



An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV

THE ANGIOSPERM PHYLOGENY GROUP^{1*}

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An update of the Angiosperm Phylogeny Group (APG) classification of the orders and families of angiosperms is presented. Several new orders are recognized: Boraginales, Dilleniales, Icaciniales, Metteniusiales and Vahliales. This brings the total number of orders and families recognized in the APG system to 64 and 416, respectively. We propose two additional informal major clades, superrosids and superasterids, that each comprise the additional orders that are included in the larger clades dominated by the rosids and asterids. Families that made up potentially monofamilial orders, Dasypogonaceae and Sabiaceae, are instead referred to Arecales and Proteales, respectively. Two parasitic families formerly of uncertain positions are now placed: Cynomoriaceae in Saxifragales and Apodanthaceae in Cucurbitales. Although there is evidence that some families recognized in APG III are not monophyletic, we make no changes in Dioscoreales and Santalales relative to APG III and leave some genera in Lamiales unplaced (e.g. *Peltanthera*). These changes in familial circumscription and recognition have all resulted from new results published since APG III, except for some changes simply due to nomenclatural issues, which include substituting Asphodelaceae for Xanthorrhoeaceae (Asparagales) and Francoaceae for Melianthaceae (Geraniales); however, in Francoaceae we also include Bersamaceae, Ledocarpaceae, Rhynchothecaceae and Vivianiaceae. Other changes to family limits are not drastic or numerous and are mostly focused on some members of the lamiids, especially the former Icacinaceae that have long been problematic with several genera moved to the formerly monogeneric Metteniusaceae, but minor changes in circumscription include Aristolochiaceae (now including Lactoridaceae and Hydnoraceae; Aristolochiales), Maundiaceae (removed from Juncaginaceae; Alismatales), Restionaceae (now re-including Anarthriaceae and Centrolepidaceae; Poales), Buxaceae (now including Haptanthaceae; Buxales), Peraceae (split from Euphorbiaceae; Malpighiales), recognition of Petenaeaceae (Huerteales), Kewaceae, Limeaceae, Macarthuraceae and Microteaceae (all Caryophyllales), Petiveriaceae split from Phytolaccaceae (Caryophyllales), changes to the generic composition of Ixonanthaceae and Irvingiaceae (with transfer of *Allantosperrum* from the former to the latter; Malpighiales), transfer of *Pakaraimaea* (formerly Dipterocarpaceae) to Cistaceae (Malvales), transfer of *Borthwickia*, *Forchhammeria*, *Stixis* and *Tirania* (formerly all Capparaceae) to Resedaceae (Brassicales), Nyssaceae split from Cornaceae (Cornales), *Pteleocarpa* moved to Gelsemiaceae (Gentianales), changes to the generic composition of Gesneriaceae (*Sanango* moved from Loganiaceae) and Orobanchaceae (now including Lindenbergiaceae and

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Rehmanniaceae) and recognition of Mazaceae distinct from Phrymaceae (all Lamiales). © 2016 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2016, **181**, 1–20

ADDITIONAL KEYWORDS: Apodanthaceae – Aristolochiaceae – Boraginales – Cistaceae – Cynomoriaceae – Dasyogonaceae – Dilleniales – Francoaceae – Gesneriaceae – Icacinales – Metteniusales – Orobanchaceae – Phrymaceae – Phytolaccaceae – Resedaceae – Restionaceae – Sabiaceae – Santalales – Vahliales.

HISTORICAL INTRODUCTION

In 1998, the first Angiosperm Phylogeny Group (APG) classification of the orders and families of flowering plants (which we will term APG I; APG, 1998) was published, and this classification initiated a new approach to this long tradition. APG I was not written by one or two authoritative individuals; rather the APG process tried to produce a consensus classification that reflected results and opinions of experts in many groups of flowering plants. The initial focus was to produce a classification of families in orders, without too much emphasis on the issue of family delimitation; in 1998, few families had been appropriately studied, and so such issues had limited consideration in APG I. Exceptions were families, such as Saxifragaceae (Morgan & Soltis, 1993), Geraniaceae (Price & Palmer, 1993), Liliaceae (Chase *et al.*, 1995), Onagraceae (Conti, Fischbach & Sytsma, 1993) and Ericaceae (Judd & Kron, 1993; Kron & Chase, 1993), that had been the focus of early molecular studies, some of them due to their suspected polyphyletic nature (e.g. Saxifragaceae *sensu* Cronquist, 1981). Because the rule of priority does not apply at the level of order, the biggest issue in APG I was standardization of names being applied to orders so that researchers (many of them using molecular techniques) studying similar sets of families were not using different names. Prevention of chaos was the objective, and consensus was relatively easily reached. The summary consensus tree (fig. 1, p. 535) provided in APG I was highly unresolved, an indication of the preliminary nature of what was known at that time about higher-level (interordinal) relationships, even though the composition of what were then considered orders was reasonably clear.

The general scheme of the arrangement of major groups was also clear: a grade of isolated taxa (the ANA grade, or ANITA grade as it was then called) leading to the major radiation of angiosperms, a clade of all monocots, a clade of magnoliid families and a large eudicot (tricolpate) clade composed of several small clades and two major groups, rosids and asterids, each composed of two major subclades.

As the general framework of angiosperm relationships became clearer, the focus started to shift toward issues of family delimitation, with an emphasis on those that most angiosperm taxonomists had a

sense might be problematic, such as Dioscoreaceae (Caddick *et al.*, 2002), Flacourtiaceae (Chase *et al.*, 2002), Lamiaceae/Verbenaceae (Wagstaff & Olmstead, 1997), Loganiaceae (Backlund, Oxelman & Bremer, 2000), Malvaceae (Judd & Manchester, 1997; Bayer *et al.*, 1999), Rutaceae (Chase, Morton & Kalunki, 1999) and others. These early studies of putatively problematic families resulted in mostly clear-cut solutions, especially if one followed the principles of Backlund & Bremer (1998; Vences *et al.*, 2013 presented a zoological perspective on these same issues). Again, gaining a consensus was relatively straightforward, and APG II (2003) tried to make this easier by offering APG users optional circumscriptions, narrower and broader (a 'bracketed' system), permitting any permutation thereof and still allowing authors to claim that they were 'following APG'. Delimitation of families was clearly becoming a major issue, and the use of the bracketed system was, in addition to an attempt to maintain a broad consensus of support, focused much more on family delimitation and the issue of lumping versus splitting.

In response to negative reactions received by the compilers on the use of the bracketed system, this usage was abandoned in APG III (2009). In most, but not all, cases the broader circumscriptions implied by the bracketing were accepted. As reviewed by Wearn *et al.* (2013) and Christenhusz *et al.* (2015), this lumping approach was made in an effort to simplify the parts of a classification that users emphasize, principally orders and families, an approach that has generally received support. An additional effort to assess support from both taxonomists and users of classification for broader versus narrower circumscriptions was made by conducting an online survey in August 2014 (Christenhusz *et al.*, 2015), with the realization that any survey may have biases due to the way questions are phrased.

REVIEW

Higher-level classification of angiosperms has received continuing attention since APG III (2009) and enough progress has been made that an update to the APG classification is warranted. Several important studies have been published since 2009

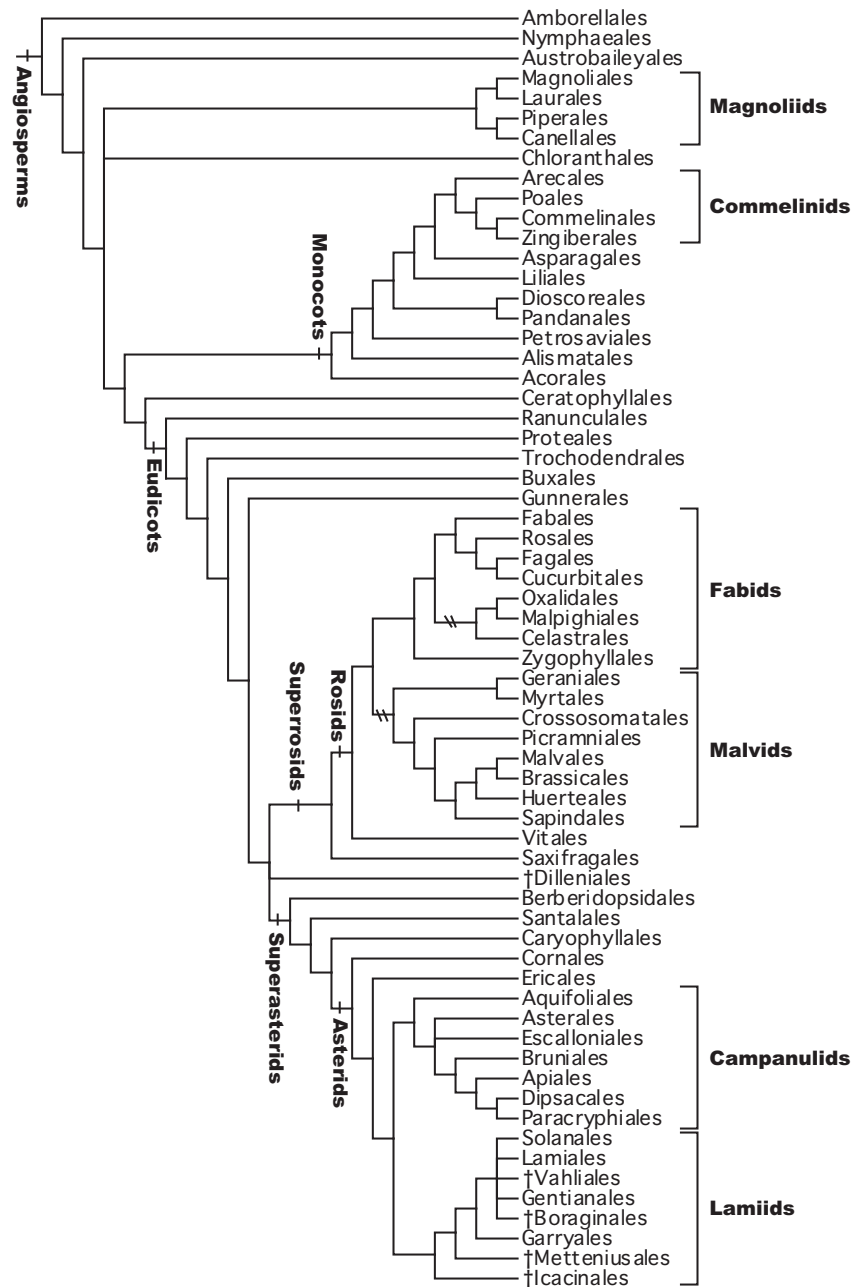


Figure 1. Interrelationships of the APG IV orders and some families supported by jackknife/bootstrap percentages >50 or Bayesian posterior probabilities >0.95 in large-scale analyses of angiosperms. See text for literature supporting these relationships. The alternative placements representing incongruence between nuclear/mitochondrial and plastid results for the Celastrales/Oxalidales/Malpighiales (COM) clade are indicated by slash marks (\\). †Orders newly recognized in APG.

(APG III), particularly those of Soltis *et al.* (2011), Ruhfel *et al.* (2014) and Stull *et al.* (2015). Soltis *et al.* (2011) used 17 genes from all three genomes for 640 angiosperm taxa, whereas Ruhfel *et al.* (2014) used 78 protein-coding plastid genes for 360 green plant taxa (including green algae). Both analyses reached similar general conclusions for the angiosperms. Stull *et al.* (2015) concentrated on the lamiids, but this was the clade in which the greatest uncertainty existed, particularly with the former Icacinaceae, which had been known to be polyphyletic (Savolainen *et al.*, 2000).

Researchers have speculated about what analyses of low-copy nuclear genes would reveal about plant relationships and whether these relationships would be different from those portrayed so far by plastid, mitochondrial and nuclear ribosomal genes. Nuclear data, particularly low-copy genes, have so far been poorly represented in broader phylogenetic studies of the angiosperms. Morton (2011) surveyed xanthine dehydrogenase (*Xdh*) for 247 genera of seed plants and obtained results generally congruent with those of previous studies, although the branching order within some larger clades was different from other

studies. Zeng *et al.* (2014) and Wickett *et al.* (2014) both analysed low-copy nuclear genes (59 and 852 genes, respectively), but relatively few angiosperms (60 and 37, respectively, the latter focused on all green plants), and reached similar conclusions about relationships to those found in the majority of earlier studies.

Although the results using low-copy nuclear genes may not substantially alter our ideas of the major framework of relationships within the angiosperms, there is at least one consistent and significant difference. Celastrales, Oxalidales and Malpighiales (the COM clade), in general found in the fabid clade of rosids (rosid I) based on the mostly plastid DNA results published up to 2011, are instead members of the malvid clade (rosid II) in trees inferred from low-copy nuclear and mitochondrial genes. This is consistent with the nuclear results of Morton (2011), Zeng *et al.* (2014) and Wickett *et al.* (2014) and mitochondrial results of Zhu *et al.* (2007) and Qiu *et al.* (2010). Sun *et al.* (2015) reviewed the history of these incongruent results and added additional studies of mitochondrial and nuclear genes. It is possible that some sort of horizontal transfer of plastid DNA, perhaps via ancient hybridization, produced this incongruence (Sun *et al.*, 2015). We have indicated this incongruence in Figure 1. It is not yet clear if this incongruence extends to Zygophyllaceae, which fell as sister to the rest of the fabid clade (including the COM clade) in plastid analyses in Sun *et al.* (2015).

In this update of APG, there are some changes from APG III as a result of placements of some genera that required erection of new families, and we recognize several new orders as a result of studies incorporating many genes/whole plastid genomes (Soltis *et al.*, 2011; Ruhfel *et al.*, 2014; Stull *et al.*, 2015), for example Boraginales, Dilleniales, Icaciniales and Metteniusales (see below). We deviate here from previous APG papers in placing the families in the linear order of Haston *et al.* (2009; LAPG) and provide comments on changes and other issues in the text below, thus keeping the linear sequence of orders and families intact. For a formal, higher-level classification of plants, see Cantino *et al.* (2007) and Chase & Reveal (2009), which can still be applied to this version of APG. Recently, linear orders and revised classifications have been published for ferns and lycopods (Smith *et al.*, 2006; Christenhusz & Chase, 2014) and gymnosperms (Christenhusz *et al.*, 2011), which provide companion classifications for the remainder of the vascular plant flora.

A NOTE ON FAMILY NAMES

Alternative names for eight flowering plant families have been extensively discussed (reviewed by McNeil

& Brummitt, 2003) and some authors strictly prefer the traditional versions (e.g. Compositae vs. Asteraceae). At the Royal Botanic Gardens, Kew, for example, Compositae and Leguminosae are formally endorsed, whereas the reverse is true for Apiaceae (not Umbelliferae), Areaceae (not Palmae), Brassicaceae (not Cruciferae), Clusiaceae (not Guttiferae), Lamiaceae (not Labiatae) and Poaceae (not Gramineae). These alternative names are considered as not based on a generic name, and they are attached to particular genera by the means of a special provision in the International Code of Nomenclature for algae, fungi and plants (McNeill *et al.*, 2012; Art. 18.5). We list these alternative names here (in parentheses) for the first time because they are of equal status in the Code, continue to receive wide use in the literature and are preferred by many working on the groups concerned; see Mabberley (2008: xi–xii) for further discussion.

The suprageneric names appearing in Martinov (1820) have been subject to extensive debate, and a proposal to treat all names as not validly published in that book has been made recently (Sennikov *et al.*, 2015). If this proposal is accepted, the authorship and dates of such names will be changed, affecting at least the name Acoraceae (all other Martinov names are conserved, and their place of publication can only be changed by the means of proposals to amend entries of conserved names; Art. 14.15). Additionally, several familial names are credited to Van Tieghem, although they appeared not in Van Tieghem's work but in reviews of his articles published in *Just's Botanischer Jahresbericht*. Because of controversies connected to acceptance and authorship of such publications, they have also been proposed to be treated as inappropriate for valid publication (Sennikov *et al.*, 2015). If this proposal is accepted, the relevant familial names should be credited to later authors who accepted Van Tieghem's names and fulfilled the conditions for their valid publication.

Two entries of conserved familial names, i.e. Actinidiaceae and Eucommiaceae, were found (Reveal, 2010) to have been published earlier than recorded in the list of conserved names. The name Actinidiaceae was also published with a different authorship (Actinidiaceae Engl. & Gilg, not Gilg & Werderm. as in Wiersema *et al.*, 2015). More additions affecting conserved familial names are from Batsch (1794), which is to be considered as the place for valid publication of Melanthiaceae and Primulaceae, both accepted and conserved with the authorship of 'Batsch ex Borkh. 1797' but validly published in 1794 by a reference in the introduction of that book to the corresponding descriptions in Batsch (1786). These entries can be corrected by means of special proposals to avoid current discrepancies in the databases.

Another issue is standardization of the authorship of conserved familial names, which is regulated by Art. 46 but not covered by Art. 14.15. At present, entries of conserved familial names have inconsistent statements of authorship when a taxon was described by one author but that name was validly published later by another author. In the list of conserved familial names, such names are attributed either to original authors (e.g. Theaceae Mirb.), presumed validating authors (e.g. Asteraceae Martinov) or both authors connected with 'ex' (e.g. Ancistrocladaceae Planch. ex Walp.). We follow the authorship as attributed by Wiersema *et al.* (2015), in anticipation that this will be standardized in the next edition of the International Code of Nomenclature for algae, fungi and plants.

ANGIOSPERM CLASSIFICATION: AN UPDATE

By way of general comment on our philosophy of adopting changes to the APG classification, we have followed here a conservative approach of accepting only changes due to new phylogenetic studies. Without new results demonstrating a well-supported need for change, we have maintained the APG III classification. There are at least two cases in which the APG IV classification does not reflect the results of published studies, Dioscoreales and Santalales, and in these cases there are either conflicting results among the published studies or insufficient support for evaluating what possible altered familial circumscriptions might be possible or preferable, respectively. In these cases, we await future resolution before altering APG III.

We place Chloranthales on a polytomy with the magnoliid and eudicots/monocots/Ceratophyllaceae clades because several recent studies (e.g. Wickett *et al.*, 2014; Zeng *et al.*, 2014) have not placed them with the magnoliids, as was indicated in APG III (2009). Support for Chloranthales as sister to the magnoliids was also low (bootstrap support 61–69%) in Ruhfel *et al.* (2014).

There are no alterations among the ANA grade or the magnoliid families and orders, except for inclusion of Hydnoraceae and Lactoridaceae in Aristolochiaceae due to paraphyly of the last (Massoni, Forest & Sauquet, 2014). It has been known that *Lactoris* Phil. was embedded in Aristolochiaceae (Qiu *et al.*, 2005; Wanke *et al.*, 2007), but this placement was considered by some to be an artefact due to a long-branch problem. No study has yet supported this hypothesis, so it seems appropriate to make this change in circumscription. Hydnoraceae have also recently been shown to be nested in Aristolochiaceae (Naumann *et al.*, 2013; Massoni *et al.*, 2014).

MONOCOTS

Since APG III (2009), little alteration of our understanding has been achieved among monocots, but several relatively minor changes are proposed here. First, we place Dasyopogonaceae in Arecales on the basis of Barrett *et al.* (2016), in which they received moderate to high support as sister to Arecaceae. Previous studies with much sparser taxonomic sampling did not strongly support this relationship (Givnish *et al.*, 2010; Ruhfel *et al.*, 2014), even though they placed Dasyopogonaceae as sister to Arecaceae.

In Alismatales, we recognize here Maundiaceae because the single genus, *Maundia* F.Muell., has a non-exclusive relationship with Juncaginaceae (Von Mering & Kadereit, 2010; Les & Tippery, 2013), in which it was previously placed (APG III, 2009). Erection of another monogeneric family in this order in which the alismatid families (not including Araceae) are already numerous and small might seem unwarranted, but the online survey (Christenhusz *et al.*, 2015) found little support for the alternative, namely expansion of Juncaginaceae to include Potamogetonaceae, Zosteraceae, Cymodoceaceae, Ruppiaceae, Posidoniaceae and Maundiaceae. The simplest solution to the problem posed by *Maundia* is the addition of another family to Alismatales.

In Dioscoreales, we maintain the circumscription of the families provided in APG III (2009), but we admit that several studies (Merckx *et al.*, 2009; Merckx, Huysmans & Smets, 2010; Merckx & Smets, 2014) have indicated that *Thismia* Griff. and its relatives and *Burmannia* L. and related genera do not form a clade. Those authors recommended that Thismiaceae, Burmanniaceae and Taccaceae be reinstated to reflect their estimates of relationships for these taxa. Caddick *et al.* (2002), upon which the APG III circumscriptions were based, had earlier found good support for the relationships as recognized in APG (2003, 2009), and Hertweck *et al.* (2015) reaffirmed this relationship in their analysis. We hope that future studies will resolve the incongruence reported in the literature for this order, and we will make any necessary changes to familial circumscription at that time.

To make the name Asphodelaceae available for use when this family in the strict sense is combined with Xanthorrhoeaceae, conservation of Asphodelaceae was proposed (Klopper, Smith & van Wyk, 2013) and approved by the Nomenclature Committee for Vascular Plants (Applequist, 2014). This action will restore the priority of Asphodelaceae over Xanthorrhoeaceae as soon as conservation is approved by the General Committee and then the Nomenclature Section of the XIX International Botanical Congress in Shenzhen, 2017.

In Poales, there have been conflicting estimates of relationships among Anarthriaceae, Centrolepidaceae and Restionaceae (reviewed by Briggs, Marchant & Perkins, 2014). To stabilize the taxonomy of this order, we enlarge Restionaceae to re-include Anarthriaceae and Centrolepidaceae so that, regardless of the outcomes of future studies, the family name will remain the same.

EUDICOTS

The classification of Ranunculales and Trochodendrales remains the same as in APG III (2009). We move Sabiaceae into Proteales on the basis of strong support found by Sun *et al.* (2016). Bootstrap support for this placement was not strong in earlier studies (Ruhfel *et al.*, 2014, 63%; Soltis *et al.*, 2011, 59%). In Buxales, we broaden the limits of Buxaceae to include Haptanthaceae (Buxaceae already included Didymelaceae in APG III, 2009). Shipunov & Shipunova (2011) found that *Haptanthus* Goldberg & C. Nelson was embedded in Buxaceae, possibly sister to *Buxus* L., so its inclusion in that family is indicated.

CORE EUDICOTS (NEITHER ROSIDS NOR ASTERIDS)

In this set of clades, only two changes are made, neither affecting familial circumscriptions. On the basis of results in Soltis *et al.* (2011) and Ruhfel *et al.* (2014), recognition of monofamilial Dilleniales is warranted. However, in the former they are well supported as sister to the large superasterid clade, whereas in the latter they are well supported as sister to the large superrosid clade. Due to this conflict, here we do not include them in either larger clade (Fig. 1). In the linear order presented here, the position of Dilleniales does not exactly accord with their phylogenetic position among the eudicots, but this set of core eudicots is paraphyletic to rosids plus asterids, thus making the sequence of the linear order arbitrary as long as they are excluded from these two larger groups.

The other change is the position of Cynomoriaceae, for which the evidence has been weak and contradictory in published studies (reviewed in APG III, 2009; and Qiu *et al.*, 2010). Recently, S. Bellot & S. Renner (unpubl. data) showed that Cynomoriaceae are well supported as members of Saxifragales, although their exact position in that order is not yet clear. Vitales, on the basis of Soltis *et al.* (2011) and Ruhfel *et al.* (2014), are again considered in the rosid clade. Both of these analyses also supported the position of Saxifra-

gales as sister to the rosid clade, and this more inclusive clade, i.e. Saxifragales + rosids, is here referred to as the superrosids (following Soltis *et al.*, 2011).

ROSIDS

Few changes to family circumscription have been made among rosids relative to APG III. The endoparasitic Apodanthaceae are now placed in Cucurbitales (Filipowicz & Renner, 2010). The sequence of families in Malpighiales diverts from that of LAPG (Haston *et al.*, 2009), because we now have a much better understanding of interfamilial relationships in that order (Soltis *et al.*, 2011; Xi *et al.*, 2012; Endress, Davis & Matthews, 2013). Also in Malpighiales, there is one newly recognized family, Peraceae, the potential need for which was discussed in APG III (2009), due to the position of Rafflesiaceae as sister to the rest of Euphorbiaceae, minus *Pera* Mutis and relatives (Davis *et al.*, 2007). This family is now accepted here as Peraceae (Endress *et al.*, 2013). In addition, two changes to familial circumscription are needed. *Allantospermum* Forman has historically alternated between Ixonanthaceae and Irvingiaceae, but most recently has been considered in Ixonanthaceae (Byng, 2014; Kubitzki, 2014). Recently, J.W. Byng (unpubl. data) has shown *Allantospermum* to be sister to the rest of Irvingiaceae rather than Ixonanthaceae.

In Huerteales, Petenaeaceae (Christenhusz *et al.*, 2010) are added as a new family. In Geraniales, Francoaceae must be substituted for Melianthaceae, due to nomenclatural priority, and we include Vivianiaceae in Francoaceae on the basis of Sytsma, Spalink & Berger (2014). Exact relationships among Francoaceae *s.s.* (*Francoa* Cav., *Greyia* Hook. & Harv. and *Tetilla* DC.), Melianthaceae (*Bersama* Fresen. and *Melianthus* L.) and Ledocarpaceae (for which Vivianiaceae is a later synonym, contrary to its use in APG III; *Balbisia* Cav., *Rhynchotheca* Ruiz & Pav., *Viviania* Cav. and *Wendtia* Meyen) are uncertain, with contradictory relationships in recent papers (Palazzesi *et al.*, 2012; Sytsma *et al.*, 2014). We opt to stabilize APG by recognizing the broader circumscription so that no matter which relationship proves to be the most robust the family name recognized does not change.

Alteration of family limits for Sapindaceae (Sapindales) was proposed by Buerki *et al.* (2010) to preserve the long-recognized temperate families, Aceraceae and Hippocastanaceae. To accomplish this required recognition of a new family, Xanthocerataceae, which Buerki *et al.* (2010) published as Xanthoceraceae. Relationships in Sapindaceae have been known since Harrington *et al.* (2005) and, given our statement of philosophy (above), we do not alter circumscription of

Sapindaceae because no new phylogenetic information has become available that addresses this issue of altered family limits. Contrary to the viewpoint of Buerki *et al.* (2010), Sapindaceae *s.l.* are easily diagnosed morphologically (Judd *et al.*, 2016).

In Malvales, circumscription of Cistaceae, Dipterocarpaceae and Sarcolaenaceae requires a minor adjustment, but the potential for further change should be noted for this set of families. In an analysis based only on *rbcL* (Ducouso *et al.*, 2004), *Pakaraimaea* Maguire & P.S.Ashton (placed in its own subfamily of Dipterocarpaceae) is sister (88% bootstrap support) to Cistaceae, and *Monotes* A.DC. and *Pseudomonotes* Maguire & P.S.Ashton (subfamily Monotoideae of Dipterocarpaceae) are weakly supported (62%) as sister to *Sarcolaena* Thouars plus *Leptolaena* Thouars (Sarcolaenaceae; 97%) and Dipterocarpoideae (84%). Here, we propose to include *Pakaraimaea* in an expanded Cistaceae. Sarcolaenaceae might also need to be included in Dipterocarpaceae; they share many morphological, anatomical and chemical characters and in Ducouso *et al.* (2004) are sister to Dipterocarpoideae to the exclusion of Monotoideae of Dipterocarpaceae. We refrain from making further changes in this group of families until a more comprehensive study (in terms of data and taxa) has been concluded. Perhaps it would be better to combine all of these into a single family, given that the limits of neither Cistaceae nor Dipterocarpaceae would be consistent with past circumscriptions. The continued use of Dipterocarpaceae (currently used for the economically most significant group) could be achieved by superconservation of the name Dipterocarpaceae, as Cistaceae currently has nomenclatural priority and is a conserved name.

In Brassicales, the generic composition of Cleomaceae and Capparaceae has continued to be diminished by studies finding that the genera belong elsewhere, with *Koerberlinia* Zucc. (Koerberliniaceae), *Pentadiplandra* Baill. (Pentadiplandraceae) and *Setchellanthus* Brandege (Setchellanthaceae) having already been placed in their own families in APG III (2009). Su *et al.* (2012) showed that *Borthwickia* W.W.Sm., *Forchhammeria* Liebm., *Stixis* Lour. and *Tirania* Pierre are collectively paraphyletic to Resedaceae and described Borthwickiaceae, whereas a separate Stixidaceae (as ‘Stixaceae’) had been previously proposed by Doweld & Reveal (2008). Here we include Borthwickiaceae and Stixidaceae in an expanded Resedaceae, members of which share some morphological characters (e.g. flowers with many stamens), although some share more characters with Gyrostemonaceae than with core Resedaceae. This prevents unnecessary inflation of family names. *Cleome* L. has been shown to be grossly paraphyletic to the other previously recognized genera of Cleo-

maceae (Feodorova *et al.*, 2010; Patchell, Roalson & Hall, 2014), leaving perhaps only a single genus in that family. Two genera of Capparaceae (*Keithia* Spreng. and *Poilanedora* Gagnep.) are a poor morphological fit with their pentamerous flowers. They most certainly belong elsewhere, and we include them at the end as unplaced genera.

SUPERASTERIDS

In Santalales, we confront a difficult question about how best to represent the phylogenetic results obtained by Malécot & Nickrent (2008) and Der & Nickrent (2008), as summarized in Nickrent *et al.* (2010), Su *et al.* (2015) and J.W. Byng (unpubl. data). APG III (2009) reported the results of the two phylogenetic papers (Der & Nickrent, 2008; Malécot & Nickrent, 2008; as summarized in Nickrent *et al.*, 2010), but refrained from making any changes to the classification. Malécot & Nickrent (2008; as summarized in Nickrent *et al.*, 2010) split ‘Olacaceae’ into eight families: Aptandraceae, Coulaceae, Erythralaceae, Octoknemaceae, Olacaceae *s.s.*, Schoepfiaceae, Strombosiaceae and Ximeniaceae. Additionally, Der & Nickrent (2008; as summarized in Nickrent *et al.*, 2010) proposed recognition of seven families in the group recognized as Santalaceae in APG III (2009): Amphorogynaceae, Cervantesiaceae, Comandraceae, Nanodeaceae, Santalaceae *s.s.*, Thesiaceae and Viscaceae. However, strong support for these relationships is lacking, particularly in ‘Olacaceae’. We therefore here opt to maintain the APG III (2009) status quo in Santalales until additional data can be brought to bear on this problematic clade. Furthermore, a recent study (J.W. Byng, unpubl. data) places Balanophoraceae *s.l.* as a monophyletic group in ‘Santalaceae’, in contrast to Su *et al.* (2015), where Balanophoraceae were divided into two clades. We acknowledge that our use of ‘Olacaceae’ and ‘Santalaceae’ does not refer to monophyletic groups and thus maintain the families as they were in APG III, but in the linear sequence we move Balanophoraceae next to ‘Santalaceae’, in which they appear to be embedded.

Familial delimitation in Caryophyllales continues to generate taxonomic conundrums focused on three problematic sets of families, although the nature of these problems is different in each case (reviewed by Hernández-Ledesma *et al.*, 2015). The first centres on Phytolaccaceae and their relationship to Nyctaginaceae, which has long posed problems. Genera previously associated with Phytolaccaceae but now with different placements have been cleaved off into their own families. In APG III (2009), these included Barbeuiaceae, Gisekiaceae, Lophiocarpaceae and Stegnospermataceae. Most recent studies (Brockington

et al., 2009, 2011; Bissinger *et al.*, 2014) have found that subfamily Rivinoideae of Phytolaccaeae are sister to Nyctaginaceae, and we propose here to accept them at the family level (Petiveriaceae, including Rivinaceae) to maintain the previous use of family names in this larger clade. The priority of Petiveriaceae C.Agardh 1824 over Rivinaceae C.Agardh 1824 was established by Meisner (1841), who combined the tribes Rivineae Dumort. and Petiverieae Bartl. under Petiveriaceae (Art. 11.5).

The second problematic area in Caryophyllales involves Cactaceae and their relationship to the former broadly defined Portulacaceae, the latter shown to be paraphyletic to Cactaceae. In APG III (2009), Anacampserotaceae, Montiaceae and Talinaceae were accepted, leaving Portulacaceae with only *Portulaca* L. To reduce the number of monogeneric families in this clade, Cactaceae could be expanded to include at least Anacampserotaceae and Portulacaceae, but this was highly unpopular in the online survey (Christenhusz *et al.*, 2015).

The third problematic family in Caryophyllales is Molluginaceae, which in their broadest sense are polyphyletic. In APG III (2009), Limeaceae and Lophiocarpaceae were recognized as distinct, and here we add three additional families (Schäferhoff, Müller & Borsch, 2009; Christenhusz *et al.*, 2014): Kewaceae (with the genus *Kewa* Christenh., which has been segregated from *Hypertelis* E.Mey. ex Fenzl, the type species *H. spergulacea* E.Mey. ex Fenzl remaining in Molluginaceae), Microteaceae and Macarthuriaceae. These all have distant relationships to each other and to the other genera to which they were thought to be related (Brockington *et al.*, 2009, 2011; Schäferhoff *et al.*, 2009; Christin *et al.*, 2011; Christenhusz *et al.*, 2014). Further sampling of Molluginaceae is required (Borsch *et al.*, 2015). Finally, *Agdestis* Moc. & Sessé ex DC. appears to be sister to *Sarcobatus* Nees (Sarcobataceae; Brockington *et al.*, 2011). Agdestidaceae may require recognition as a segregate family (Hernández-Ledesma *et al.*, 2015), but more data are needed to support this placement or to confirm the placement in Sarcobataceae.

ASTERIDS

In Ericales, Mitrastemonaceae are placed at the end of the linear sequence for the order because their exact position in that order is not yet certain. In Barkman *et al.* (2004), they were sister to Ericaceae. Hardy & Cook (2012) recovered Mitrastemonaceae as sister to most of the order except the Marcgraviaceae–Tetrameristaceae–Balsaminaceae clade.

Further studies in Cornales have also resulted in a change in family circumscriptions. Nyssaceae,

included in Cornaceae in APG III (2009), have been shown by molecular studies (Xiang *et al.*, 2011) to include Campthothaceae, Davidiaceae and Mastixiaceae, which are sister to a clade comprising Hydrostachyaceae, Loasaceae and Hydrangeaceae. They are therefore widely separated from Cornaceae, and thus Nyssaceae need to be accepted.

In Gentianales, the limits of Gelsemiaceae have been altered here by the inclusion of *Pteleocarpa* Oliv., which had previously been considered problematic; it had been included by various authors in Boraginaceae, Cardiopteridaceae and Icacinaceae. It was always an odd element in any family and was thus sometimes placed in its own family, Pteleocarpaceae (Brummitt, 2011). Refulio-Rodríguez & Olmstead (2014) and Struwe *et al.* (2014) demonstrated that it falls as sister to Gelsemiaceae, and we expand that family to include it, in agreement with their findings.

Ongoing studies in Lamiales have resulted in several unstudied genera being placed, for example *Sanango* Bunting & Duke (previously considered Loganiaceae) as sister to Gesneriaceae (Perret *et al.*, 2012), *Peltanthera* Benth. as sister to Gesneriaceae plus *Sanango* and Calceolariaceae, and *Rehmannia* Libosch. ex Fisch. & C.A.Mey. as sister to Orobanchaceae (not in Scrophulariaceae, as previously thought; Xia, Wang & Smith, 2009; Refulio-Rodríguez & Olmstead, 2014). The history of investigating relationships in Lamiales has some similarities to work on the monocot order Asparagales, in which the old family limits were completely altered by the results of phylogenetic studies. Because no previously suggested relationships could be relied upon in Asparagales, narrow family limits were initially accepted (APG, 1998), but as molecular studies progressed and more taxa were sampled with more molecular data (e.g. Fay *et al.*, 2000; Pires *et al.*, 2006), relationships became clear and larger family limits could be applied (APG II, 2003; APG III, 2009). These newly circumscribed families were heterogeneous, but the wider limits as applied in APG III (2009) have been generally well accepted (Wearn *et al.*, 2013). In Lamiales, the old delimitations of Acanthaceae, Lamiaceae, Scrophulariaceae, etc., were contradicted by molecular studies, and although we still use many of these names, their circumscriptions are now vastly different. In addition, we have seen the proliferation of small families (13), just as in Asparagales (APG, 1998, had 29 families in Asparagales vs. 12 here). A similar condensation in the number of families recognized in Lamiales may be needed, for the reasons discussed by Christenhusz *et al.* (2015). However, for now, we propose the following minor changes: (1) enlarging Gesneriaceae to include *Sanango*, (2) enlarging Orobanchaceae to include Rehmanniaceae and (3)

acceptance of Mazaceae as separate from Phrymaceae, which with Paulowniaceae form a grade leading to Orobanchaceae (Albach *et al.*, 2009; Xia *et al.*, 2009; Schäferhoff *et al.*, 2010; Fischer, Schäferhoff & Müller, 2012). Tentatively, we maintain Calceolariaceae and *Peltanthera* as distinct from Gesneriaceae, although more study of these closely related taxa is needed. Eventually either *Peltanthera* will need to be recognized in its own family or *Peltanthera* and Calceolariaceae could be included in an expanded Gesneriaceae. A formal infrafamilial classification of Gesneriaceae would be needed if an expanded circumscription is adopted, but the position of many genera in Lamiales is still uncertain (e.g. *Wightia* Wall.; Zhou *et al.*, 2014) so further familial realignment is likely in the future.

Icacinaceae in their modern, pre-molecular circumscription comprised *c.* 54 genera and 400 species, but they were known to be non-monophyletic from the time of Savolainen *et al.* (2000). Kårehed (2001) showed the scope of the problem in greater detail, but the low levels of *rbcL* gene sequence divergence among early-diverging lamiids precluded circumscription of well-supported taxa. Using three plastid genes (*ndhF*, *matK* and *rbcL*), Byng *et al.* (2014) fared somewhat better, but still failed to find a set of well-supported relationships that could serve as the basis of a new classification for these genera/clades. Stull *et al.* (2015) sequenced 50 complete plastid genomes and, combining these with previous data, proposed a reduction in the size of Icacinaceae, expansion of Metteniusaceae and recognition of two new-to-APG orders, Icacinales (with Icacinaceae and monogeneric Oncothecaceae) and Metteniusiales (with Metteniusiaceae including Emmotaceae and the *Apodytes* E.Mey. ex Arn. clade). Metteniusaceae here comprise 11 genera, expanded from one in APG III (2009), whereas Icacinaceae are reduced to 25 genera (Byng, 2014; Byng *et al.*, 2014; Stull *et al.*, 2015). Of other families previously segregated from Icacinaceae *s.l.* by Kårehed (2001), Stemonuraceae and Cardiopteridaceae are retained in Aquifoliales and Pennantiaceae in Apiales, respectively. This brings resolution and a well-supported conclusion to the investigation of the limits of orders and families in this part of the lamiids.

Given the ongoing uncertainty over the exact placement of Boraginaceae *s.l.*, we recognize an order, Boraginales, to accommodate the family. Refulio-Rodríguez & Olmstead (2014) found Boraginales as sister to Lamiales, but only in the Bayesian analysis was this placement well supported. Stull *et al.* (2015) placed Boraginales as sister to Gentianales, but again only in their Bayesian analysis was this well supported. Here we consider Boraginales to comprise a single family, Boraginaceae *s.l.*, including Boraginaceae *s.s.*, Codonaceae, Cordiaceae, Ehreti-

aceae, Lennoaceae, Wellsteddiaceae, Heliotropiaceae, Hydrophyllaceae and the *Nama* L. clade (often referred to as 'Namaceae', a name that has not been formally published), which have been proposed by several authors (Weigend & Hilger, 2010; as reviewed by Stevens, 2001). The need to dismember a group shown in all analyses to be monophyletic was questioned and strongly rejected as an option by the online survey (Christenhusz *et al.*, 2015).

Finally, here we treat Vahliaceae, unplaced to order in APG III (2009), as another monofamilial order, Vahliales. *Vahlia* Thunb. was sister to Solanales in Refulio-Rodríguez & Olmstead (2014), but only in the Bayesian analysis was this position well supported. In Stull *et al.* (2015), *Vahlia* was sister to Lamiales but with low support in both Bayesian and parsimony analyses.

Recently the Nomenclature Committee for Vascular Plants (NCVP) has approved the conservation of Viburnaceae (Applequist, 2013), thus proposing it be the correct name for Adoxaceae *sensu* APG. This outcome was contrary to the intention of the original proposal (Reveal, 2008), which aimed to maintain nomenclatural stability. We therefore do not accept this decision of the NCVP in the hope that the General Committee will not approve it in its report to the next botanical congress (cf. Applequist, 2013).

Of the taxa of uncertain position in APG III (2009), we have now placed Apodanthaceae in Cucurbitales (Filipowicz & Renner, 2010), Cynomoriaceae in Saxifragales (see above), *Petenaea* Lundell in Petenaeaceae of Huerteales (Christenhusz *et al.*, 2010) and *Nicobariodendron* Vasudeva Rao & Chakrab. in Celastraceae (Simmons, 2004). We have added several genera of uncertain position to the only remaining genus from APG III (2009), *Gumillea*, hoping that by drawing attention to these, we increase the likelihood that they will be studied further.

Overall, the changes from APG III (2009) to APG IV are minimal. Stability is an important aspect of our approach to this classification, and the APG system has remained remarkably consistent since its inception. Little remains now that requires attention, although reorganizations and changes of familial circumscriptions will continue, particularly in Caryophyllales, Lamiales and Santalales, for which more data are needed to provide a robust picture of generic and familial relationships. The advent of routine whole-plastid genome sequencing and nuclear gene sequencing should remedy this situation, as it has done for the early-diverging lamiids. Of course, new phylogenetic understanding may necessitate description of new families, as were the cases with Kewaceae, Macarthuraceae, Microteaceae and Petenaeaceae, but this appears to be the most likely source of new data that will require future alteration of the APG system.

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SUPPORTING INFORMATION

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

Data S1. Angiosperm phylogeny classification of flowering plants (APG IV) with the families organized alphabetically within orders.

Appendix

Linear classification of flowering plants (APG IV)

*Changed circumscription of a family or families added since APG III (2009).

†Orders added since APG III (2009).

Numbers in square brackets are those of LAPG (Haston *et al.*, 2009).

Amborellales Melikyan *et al.*

1 [1]. Amborellaceae Pichon, *nom. cons.*

Nymphaeales Salisb. ex Bercht. & J.Presl

2 [2]. Hydatellaceae U.Hamann
3 [3]. Cabombaceae Rich. ex A.Rich., *nom. cons.*
4 [4]. Nymphaeaceae Salisb., *nom. cons.*

Austrobaileyales Takht. ex Reveal

5 [5]. Austrobaileyaceae Croizat, *nom. cons.*
6 [6]. Trimeniaceae Gibbs, *nom. cons.*
7 [7]. Schisandraceae Blume, *nom. cons.*

MESANGIOSPERMS

MAGNOLIIDS

Canellales Cronq.

8 [9]. Canellaceae Mart., *nom. cons.*
9 [10]. Winteraceae R.Br. ex Lindl., *nom. cons.*

Piperales Bercht. & J.Presl

10 [11]. Saururaceae Rich. ex T.Lestib., *nom. cons.*
11 [12]. Piperaceae Giseke, *nom. cons.*
12 [15]. *Aristolochiaceae Juss., *nom. cons.* (including Asaraceae Vent., Hydnoraceae C.Agardh, *nom. cons.*, Lactoridaceae Engl., *nom. cons.*)

Magnoliales Juss. ex Bercht. & J.Presl

13 [16]. Myristicaceae R.Br., *nom. cons.*
14 [17]. Magnoliaceae Juss., *nom. cons.*
15 [18]. Degeneriaceae I.W.Bailey & A.C.Sm., *nom. cons.*
16 [19]. Himantandraceae Diels, *nom. cons.*
17 [20]. Eupomatiaceae Orb., *nom. cons.*
18 [21]. Annonaceae Juss., *nom. cons.*

Laurales Juss. ex Bercht. & J.Presl

19 [22]. Calycanthaceae Lindl., *nom. cons.*
20 [23]. Siparunaceae Schodde
21 [24]. Gomortegaceae Reiche, *nom. cons.*
22 [25]. Atherospermataceae R.Br.
23 [26]. Hernandiaceae Blume, *nom. cons.*
24 [27]. Monimiaceae Juss., *nom. cons.*
25 [28]. Lauraceae Juss., *nom. cons.*

INDEPENDENT LINEAGE: UNPLACED TO MORE INCLUSIVE
CLADE

Chloranthales Mart.

26 [8]. Chloranthaceae R.Br. ex Sims, *nom. cons.*

MONOCOTS

Acorales Mart.

27 [29]. Acoraceae Martinov

Alismatales R.Br. ex Bercht. & J.Presl

- 28 [30]. Araceae Juss., *nom. cons.*
 29 [31]. Tofieldiaceae Takht.
 30 [32]. Alismataceae Vent., *nom. cons.*
 31 [33]. Butomaceae Mirb., *nom. cons.*
 32 [34]. Hydrocharitaceae Juss., *nom. cons.*
 33 [35]. Scheuchzeriaceae F.Rudolphi, *nom. cons.*
 34 [36]. Aponogetonaceae Planch., *nom. cons.*
 35 [37]. *Juncaginaceae Rich., *nom. cons.*
 36. *Maundiaceae Nakai
 37 [38]. Zosteraceae Dumort., *nom. cons.*
 38 [39]. Potamogetonaceae Bercht. & J.Presl, *nom. cons.*
 39 [40]. Posidoniaceae Vines, *nom. cons.*
 40 [41]. Ruppiaceae Horan., *nom. cons.*
 41 [42]. Cymodoceaceae Vines, *nom. cons.*

Petrosaviales Takht.

42 [43]. Petrosaviaceae Hutch., *nom. cons.*

Dioscoreales Mart.

- 43 [44]. Nartheciaceae Fr. ex Bjurzon
 44 [45]. 'Burmanniaceae' Blume, *nom. cons.*
 45 [46]. Dioscoreaceae R.Br., *nom. cons.*

Pandanales R.Br. ex Bercht. & J.Presl

- 46 [47]. Triuridaceae Gardner, *nom. cons.*
 47 [48]. Velloziaceae J.Agardh, *nom. cons.*
 48 [49]. Stemonaceae Caruel, *nom. cons.*
 49 [50]. Cyclanthaceae Poit. ex A.Rich., *nom. cons.*
 50 [51]. Pandanaceae R.Br., *nom. cons.*

Liliales Perleb

- 51 [52]. Campynemataceae Dumort.
 52 [60]. Corsiaceae Becc., *nom. cons.*
 53 [53]. Melanthiaceae Batsch ex Borkh., *nom. cons.*
 54 [54]. Petermanniaceae Hutch, *nom. cons.*
 55 [55]. Alstroemeriaceae Dumort., *nom. cons.*
 56 [56]. Colchicaceae DC., *nom. cons.*
 57 [57]. Philesiaceae Dumort., *nom. cons.*
 58 [58]. Ripogonaceae Conran & Clifford
 59 [59]. Smilacaceae Vent., *nom. cons.*
 60 [61]. Liliaceae Juss., *nom. cons.*

Asparagales Link

- 61 [62]. Orchidaceae Juss., *nom. cons.*
 62 [63]. Boryaceae M.W.Chase *et al.*
 63 [64]. Blandfordiaceae R.Dahlgren & Clifford
 64 [65]. Asteliaceae Dumort.
 65 [66]. Lanariaceae H.Huber ex R.Dahlgren
 66 [67]. Hypoxidaceae R.Br., *nom. cons.*
 67 [69]. Doryanthaceae R.Dahlgren & Clifford
 68 [70]. Ixioliriaceae Nakai (as 'Ixiolirionaceae'; spelling corrected)
 69 [68]. Tecophilaeaceae Leyb., *nom. cons.*
 70 [71]. Iridaceae Juss., *nom. cons.*
 71 [72]. Xeronemataceae M.W.Chase *et al.*
 72 [73]. Asphodelaceae Juss., *nom. cons. prop.* (including Xanthorrhoeaceae Dumort., *nom. cons.*)
 73 [74]. Amaryllidaceae J.St.-Hil., *nom. cons.*
 74 [75]. Asparagaceae Juss., *nom. cons.*

Arecales Bromhead

- 75 [90]. Dasypogonaceae Dumort.
 76 [76]. Arecaceae Bercht. & J.Presl, *nom. cons.* (= Palmae Juss., *nom. cons.*)

Commelinales Mirb. ex Bercht. & J.Presl

- 77 [77]. Hanguanaceae Airy Shaw
 78 [78]. Commelinaceae Mirb., *nom. cons.*
 79 [79]. Philydraceae Link, *nom. cons.*
 80 [80]. Pontederiaceae Kunth, *nom. cons.*
 81 [81]. Haemodoraceae R.Br., *nom. cons.*

Zingiberales Griseb.

- 82 [82]. Strelitziaceae Hutch., *nom. cons.*
 83 [83]. Lowiaceae Ridl., *nom. cons.*
 84 [84]. Heliconiaceae Vines
 85 [85]. Musaceae Juss., *nom. cons.*
 86 [86]. Cannaceae Juss., *nom. cons.*
 87 [87]. Marantaceae R.Br., *nom. cons.*
 88 [88]. Costaceae Nakai
 89 [89]. Zingiberaceae Martinov, *nom. cons.*

Poales Small

- 90 [91]. Typhaceae Juss., *nom. cons.*
 91 [92]. Bromeliaceae Juss., *nom. cons.*
 92 [93]. Rapateaceae Dumort., *nom. cons.*
 93 [94]. Xyridaceae C.Agardh, *nom. cons.*
 94 [95]. Eriocaulaceae Martinov, *nom. cons.*
 95 [96]. Mayacaceae Kunth, *nom. cons.*
 96 [97]. Thurniaceae Engl., *nom. cons.*
 97 [98]. Juncaceae Juss., *nom. cons.*
 98 [99]. Cyperaceae Juss., *nom. cons.*

- 99 [102]. *Restionaceae R.Br., *nom. cons.* (including Anarthriaceae D.W.Cutler & Airy Shaw, Centrolepidaceae Endl., *nom. cons.*)
 100 [103]. Flagellariaceae Dumort., *nom. cons.*
 101 [104]. Joinvilleaceae Toml. & A.C.Sm.
 102 [105]. Ecdeiocoleaceae D.W.Cutler & Airy Shaw
 103 [106]. Poaceae Barnhart, *nom. cons.* (= Gramineae Juss., *nom. cons.*)

PROBABLE SISTER OF EUDICOTS

Ceratophyllales Link

- 104 [107]. Ceratophyllaceae Gray, *nom. cons.*

EUDICOTS

Ranunculales Juss. ex Bercht. & J.Presl

- 105 [108]. Eupteleaceae K.Wilh., *nom. cons.*
 106 [109]. Papaveraceae Juss., *nom. cons.*
 107 [110]. Circaeasteraceae Hutch., *nom. cons.*
 108 [111]. Lardizabalaceae R.Br., *nom. cons.*
 109 [112]. Menispermaceae Juss., *nom. cons.*
 110 [113]. Berberidaceae Juss., *nom. cons.*
 111 [114]. Ranunculaceae Juss., *nom. cons.*

Proteales Juss. ex Bercht. & J.Presl

- 112 [115]. Sabiaceae Blume, *nom. cons.*
 113 [116]. Nelumbonaceae A.Rich., *nom. cons.*
 114 [117]. Platanaceae T.Lestib., *nom. cons.*
 115 [118]. Proteaceae Juss., *nom. cons.*

Trochodendrales Takht. ex Cronq.

- 116 [119]. Trochodendraceae Eichler, *nom. cons.*

Buxales Takht. ex Reveal

- 117 [121]. *Buxaceae Dumort., *nom. cons.* (including Haptanthaceae C.Nelson)

CORE EUDICOTS

Gunnerales Takht. ex Reveal

- 118 [122]. Myrothamnaceae Nied., *nom. cons.*
 119 [123]. Gunneraceae Meisn., *nom. cons.*

†Dilleniales DC. ex Bercht. & J.Presl

- 120 [124]. Dilleniaceae Salisb., *nom. cons.*

SUPERROSIDS

Saxifragales Bercht. & J.Presl

- 121 [125]. Peridiscaceae Kuhl., *nom. cons.*
 122 [126]. Paeoniaceae Raf., *nom. cons.*
 123 [127]. Altingiaceae Lindl., *nom. cons.*
 124 [128]. Hamamelidaceae R.Br., *nom. cons.*
 125 [129]. Cercidiphyllaceae Engl., *nom. cons.*
 126 [130]. Daphniphyllaceae Müll.Arg., *nom. cons.*
 127 [131]. Iteaceae J.Agardh, *nom. cons.*
 128 [132]. Grossulariaceae DC., *nom. cons.*
 129 [133]. Saxifragaceae Juss., *nom. cons.*
 130 [134]. Crassulaceae J.St.-Hil., *nom. cons.*
 131 [135]. Aphanopetalaceae Doweld
 132 [136]. Tetracarpaeaceae Nakai
 133 [137]. Penthoraceae Rydb. ex Britton, *nom. cons.*
 134 [138]. Haloragaceae R.Br., *nom. cons.*
 135 [139]. Cynomoriaceae Endl. ex Lindl., *nom. cons.*

ROSIDS

Vitales Juss. ex Bercht. & J.Presl

- 136 [140]. Vitaceae Juss., *nom. cons.*

Zygophyllales Link

- 137 [141]. Krameriaceae Dumort., *nom. cons.*
 138 [142]. Zygophyllaceae R.Br., *nom. cons.*

Fabales Bromhead

- 139 [143]. Quillajaceae D.Don
 140 [144]. Fabaceae Lindl., *nom. cons.* (= Leguminosae Juss., *nom. cons.*)
 141 [145]. Surianaceae Arn., *nom. cons.*
 142 [146]. Polygalaceae Hoffmanns. & Link, *nom. cons.*

Rosales Bercht. & J.Presl

- 143 [147]. Rosaceae Juss., *nom. cons.*
 144 [148]. Barbeyaceae Rendle, *nom. cons.*
 145 [149]. Dirachmaceae Hutch.
 146 [150]. Elaeagnaceae Juss., *nom. cons.*
 147 [151]. Rhamnaceae Juss., *nom. cons.*
 148 [152]. Ulmaceae Mirb., *nom. cons.*
 149 [153]. Cannabaceae Martinov, *nom. cons.*
 150 [154]. Moraceae Gaudich., *nom. cons.*
 151 [155]. Urticaceae Juss., *nom. cons.*

Fagales Engl.

- 152 [156]. Nothofagaceae Kuprian.
 153 [157]. Fagaceae Dumort., *nom. cons.*
 154 [158]. Myricaceae Rich. ex Kunth, *nom. cons.*
 155 [159]. Juglandaceae DC. ex Perleb, *nom. cons.*
 156 [160]. Casuarinaceae R.Br., *nom. cons.*
 157 [161]. Ticodendraceae Gómez-Laur. & L.D.Gómez
 158 [162]. Betulaceae Gray, *nom. cons.*

Cucurbitales Juss. ex Bercht. & J.Presl

- 159 [163]. *Apodanthaceae Tiegh. ex Takht.
 160 [164]. Anisophylleaceae Ridl.
 161 [165]. Corynocarpaceae Engl., *nom. cons.*
 162 [166]. Coriariaceae DC., *nom. cons.*
 163 [167]. Cucurbitaceae Juss., *nom. cons.*
 164 [168]. Tetramelaceae Airy Shaw
 165 [169]. Daticaceae Dumort., *nom. cons.*
 166 [170]. Begoniaceae C.Agardh, *nom. cons.*

[COM-clade; placement uncertain]

Celastrales Link

- 167 [171]. Lepidobotryaceae J.Léonard, *nom. cons.*
 168 [172]. Celastraceae R.Br., *nom. cons.*

Oxalidales Bercht. & J.Presl

- 169 [173]. Huaceae A.Chev.
 170 [174]. Connaraceae R.Br., *nom. cons.*
 171 [175]. Oxalidaceae R.Br., *nom. cons.*
 172 [176]. Cunoniaceae R.Br., *nom. cons.*
 173 [177]. Elaeocarpaceae Juss., *nom. cons.*
 174 [178]. Cephalotaceae Dumort., *nom. cons.*
 175 [179]. Brunelliaceae Engl., *nom. cons.*

Malpighiales Juss. ex Bercht. & J.Presl

- 176 [180]. Pandaceae Engl. & Gilg, *nom. cons.*
 177 [207]. *Irvingiaceae Exell & Mendonça, *nom. cons.*
 (including *Allantospermum* Forman)
 178 [186]. Ctenolophonaceae Exell & Mendonça
 179 [181]. Rhizophoraceae Pers., *nom. cons.*
 180 [182]. Erythroxylaceae Kunth, *nom. cons.*
 181 [187]. Ochnaceae DC., *nom. cons.*
 182 [212]. Bonnetiaceae L.Beauvis. ex Nakai
 183 [211]. Clusiaceae Lindl., *nom. cons.* (= Guttiferae
 Juss., *nom. cons.*)
 184 [210]. Calophyllaceae J.Agardh
 185 [213]. Podostemaceae Rich. ex Kunth, *nom. cons.*
 186 [214]. Hypericaceae Juss., *nom. cons.*
 187 [205]. Caryocaraceae Voigt, *nom. cons.*
 188 [197]. Lophopyxidaceae H.Pfeiff.

- 189 [198]. Putranjivaceae Meisn.
 190 [185]. Centroplacaceae Doweld & Reveal
 191 [190]. Elatinaceae Dumort., *nom. cons.*
 192 [191]. Malpighiaceae Juss., *nom. cons.*
 193 [192]. Balanopaceae Benth. & Hook.f., *nom. cons.*
 194 [193]. Trigoniaceae A.Juss., *nom. cons.*
 195 [194]. Dichapetalaceae Baill., *nom. cons.*
 196 [195]. Euphroniaceae Marc.-Berti
 197 [196]. Chrysobalanaceae R.Br., *nom. cons.*
 198 [206]. Humiriaceae A.Juss., *nom. cons.*
 199 [204]. Achariaceae Harms, *nom. cons.*
 200 [202]. Violaceae Batsch, *nom. cons.*
 201 [203]. Goupiaceae Miers
 202 [199]. Passifloraceae Juss. ex Roussel, *nom. cons.*
 203 [200]. Lacistemataceae Mart., *nom. cons.*
 204 [201]. Salicaceae Mirb., *nom. cons.*
 205 [—]. *Peraceae Klotzsch
 206 [183]. Rafflesiaceae Dumort., *nom. cons.*
 207 [184]. *Euphorbiaceae Juss., *nom. cons.*
 208 [208]. Linaceae DC. ex Perleb, *nom. cons.*
 209 [209]. *Ixonanthaceae Planch. ex Miq., *nom. cons.*
 210 [188]. Picrodendraceae Small, *nom. cons.*
 211 [189]. Phyllanthaceae Martinov, *nom. cons.*

Geraniales Juss. ex Bercht. & J.Presl

- 212 [215]. Geraniaceae Juss., *nom. cons.*
 213 [217]. *Francoaceae A.Juss., *nom. cons.* (including
 Bersamaceae Doweld, Greyiaceae Hutch., *nom. cons.*,
 Ledocarpaceae Meyen, Melianthaceae Horan., *nom.*
cons., Rhynchothecaceae A.Juss., Vivianiaceae
 Klotzsch, *nom. cons.*)

Myrtales Juss. ex Bercht. & J.Presl

- 214 [218]. Combretaceae R.Br., *nom. cons.*
 215 [219]. Lythraceae J.St.-Hil., *nom. cons.*
 216 [220]. Onagraceae Juss., *nom. cons.*
 217 [221]. Vochysiaceae A.St.-Hil., *nom. cons.*
 218 [222]. Myrtaceae Juss., *nom. cons.*
 219 [223]. Melastomataceae Juss., *nom. cons.*
 220 [224]. Crypteroniaceae A.DC., *nom. cons.*
 221 [225]. Alzateaceae S.A.Graham
 222 [226]. Penaeaceae Sweet ex Guill., *nom. cons.*

Crossosomatales Takht. ex Reveal

- 223 [227]. Aphloiaceae Takht.
 224 [228]. Geissolomataceae A.DC., *nom. cons.*
 225 [229]. Strasburgeriaceae Tiegh., *nom. cons.*
 226 [230]. Staphyleaceae Martinov, *nom. cons.*
 227 [231]. Guamatelaceae S.H.Oh & D.Potter
 228 [232]. Stachyuraceae J.Agardh, *nom. cons.*
 229 [233]. Crossosomataceae Engl., *nom. cons.*

Picramniales Doweld

Picramniales Doweld

230 [234]. Picramniaceae Fernando & Quinn

Huerteales Doweld

231 [244]. Gerrardinaceae M.H.Alford

232 [—]. *Petenaeeae Christenh. *et al.*

233 [245]. Tapisciaceae Takht.

234 [246]. Dipentodontaceae Merr., *nom. cons.*

Sapindales Juss. ex Bercht. & J.Presl

235 [235]. Biebersteiniaceae Schnizl.

236 [236]. Nitrariaceae Lindl.

237 [237]. Kirkiaceae Takht.

238 [238]. Burseraceae Kunth, *nom. cons.*239 [239]. Anacardiaceae R.Br., *nom. cons.*240 [240]. Sapindaceae Juss., *nom. cons.* (including Xanthocerataceae Buerki *et al.*, as 'Xanthoceraceae')241 [241]. Rutaceae Juss., *nom. cons.*242 [242]. Simaroubaceae DC., *nom. cons.*243 [243]. Meliaceae Juss., *nom. cons.*

Malvales Juss. ex Bercht. & J.Presl

244 [247]. Cytinaceae A.Rich.

245 [248]. Muntingiaceae C.Bayer *et al.*246 [249]. Neuradaceae Kostel., *nom. cons.*247 [250]. Malvaceae Juss., *nom. cons.*

248 [251]. Sphaerosepalaceae Bullock

249 [252]. Thymelaeaceae Juss., *nom. cons.*250 [253]. Bixaceae Kunth, *nom. cons.*251 [255]. *Cistaceae Juss., *nom. cons.* (including *Pakaraimaea* Maguire & P.S.Ashton)252 [254]. Sarcolaenaceae Caruel, *nom. cons.*253 [256]. *Dipterocarpaceae Blume, *nom. cons.*

Brassicales Bromhead

254 [257]. Akaniaceae Stapf, *nom. cons.*255 [258]. Tropaeolaceae Juss. ex DC., *nom. cons.*256 [259]. Moringaceae Martinov, *nom. cons.*257 [260]. Caricaceae Dumort., *nom. cons.*258 [261]. Limnanthaceae R.Br., *nom. cons.*

259 [262]. Setchellanthaceae Iltis

260 [263]. Koeberliniaceae Engl., *nom. cons.*261 [264]. Bataceae Mart. ex Perleb, *nom. cons.*262 [265]. Salvadoraceae Lindl., *nom. cons.*

263 [266]. Emblingiaceae Airy Shaw

264 [267]. Tovariaceae Pax, *nom. cons.*

265 [268]. Pentadiplandraceae Hutch. & Dalziel

266 [269]. Gyrostemonaceae A.Juss., *nom. cons.*267 [270]. *Resedaceae Martinov, *nom. cons.* (including Borthwickiaceae J.X.Su *et al.*, Stixidaceae Doweld as 'Stixaceae', *Forchhammeria* Liebm.)268 [271]. *Capparaceae Juss., *nom. cons.*

269 [272]. Cleomaceae Bercht. & J.Presl

270 [273]. Brassicaceae Burnett, *nom. cons.* (= Cruciferae Juss., *nom. cons.*)

SUPERASTERIDS

Berberidopsidales Doweld

271 [274]. Aextoxicaceae Engl. & Gilg, *nom. cons.*

272 [275]. Berberidopsidaceae Takht.

Santalales R.Br. ex Bercht. & J.Presl

273 [277]. 'Olacaceae' R.Br., *nom. cons.* [not monophyletic] (including Aptandraceae Miers, Coulaceae Tiegh., Erythralaceae Planch. ex Miq., *nom. cons.* Octoknemaceae Soler. *nom. cons.*, Strombosiaceae Tiegh., Ximeniaceae Horan.)274 [278]. Opiliaceae Valetton, *nom. cons.*275 [276]. Balanophoraceae Rich., *nom. cons.*276 [279]. 'Santalaceae' R.Br., *nom. cons.* [not monophyletic if Balanophoraceae are embedded] (including Amphorogynaceae Nickrent & Der, Cervantesiaceae Nickrent & Der, Comandraceae Nickrent & Der, Nanodeaceae Nickrent & Der, Thesiaceae Vest, Viscaceae Batsch)277 [281]. Misodendraceae J.Agardh, *nom. cons.*

278 [282]. Schoepfiaceae Blume

279 [280]. Loranthaceae Juss., *nom. cons.*

Caryophyllales Juss. ex Bercht. & J.Presl

280 [283]. Frankeniaceae Desv., *nom. cons.*281 [284]. Tamaricaceae Link, *nom. cons.*282 [285]. Plumbaginaceae Juss., *nom. cons.*283 [286]. Polygonaceae Juss., *nom. cons.*284 [287]. Droseraceae Salisb., *nom. cons.*285 [288]. Nepenthaceae Dumort, *nom. cons.*286 [289]. Drosophyllaceae Chrtek *et al.*287 [290]. Dioncophyllaceae Airy Shaw, *nom. cons.*288 [291]. Ancistrocladaceae Planch. ex Walp., *nom. cons.*

289 [292]. Rhabdodendraceae Prance

290 [293]. Simmondsiaceae Tiegh.

291 [294]. Physenaceae Takht.

292 [295]. Asteropeiaceae Takht. ex Reveal & Hoogland

293 [—]. *Macarthuriaceae Christenh.

294 [—]. *Microteaceae Schäferhoff & Borsch

295 [296]. Caryophyllaceae Juss., *nom. cons.*296 [297]. Achatocarpaceae Heimerl, *nom. cons.*297 [298]. Amaranthaceae Juss., *nom. cons.*

298 [299]. Stegnospermataceae Nakai

299 [300]. *Limeaceae Shipunov ex Reveal

- 300 [301]. Lophiocarpaceae Doweld & Reveal
 301 [—]. *Kewaceae Christenh.
 302 [302]. Barbeuiaceae Nakai
 303 [303]. Gisekiaceae Nakai
 304 [304]. Aizoaceae Martinov, *nom. cons.*
 305 [305]. *Phytolaccaceae R.Br., *nom. cons.*
 306 [—]. *Petiveriaceae C.Agardh (including Rivinaceae C.Agardh)
 307 [306]. Sarcobataceae Behnke
 308 [307]. Nyctaginaceae Juss., *nom. cons.*
 309 [308]. *Molluginaceae Bartl., *nom. cons.*
 310 [309]. Montiaceae Raf.
 311 [310]. Didiereaceae Radlk., *nom. cons.*
 312 [311]. Basellaceae Raf., *nom. cons.*
 313 [312]. Halophytaceae S.Soriano
 314 [313]. Talinaceae Doweld
 315 [314]. Portulacaceae Juss., *nom. cons.*
 316 [315]. Anacampserotaceae Egli & Nyffeler
 317 [316]. Cactaceae Juss., *nom. cons.*

ASTERIDS

Cornales Link

- 318 [—]. *Nyssaceae Juss. ex Dumort., *nom. cons.*
 319 [317]. Hydrostachyaceae Engl., *nom. cons.*
 320 [321]. Hydrangeaceae Dumort., *nom. cons.*
 321 [322]. Loasaceae Juss., *nom. cons.*
 322 [318]. Curtisiaceae Takht.
 323 [319]. Grubbiaceae Endl. ex Meisn., *nom. cons.*
 324 [320]. Cornaceae Bercht. & J.Presl, *nom. cons.*

Ericales Bercht. & J.Presl

- 325 [323]. Balsaminaceae A.Rich., *nom. cons.*
 326 [324]. Marcgraviaceae Bercht. & J.Presl, *nom. cons.*
 327 [325]. Tetrameristaceae Hutch.
 328 [326]. Fouquieriaceae DC., *nom. cons.*
 329 [327]. Polemoniaceae Juss., *nom. cons.*
 330 [328]. Lecythidaceae A.Rich., *nom. cons.*
 331 [329]. Sladeniaceae Airy Shaw
 332 [330]. Pentaphragmaceae Engl., *nom. cons.*
 333 [331]. Sapotaceae Juss., *nom. cons.*
 334 [332]. Ebenaceae Gürke, *nom. cons.*
 335 [333]. Primulaceae Batsch ex Borkh., *nom. cons.*
 336 [334]. Theaceae Mirb., *nom. cons.*
 337 [335]. Symplocaceae Desf., *nom. cons.*
 338 [336]. Diapensiaceae Lindl., *nom. cons.*
 339 [337]. Styracaceae DC. & Spreng., *nom. cons.*
 340 [338]. Sarraceniaceae Dumort., *nom. cons.*
 341 [339]. Roridulaceae Martinov, *nom. cons.*
 342 [340]. Actinidiaceae Gilg & Werderm., *nom. cons.*
 343 [341]. Clethraceae Klotzsch, *nom. cons.*
 344 [342]. Cyrillaceae Lindl., *nom. cons.*
 345 [344]. Ericaceae Juss., *nom. cons.*
 346 [343]. Mitrastemonaceae Makino, *nom. cons.*

[placement in order unclear]

†Icacinales Tiegh.

- 347 [345]. Oncothecaceae Kobuski ex Airy Shaw
 348 [347]. *Icacinaceae Miers, *nom. cons.*

†Metteniusales Takht.

- 349 [346]. *Metteniusaceae H.Karst. ex Schnizl.

Garryales Mart.

- 350 [348]. Eucommiaceae Engl., *nom. cons.*
 351 [349]. Garryaceae Lindl., *nom. cons.*

Gentianales Juss. ex Bercht. & J.Presl

- 352 [350]. Rubiaceae Juss., *nom. cons.*
 353 [351]. Gentianaceae Juss., *nom. cons.*
 354 [352]. Loganiaceae R.Br. ex Mart., *nom. cons.*
 355 [353]. *Gelsemiaceae L.Struwe & V.A.Albert
 (including Pteleocarpaceae Brummitt)
 356 [354]. Apocynaceae Juss., *nom. cons.*

†Boraginales Juss. ex Bercht. & J.Presl

- 357 [356]. Boraginaceae Juss., *nom. cons.* (including Codonaceae Weigend & Hilger)

†Vahliales Doweld

- 358 [355]. Vahliaceae Dandy

Solanales Juss. ex Bercht. & J.Presl

- 359 [357]. Convolvulaceae Juss., *nom. cons.*
 360 [358]. Solanaceae Juss., *nom. cons.*
 361 [359]. Montiniaceae Nakai, *nom. cons.*
 362 [360]. Sphenocleaceae T.Baskerv., *nom. cons.*
 363 [361]. Hydroleaceae R.Br.

Lamiales Bromhead

- 364 [362]. Plocospermataceae Hutch.
 365 [363]. Carlemanniaceae Airy Shaw
 366 [364]. Oleaceae Hoffmanns. & Link, *nom. cons.*
 367 [365]. Tetrachondraceae Wettst.
 368 [366]. Calceolariaceae Olmstead
 369 [367]. *Gesneriaceae Rich. & Juss., *nom. cons.* (note: position of *Peltanthera* Benth. is problematic and here considered unplaced to family)
 370 [368]. Plantaginaceae Juss., *nom. cons.*
 371 [369]. Scrophulariaceae Juss., *nom. cons.*
 372 [370]. Stilbaceae Kunth, *nom. cons.*
 373 [371]. Linderniaceae Borsch *et al.*
 374 [383]. Byblidaceae Domin, *nom. cons.*
 375 [384]. Martyniaceae Horan., *nom. cons.*
 376 [372]. Pedaliaceae R.Br., *nom. cons.*

- 377 [378]. Acanthaceae Juss., *nom. cons.*
 378 [379]. Bignoniaceae Juss., *nom. cons.*
 379 [377]. Lentibulariaceae Rich., *nom. cons.*
 380 [381]. Schlegeliaceae Reveal
 381 [380]. Thomandersiaceae Sreem.
 382 [382]. Verbenaceae J.St.Hil., *nom. cons.*
 383 [373]. Lamiaceae Martinov, *nom. cons.* (= Labiatae Juss., *nom. cons.*)
 384 [—].*Mazaceae Reveal
 385 [374]. *Phrymaceae Schauer, *nom. cons.*
 386 [375]. Paulowniaceae Nakai
 387 [376]. *Orobanchaceae Vent., *nom. cons.* (including Lindenbergiaceae Doweld, Rehmanniaceae Reveal)

Aquifoliales Senft

- 388 [385]. Stemonuraceae Kårehed
 389 [386]. Cardiopteridaceae Blume, *nom. cons.*
 390 [387]. Phyllonomaceae Small
 391 [388]. Helwingiaceae Decne.
 392 [389]. Aquifoliaceae Bercht. & J.Presl, *nom. cons.*

Asterales Link

- 393 [390]. Rousseeaceae DC.
 394 [391]. Campanulaceae Juss., *nom. cons.*
 395 [392]. Pentaphragmataceae J.Agardh, *nom. cons.*
 396 [393]. Styliaceae R.Br., *nom. cons.*
 397 [394]. Alseuosmiaceae Airy Shaw
 398 [395]. Phellinaceae Takht.
 399 [396]. Argophyllaceae Takht.
 400 [397]. Menyanthaceae Dumort., *nom. cons.*
 401 [398]. Goodeniaceae R.Br., *nom. cons.*
 402 [399]. Calyceraceae R.Br. ex Rich., *nom. cons.*
 403 [400]. Asteraceae Bercht. & J.Presl, *nom. cons.* (= Compositae Giseke, *nom. cons.*)

Escalloniales Link

- 404 [401]. Escalloniaceae R.Br. ex Dumort., *nom. cons.*

Bruniales Dumort.

- 405 [402]. Columelliaceae D.Don, *nom. cons.*
 406 [403]. Bruniaceae R.Br. ex DC., *nom. cons.*

Paracryphiales Takht. ex Reveal

- 407 [404]. Paracryphiaceae Airy Shaw

Dipsacales Juss. ex Bercht. & J.Presl

- 408 [405]. Adoxaceae E.Mey., *nom. cons.* (= Viburnaceae Raf., *nom. cons. prop.*)
 409 [406]. Caprifoliaceae Juss., *nom. cons.*

Apiales Nakai

- 410 [407]. Pennantiaceae J.Agardh
 411 [408]. Torricelliaceae Hu
 412 [409]. Griselinaceae Takht., *nom. cons. prop.*
 413 [410]. Pittosporaceae R.Br., *nom. cons.*
 414 [411]. Araliaceae Juss., *nom. cons.*
 415 [412]. Myodocarpaceae Doweld
 416 [413]. Apiaceae Lindl., *nom. cons.* (= Umbelliferae Juss., *nom. cons.*)

Incertae sedis

- Atrichodendron* Gagnep. (specimen poorly preserved, and thus difficult to know to which family it should belong; it is definitely not Solanaceae where it was previously placed, S. Knapp, pers. comm.)
Coptocheile Hoffmanns. (described in Gesneriaceae and may belong there but may belong elsewhere in Lamiales)
Gumillea Ruiz & Pav. (originally placed in Cunoniaceae, where it certainly does not belong; it may be close to Picramniales or Huerteales)
Hirania Thulin (described in Sapindales and stated to be related to *Diplopeltis*, but may belong elsewhere; phylogenetic evidence is wanting)
Keithia Spreng. (described in Capparaceae, but may belong elsewhere in Brassicales)
Poilanedora Gagnep. (described in Capparaceae, but does not seem to belong there)
Rumphia L. (only known from illustration)