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 Orchideae (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 Wullschlaegelieae for achlorophyllous Wullschlaegelia, which had tentatively been placed in Calypsoeae. Another genus, Devogelia, takes the place of Thaia as incertae sedis in Epidendroideae. Gastroideae are clearly placed among the tribes in the neottioid 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: Vandeae/Podochileae/Collabieae, Cymbidieae, Malaxideae and Epidendreae, 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 Adrorhizinae, the first now included in Epidendreae and the second in Vandeae. Collabiinae, also probably related to Vandeae, 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.


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
The 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 Orchidaceae, 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 Neottiioideae 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 Stifttioidae (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 *Tomzanonia* 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 Apostasiioideae 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, Pogonieae 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. *Cleistes* 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 tropical American species, including the type species, *C. grandiflora* (Aubl). Schltr. The position of achlorophyllous *Pogoniosis* 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, Epidendroidae). 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 *Pogoniosis* 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 spirantheid embryo (Clements, 1999).

**Cranichideae**

Within Chloraeae, phylogenetic analyses (Chemisquy & Marrone, 2010; Cisternas et al., 2012b) have shown that *Goeblasta 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*; *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 *Bieniera* Rchb.f and *Ulantha* Hook., and created some new genera mostly based on column and perianth features (*Jouyella* Schlach., *Chileorchis* Schlach. and *Correorchis* Schlach.), 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.

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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 Pontthieva and included in that genus. In Salazar (2003b), Nothostele was treated as a member of Cranichidinae, but Batista et al. (2011) demonstrated that the sole species, Nothostele acianthiformis (Rchb.f. & Warn.) 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 Platylepis A.Rich., it is tentatively recognized here. In addition, Meneguzzo (2012) transferred Ligeophila Garay and Platyleysis to Aspidogyno 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/Cranichidinae 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 Spiranthinae 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 genus, most commonly treated as Cyclopogon glabrescens (T.Hashim.) Dodson, falls as sister to the pair of Eurystyls 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 Sotosa (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.
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 Rehb.) is sister to Cynicaulus (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/Elytranthera with nrITS DNA sequences (Jones et al., 2001) or Caladenia/Cynicaulus 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 Corycinae, Corycium and Pterygodium are not monophyletic, and the relationships of the genera in Corycinae 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 Corycinae plus Orchidinae, including Huttonaea (Bytehier et al., 2008), with the last weakly supported as sister to Disa (including Herscheliantus, Monadenia and Schizodorum as before; Bytehier, Bellstedt & Linder, 2007). We include Ceratandra, Corycium, Eotovella and Pterygodium in Corycinae, 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 sub-tribe 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 Hu, Cercarochis Schlr. and Chondradenia Maxim. ex P.Maek., and Diphyllax 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 Prigodine et al. (2001a). Neolindleya has recently been included in Galearis (Jin et al., 2014). Tsaiorchis was considered as a synonym of Anitostigma Schlr. in Prigodine 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 Habe- naria or Brachycorythis based on morphology (Luo, Zhu & Kurzweil, 2005; Prigodine et al., 2014), falls within Hemipilia in Jin et al. (2014), and so we include it there. Ponerorchis and Neottianthe are nested within Anitostigma, 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) 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 Nuijiangia 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 holomycotropic genus Silvorchis, with only one, presumably extinct species from Java, was included in subtribe Epipoginae 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 Neottioidae. In Triphoreae, we recognize two subtribes in parallel with the treatment in Pridgeon et al. (2005), with the addition of heteromycotropic 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.

**Wullschlaegelieae**

The position of Wullschlaegeliea 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 Wullschlaegeliea 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 Neottioidae. *Thaia* was originally described from Thailand as holomycotropic (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 Coelogyininae. *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 Coelogyininae.

No further work or nomenclatural changes have been made to Coelogyininae 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, Nabaluia, 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 Collabiaeae, 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 Bletiinae (Arethusaeeae). On the basis of results in Goldman et al. (2001), Chase et al. (2003) first recognized an expanded circumscription of Collabiaeae 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 Gorniak et al. (2010), we recognize the group as a tribe due to their position as sister to a clade including Vandeae 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 Collabiaeae. 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 Preptanthex 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 Collabiaeae, despite its deviating morphology (it is an epiphyte, whereas most members of Collabiaeae 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 relationship to Malaxideae in Gorniak 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 Cymbidiiinae and Eulophiinae are still unclear, and the treatment here still requires confirmation. Cymbidiiinae (Batista et al., 2014) should include at least Acriopsis, Thecopus and Thecostele, in addition to those genera included here in Chase et al. (2003). Porphyrogloittis, from Peninsular Malaysia, Borneo and Sumatra, is included here, but only tentatively; in habit, it resembles Neotropical Cyrtopodium (Cytopodiinae). 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 (Polystachyiinae; Vandeae; Dressler, 1993). Graphorkis was moved here from Cymbidiiinae (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 Eulophiinae.
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 (Rehb.f.), which falls in different positions with nrITS and plastid DNA inMartos 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, Cyrtopodinae, as in Pridgeon et al. (2005). Cyrtopodium continues to occupy an isolated position in Cymbidieae, 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 Cymbidieae, Cyrtopodinae were found to be sister to all Cymbidieae, 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 Bentham., 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, Gorniak & 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., Pityphylum, Rhetinantha M.A.Blanco, Sauvetrea 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 Angulooa. This group of species was also described by Ryan & Oakley (2003) as Ifa A.Ryan & Oakley, but it had been preceded by Sudamerlycaste; it was treated by Pridgeon et al. (2009) as Ifa 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, Psychopsisella 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 Santanderiella P. Ortiz with Notyliosis. Pachyphyllum Kunth and Raycedenko 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 Raycedenko 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 (Papadopulos 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 Chondrodendron, 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. Vargasella (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 Vargasella 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. Górniak 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 Freudentstein & 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 Praga & 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. Draconanthas is also newly accepted here as well as being included in Pridgeon et al. (2005). Kraenzlinellina 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 Anathaliis barbulata (Lindl.) Pridgeon & M.W.Chase because, in an nrITS analysis, they fell closer to other genera than to the rest of Anathaliis, but support for this result was poor (none of the relevant nodes separating the species ascribed to Lankesteriana from the rest of Anathaliis 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 Philoeophilia 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. araguaensis 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 Rchb.f.

New genera for parts of Epidendrum, such as Takulumenä 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). Platyglossis L.O.Williams and Hexisea Lindl. have been included in Scaphyglossis 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 Górniai 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. Didicea King & Prain has been included in Tipularia in accord with Pridgeon et al. (2005) and Wu, Raven & Hong (2009). Wullschaegelia was placed here tentatively in Chase et al. (2003), but its position was queried. In Górniai et al. (2010), it fell in an isolated position among the neottioids, and here we reinstate Wullschaegelia 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. Górniai 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.

Podochilinae

In Podochilinae, Podochilinae were combined with Eriinae based on interdigitation of the two subtribes in Pridgeon et al. (2005). Thelasinae minus Ridleyella are sister to Eriinae, whereas Ridleyella is sister to the rest of Podochilinae (van den Berg et al., 2005). On this basis, it is appropriate to recognize Podochilinae as an independent tribe but, in 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). Chitonochnilus 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 Appendixa because of their similar habit and floral morphology, in which genus the necessary combinations already exist.

Vandeae

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 Adrorhizinae were demonstrated to be members of Vandeae (bootstrap percentage 84%), but not to share an exclusive relationship. The association of Agrostophyllinae with Vandeae 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 Cymbidiae (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 Vandeae; these relationships obviously still require further investigation. In morphological terms, Bromheadia is highly dissimilar to Adrorhizon and Sirhookera.

Polystachyninae were included in Vandiae 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 Polystachyninae here, but this relationship should be the focus of additional study. Relative to Chase et al. (2003), Imerinaea was moved to Euophilinae of Cymbidiae (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 Chelystachys Mytnik & Szlach., Isochilos-tachys Mytnik & Szlach. and Neobenthamia Mytnik, Szlach. & Baranow, as proposed by Mytnik-Ejsmont (2011) and coworkers.

Updating Chase et al. (2003), Aerangidinae have been included in Angraceae (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. Erasantae has been added (Cribb, Hermans & Roberts, 2007) because it falls far from Aeranthae, 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).
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 Ascocentrum 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.Wolf, 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 and the recently proposed Theana Aver. A broader circumscription of Holcoglossum was maintained that includes several recently described genera: Penkimia Phukan & Odyuo, Chenorchis 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 Porphyrodése Schltr. The recently described Monanochilus (Schltr.) R.Rice is considered to be a synonym of Sarcocchilus, having been a section of that genus. Luxomorchis Rauschert is a synonym of Smithsonia. Microtatorchis Schltr. is a synonym of Tueniophyllum; they differ chiefly in the former having leaves and the latter not. Cordiglottis J.J.Sm. differs from Thrixpermum mostly in its terete leaves and some minor lip characters; some terete-leaved Thrixpermum 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 Tuberoselium 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 Tuberoselium. In Cleisostoma, we included Blumeorchis Szlach. and Ormerodia Szlach., both described since 2003. As currently circumscribed, Cleisostoma is clearly polythetic; further analyses are needed to determine whether it should be split or expanded by merging other genera with it, such as Pelatanthera and Rhynchogyna (both still recognized here). Harraella 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 Devogeilia Schuitema 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 Eulophineae, Malaxidinae and Collableae (all Epipendroideae). 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). Devogeilia 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 phyllogenetic 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 publications 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 havenarids) 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 havenarids 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 Vanuclae). As noted above, Podochilinae 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 neotiioid 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 APPOSTASIOIDEAE**

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

**SUBFAMILY VANILLOIDEAE**

Tribe Pogonieae


Tribe Vanilleae

Clemattepistephium 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 Blume ex Mill. (105).

**SUBFAMILY CYRIPEDIOIDEAE**

Cypripedium L. (51), Mexpedium 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), Gaviaole Poepp. (15).

Subtribe Galeottiellinae:
Galeottiella Schltr. (6).

Subtribe Goodyerinae:

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:

Tribe Diurideae
Subtribe Acianthinae:
Acianthus R.Br. (20), Corybas Salisb. (132), Cyrtozephyrion R.Br. (5), Stigmatodactylus Maxim. ex Makino (10), Townsonia Cheeseeman (2).

Subtribe Caladeniinae:

Subtribe Cryptostylidinae:
Cryptostylis Schltr. (1), Cryptostylis R.Br. (23).

Subtribe Diuridinae:
Diuris Sm. (71), Orthoceras R.Br. (2).

Subtribe Drakaeinae‡:
Arthrodorum F.Muell. (15), Caleana R.Br. (1), Chiloglottis R.Br. (23), Drakaea Lindl. (10), Paracaleana Blaxell (13), Spiculaea Lindl. (1).

Subtribe Megastylidinae‡:

Subtribe Prasophyllinae‡:
Genoplesium R.Br. (47), Microtis R.Br. (19), Prasophyllum R.Br. (131).

Subtribe Rhizanthellinae:
Rhizanthella R.S.Rogers (3).

Subtribe Thelymitrinae:

Tribe Orchideae
Subtribe Brownleeinae:
Brownleea Harv. ex Lindl. (8), Disperis Sw. (78).

Subtribe Coryciinae‡:
Cerandra Lindl. (6), Corycium Sw. (15), Eotetra Kurzweil & H.P.Linder (1), Pterygodium Sw. (19).
Subtribe Disinae:
Disa P.J.Bergius (182), Huttonea Harv. (5), Pachites† Lindl. (2).

Subtribe Orchidinae:

SUBFAMILY EPIDENDROIDEAE

Tribe Neottiaceae

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

Tribe Tropicidaceae
Corymborkis Thouars (6), Tropidia Lindl. (31).

Tribe Triphoreae
Subtribe Diceratostelinae:
‡Diceratostele Summerh. (1).

Subtribe Triphorinae‡:

Tribe Xerorchidaceae‡
Xerorchis Schltr. (2).

Tribe Wullschlaegelieae‡
Wullschlaegelia† Rchb.f. (2).

Tribe Gastrodieceae
Auxopus Schltr. (4), Didymopseilissa Garay (8), Didymopseilissa Griff. (17), Gastrodia R.Br. (60), Uleiorchis Hoehne (2).

Tribe Nervilieae
Subtribe Nervilininae‡:
Nervilia Comm. ex Gaudich. (67).

Subtribe Epipogininae‡:
Epipogium Borkh. (3), Stereosandra Blume (1).

Tribe Thaieae‡
Thaia† Seidenf. (1).

Tribe Arethuceae
Subtribe Arethuceinae:

Tribe Malaxidaceae‡
Subtribe Dendrobininae:
Bulbophyllum Thouars (1867), Dendrobium Sw. (1509).

Subtribe Malaxidinae‡:

Tribe Cymbidiceae
Subtribe Cymbidinae:
Acrolophia Pfister (7), Ansellia Lindl. (1), Claderia† Hook.f. (2), Cymbidiella Rolfe (3), Dipodium R.Br.


Subtribe Cyrtopodiinae: Cyrtopodium R.Br. (47).


Subtribe Eriopsisidinae: 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), Neomorea Rolfe (1), Rudolfiella Hoehe (6), Scuticaria Lindl. (11), Sudamerlycaste* Archila (42), Teuscheria Garay (7), Xylobium Lindl. (30).


Tribe Epidendreae
Subtribe Bletiinae: Basiphyllaelae Schltr. (7), Bletia Ruiz & Pav. (33), Chysis† Lindl. (10), Hexalectris Raf. (10).

Subtribe Pleurothallidinae:

Acianthera Scheidw. (118), Anathallis Barb.Rodr. (152), Andinia (Luer) Luer (13), Barbosella Schltr. (19), Brachidium Schltr. (75), Chamelophyton Garay (1), Dilomilis Raf. (5), Diodonopsis P.O'Byrne (1), Dractionthes* (Luer) Luer (2), Dracula Luer (127), Dresslerella Luer (13), Dryadella Luer (54), Echinosepala P.O'Byrne & M.W.Chase (11), Frondaria 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), Philoephila Hoehne & Schltr. (11), Platystele Schltr. (101), Pleurothallium R.Br. (551), Pleurothallopsis Porto & Brade (18), Porroglossum Schltr. (43), Restrepia Kuntze (53), Restrepia Luer (13), Tomzanonia Nú (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:


Subtribe Agrostophyllinae:

Agrostophyllum Blume (100), Earina Lindl. (7). Subtribe Collabiaeae:

Acanthephippium Blume (13), Ancistrochilus Rolfe (2), Ania Lindl. (11), Calanthe R.Br. (216), Cephalantheropsis Guillaumin (4), ChrysoGLOSSUM Blume (4), Collabium Blume (14), Diglyphosa Blume (3), Eriodes Rolfe (1), Gastrochilus 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 Podochlaeae


Adrorhizon Hook.f. (1), Bromheadia† Lindl. (30), Sirhookera Kuntze (2). Subtribe Polystachyinae:

Hederorkis Thouars (2), Polystachya Hook. (234). Subtribe Aeridinae:


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Subtribe Angraecinae:


Incertae sedis (in Epidendroideae)

Devogelia* Schuit. (1).