgkia* Lindl. is now included in *Laelia*, which was explained in Pridgeon *et al.* (2005), but the species of *Myrmecophila*, often included in *Schomburgkia*, are related to *Barkeria*, *Caularthron*, *Orleanesia* and *Epidendrum* (van den Berg *et al.*, 2009), not *Laelia*, and so they have been maintained as a distinct genus. *Sophronitis* Lindl., which was considered to include the species of rupicolous *Laelia* in Chase *et al.* (2003) or *Hadrolaelia* (Schltr.) Chiron & V.P.Castro, is now considered as a synonym of *Cattleya* (van den Berg, 2008). At the time that the transfers from *Laelia* were made to *Sophronitis* (van den Berg & Chase, 2000), it had been debated whether this broader version of *Cattleya* would be preferable, but eventually it became clear that the latter treatment should prevail. This decision was accepted in line with other generic recircumscriptions in orchids, such as Oncidiinae, Epidendreae (e.g. *Epidendrum*), *Bulbophyllum* and *Dendrobium*.

Calypso and its relatives have long been considered as an independent tribe but, in Górniak *et al.* (2010) and Freudenstein & Chase (2015), this clade is well supported as a member of the same major clade as Epidendreae, making its treatment as a subtribe of that tribe appropriate. There have been several changes in the composition of Calypsoinae. *Didicicia* King & Prain has been included in *Tipularia* in accord with Pridgeon *et al.* (2005) and Wu, Raven & Hong (2009). *Wulfschlaegelia* was placed here tentatively in Chase *et al.* (2003), but its position was queried. In Górniak *et al.* (2010), it fell in an isolated position among the neottioids, and here we reinstate *Wulfschlaegeliae* for it. A new achlorophyllous genus from China, *Danxiaorchis*, has been described (Zhai *et al.*, 2013) and also demonstrated to be sister to achlorophyllous *Yoania*. Finally, in Freudenstein & Chase (2015), *Coelia* is sister to Calypsoinae with high bootstrap support, and it seems that this difficult-to-place genus has at last found a well-supported placement.

One of the subtribes listed in Chase *et al.* (2003) as unplaced was Agrostophyllinae, which here are included in Epidendreae, but with a much-reduced circumscription, including only two genera, *Agrostophyllum* and *Earina*, which share elaters (Dressler, 1993), also present in *Polystachya* (see below); these must have originated twice based on the results of phylogenetic analysis. Dressler (1993) considered these to be members of the group he named Epidendreae II. Górniak *et al.* (2010) and Freudenstein & Chase (2015) both found this subtribe to be members of an expanded Epidendroideae with high support (98% and 97%, respectively). Several species of *Earina* have striking floral and vegetative similarities to *Nemaconia* (Ponerinae), which adds some morphological weight to this change.

Podochileae

In Podochileae, Podochilinae were combined with Eriinae based on interdigitation of the two subtribes in Pridgeon *et al.* (2005). Thelasiinae minus *Ridleyella* are sister to Eriinae, whereas *Ridleyella* is sister to the rest of Podochileae (van den Berg *et al.*, 2005). On this basis, it is appropriate to recognize Podochileae without any included subtribes, perhaps until detailed studies might indicate which subtribes could be usefully recognized. Since Chase *et al.* (2003), substantial changes have been made to the generic circumscription of *Eria*, which has been shown to be polyphyletic (Pridgeon *et al.*, 2005; Y.-P. Ng, H. Æ. Pedersen & A. Schuiteman, unpubl. data). Many of the genera recognized in Pridgeon *et al.* (2005) did not have combinations published at that time for the species that would putatively have been included in them, but these have been made by several authors subsequently (e.g. Ng & Cribb, 2005; Wood, 2005; Cootes & Suarez, 2008;

Ormerod, 2012). It still remains to be seen whether the proposed newly recognized, mostly resurrected, genera hold up once a phylogenetic analysis with greatly increased sampling of species is completed, but such a study is in progress (Y.-P. Ng, H. Æ. Pedersen & A. Schuiteman, unpubl. data). *Oxystophyllum* was previously included in *Dendrobium* as *D.* section *Oxystophyllum* (Blume) Miq., but Clements (2003) demonstrated that this group of species were not in fact related to *Dendrobium*, but were instead members of Podochileae. This is similar to the case of *Pseuderia*, which Yukawa, Cameron & Chase (1996) had earlier demonstrated was not related to *Dendrobium*. *Pseuderia* was omitted by mistake from the treatment of Podochileae in Pridgeon *et al.* (2005), but was included in the addendum of Pridgeon *et al.* (2014). *Chitonochilus* Schltr., a monospecific genus formerly in Podochileae, is now considered to be a synonym of *Agrostophyllum* (Pridgeon *et al.*, 2014). *Chilopogon* Schltr. and *Cyphochilus* Schltr., recognized in Pridgeon *et al.* (2005), are easily accommodated in *Appendicula* because of their similar habit and floral morphology, in which genus the necessary combinations already exist.

Vandaeae

Agrostophyllinae in Chase *et al.* (2003) were unplaced, but have since been demonstrated to be polyphyletic in this broader circumscription. *Adrorhizon* and *Sirhookera* are here placed in Adrorhizinae (see below); *Aglossorrhyncha* is here placed in Coelogyninae (see above) based on its morphological similarity to *Glomera*, which includes *Glossorrhyncha* Ridl., *Ischnocentrum* Schltr. and *Sepalosiphon* Schltr. In Pridgeon *et al.* (2014), Agrostophyllinae and Adrorhizoninae were demonstrated to be members of Vandaeae (bootstrap percentage 84%), but not to share an exclusive relationship. The association of Agrostophyllinae with Vandaeae was first found in van den Berg *et al.* (2005), but weakly supported, whereas, in Górniak *et al.* (2010), this relationship was well supported.

Adrorhizinae are newly resurrected. They were recognized by Dressler (1993), who reported that the pollinia were similar to those of Agrostophyllinae and the seeds were similar to those of *Polystachya* (see below). We also include here *Bromheadia* which, in Chase *et al.* (2003), was in its own subtribe in Cymbideae (as in Dressler, 1993), although, at that time, it had not been included in any molecular analysis. Pridgeon *et al.* (2014) showed that *Bromheadia* is strongly supported as related to *Adrorhizon* and *Sirhookera*, but, in Górniak *et al.* (2010), *Bromheadia* is not supported as uniquely related to *Adrorhizon* and *Sirhookera*, although it falls near them in Vandaeae; these relationships obviously still require further investigation. In morphological terms, *Bromheadia* is highly dissimilar to *Adrorhizon* and *Sirhookera*.

Polystachyinae were included in Vandaeae in Chase *et al.* (2003) on the basis of analyses in which this relationship had appeared (e.g. van den Berg *et al.*, 2005, seen in 2003 prior to its publication). An exclusive relationship of *Hederorkis* to *Polystachya* has not been demonstrated (Pridgeon *et al.*, 2014), but it also has not been strongly refuted. Thus, we keep *Hederorkis* in Polystachyinae here, but this relationship should be the focus of additional study. Relative to Chase *et al.* (2003), *Imerinaea* was moved to Eulophiinae of Cymbidieae (see above), and *Neobenthamia* Rolfe has been included in *Polystachya* on the basis of Russell *et al.* (2010a, b). We have seen no convincing arguments to split up the monophyletic and easily recognized genus *Polystachya* into smaller genera, such as *Chelystachya* Mytnik & Szlach., *Isochilostachya* Mytnik & Szlach. and *Neoburtia* Mytnik, Szlach. & Baranow, as proposed by Mytnik-Ejsmont (2011) and coworkers.

Updating Chase *et al.* (2003), Aerangidinae have been included in Angraecinae (Micheneau *et al.*, 2008). The only genus in the earlier classification not included here is *Bonniera* Cordem., which is deeply embedded in *Angraecum* (Micheneau *et al.*, 2008). *Angraecum*, the largest genus of the subtribe, is polyphyletic and, once the phylogenetics of the subtribe beyond the American taxa (Carlward *et al.*, 2006) and the Mascarene species (Micheneau *et al.*, 2008) have been better studied, substantial alteration of the generic limits is anticipated. *Erasanthe* has been added (Cribb, Hermans & Roberts, 2007) because it falls far from *Aeranthus*, in which this species had been previously included.

Aeridinae have presented a large number of problems throughout their history, and several major shifts have occurred. In the words of Dressler (1993), the genera of Aeridinae are 'very finely split'. Their flowers are complex and provide a seeming wealth of characters, such as variation in the number and fusion of pollinia and a column foot, upon which to base generic concepts, but these are generally unreliable, presumably because of parallel adaptations to similar pollinators. On the basis of recently published phylogenetic studies (Padolina, Lindner & Simpson, 2005; Topik, Yukawa & Ito, 2005; Carlward *et al.*, 2006; Tsai, Huang & Chou, 2006; Kocyan *et al.*, 2008; Fan *et al.*, 2009; Liu *et al.*, 2011; Gardiner *et al.*, 2013) and particularly on the most thoroughly sampled study by Kocyan in Pridgeon *et al.* (2014), generic changes have begun to be made (Gardiner, 2012; Kocyan & Schuiteman, 2013). Many clades were still highly unresolved or poorly supported in these studies and, until such time as more reliable results with much better sampling are obtained, further changes cannot be undertaken. For much more detailed treatments, the reader is referred to Pridgeon *et al.* (2014). We

describe briefly here the changes that have taken place since Chase *et al.* (2003).

The two most important genera horticulturally have been expanded to include the genera embedded in them, as well as some that are their sister taxa. In *Vanda*, we include *Ascocentropsis* Senghas & H.Schildh. (synonym *Gunnaria* Z.L.Liu & L.J.Chen), *Ascocentrum* Schltr., *Christensonia* Haager, *Eparmatostigma* Garay and *Neofinetia* Hu (Gardiner, 2012; Gardiner *et al.*, 2013). Although *Neofinetia* is sister to *Vanda s.l.* and, unlike the embedded genera, could have been maintained, the perspective taken here was that the species concerned have previously been treated in *Vanda* (the first species of *Neofinetia* described was placed in *Vanda*), and thus to simplify the taxonomy a broad generic concept was adopted. In *Phalaenopsis* are included *Grussia* M.Wolff, *Hygrochilus* Pfitzer, *Lesliea* Seidenf., *Nothodoritis* Z.H.Tsi, *Ornithochilus* (Lindl.) Wall. ex Benth. and *Sedirea* Garay & H.Sweet (Pridgeon *et al.*, 2014).

Abdominea J.J.Sm., *India* A.N.Rao, *Malleola* J.J.Sm., *Megalotus* Garay and the recently proposed *Samarorchis* Ormerod have been included in *Robiquetia*. *Arachnis* includes *Armodorium* Breda and *Esmeralda* Rchb.f. *Grosourda* includes *Ascochilopsis* Carr and *Ascochilus* Ridl., together with the recently described *Theana* Aver. A broader circumscription of *Holcoglossum* was maintained that includes several recently described genera: *Penkimia* Phukan & Odyuo, *Chenororchis* Z.L.Liu, S.C.Chen & L.J.Chen and *Tsiorchis* Z.L.Liu, S.C.Chen & L.J.Chen. *Luisia* includes the recently described *Lockia* Aver. *Renanthera* has been expanded to include *Ascoglossum* Schltr., *Renantherella* Ridl. and *Porphyrodesme* Schltr. The recently described *Monanthochilus* (Schltr.) R.Rice is considered to be a synonym of *Sarcochilus*, having been a section of that genus. *Loxomorchis* Rauschert is a synonym of *Smithsonia*. *Microtatorchis* Schltr. is a synonym of *Taeniophyllum*; they differ chiefly in the former having leaves and the latter not. *Cordiglottis* J.J.Sm. differs from *Thrixspermum* mostly in its terete leaves and some minor lip characters; some terete-leaved *Thrixspermum* species have also been described, and *Cordiglottis* was considered to be a synonym of the latter in Pridgeon *et al.* (2014). *Ceratochilus* Blume, *Staurochilus* Ridl. and *Ventricularia* Garay are considered as synonyms of *Trichoglottis*. The distinction between *Trachoma* and *Tuberolabium* has been problematic, but the phylogenetic study by Kocyan published in Pridgeon *et al.* (2014) demonstrated that the two are distinct; however, some species of the latter needed to be transferred to the former (Kocyan & Schuiteman, 2013). *Parapteroceras* Aver. is considered as a synonym of *Tuberolabium*. In *Cleisostoma*, we included *Blumeorchis* Szlach. and *Ormerodia* Szlach., both described since 2003. As

currently circumscribed, *Cleisostoma* is clearly polyphyletic; further analyses are needed to determine whether it should be split or expanded by merging other genera with it, such as *Pelatantheria* and *Rhynchogyna* (both still recognized here). *Haraella* Kudô was included in *Gastrochilus* together with the recently described *Luisiopsis* C.S.Kumar & P.C.S.Kumar. The position of the single species of *Luisiopsis*, *L. inconspicua* (Hook.f.) C.S.Kumar & P.C.S.Kumar, is still uncertain; it is not clear whether it is a species of *Gastrochilus* with the vegetative morphology of *Luisia* or a species of *Luisia* with the floral morphology of *Gastrochilus*. Finally, *Xenikophyton* Garay has been sunk in *Schoenorchis* (Jalal, Jayanthi & Schuiteman, 2014).

INCERTAE SEDIS

The monospecific genus *Devogelia* Schuit. was described on the basis of three herbarium collections and one spirit sample from Obi Island in the Moluccas and the Bird's Head Peninsula of New Guinea. It is now known to occur in Papua New Guinea as well. The only known species displays a puzzling combination of characters, seemingly amalgamating features from Eulophiinae, Malaxidinae and Collabieae (all Epidendroideae). It is a terrestrial orchid with creeping rhizomes, unifoliate, homoblastic pseudobulbs, long-petiolate, stiffly plicate leaves, tall, terminal inflorescences carrying small *Claderia*-like flowers opening in succession, and four, apparently naked pollinia (Schuiteman, 2004). *Devogelia* may represent a distinct tribe, but, until fresh material can be examined and DNA analysed, its position must remain uncertain.

FINAL REMARKS AND OUTLOOK FOR THE NEXT DECADE

With the publication of the last volume of *Genera Orchidacearum* in early 2014 (Pridgeon *et al.*, 2014), Orchidaceae can be considered as one of the best documented of all angiosperm families, but this does not mean that the task of understanding the evolution of this immense family is complete. The great strides in the understanding of the phylogenetic relationships of the family represent a revolution for other kinds of studies that seek to understand the evolution of the key orchid traits. When Dressler (1993) was published, we neither knew to which group of monocots the orchids were related nor how many major clades existed within the family, both of which inhibited scientists in other fields from using orchids as a study group. That situation is now completely different, and the burgeoning number of other types of orchid papers being published is testament to the effect of *Genera Orchidacearum* in stimulating

and setting the context for an improved understanding of orchid biology.

Phylogenetic studies of orchids are already beginning to see the results of the use of next-generation sequencing to advance our understanding of higher level relationships. The first target has been the sequencing of whole plastid genomes (plastomes), and the results of Givnish *et al.* (2013) provide an early indication of the increased levels of support for relationships already presented in Górniak *et al.* (2010) and Freudenstein & Chase (2015). The term ‘chloroplast genomics’ is widely used for this endeavour, but this term is incorrect because chloroplasts are just one type of plastid present in plants (the others include chromoplasts and leucoplasts); thus, when sequencing using standard methods, template DNA contains a mixture of plastid types, and so the correct term is the more general one: plastome or plastid genome. Whole-genome and transcriptome sequencing is now becoming a reality in Orchidaceae, given the technological advances allowed by next-generation sequencing, but publication of the results of this type of study is most likely still a couple of years away, given the expensive nature of these approaches and our inability to understand how to use low-copy nuclear genes in phylogenetic studies when some such alleles can be older than species and most diploids have two alleles with different phylogenetic histories (i.e. coalescent times are different from those of speciation events). An additional problem is that, with current next-generation sequencing technologies, the DNA samples used in previous standard sequencing studies are not suitable as templates, although this problem is likely to be overcome by future next-generation sequencing technologies that are being tested in many laboratories, such as single-strand sequencing (e.g. Gansauge & Meyer, 2013), which is also suitable for the sequencing of ancient DNA samples. Perhaps some of these problems can be addressed by using the repetitive parts of the nuclear genome, which has been proposed and preliminarily studied by Dodsworth *et al.* (2015) in several plant groups (monocots and eudicots) and animals (*Drosophila*). It should be admitted that these approaches are likely to be most important at the species and intergeneric levels and are unlikely to have much impact on higher level studies. Likewise, epigenetics is an important factor to consider at the population/species interface (Paun *et al.*, 2009, 2010), but is unlikely to affect orchid classification.

In terms of specific problematic groups, as noted earlier, a major challenge is to resolve relationships among Old World *Habenaria*, which implies sampling broadly among representatives of as many as possible of the roughly 25 genera of the former ‘Habenariinae’ (Orchidinae group 2 *sensu* Pridgeon *et al.*, 2003), as the molecular phylogenetic analyses of Batista *et al.* (2013)

(focused on Neotropical habenarids) and Jin *et al.* (2014) (with an emphasis on Asian taxa) indicated that many such genera are intermingled with species of polyphyletic *Habenaria*. The major gap seems to be the African species. The only study focused on African habenarids is that of Ponsie *et al.* (2007, on *Bonatea*), but their sampling was narrowly focused and therefore did not allow for a truly stringent assessment of generic monophyly. The other remaining challenges include a well-sampled phylogenetic analysis of Goodyerinae, in which generic delimitation is currently speculative, and resolution of the *Angraecum* and *Cleisostoma* alliances (Angraecinae and Aeridinae, respectively, of Vandeeae). As noted above, Podochileae are under study, but these too need a great deal of work. In spite of a great deal of progress, there are still major problems in understanding the higher level relationships between and within tribes. A quick look at the many polytomies in Figure 1 demonstrates that more work is needed to sort out subtribal relationships within many tribes (e.g. Diurideae and Cymbidieae), and tribal relationships within Orchidoideae and among the neottiid complex at the base of Epidendroideae. Next-generation sequencing can be expected to help in these matters. When we look back at Chase *et al.* (2003), we can see that progress has been substantial and major, and, if we can then extrapolate, we predict that, in the next 10 years, all of these challenges will be met. In the relative scheme of what was known about orchids in 1993 (Dressler, 1993), the past 20 years have seen the resolution of many major questions. Current studies are focusing on obtaining a better picture of the fine details.

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APPENDIX

Relative to Chase *et al.* (2003); *newly described or recognized genera; †altered tribal or subtribal placement; ‡newly recognized tribe or subtribe; number of species in parentheses from Govaerts (2014).

SUBFAMILY APOSTASIOIDEAE

Apostasia Blume (6), *Neuwiedia* Blume (8).

SUBFAMILY VANILLOIDEAE

Tribe Pogonieae

Cleistis Rich. ex Lindl. (64), *Cleistesiopsis** Pansarin & F.Barros (2), *Duckeella* Porto & Brade (3), *Isotria* Raf. (2), *Pogonia* Juss. (5).

Tribe Vanilleae

Clematepistephium N.Hallé (1), *Cyrtosia* Blume (5), *Epistephium* Kunth (21), *Eriaxis* Rchb.f. (1), *Erythrorchis* Blume (2), *Galeola* Lour. (6), *Lecanorchis* Blume (20), *Pseudovanilla* Garay (8), *Vanilla* Plum. ex Mill. (105).

SUBFAMILY CYPRIPEIDIOIDEAE

Cypripedium L. (51), *Mexipedium* V.A.Albert & M.W.Chase (1), *Paphiopedilum* Pfitzer (86), *Phragmipedium* Rolfe (26), *Selenipedium* Rchb.f. (5).

SUBFAMILY ORCHIDOIDEAE

Tribe Codonorchideae

Codonorchis Lindl. (1).

Tribe Cranichideae

Subtribe Chloraeinae:

Bipinnula (11), *Chloraea* Comm. ex Juss. (52), *Gavilea* Poepp. (15).

Subtribe Cranichidinae:

Aa Rchb.f. (25), *Altensteinia* Kunth (7), *Baskervilla* Lindl. (10), *Cranichis* Sw. (53), *Fuertesilla* Schltr. (1), *Galeoglossum** A.Rich & Galeotti (3), *Gomphichis* Lindl. (24), *Myrosmodes* Rchb.f. (12), *Ponthieva* R.Br.

in W.T.Aiton (66), *Porphyrostachys* Rchb.f. (2), *Prescottia* Lindl. (26), *Pseudocentrum* Lindl. (7), *Pterichis* Lindl. (20), *Solenocentrum* Schltr. (4), *Stenoptera* C.Presl (7).

Subtribe Galeottiellinae:

Galeottiella Schltr. (6).

Subtribe Goodyerinae:

Aenhenrya Gopalan (1), *Anoectochilus* Blume (43), *Aspidogyne* Garay (60), *Chamaegastrodia* Makino & F.Maek. (3), *Cheirostylis* Blume (53), *Cystorchis* Blume (21), *Danhatchia* Garay & Christenson (1), *Dossinia* C.Morren (1), *Erythrodes* Blume (26), *Eurycentrum* Schltr. (7), *Gonatostylis* Schltr. (2), *Goodyera* R.Br. in W.T.Aiton (98), *Halleorchis* Szlach. & Olszewski (1), *Herpysma* Lindl. (1), *Hetaeria* Blume (29), *Hylophila* Lindl. (7), *Kreodanthus* Garay (14), *Kuhlhasseltia* J.J.Sm. (9), *Lepidogyne* Blume (1), *Ludisia* A.Rich. (1), *Macodes* Lindl. (11), *Microchilus* C.Presl (137), *Myrmecis* Blume (17), *Odontochilus* Blume (25), *Orchipedum* Breda (3), *Pachyplectron* Schltr. (3), *Papuaea* Schltr. (1), *Platylepis* A.Rich. (17), *Rhamphorhynchus* Garay (1), *Rhomboda* Lindl. (22), *Schuitemanina** Ormerod (1), *Stephanotherys* Garay (5), *Vrydagzynea* Blume (43), *Zeuxine* Lindl. (74).

Subtribe Manniellinae:

Manniella Rchb.f. (2).

Subtribe Pterostylidinae:

Pterostylis R.Br. (211), *Achlydosa**† M.A.Clem. & D.L.Jones (1).

Subtribe Discyphinae‡:

Discyphus Schltr. (1).

Subtribe Spiranthinae:

Aracamunia Carnevali & I.Ramírez (1), *Aulosepalum* Garay (7), *Beloglottis* Schltr. (7), *Brachystele* Schltr. (21), *Buchtienia* Schltr. (3), *Coccineorchis* Schltr. (7), *Cotylolabium* Garay (1), *Cybebus* Garay (1), *Cyclopon* C.Presl (83), *Degranvillea* Determann (1), *Deiregyne* Schltr. (18), *Dichromanthus* Garay (4), *Eltroplectris* Raf. (13), *Eurystyles* Wawra (20), *Funkiella* Schltr. (27), *Hapalorchis* Schltr. (10), *Helonoma* Garay (4), *Kionophyton* Garay (4), *Lankesterella* Ames (11), *Lyroglossa* Schltr. (2), *Mesadenella* Pabst & Garay (7), *Mesadenus* Schltr. (7), *Nothostele*† Garay (2), *Odontorrhynchus* M.N.Correa (6), *Pelexia* Poit. ex Rich. (77), *Physogyne* Garay (3), *Pseudogood- yera* Schltr. (1), *Pteroglossa* Schltr. (11), *Quechua** Salazar & L.Jost (1), *Sacoila* Raf. (7), *Sarcoglottis* C.Presl (48), *Sauroglossum* Lindl. (11), *Schiedeella* Schltr. (24), *Skeprostachys* Garay (13), *Sotoa** Salazar (1), *Spiranthes* Rich. (34), *Stalkya* Garay (1),

Stenorrhynchus Rich. ex Spreng. (5), *Svenkoeltzia* Burns-Bal. (3), *Thelyschista* Garay (1), *Veyretia* Szlach. (11).

Tribe Diurideae

Subtribe Acianthinae:

Acianthus R.Br. (20), *Corybas* Salisb. (132), *Cyrtostylis* R.Br. (5), *Stigmatodactylus* Maxim. ex Makino (10), *Townsonia* Cheeseman (2).

Subtribe Caladeniinae:

Adenochilus Hook.f. (2), *Aporostylis* Rupp & Hatch (1), *Caladenia* R.Br. (267), *Cyanicula* Hopper & A.P.Brown (10), *Elythranthera* (Endl.) A.S.George (2), *Ericksonella** Hopper & A.P.Br. (1), *Eriochilus* R.Br. (9), *Glossodia* R.Br. (2), *Leptoceras* (R.Br.) Lindl. (1), *Pheladenia** D.L.Jones & M.A.Clem. (1), *Praecoxanthus* Hopper & A.P.Brown (1).

Subtribe Cryptostylidinae:

Coilochilus Schltr. (1), *Cryptostylis* R.Br. (23).

Subtribe Diuridinae:

Diuris Sm. (71), *Orthoceras* R.Br. (2).

Subtribe Drakaeinae‡:

Arthrochilus F.Muell. (15), *Caleana* R.Br. (1), *Chiloglottis* R.Br. (23), *Drakaea* Lindl. (10), *Paracaleana* Blaxell (13), *Spiculaea* Lindl. (1).

Subtribe Megastylidinae‡:

Burnettia Lindl. (1), *Leporella* A.S.George (1), *Lyperanthus* R.Br. (2), *Megastylis* (Schltr.) Schltr. (7), *Pyrorchis* D.L.Jones & M.A.Clements (2), *Rimacola* Rupp (1), *Waireia* D.L.Jones, Molloy & M.A.Clements (1).

Subtribe Prasophyllinae‡:

Genoplesium R.Br. (47), *Microtis* R.Br. (19), *Prasophyllum* R.Br. (131).

Subtribe Rhizanthellinae:

Rhizanthella R.S.Rogers (3).

Subtribe Thelymitrinae:

Calochilus R.Br. (27), *Epiblema* R.Br. (1), *Thelymitra* J.R.Forst. & G.Forst. (110).

Tribe Orchideae

Subtribe Brownleeinae:

Brownleea Harv. ex Lindl. (8), *Disperis* Sw. (78).

Subtribe Coryciinae‡:

Ceratandra Lindl. (6), *Corycium* Sw. (15), *Evotella* Kurzweil & H.P.Linder (1), *Pterygodium* Sw. (19).

Subtribe Disinae:

Disa P.J.Bergius (182), *Huttonaea* Harv. (5), *Pachites*† Lindl. (2).

Subtribe Orchidinae:

Aceratorchis Schltr. (1), *Anacamptis* Rich. (11), *Androcorys* Schltr. (10), *Bartholina* R.Br. (2), *Benthamia* A.Rich. (29), *Bhutanthera** J.Renz (5), *Bonatea* Willd. (13), *Brachycorythis* Lindl. (36), *Centrostigma* Schltr. (3), *Chamorchis* Rich. (1), *Cynorkis* Thouars (156), *Dactylorhiza* Neck. ex Nevski (40), *Diplomeris* D.Don (3), *Dracomonticola* H.P.Linder & Kurzweil (1), *Galearis* Raf. (10), *Gennaria* Parl. (1), *Gymnadenia* R.Br. (23), *Habenaria* Willd. (835), *Hemipilia* Lindl. (13), *Hsenhsua** X.H.Jin, Schuit. & W.T.Jin (1), *Hermannium* L. (19), *Himantoglossum* Spreng. (11), *Holothrix* Rich. ex Lindl. (45), *Megalorchis* H.Perrier (1), *Neobolusia* Schltr. (3), *Neotinea* Rchb.f. (4), *Oligophyton* H.P.Linder (1), *Ophrys* L. (34), *Orchis* Tourn. ex L. (21), *Pecteilis* Raf. (8), *Peristylus* Blume (103), *Physoceras* Schltr. (12), *Platanthera* Rich. (136), *Platycoryne* Rchb.f. (19), *Ponerorchis* Rchb.f. (55), *Porolabium* Tang & F.T.Wang (1), *Pseudorchis* Ség. (1), *Roeperocharis* Rchb.f. (5), *Satyrium* L. (86), *Schizochilus* Sond. (11), *Serapias* L. (13), *Silvorchis*† J.J.Sm. (3), *Sirindhornia** H.A.Pedersen & Suksathan (3), *Stenoglottis* Lindl. (7), *Steveniella* Schltr. (1), *Thulinia* P.J.Cribb (1), *Traunsteinera* Rchb. (2), *Tsaiorchis** Tang & F.T.Wang (1), *Tylostigma* Schltr. (8), *Veyretella* Szlach. & Olszewski (2).

SUBFAMILY EPIDENDROIDEAE

Tribe Neottieae

Aphyllorchis Blume (22), *Cephalanthera* Rich. (19), *Epipactis* Zinn (49), *Limodorum* Boehm. (3), *Neottia* Guett. (64), *Palmorchis* Barb.Rodr. (21).

Tribe Sobralieae

Elleanthus C.Presl (111), *Epilyna* Schltr. (2), *Sertifera* Lindl. (7), *Sobralia* Ruiz & Pav. (149).

Tribe Tropidieae

Corymborkis Thouars (6), *Tropidia* Lindl. (31).

Tribe Triphoreae

Subtribe Diceratostelinae:
‡*Diceratostele* Summerh. (1).

Subtribe Triphorinae‡:

Monophyllorchis Schltr. (1), *Pogoniopsis*† Rchb.f. (2), *Psilochilus* Barb.Rodr. (7), *Triphora* Nutt. (18).

Tribe Xerorchideae‡

Xerorchis Schltr. (2).

Tribe Wulschlaegeliae‡

Wulschlaegelia† Rchb.f. (2).

Tribe Gastrodieae

Auxopus Schltr. (4), *Didymoplexiella* Garay (8), *Didymoplexis* Griff. (17), *Gastrodia* R.Br. (60), *Uleiorchis* Hoehne (2).

Tribe Nervilieae

Subtribe Nerviliinae‡:
Nervilia Comm. ex Gaudich. (67).

Subtribe Epipogiinae‡:

Epipogium Borkh. (3), *Stereosandra* Blume (1).

Tribe Thaieae‡

Thaia† Seidenf. (1).

Tribe Arethuseae

Subtribe Arethusinae:
Anthogonium Wall. ex Lindl. (9), *Arethusa* L. (1), *Arundina* Blume (2), *Calopogon* R.Br. (5), *Eleorchis* Maek. (1).

Subtribe Coelogyninae:

Aglossorrhyncha† Schltr. (13), *Bletilla* Rchb.f. (5), *Bracisepalum* J.J.Sm. (2), *Bulleyia* Schltr. (1), *Chelonistele* Pfitzer (13), *Coelogyne* Lindl. (200), *Dendrochilum* Blume (278), *Dickasonia* L.O.Williams (1), *Dilochia* Lindl. (8), *Entomophobia* de Vogel (1), *Geesinkorchis* de Vogel (4), *Glomera* Blume (131), *Gynoglottis* J.J.Sm. (1), *Ischnogyne* Schltr. (1), *Nabalua* Ames (3), *Neogyna* Rchb.f. (1), *Otochilus* Lindl. (5), *Panisea* Lindl. (11), *Pholidota* Lindl. (39), *Pleione* D.Don (21), *Thunia* Rchb.f. (5).

Tribe Malaxideae‡

Subtribe Dendrobiinae:
Bulbophyllum Thouars (1867), *Dendrobium* Sw. (1509).

Subtribe Malaxidinae‡:

*Alatiliparis** Marg. & Szlach. (5), *Crepidium** Blume (260), *Crossoglossa* Dressler & Dodson (26), *Crossoliparis** Marg. (1), *Dienia** Lindl. (6), *Hammarbya** Kuntze (1), *Hippeophyllum* Schltr. (10), *Liparis* Rich. (426), *Malaxis* Sol. ex Sw. (182), *Oberonia* Lindl. (323), *Oberonioides** Szlach. (2), *Orestias* Ridl. (4), *Stichorkis** Thouars (8), *Tamayorkis** Szlach. (1).

Tribe Cymbidieae

Subtribe Cymbidiinae:
Acriopsis† Reinw. ex Blume (9), *Cymbidium* Sw. (71), *Grammatophyllum* Blume (12), *Porphyroglottis* Ridl. (1), *Thecopus*† Seidenf. (2), *Thecostele*† Rchb.f. (1).

Subtribe Eulophiinae:

Acrolophia Pfitzer (7), *Ansellia* Lindl. (1), *Claderia*† Hook.f. (2), *Cymbidiella* Rolfe (3), *Dipodium* R.Br.

(25), *Eulophia* R.Br. (200), *Eulophiella* Rolfe (5), *Geodorum* Jacks. (12), *Grammangis* Rchb.f. (2), *Graphorkis*† Thouars (4), *Imerinaea*† Schltr. (1), *Oeceoclades* Lindl. (38), *Paralophia** P.J.Cribb & Hermans (2).

Subtribe Catasetinae:

Catasetum Rich. ex Kunth (176), *Clowesia* Lindl. (7), *Cyanaeorchis*† Barb.Rodr. (3), *Cycnoches* Lindl. (34), *Dressleria* Dodson (11), *Galeandra* Lindl. (38), *Grobya* Lindl. (5), *Mormodes* Lindl. (80).

Subtribe Cyrtopodiinae‡:

Cyrtopodium R.Br. (47).

Subtribe Coeliopsidinae:

Coeliopsis Rchb.f. (1), *Lycomormium* Rchb.f. (5), *Peristeria* Hook. (13).

Subtribe Eriopsidinae:

Eriopsis Lindl. (5).

Subtribe Maxillariinae:

Anguloa Ruiz & Pav. (9), *Bifrenaria* Lindl. (21), *Guanchezia* G.A.Romero & Carnevali (1), *Horvatia* Garay (1), *Lycaste* Lindl. (32), *Maxillaria* Ruiz & Pav. (658), *Neomoorea* Rolfe (1), *Rudolphiella* Hoehne (6), *Scuticaria* Lindl. (11), *Sudamerlycaste** Archila (42), *Teuscheria* Garay (7), *Xylobium* Lindl. (30).

Subtribe Oncidiinae:

Aspasia Salisb. (7), *Brassia* R.Br. (64), *Caluera* Dodson & Determann (3), *Capanemia* Barb.Rodr. (9), *Caucaea* Schltr. (9), *Centroglossa* Barb.Rodr. (5), *Chytroglossa* Rchb.f. (3), *Cischweinfia* Dressler & N.H.Williams (11), *Comparettia* Poepp. & Endl. (78), *Cuitlauzina* La Llave & Lex. (7), *Cypholoron* Dodson & Dressler (2), *Cyrtochiloides* N.H.Williams & M.W.Chase (3), *Cyrtochilum* Kunth (137), *Dunstervillea* Garay (1), *Eloyella* P.Ortiz (10), *Erycina* Lindl. (7), *Fernandezia* Ruiz & Pav. (51), *Gomesa* R.Br. (119), *Grandiphyllum** Docha Neto (7), *Hintonella* Ames (1), *Hofmeisterella* Rchb.f. (2), *Ionopsis* Kunth (6), *Leochilus* Knowles & Westc. (12), *Lockhartia* Hook. (28), *Macradenia* R.Br. (11), *Macroclinium* Barb.Rodr. (42), *Miltonia* Lindl. (12), *Miltoniopsis* God.-Leb. (5), *Notylia* Lindl. (56), *Notyliopsis* P.Ortiz (2), *Oliveriana* Rchb.f. (6), *Oncidium* Sw. (311), *Ornithocephalus* Hook. (55), *Otoglossum* (Schltr.) Garay & Dunst. (13), *Phymatidium* Lindl. (10), *Platyrrhiza* Barb.Rodr. (1), *Plectrophora* H.Focke (10), *Polyotidium* Garay (1), *Psychopsiella** Lückel & Braem (1), *Psychopsis* Raf. (4), *Pterostemma* Kraenzl. (3), *Quekettia* Lindl. (4), *Rauhiella* Pabst & Braga (3), *Rhynchostele* Rchb.f. (17), *Rodriguezia* Ruiz & Pav. (48), *Rossioglossum* (Schltr.) Garay & G.C.Kenn. (9), *Sanderella* Kuntze

(2), *Saundersia* Rchb.f. (2), *Schunkea* Senghas (1), *Seegeriella* Senghas (2), *Solenidium* Lindl. (3), *Suarezia* Dodson (1), *Sutrina* Lindl. (2), *Systeloglossum* Schltr. (5), *Telipogon* Kunth (205), *Thysanoglossa* Porto & Brade (3), *Tolumnia* Raf. (27), *Trichocentron* Poepp. & Endl. (70), *Trichoceros* Kunth (10), *Trichopilia* Lindl. (44), *Trizeuxis* Lindl. (1), *Vitekorchis** Romowicz & Szlach. (4), *Warmingia* Rchb.f. (4), *Zelenkoa* M.W.Chase & N.H.Williams (1), *Zygostates* Lindl. (22).

Subtribe Stanhopeinae:

Acineta Lindl. (17), *Braemia* Jenny (1), *Cirrhaea* Lindl. (7), *Coryanthes* Hook. (59), *Embreea* Dodson (2), *Gongora* Ruiz & Pav. (74), *Horichia* Jenny (1), *Houlletia* Brongn. (9), *Kegeliella* Mansf. (4), *Lacaena* Lindl. (2), *Lueckelia* Jenny (1), *Lueddemannia* Linden & Rchb.f. (3), *Paphinia* Lindl. (16), *Polycycnis* Rchb.f. (17), *Schlimia* Planch. & Linden (7), *Sievekingia* Rchb.f. (16), *Soterosanthus* F.Lehm. ex Jenny (1), *Stanhopea* J.Frost ex Hook. (61), *Trevoria* F.Lehm. (5), *Vasquezella* Dodson (1).

Subtribe Zygopetalinae:

*Aetheorhyncha** Dressler (1), *Aganisia* Lindl. (4), *Batemannia* Lindl. (5), *Benzingia* Dodson (9), *Chaubardia* Rchb.f. (3), *Chaubardiella* Garay (8), *Cheiradenia* Lindl. (1), *Chondrorhyncha* Lindl. (7), *Chondroscaphe* (Dressler) Senghas & G.Gerlach (14), *Cochleanthes* Raf. (4), *Cryptarrhena* R.Br. (3), *Daioityla** Dressler (4), *Dichaea* Lindl. (118), *Echinorhyncha** Dressler (5), *Euryblema** Dressler (2), *Galeottia* A.Rich. (12), *Hoehneella* Ruschi (2), *Huntleya* Bateman ex Lindl. (14), *Ixyophora** Dressler (5), *Kefersteinia* Rchb.f. (70), *Koellensteinia* Rchb.f. (17), *Neogardneria* Schltr. ex Garay (1), *Otostylis* Schltr. (4), *Pabstia* Garay (5), *Paradisanthus* Rchb.f. (4), *Pescatoria* Rchb.f. (23), *Promenaea* Lindl. (18), *Stenia* Lindl. (22), *Stenotyla** Dressler (9), *Vargasiella* C.Schweinf. (1), *Warczewiczella** Rchb.f. (11), *Warrea* Lindl. (3), *Warreella* Schltr. (2), *Warreopsis* Garay (4), *Zygopetalum* Hook. (14), *Zygosepalum* (Rchb.f.) Rchb.f. (8).

Tribe Epidendreae

Subtribe Bletinae:

Basiphyllaea Schltr. (7), *Bletia* Ruiz & Pav. (33), *Chysis*†Lindl. (10), *Hexalectris* Raf. (10).

Subtribe Laeliinae:

Acorchis Dressler (1), *Adamantina* van den Berg & C.N.Conç (1), *Alamania* Llave & Lex. (1), *Arpophyllum* Llave & Lex. (3), *Artorima* Dressler & G.E.Pollard (1), *Barkeria* Knowl. & Westc. (17), *Brassavola* R.Br. (22), *Broughtonia* R.Br. (6), *Cattleya* Lindl. (113), *Caularthron* Raf. (4), *Constantia** Barb.Rodr.

(6), *Dimerandra* Schltr. (8), *Dinema* Lindl. (1), *Domingoa* Schltr. (4), *Encyclia* Hook. (165), *Epidendrum* L. (1413), *Guarianthe* Dressler & W.E.Higgins (4), *Hagsatera* R.González (2), *Homalopetalum* Rolfe (8), *Isabelia* Barb.Rodr. (3), *Jacquinella* Schltr. (12), *Laelia* Lindl. (23), *Leptotes* Lindl. (9), *Loefgrenianthus* Hoehne (1), *Meiracyllium* Rchb.f. (2), *Microepidendrum** Brieger ex W.E.Higgins (1), *Myrmecophila* Rolfe (10), *Nidema* Britton & Millsp. (2), *Oestlundia* W.E.Higgins (4), *Orleanesia* Barb.Rodr. (9), *Prosthechea* Knowles & Westc. (117), *Pseudolaelia* Porto & Brade (18), *Psychilis* Raf. (14), *Pygmaeorchis* Brade (2), *Quisqueya* Dod (4), *Rhynchoaelia* Schltr. (2), *Scaphyglottis* Poepp. & Endl. (69), *Tetramicra* Lindl. (14).

Subtribe Pleurothallidinae:

Acianthera Scheidw. (118), *Anathallis* Barb.Rodr. (152), *Andinia* (Luer) Luer (13), *Barbosella* Schltr. (19), *Brachionidium* Lindl. (75), *Chamelophyton* Garay (1), *Dilomilis* Raf. (5), *Diodonopsis* Pridgeon & M.W.Chase (5), *Draconanthes** (Luer) Luer (2), *Dracula* Luer (127), *Dresslerella* Luer (13), *Dryadella* Luer (54), *Echinosepala* Pridgeon & M.W.Chase (11), *Fronitaria* Luer (1), *Kraenzlinella** Kuntze (9), *Lepanthes* Sw. (1085), *Lepanthopsis* (Cogn.) Ames (43), *Masdevallia* Ruiz & Pav. (589), *Myoxanthus* Poepp. & Endl. (48), *Neocogniauxia* Schltr. (2), *Octomeria* D.Don (159), *Pabstiella** Brieger & Senghas (29), *Phloeophila* Hoehne & Schltr. (11), *Platystele* Schltr. (101), *Pleurothallis* R.Br. (551), *Pleurothallopsis* Porto & Brade (18), *Porroglossum* Schltr. (43), *Restrepia* Kunth (53), *Restrepiella* Garay & Dunst. (2), *Sansonia** Chiron (2), *Scaphosepalum* Pfitzer (46), *Specklinia* Lindl. (135), *Stelis* Sw. (879), *Teagueia* (Luer) Luer (13), *Tomzania* Nir (1), *Trichosalpinx* Luer (111), *Trisetella* Luer (23), *Zootrophion* Luer (22).

Subtribe Ponerinae:

Helleriella A.D.Hawkes (2), *Isochilus* R.Br. (13), *Nemaconia** Knowles & Westc. (6), *Ponera* Lindl. (2).

Subtribe Calypsoinae†:

Aplectrum Nutt. (1), *Calypso* Salisb. (1), *Changnienia* S.S.Chien (1), *Coelia*† Lindl. (5), *Corallorhiza* Gagnebin (11), *Cremastra* Lindl. (4), *Dactylostalix* Rchb.f. (1), *Danxiaorchis*† J.W.Zhai, F.W.Xing & Z.J.Liu (1), *Ephippianthus* Rchb.f. (2), *Govenia* Lindl. (24), *Oreorchis* Lindl. (16), *Tipularia* Nutt. (7), *Yuania* Maxim. (4).

Subtribe Agrostophyllinae†:

Agrostophyllum Blume (100), *Earina* Lindl. (7).

Tribe Collabieae‡

Acanthephippium Blume (13), *Ancistrochilus* Rolfe (2), *Ania* Lindl. (11), *Calanthe* R.Br. (216), *Cephalan-*

theropsis Guillaumin (4), *Chrysoglossum* Blume (4), *Collabium* Blume (14), *Diglyphosa* Blume (3), *Eriodes* Rolfe (1), *Gastrorchis* Thouars (8), *Hancockia* Rolfe (1), *Ipsea* Lindl. (3), *Nephelaphyllum* Blume (11), *Pachystoma* Blume (3), *Phaius* Lour. (45), *Pilophyllum*† Schltr. (1), *Plocoglottis* Blume (41), *Risleya*† King & Pantl. (1), *Spathoglottis* Blume (48), *Tainia* Blume (23).

Tribe Podochileae

Appendicula Blume (146), *Ascidieria* Seidenf. (8), *Bryobium** Lindl. (8), *Callostylis** Blume (5), *Campanulorchis** Brieger in F.R.R.Schlechter (5), *Ceratostylis* Blume (147), *Conchidium** Griff. (10), *Cryptochilus* Wall. (5), *Dilochiopsis** (Hook.) Brieger in F.R.R.Schlechter (1), *Epiblastus* Schltr. (22), *Eria* Lindl. (237), *Mediocalcar* J.J.Sm. (17), *Mycaranthes** Blume (36), *Notheria** P.O'Byrne and J.J.Verm. (15), *Octarrhena* Thwaites (52), *Oxystophyllum** Blume (36), *Phreatia* Lindl. (211), *Pinalia** Lindl. (105), *Poaephyllum* Ridl. (6), *Podochilus* Blume (62), *Porpax* Lindl. (13), *Pseuderia* Schltr. (20), *Ridleyella* Schltr. (1), *Sarcostoma* Blume (5), *Stolzia* Schltr. (15), *Thelasis* Blume (26), *Trichotosia* Blume (78).

Tribe Vandae

Subtribe Adrorrhizinae‡:

Adrorrhizon Hook.f. (1), *Bromheadia*† Lindl. (30), *Sirhookera* Kuntze (2).

Subtribe Polystachyinae:

Hederorkis Thouars (2), *Polystachya* Hook. (234).

Subtribe Aeridinae:

Acampe Lindl. (8), *Adenoncos* Blume (17), *Aerides* Lour. (25), *Amesiella* Schltr. ex Garay (3), *Arachnis* Blume (14), *Biermannia* King & Pantl. (11), *Bogoria* J.J.Sm. (4), *Brachypeza* Garay (10), *Calymmanthera* Schltr. (5), *Ceratocentron* Senghas (1), *Chamaeanthus* Schltr. (3), *Chiloschista* Lindl. (20), *Chroniochilus* J.J.Sm. (4), *Cleisocentron* Brühl (6), *Cleisomeria* Lindl. ex D.Don in Loud. (2), *Cleisostoma* Blume (88), *Cleisostomopsis** Seidenf. (2), *Cottonia* Wight (1), *Cryptopylos* Garay (1), *Deceptor** Seidenf. (1), *Dimorphorchis* Rolfe (5), *Diplocentrum* Lindl. (2), *Diploprora* Hook.f. (2), *Dryadorchis* Schltr. (5), *Drymoanthus* Nicholls (4), *Dyakia* Christenson (1), *Eclecticus** P.O'Byrne (1), *Gastrochilus* D.Don (56), *Grosourdyia* Rchb.f. (11), *Gunnarella* Senghas (9), *Holcoglossum* Schltr. (14), *Hymenorchis* Schltr. (12), *Jejewoodia** Szlach. (6), *Luisia* Gaudich. (39), *Macropodanthus* L.O.Williams (8), *Micropera* Lindl. (21), *Microsaccus* Blume (12), *Mobilabium* Rupp (1), *Omoea* Blume (2), *Ophioglossella** Schuit. & Ormerod (1), *Papilionanthe* Schltr. (11), *Papillilabium* Dockrill (1), *Paraphalaenopsis* A.D.Hawkes (4), *Pelatantheria*

Ridl. (8), *Pennilabium* J.J.Sm. (15), *Peristeranthus* T.E.Hunt (1), *Phalaenopsis* Blume (70), *Phragmorchis* L.O.Williams (1), *Plectorrhiza* Dockrill (3), *Pomato-calpa* Breda (25), *Porrorrhachis* Garay (2), *Pteroceras* Hassk. (27), *Renanthera* Lour. (20), *Rhinerrhiza* Rupp (1), *Rhinerrhizopsis** Ormerod (3), *Rhynchogyna* Seidenf. & Garay (3), *Rhynchostylis* Blume (3), *Robiquetia* Gaudich. (45), *Saccolabiopsis* J.J.Sm. (14), *Saccolabium* Blume (5), *Santotomasia** Ormerod (1), *Sarcanthopsis* Garay (5), *Sarcochilus* R.Br. (25), *Sarcoglyphis* Garay (12), *Sarcophyton* Garay (3), *Schistotylus* Dockrill (1), *Schoenorchis* Reinw. ex Blume (25), *Seidenfadenia* Garay (1), *Seidenfadeniella** C.S.Kumar (2), *Singchia** Z.J.Liu & L.J.Chen (1), *Smithsonia* C.J.Saldanha (3), *Smitinandia* Holttum (3), *Spongiola** J.J.Wood & A.L.Lamb (1), *Stereochilus* Lindl. (7), *Taeniophyllum* Blume (185), *Taprobanea** Christenson (1), *Thrixspermum* Lour. (161), *Trachoma** Garay (14), *Trichoglottis* Blume (69), *Tuberolabium* Yaman. (11), *Uncifera* Lindl. (6), *Vanda* R.Br. (73), *Vandopsis* Pfitzer in Engler & Prantl (4).

Subtribe Angraecinae:

Aerangis Rchb.f. (58), *Aeranthes* Lindl. (43), *Ambrella* H.Perrier (1), *Ancistrorhynchus* Finet (17), *Angrae-*

copsis Kraenzl. (22), *Angraecum* Bory (221), *Beclardia* A.Rich. (2), *Bolusiella* Schltr. (6), *Calyptrochilum* Kraenzl. (2), *Campylocentrum* Benth. (65), *Cardi-ochilos* P.J.Cribb (1), *Chauliodon* Summerh. (1), *Cribbia* Senghas (4), *Cryptopus* Lindl. (4), *Cyrtorchis* Schltr. (18), *Dendrophyllax* Rchb.f. (14), *Diaphananthe* Schltr. (33), *Dinklageella* Mansf. (4), *Distylodon* Summerh. (1), *Eggelingia* Summerh. (3), *Erasanthe* P.J.Cribb, Hermans & D.L. Roberts (1), *Eurychone* Schltr. (2), *Jumellea* Schltr. (59), *Lemurella* Schltr. (4), *Lemurorchis* Kraenzl. (1), *Listrostachys* Rchb.f. (1), *Margelliantha* P.J.Cribb (6), *Microcoelia* Lindl. (30), *Mystacidium* Lindl. (10), *Neobathiea* Schltr. (5), *Nephrangis* Summerh. (2), *Oeonia* Lindl. (5), *Oeoniella* Schltr. (2), *Ossiculum* P.J.Cribb & Laan (1), *Plectrelminthus* Raf. (1), *Podangis* Schltr. (1), *Rangar-eris* (Schltr.) Summerh. (6), *Rhaesteria* Summerh. (1), *Rhipidoglossum* Schltr. (35), *Sobennikoffia* Schltr. (4), *Solenangis* Schltr. (8), *Sphyrarhynchus* Mansf. (1), *Summerhayesia* P.J.Cribb (2), *Taeniorrhiza* Summerh. (1), *Triceratorhynchus* Summerh. (1), *Tri-dactyle* Schltr. (47), *Ypsilopus* Summerh. (5).

Incertae sedis (in *Epidendroideae*)

*Devogelia** Schuit. (1).