

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

THE ANGIOSPERM PHYLOGENY GROUP*¹

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A revised and updated classification for the families of flowering plants is provided. Many recent studies have yielded increasingly detailed evidence for the positions of formerly unplaced families, resulting in a number of newly adopted orders, including Amborellales, Berberidopsidales, Bruniales, Buxales, Chloranthales, Escalloniales, Huerteales, Nymphaeales, Paracryphiales, Petrosaviales, Picramniales, Trochodendrales, Vitales and Zygophyllales. A number of previously unplaced genera and families are included here in orders, greatly reducing the number of unplaced taxa; these include Hydatellaceae (Nymphaeales), Haptanthaceae (Buxales), Peridiscaceae (Saxifragales), Huaceae (Oxalidales), Centroplocaceae and Rafflesiaceae (both Malpighiales), Aphloiaceae, Geissolomataceae and Strasburgeriaceae (all Crossosomatales), Picramniaceae (Picramniales), Dipentodontaceae and Gerrardinaceae (both Huerteales), Cytinaceae (Malvales), Balanophoraceae (Santalales), Mitrastemonaceae (Ericales) and Boraginaceae (now at least known to be a member of lamiid clade). Newly segregated families for genera previously understood to be in other APG-recognized families include Petermanniaceae (Liliales), Calophyllaceae (Malpighiales), Capparaceae and Cleomaceae (both Brassicales), Schoepfiaceae (Santalales), Anacampserotaceae, Limeaceae, Lophiocarpaceae, Montiaceae and Talinaceae (all Caryophyllales) and Linderiaceae and Thomandersiaceae (both Lamiales). Use of bracketed families is abandoned because of its unpopularity, and in most cases the broader circumscriptions are retained; these include Amaryllidaceae, Asparagaceae and Xanthorrhaceae (all Asparagales), Passifloraceae (Malpighiales), Primulaceae (Ericales) and several other smaller families. Separate papers in this same volume deal with a new linear order for APG, subfamilial names that can be used for more accurate communication in Amaryllidaceae *s.l.*, Asparagaceae *s.l.* and Xanthorrhaceae *s.l.* (all Asparagales) and a formal supraordinal classification for the flowering plants. © 2009 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2009, 161, 105–121.

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INTRODUCTION

Since the previous APG classification (APG II, 2003), a great deal more information about flowering plant relationships has emerged, and a more refined and better-resolved classification is now possible. If a well-supported hypothesis of monophyly is a necessary prerequisite for a group to be named, it is not sufficient. Not all clades need be named and, indeed, it would barely be practicable to do this, so to decide which clades should be named, additional criteria can be invoked. Backlund & Bremer (1998) provided a useful discussion on the principles of rank-based phylogenetic classification that is applicable at all levels apart from species and immediately above (see Albach *et al.*, 2004; Entwisle & Weston, 2005; Pfeil & Crisp, 2005, *etc.*, for examples). We follow these principles here. Backlund and Bremer's main principle is that taxa that are recognized formally should be monophyletic. However, this does not indicate which particular clades should be named as families, orders *etc.*

It is helpful if (1) taxa formally recognized are easily recognizable, (2) groups that are well established in the literature are preserved, (3) the size of groups is taken into account (particularly small ones, which should be combined with others whenever possible) and (4) nomenclatural changes are minimized (Backlund & Bremer, 1998). Thus, on the one hand, numerous small groups have little to recommend them, as individually they summarize only a small amount of information and tend to clog the memory, whereas groups that are too large may have few obvious shared traits that can be used to recognize them. Asparagales and Lamiales in particular have a number of problems in this regard and include families that are still in a state of flux in this respect.

Changes are being made to the classification adopted by APG II for several reasons, but bearing the Backlund and Bremer guidelines in mind.

1. In the earlier versions of the Angiosperm Phylogeny Group classification, alternative circumscriptions were permitted for some families. However, this seems unnecessary and more likely to cause confusion than clarity. Here we indicate one of the alternatives, a choice based in part on the circumscriptions adopted by textbooks (e.g. Judd *et al.*, 2007), dictionaries (e.g. Mabberley, 2008) and the general literature. Note that, in preparation for the third edition of *The Plant Book*, Mabberley (2008: xi, 927, 929) consulted widely among taxonomists about which alternative they preferred, and, more recently, the issue of these alternative circumscriptions was discussed by researchers representing several European herbaria (e.g. K, E, BM, P, G and the Dutch herbaria collectively) that are in the process of reorganizing their collections

along APG lines. They have all agreed to adopt APG III as their standard and the linear order of Haston *et al.* (2009). In general, the broader circumscriptions have been favoured and are adopted here.

2. Papers over the last few years have clarified the positions of isolated families including Ceratophyllaceae, Chloranthaceae and Picramniaceae (Jansen *et al.*, 2007; Moore *et al.*, 2007; Wang *et al.*, 2009), and this has necessitated addition of orders not previously recognized by APG.
3. A few genera/families, members of which had either not been sequenced before or for which chimaeric sequences were produced, were wrongly placed. Thus, families like Guamatelaceae have been added; *Guamatela* used to be placed in Rosaceae, but molecular data places it in Crossosomatales (Oh & Potter, 2006). Hydatelaceae have been moved from Poales to Nymphaeales (Saarela *et al.*, 2007).
4. There are a few cases where the general pattern of relationships has not changed much since APG II, but our appreciation of the pattern of variation has. For example, this helps justify inclusion of Ixerbaceae in Strasburgeriaceae.
5. Finally, a few family circumscriptions suggested by APG II did not reflect general usage, so we have modified these, an example being the broadly circumscribed Brassicaceae, which are here split into three families.

In general, we have tried not to change the status of families if they have long been recognized, unless there are other good reasons for combining them. However, we have taken the opportunity to combine mono- or oligogeneric families. Most of the family-level changes mentioned below have resulted in the families now recognized being relatively well characterized. However, we realize that it is almost impossible to achieve universal agreement for change – of any sort. Note that we do not see the APG classification as continuing to mutate for the indefinite future. Given the amount of phylogenetic work that has taken place in the last five years, the changes proposed here are modest. We hope the classification below will be found to be reasonable and, hence, will not need much further change, although we do note those few areas where there is particular phylogenetic uncertainty that may necessitate further revision of familial or ordinal limits. For further discussion on the variation in the groups discussed, potential apomorphies, *etc.*, see the literature cited and Stevens (2001); particularly important recent work includes Wang *et al.* (2009: rosids), Tank & Donoghue (in press), Moore *et al.* (2008, in press: core eudicots), Wurdack & Davis (2009: Malpighiales) and

Refulio-Rodriguez & Olmstead (2008, pers. comm.: Lamiales).

For those researchers who wish to employ a formal, higher-level classification for the land plants, Chase & Reveal (2009) have proposed a system. It is based on the recognition that most previous systems have inflated the ranks of the angiosperms and the other major groups of land plants. In this system, all embryophytes are a class, and, therefore, the angiosperms are recognized collectively as a single subclass, Magnoliidae, which necessitated the use of superorders for the major angiosperm clades recognized here (rosids, asterids etc.).

The general sequence of orders follows the left to right sequence of the largely ladderized tree in Haston *et al.* (2009). Within orders, the sequence of families is alphabetical. Symbols: *new family placement; †newly recognized order for the APG system; §new family circumscription described in the text; \$families that represent the broader circumscription of options available in APG II and favoured here, \$\$families that were in square brackets in APG II, the narrower circumscriptions favoured here. The list reflects a starting date for all flowering plant family names as 4 August 1789 (Jussieu, *Genera plantarum*). Full citations are available elsewhere (Reveal, 2008 – onward). A summarized phylogenetic tree representing the relationships among the major groups recognized here is presented in Figure 1.

CLASSIFICATION OF FLOWERING PLANTS

†Amborellales Melikyan, A.V.Bobrov & Zaytzeva (1999)

Amborellaceae Pichon (1948), nom. cons.

The evidence that Amborellaceae are sister to all other angiosperms is clear (e.g. Hansen *et al.*, 2007; Jansen *et al.*, 2007; Moore *et al.*, 2007). However, even if they were sister to Nymphaeales (e.g. Goremykin, Viola & Hellwig, 2009), they should be kept separate as their inclusion in Nymphaeales would result in a taxon without characters.

†Nymphaeales Salisb. ex Bercht. & J.Presl (1820)

\$\$Cabombaceae Rich. ex A.Rich. (1822), nom. cons.

*Hydatellaceae U.Hamann (1976)

\$\$Nymphaeaceae Salisb. (1805), nom. cons.

There seems to be a general preference for keeping Cabombaceae and Nymphaeaceae separate, although both are small in terms of species. The two families are easily characterizable. The inclusion of Hydatellaceae (previously included in Poales) here was unexpected, but it is well supported morphologically and embryologically (Saarela *et al.*, 2007; Friedman, 2008; Rudall *et al.*, 2008).

Austrobaileyales Takht. ex Reveal (1992)

Austrobaileyaceae Croizat (1943), nom. cons.

§Schisandraceae Blume (1830), nom. cons. (including Illiciaceae A.C.Sm., nom. cons.)

Trimeniaceae L.S.Gibbs (1917), nom. cons.

Schisandraceae *s.l.* are well characterized.

†Chloranthales R.Br. (1835)

Chloranthaceae R.Br. ex Sims (1820), nom. cons.

Chloranthaceae are probably sister to magnoliids (Moore *et al.*, 2007). Separate ordinal status is warranted because of their phylogenetic position; they are also morphologically distinctive.

MAGNOLIIDS

Canellales Cronquist (1957)

Canellaceae Mart. (1832), nom. cons.

Winteraceae R.Br. ex Lindl. (1830), nom. cons.

Piperales Bercht. & J.Presl (1820)

Aristolochiaceae Juss. (1789), nom. cons.

Hydnoraceae C.Agardh (1821), nom. cons.

Lactoridaceae Engl. (1888), nom. cons.

Piperaceae Giseke (1792), nom. cons.

Saururaceae F.Voigt (1811), nom. cons.

The relationships of Hydnoraceae are unclear within Piperales.

Laurales Juss. ex Bercht. & J.Presl (1820)

Atherospermataceae R.Br. (1814)

Calycanthaceae Lindl. (1819), nom. cons.

Gomortegaceae Reiche (1896), nom. cons.

Hernandiaceae Blume (1826), nom. cons.

Lauraceae Juss. (1789), nom. cons.

Monimiaceae Juss. (1809), nom. cons.

Siparunaceae Schodde (1970)

Magnoliales Juss. ex Bercht. & J.Presl (1820)

Annonaceae Juss. (1789), nom. cons.

Degeneriaceae I.W.Bailey & A.C.Sm. (1942), nom. cons.

Eupomatiaceae Orb. (1845), nom. cons.

Himantandraceae Diels (1917), nom. cons.

Magnoliaceae Juss. (1789), nom. cons.

Myristicaceae R.Br. (1810), nom. cons.

MONOCOTS

Acorales Link (1835)

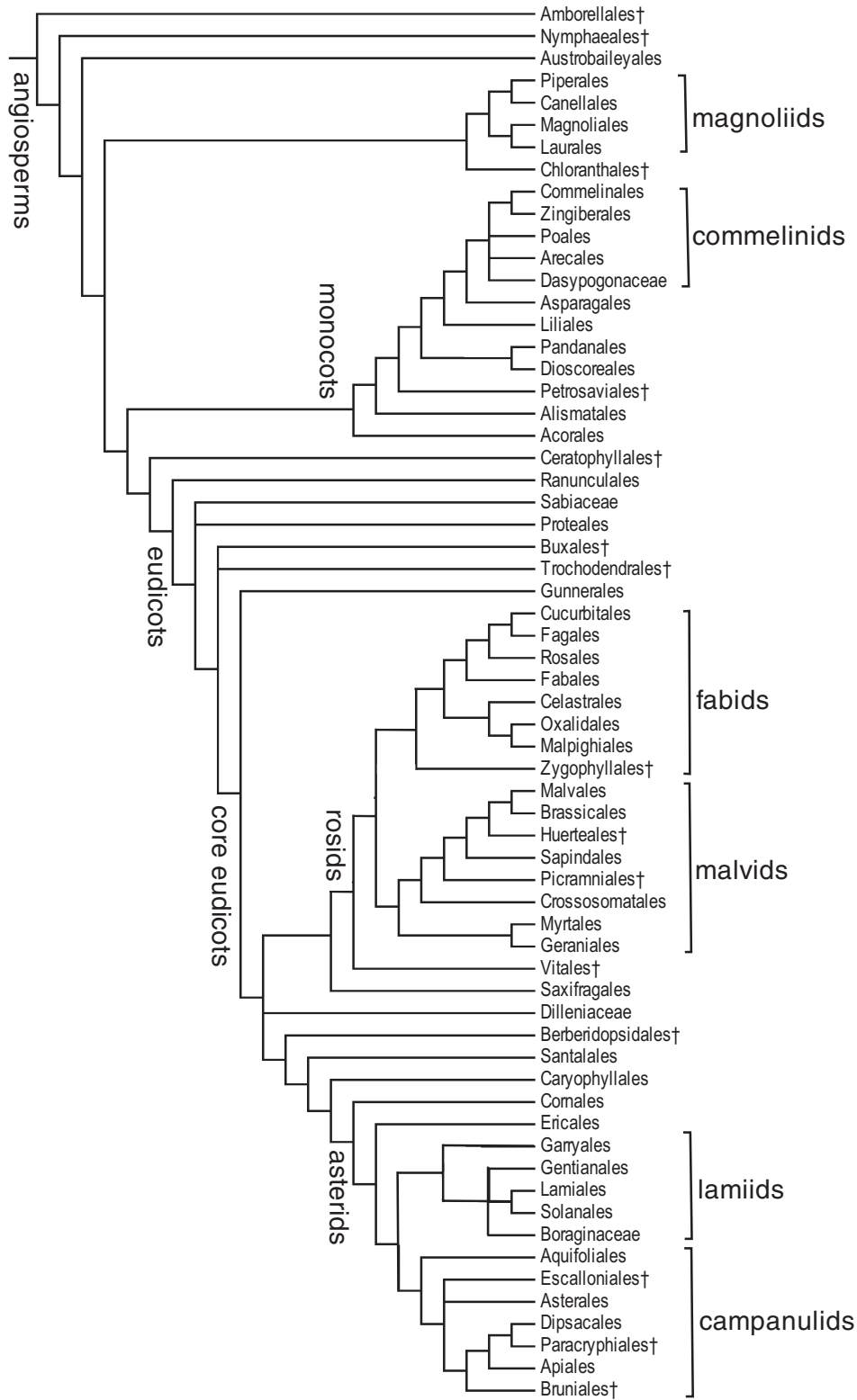
Acoraceae Martinov (1820)

Alismatales R.Br. ex Bercht. & J.Presl (1820)

§Alismataceae Vent. (1799), nom. cons. (including Limnocharitaceae Takht. ex Cronquist)

Aponogetonaceae Planch. (1856), nom. cons.

Araceae Juss. (1789), nom. cons.



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Figure 1. Interrelationships of the APG III orders and some families supported by jackknife/bootstrap percentages greater than 50 or Bayesian posterior probabilities greater than 0.95 in large-scale analyses of angiosperms. See text for literature supporting these relationships. Newly-recognized-for-APG orders are denoted (†). Some eudicot families not yet classified to order are not shown.

Butomaceae Mirb. (1804), nom. cons.
 Cymodoceaceae Vines (1895), nom. cons.
 Hydrocharitaceae Juss. (1789), nom. cons.
 Juncaginaceae Rich. (1808), nom. cons.
 Posidoniaceae Vines (1895), nom. cons.
 Potamogetonaceae Bercht. & J.Presl (1823),
 nom. cons.
 Ruppiaceae Horan. (1834), nom. cons.
 Scheuchzeriaceae F.Rudolphi (1830), nom. cons.
 Tofieldiaceae Takht. (1995)
 Zosteraceae Dumort. (1829), nom. cons.

Convincing evidence for the monophyly of Alismataceae *s.s.* is lacking (e.g. Chen *et al.*, 2004a, b) and the family does not have any apomorphies. When combined with Limnocharitaceae, a family that was only relatively recently described (Cronquist, 1981), the enlarged family has several distinctive characters. It may be necessary to split off *Maundia* from Juncaginaceae (Iles *et al.*, 2009; S. von Mering & J. W. Kadereit, pers. comm.), and Maundiaceae Nakai is available. However, it might be better in this case to create a larger single family for the larger clade. More study is needed before another monogeneric family is recognized in Alismatales.

†Petrosaviales Takht. (1997)

Petrosaviaceae Hutch. (1934), nom. cons.

The isolated position of Petrosaviaceae here is well supported (e.g. Tamura *et al.*, 2004; Chase *et al.*, 2006), hence its ordinal status.

Dioscoreales R.Br. (1835)

Burmanniaceae Blume (1827), nom. cons.
 Dioscoreaceae R.Br. (1810), nom. cons.
 Nartheciaceae Fr. ex Bjurzon (1846)

Thismiaceae J.Agardh (1858) may turn out to be in a clade separate from Burmanniaceae and, similarly, the morphologically distinctive Taccaceae Dumort. (1829), nom. cons., from Dioscoreaceae. Phylogenetic relationships in Dioscoreales that support such changes have been found by Merckx *et al.* (2006) and Merckx & Bidartondo (2008), and Merckx *et al.* (2009) even suggest that Thismiaceae *s.s.* may be paraphyletic. Given the problems in understanding relationships of mycoheterotrophic groups, we have been conservative and not adopted any altered circumscriptions at this stage.

Pandanales R.Br. ex Bercht. & J.Presl (1820)

Cyclanthaceae Poit. ex A.Rich. (1824), nom. cons.
 Pandanaceae R.Br. (1810), nom. cons.
 Stemonaceae Caruel (1878), nom. cons.
 Triuridaceae Gardner (1843), nom. cons.
 Velloziaceae J.Agardh (1858), nom. cons.

Liliales Perleb (1826)

‡Alstroemeriaceae Dumort. (1829), nom. cons.
 (including Luzuriagaceae Lotsy)
 Campynemataceae Dumort. (1829)
 Colchicaceae DC. (1804), nom. cons.
 Corsiaceae Becc. (1878), nom. cons.
 Liliaceae Juss. (1789), nom. cons.
 Melanthiaceae Batsch ex Borkh. (1797), nom. cons.
 *Petermanniaceae Hutch. (1934), nom. cons.
 Philesiaceae Dumort. (1829), nom. cons.
 Ripogonaceae Conran & Clifford (1985)
 Smilacaceae Vent. (1799), nom. cons.

Petermanniaceae are morphologically and phylogenetically distinct. Luzuriagaceae, consisting of two small genera with generalized lily floral morphology, are sister to Alstroemeriaceae and have the same distinctive twisted petioles, so combination is in order (see also Mabberley, 2008).

Asparagales Link (1829)

‡Amaryllidaceae J.St.-Hil., nom. cons. (including Agapanthaceae F.Voigt, Alliaceae Borkh., nom. cons.)
 ‡Asparagaceae Juss. (1789), nom. cons. (including Agavaceae Dumort., nom. cons., Aphyllanthaceae Burnett, Hesperocallidaceae Traub, Hyacinthaceae Batsch ex Borkh., Laxmanniaceae Bubani, Ruscaceae M.Roem., nom. cons., Themidaceae Salisb.)
 Asteliaceae Dumort. (1829)
 Blandfordiaceae R.Dahlgren & Clifford (1985)
 Boryaceae M.W.Chase, Rudall & Conran (1997)
 Doryanthaceae R.Dahlgren & Clifford (1985)
 Hypoxidaceae R.Br. (1814), nom. cons.
 Iridaceae Juss. (1789), nom. cons.
 Ixioliriaceae Nakai (1943)
 Lanariaceae R.Dahlgren & A.E.van Wyk (1988)
 Orchidaceae Juss. (1789), nom. cons.
 Tecophilaeaceae Leyb. (1862), nom. cons.
 ‡Xanthorrhoeaceae Dumort. (1829), nom. cons. (including Asphodelaceae Juss. and Hemerocallidaceae R.Br.)
 Xeronemataceae M.W.Chase, Rudall & M.F.Fay (2000)

An expanded Amaryllidaceae, including Agapanthaceae and Alliaceae, are recognized here (Amaryllidaceae was recently conserved over Alliaceae, despite Alliaceae being the older name). Several characters support the combined group. Agapanthaceae, if kept separate, are weakly characterized; the family is monogeneric.

The area around Asparagaceae is difficult from the standpoint of circumscription. Although Asparagaceae *s.l.* are heterogeneous and poorly characterized, Asparagaceae *s.s.*, Agavaceae, Laxmanniaceae, Rus-

ceae and even Hyacinthaceae have few if any distinctive features. Agavaceae and Ruscaceae *sensu* APG II (2003) are heterogeneous and have been divided into several families in the past, further confusing the issue. This solution at least keeps the number of difficult-to-recognize families to a minimum; Amaryllidaceae *s.l.* and Asparagaceae *s.l.* are easily differentiated by umbels with a pair of enclosing bracts vs. racemes or rarely umbels, but if umbels are present they contain three or more bracts (e.g. *Brodiaea*, *Milla* and relatives, Themidaceae) and lack the enclosing pair of bracts. Xanthorrhoeaceae *s.l.* have been maintained for similar reasons to Asparagaceae *s.l.* Xanthorrhoeaceae *s.s.* are monogeneric, and Asphodelaceae are impossible to distinguish from genera such as *Anthericum* in Asparagaceae *s.l.*

For convenience and better communication, a subfamilial classification of Amaryllidaceae, Asparagaceae and Xanthorrhoeaceae *sensu* APG III is proposed in Chase, Reveal & Fay (2009). This will allow researchers to use a subfamily name where previously they would have used one of the APG II bracketed family names.

COMMELINIDS

Dasypogonaceae Dumort. (1829)

Relationships of Dasypogonaceae remain unclear. They are not particularly distinctive morphologically and so do not warrant immediate ordinal status, although Dasypogonales Doweld is available. They could probably be combined with one of the other commelinid orders should they fall as sister groups.

Arecales Bromhead (1840)

Areaceae Bercht. & J.Presl (1820), nom. cons.

Commelinales Mirb. ex Bercht. & J.Presl (1820)

Commelinaceae Mirb. (1804), nom. cons.

Haemodoraceae R.Br. (1810), nom. cons.

Hanguanaceae Airy Shaw (1965)

Philydraceae Link (1821), nom. cons.

Pontederiaceae Kunth (1816), nom. cons.

Poales Small (1903)

Anarthriaceae D.F.Cutler & Airy Shaw (1965)

Bromeliaceae Juss. (1789), nom. cons.

Centrolepidaceae Endl. (1836), nom. cons.

Cyperaceae Juss. (1789), nom. cons.

Ecdeiocoleaceae D.F.Cutler & Airy Shaw (1965)

Eriocaulaceae Martinov (1820), nom. cons.

Flagellariaceae Dumort. (1829), nom. cons.

Joinvilleaceae Toml. & A.C.Sm. (1970)

Juncaceae Juss. (1789), nom. cons.

Mayacaceae Kunth (1842), nom. cons.

Poaceae Barnhart (1895), nom. cons.

Rapateaceae Dumort. (1829), nom. cons.

Restionaceae R.Br. (1810), nom. cons.

Thurniaceae Engl. (1907), nom. cons.

§Typhaceae Juss. (1789), nom. cons. (including Sparganiaceae Hanin, nom. cons.)

Xyridaceae C.Agardh (1823), nom. cons.

Sparganiaceae are included in Typhaceae; the two families are monogeneric, occupy similar habitats and share a number of features. That they were treated separately in APG II was a mistake (M. W. Chase, pers. comm.). They have in the past been combined; Mabberley (2008) suggested that their combination would be in order.

Zingiberales Griseb. (1854)

Cannaceae Juss. (1789), nom. cons.

Costaceae Nakai (1941)

Heliconiaceae Vines (1895)

Lowiaceae Ridl. (1924), nom. cons.

Marantaceae R.Br. (1814), nom. cons.

Musaceae Juss. (1789), nom. cons.

Strelitziaceae Hutch. (1934), nom. cons.

Zingiberaceae Martinov (1820), nom. cons.

PROBABLE SISTER OF EUDICOTS

Ceratophyllales Link (1829)

Ceratophyllaceae Gray (1822), nom. cons.

The molecular evidence that Ceratophyllaceae are sister to eudicots is becoming clearer (Jansen *et al.*, 2007; Moore *et al.*, 2007, but cf. Goremykin *et al.*, 2009). In this and all other relationships that have been suggested for Ceratophyllaceae, including sister to the monocots or Chloranthaceae (Endress & Doyle, 2009), they are morphologically divergent from their putative closest relatives.

EUDICOTS

Ranunculales Juss. ex Bercht. & J.Presl (1820)

Berberidaceae Juss. (1789), nom. cons.

§Circaeasteraceae Hutch. (1926), nom. cons. (including Kingdoniaceae Airy Shaw)

Eupteleaceae K.Wilh. (1910), nom. cons.

Lardizabalaceae R.Br. (1821), nom. cons.

Menispermaceae Juss. (1789), nom. cons.

§Papaveraceae Juss. (1789), nom. cons. (including Fumariaceae Marquis, nom. cons., Pteridophyllaceae Nakai ex Reveal & Hoogland)

Ranunculaceae Juss. (1789), nom. cons.

We adopt broad limits for Circaeasteraceae and Papaveraceae, as this is commonly done (Judd *et al.*, 2007; Mabberley, 2008), and the two families are well characterized in their broader circumscriptions. The two families into which Circaeasteraceae have been divided (Circaeasteraceae and Kingdoniaceae)

are both monogeneric; they are herbaceous and their leaves have the same distinctive dichotomous venation.

Sabiaceae Blume (1851), nom. cons.

Although Moore *et al.* (2008) placed Sabiaceae as sister to Proteales, support is only moderate. However, if further work confirms this position, Sabiaceae will be included in a broadened circumscription of Proteales; the two have features in common. Sabiaceae remain poorly known.

Proteales Juss. ex Bercht. & J.Presl (1820)

Nelumbonaceae A.Rich. (1827), nom. cons.

\$\$Platanaceae T.Lestib. (1826), nom. cons.

\$\$Proteaceae Juss. (1789), nom. cons.

Platanaceae, although monogeneric, are morphologically distinct from Proteaceae, and the two have never been combined previously; members of the broader family would have few features in common.

†Trochodendrales Takht. ex Cronquist (1981)

\$Trochodendraceae Eichler (1865), nom. cons. (including Tetracentraceae A.C.Sm., nom. cons.).

A separate order for this morphologically distinct clade is warranted; the two monospecific genera in Trochodendraceae *s.l.*, *Tetracentron* and *Trochodendron*, have much in common.

†Buxales Takht. ex Reveal (1996)

\$Buxaceae Dumort. (1822), nom. cons. (including Didymelaceae Leandri)

*Haptanthaceae C.Nelson (2002)

The limits of Buxaceae are expanded. The monogeneric Didymelaceae have the same distinctive pollen and chemistry as at least part of Buxaceae, although there is currently no evidence for the paraphyly of the latter. Some morphological features suggest that Haptanthaceae are best placed here, but they are distinct from all other angiosperms (Doust & Stevens, 2005). An order for the two families is warranted. Note that relationships of Trochodendrales and Buxales remain unclear, although they are certainly to be placed in this part of the tree.

CORE EUDICOTS

Gunnerales Takht. ex Reveal (1992)

\$\$Gunneraceae Meisn. (1842), nom. cons.

\$\$Myrothamnaceae Nied. (1891), nom. cons.

The two families share no important features and so are kept separate, although both are monogeneric.

Dilleniaceae Salisb. (1807), nom. cons.

This family has no stable position as yet (Moore *et al.*, in press). The ordinal name, Dilleniales DC. ex Bercht. & J.Presl, is available.

Saxifragales Bercht. & J.Presl (1820)

Altingiaceae Horan. (1841), nom. cons.

Aphanopetalaceae Doweld (2001)

Cercidiphyllaceae Engl. (1907), nom. cons.

Crassulaceae J.St.-Hil. (1805), nom. cons.

Daphniphyllaceae Müll.-Arg. (1869), nom. cons.

Grossulariaceae DC. (1805), nom. cons.

\$\$Haloragaceae R.Br. (1814), nom. cons.

Hamamelidaceae R.Br. (1818), nom. cons.

\$Iteaceae J.Agardh (1858), nom. cons. (including

Pterostemonaceae Small, nom. cons.)

Paeoniaceae Raf. (1815), nom. cons.

\$\$Penthoraceae Rydb. ex Britt. (1901), nom. cons.

*\$Peridiscaceae Kuhl. (1950), nom. cons. (including Medusandraceae Brenan, nom. cons., *Soyauxia* Oliver)

Saxifragaceae Juss. (1789), nom. cons.

\$\$Tetracarpaeaceae Nakai (1943)

The limits of Iteaceae are broadened because the combined clade is well characterized and Pterostemonaceae are monogeneric. The limits of Haloragaceae are drawn narrowly as the inclusion of Penthoraceae and Tetracarpaeaceae would result in a family with no obvious characters and totally novel limits. The three families are individually tolerably well characterized. Recent molecular analyses strongly support a placement of Peridiscaceae within Saxifragales, as sister to all other members of this clade (Soltis *et al.*, 2007a; Jian *et al.*, 2008), rather than in Malpighiales as previously proposed. Peridiscaceae continue to be expanded (Davis & Chase, 2004; Wurdack & Davis, 2009), but all members of the expanded family have similar distinctive seeds etc.

Cynomoriaceae are another family of holoparasitic angiosperms that have been difficult to place. Some molecular analyses had placed them in Santalales (Jian *et al.*, 2008), although with little support. However, Barkman *et al.* (2007) found no support for a position in that order or anywhere else. Nevertheless, Nickrent (2002) and Nickrent *et al.* (2005) suggested that Cynomoriaceae should be placed in Saxifragales, but the evidence for placing them here versus in Santalales is not strong. Confounding the placement of this taxon is evidence for horizontal gene transfer involving its host for some mitochondrial genes (Barkman *et al.*, 2007). Zhang, Li & Li (2009) analyzed sequences from the plastid inverted repeat and found that *Cynomorium* fell as sister to Rosaceae (Rosales) with high bootstrap support (99%). Due to these discordant results, we do not assign Cynomoriaceae to an order here.

ROSIDS

†Vitales Juss. ex Bercht. & J.Presl (1820)
Vitaceae Juss. (1789), nom. cons.

Vitaceae remain isolated and ordinal status is appropriate. They are sister to the fabids + malvids (rosid I + II) clade in most recent analyses, albeit without strong support (reviewed in Wang *et al.*, 2009).

FABIDS

†Zygophyllales Link (1829)
\$\$Krameriaceae Dumort. (1829), nom. cons.
\$\$Zygophyllaceae R.Br. (1814), nom. cons.

Although Krameriaceae are monogeneric, they are readily distinguished from the heterogeneous Zygophyllaceae; the two are sister taxa. Combining the two would simply make a heterogeneous Zygophyllaceae still more so. An order is needed for this family pair as it is placed with strong support as sister to a clade containing more than two fabid orders in the analysis by Wang *et al.* (2009).

Celastrales Link (1829)
\$Celastraceae R.Br. (1814), nom. cons. (including Lepuropetalaceae Nakai, Parnassiaceae Martinov, nom. cons., Pottingeriaceae Takht.)
Lepidobotryaceae J.Léonard (1950), nom. cons.

The limits of Celastraceae are broadened because the three small families included show every sign of making Celastraceae paraphyletic if excluded (Zhang & Simmons, 2006). The dismemberment of Celastraceae needed to maintain the families, of which only Parnassiaceae are well known, would be extensive and yield poorly characterized families, and Celastraceae *s.l.* are better characterized than Celastraceae, excluding Parnassiaceae (for morphology, see Matthews & Endress, 2005a).

Oxalidales Bercht. & J.Presl (1820)
Brunelliaceae Engl. (1897), nom. cons.
Cephalotaceae Dumort. (1829), nom. cons.
Connaraceae R.Br. (1818), nom. cons.
Cunoniaceae R.Br. (1814), nom. cons.
Elaeocarpaceae Juss. ex DC. (1816), nom. cons.
*Huaceae A.Chev. (1947)
Oxalidaceae R.Br. (1818), nom. cons.

Huaceae are tentatively included in Oxalidales because a number of recent studies (e.g. Wurdack & Davis, 2009) have indicated that they are sister to Oxalidales as recognized in previous versions of APG. This is not a well-characterized clade, and it remains poorly understood.

Malpighiales Juss. ex Bercht. & J.Presl (1820)
Achariaceae Harms (1897), nom. cons.

Balanopaceae Benth. & Hook.f. (1880), nom. cons.
Bonnetiaceae L.Beauvis. ex Nakai (1948)
*Calophyllaceae J.Agardh
Caryocaraceae Voigt (1845), nom. cons.
*Centroplacaceae Doweld & Reveal (2005)
\$\$Chrysobalanaceae R.Br. (1818), nom. cons.
\$Clusiaceae Lindl. (1836), nom. cons.
Ctenolophonaceae Exell & Mendonça (1951)
\$\$Dichapetalaceae Baill. (1886), nom. cons.
Elatinaceae Dumort. (1829), nom. cons.
\$\$\$Erythroxylaceae Kunth (1822), nom. cons. (including *Aneulophus* Benth.)
Euphorbiaceae Juss. (1789), nom. cons.
\$\$Euphroniaceae Marc.-Berti (1989)
Goupiaceae Miers (1862)
Humiriaceae A.Juss. (1829), nom. cons.
Hypericaceae Juss. (1789), nom. cons.
Irvingiaceae Exell & Mendonça (1951), nom. cons.
Ixonanthaceae Planch. ex Miq. (1858), nom. cons.
Lacistemataceae Mart. (1826), nom. cons.
Linaceae DC. ex Perleb (1818), nom. cons.
Lophopyxidaceae H.Pfeiff. (1951)
Malpighiaceae Juss. (1789), nom. cons.
\$Ochnaceae DC. (1811), nom. cons. (including Medusagynaceae Engl. & Gilg, nom. cons., Quinaceae Choisy, nom. cons.)
Pandaceae Engl. & Gilg (1912–1913), nom. cons.
\$Passifloraceae Juss. ex Roussel (1806), nom. cons. [including Malesherbiaceae D.Don, nom. cons., Turneraceae Kunth ex DC. (1828), nom. cons.]
Phyllanthaceae Martinov (1820), nom. cons.
Picrodendraceae Small (1917), nom. cons.
Podostemaceae Rich. ex Kunth (1816), nom. cons.
Putranjivaceae Meisn. (1842)
*Rafflesiaceae Dumort. (1829), nom. cons.
\$\$Rhizophoraceae Pers. (1807), nom. cons.
Salicaceae Mirb. (1815), nom. cons.
\$\$Trigoniaceae A.Juss. (1849), nom. cons.
Violaceae Batsch (1802), nom. cons.

The holoparasitic Rafflesiaceae are best assigned to Malpighiales, perhaps making Euphorbiaceae *s.s.* paraphyletic (e.g. Davis & Wurdack, 2004; Davis *et al.*, 2007); the recognition of Peraceae Klotzsch (1859) would be needed to maintain monophyly of Euphorbiaceae. However, pending further studies, Peraceae are not recognized here. Limits of clades in the Bonnetiaceae–Podostemaceae area are becoming clearer (Wurdack & Davis, 2009), and this necessitates the removal of Calophyllaceae from Clusiaceae. The alternatives would be a family that included both of these families and Bonnetiaceae, Hypericaceae and Podostemaceae or one that included the last two families plus Calophyllaceae; in both cases Hypericaceae would be the correct name. The four families in the area of Chrysobalanaceae, Dichapetalaceae,

Euphroniaceae and Trigoniaceae are kept separate as, although clearly related, a broadly drawn Chryso-balanaceae would be heterogeneous (see Matthews & Endress, 2008, for the morphology of this group). *Bhesa* (formerly of Celastraceae) and *Centroplocus* (formerly of Euphorbiaceae) form an isolated clade (Davis *et al.*, 2005; Wurdack & Davis, 2009) that has distinguishing features; recognition of a bigeneric Centroplacaceae is reasonable. Salicaceae are broadly drawn, i.e. including Samydaceae Vent. and Scyphostegiaceae Hutch. Although the combined clade is only moderately distinct morphologically and less so phylogenetically (Chase *et al.*, 2002), recognition of more families in this area is premature pending a more detailed sampling of the genera. *Trichostephanus* Gilg, unplaced previously, shares wood anatomy, disc lobing and seed structure with Samydeae Vent. (= Salicaceae), and unpublished DNA data support this placement (M. Alford, pers. comm.). Rhizophoraceae are kept separate from their sister taxon, Erythroxylaceae, although *Aneulophus*, of Erythroxylaceae, is to a certain extent morphologically intermediate; the two families have hitherto not been combined. Passifloraceae and Ochnaceae are broadly delimited here yet remain readily characterizable; relationships between the component clades within the two families are uncertain, and both Medusagnaceae (Ochnaceae *s.l.*) and Malesherbiaceae (Passifloraceae *s.l.*) are monogeneric.

Cucurbitales Juss. ex Bercht. & J.Presl (1820)

- Anisophylleaceae Ridl. (1922)
- Begoniaceae C.Agardh (1824), nom. cons.
- Coriariaceae DC. (1824), nom. cons.
- Corynocarpaceae Engl. (1897), nom. cons.
- Cucurbitaceae Juss. (1789), nom. cons.
- Daticaceae Dumort. (1829), nom. cons.
- Tetramelaceae Airy Shaw (1965)

Fabales Bromhead (1838)

- Fabaceae Lindl. (1836), nom. cons.
- Polygalaceae Hoffmanns. & Link (1809), nom. cons.
- Quillajaceae D.Don (1831)
- Surianaceae Arn. (1834), nom. cons.

Fagales Engl. (1892)

- Betulaceae Gray (1822), nom. cons.
- Casuarinaceae R.Br. (1814), nom. cons.
- Fagaceae Dumort. (1829), nom. cons.
- §Juglandaceae DC. ex Perleb (1818), nom. cons. [including Rhoipteleaceae Hand.-Mazz. (1932), nom. cons.]
- Myricaceae A.Rich. ex Kunth (1817), nom. cons.
- Nothofagaceae Kuprian (1962)
- Ticodendraceae Gómez-Laur. & L.D.Gómez (1991)

Juglandaceae are expanded to include their sister clade, the monogeneric Rhoipteleaceae. The two look

similar, even although Rhoipteleaceae have superior and Juglandaceae inferior ovaries; ovary position is variable in many families, and in other such cases, e.g. Ebenaceae (including Lissocarpaceae), we have recognized the larger unit.

Rosales Bercht. & J.Presl (1820)

- Barbeyaceae Rendle (1916), nom. cons.
- Cannabaceae Martinov (1820), nom. cons.
- Dirachmaceae Hutch. (1959)
- Elaeagnaceae Juss. (1789), nom. cons.
- Moraceae Gaudich. (1835), nom. cons.
- Rhamnaceae Juss. (1789), nom. cons.
- Rosaceae Juss. (1789), nom. cons.
- Ulmaceae Mirb. (1815), nom. cons.
- Urticaceae Juss. (1789), nom. cons.

MALVIDS

Geraniales Juss. ex Bercht. & J.Presl (1820)

- §Geraniaceae Juss. (1789), nom. cons. (including Hypseocharitaceae Wedd.)
- §Melianthaceae Horan. (1834), nom. cons. (including Francoaceae A.Juss., nom. cons.)
- §Vivianiaceae Klotzsch, nom. cons. prop. (including Ledocarpaceae Meyen)

Geraniales are a heterogeneous and poorly known order. The inclusion of the monogeneric Hypseocharitaceae in Geraniaceae, monogeneric Francoaceae in Melianthaceae and bigeneric Ledocarpaceae in Vivianiaceae leaves these expanded families with a number of characters.

Myrtales Juss. ex Bercht. & J.Presl (1820)

- Alzateaceae S.A.Graham (1985)
- Combretaceae R.Br. (1810), nom. cons.
- Crypteroniaceae A.DC. (1868), nom. cons.
- Lythraceae J.St.-Hil. (1805), nom. cons.
- §Melastomataceae Juss. (1789), nom. cons. (including Memecylaceae DC., nom. cons.)
- §Myrtaceae Juss. (1789), nom. cons. (including Heteropyxidaceae Engl. & Gilg, nom. cons., Psiloxylaceae Croizat)
- Onagraceae Juss. (1789), nom. cons.
- §Penaeeae Sweet ex Guill. (1828), nom. cons. (including Oliniaceae Arn., nom. cons., Rhynchocalycaceae L.A.S.Johnson & B.G.Briggs)
- Vochysiaceae A.St.-Hil. (1820), nom. cons.

In Melastomataceae, and still more in Myrtaceae, common usage is for broadened family circumscriptions. Both Heteropyxidaceae and Psiloxylaceae are small families and when included in Myrtaceae *s.l.* that family remains characterized by possession of pellucid glands containing ethereal oils.

A close relationship between Crypteroniaceae, Penaeeae, Oliniaceae, Alzataeeae and Rhyn-

chocalyceae is clear; Van Beusekom-Osinga & van Beusekom (1975) included the last two families in the first. All families are morphologically similar, although they show variation in floral morphology and embryo sac, in particular. Some combination is in order, and Penaeaceae have been expanded to include Rhynchocalycaceae and Oliniaceae; Penaeaceae *s.l.* can be characterized.

Crossosomatales Takht. ex Reveal (1993)

- *Aphloiaceae Takht. (1985)
- Crossosomataceae Engl. (1897), nom. cons.
- *Geissolomataceae A.DC. (1856)
- *Guamatelaceae S.Oh & D.Potter (2006)
- Stachyuraceae J.Agardh (1858), nom. cons.
- Staphyleaceae Martinov (1820), nom. cons.
- *§Strasburgeriaceae Soler. (1908), nom. cons. (including Ixerbaceae Griseb. ex Doweld & Reveal)

The addition of several families to Crossosomatales is well justified (e.g. Sosa & Chase, 2003; Soltis *et al.*, 2007b; Wang *et al.*, 2009), although monogeneric Guamatelaceae are a somewhat surprising addition, *Guamatela* having previously been included in Rosaceae (Oh & Potter, 2006). For the most part, relationships among families included in Crossosomatales have not been suggested before. The order is heterogeneous, although the families are all small. Nevertheless, Matthews & Endress (2005b, 2006) found a number of floral features to be at least common in the order. The sister taxa Strasburgeriaceae and Ixerbaceae are two monogeneric families that agree in several characters, including base chromosome number and stamen and gynoecial morphology etc.; combination is in order. As the order is now defined, Staphyleales Mart. (1835) is an older name for Crossosomatales Takht. ex Reveal (1993). It need not be adopted, however.

†Picroamniales Doweld (2001)

- *Picroamniaceae Fernando & Quinn (1995)

Picroamniaceae were previously unplaced rosids, but there is now strong support for a position in the rosid II/malvid clade (Wang *et al.*, 2009).

†Huerteales Doweld (2001)

- *Dipentodontaceae Merr. (1941), nom. cons.
- *Gerrardinaceae Alford (2006)
- Tapisciaceae Takht. (1987)

This assemblage of three small families is well supported, and recognition of Huerteales is appropriate given their position. Within Huerteales, the recently described Gerrardinaceae (*Gerrardina* was previously placed in Flacourtiaceae) are sister to the rest, and Dipentodontaceae, although monogeneric like Gerrardinaceae, are distinctive (see Worberg *et al.*, 2009).

Brassicales Bromhead (1838)

- §Akaniaceae Stapf (1912), nom. cons. (including Bretschneideraceae Engl. & Gilg, nom. cons.)
- Bataceae Mart. ex Perleb (1838), nom. cons.
- §Brassicaceae Burnett (1835), nom. cons.
- *Capparaceae Juss. (1789), nom. cons.
- Caricaceae Dumort. (1829), nom. cons.
- *Cleomaceae Bercht. & J.Presl (1825)
- Emblingiaceae J.Agardh (1958)
- Gyrostemonaceae A.Juss. (1845), nom. cons.
- Koerberliniaceae Engl. (1895), nom. cons.
- Limnanthaceae R.Br. (1833), nom. cons.
- Moringaceae Martinov (1820), nom. cons.
- Pentadiplandraceae Hutch. & Dalziel (1928)
- Resedaceae Martinov (1820), nom. cons.
- Salvadoraceae Lindl. (1836), nom. cons.
- Setchellanthaceae Iltis (1999)
- Tovariaceae Pax (1891), nom. cons.
- Tropaeolaceae Juss. ex DC. (1824), nom. cons.

Inclusion of monogeneric Bretschneideraceae into the monogeneric Akaniaceae is justified by the morphological similarities of the two, which are sister taxa. Although a broad circumscription of Brassicaceae was recognized in APG (1998) and APG II (2003), the consensus prefers the recognition of three families, all of which can be characterized, albeit Capparaceae only rather poorly so. The final phylogenetic positions, and hence taxonomic disposition, of some genera, particularly those previously included in Capparaceae–Stixaceae, remain uncertain (Hall, Sytsma & Iltis, 2002; Hall, Iltis & Sytsma, 2004). Nonetheless, the name Stixaceae Doweld (2008) is available if it is required.

Malvales Juss. ex Bercht. & J.Presl (1820)

- §Bixaceae Kunth (1822), nom. cons. (including Cochlospermaceae Planch., nom. cons., Diegodendraceae Capuron,)
- Cistaceae Juss. (1789), nom. cons.
- *Cytinaceae A.Rich. (1824)
- Dipterocarpaceae Blume (1825), nom. cons.
- Malvaceae Juss. (1789), nom. cons.
- Muntingiaceae C.Bayer, M.W.Chase & M.F.Fay (1998)
- Neuradaceae Kostel. (1835), nom. cons.
- Sarcolaenaceae Caruel (1881), nom. cons.
- Sphaerosepalaceae Tiegh. ex Bullock (1959)
- Thymelaeaceae Juss. (1789), nom. cons.

A broad circumscription for Bixaceae is adopted; the three families included are all small, and the combined family can be characterized morphologically. The parasitic Cytinaceae (including *Bdallophyton* Eichl.) find their resting place here (Nickrent, 2007). The novel dismemberment of Malvaceae by Cheek (2006), see also Cheek in Heywood *et al.*, 2007) is not followed

here; the families are difficult to distinguish, and two are new (Brownlowiaceae, Durionaceae, although the first is a later name for Sparmanniaceae J. Agardh as defined by Cheek). The close relationship of the four families that make up Malvaceae *s.l.* here has been recognized since at least the time of Robert Brown. Details of relationships in the area of Cistaceae–Sarcolaenaceae–Dipterocarpaceae remain unclear, and these families may need to be combined (Kubitzki & Chase, 2002; Ducouso *et al.*, 2004); Cistaceae has priority if these are all combined as a single family.

Sapindales Juss. ex Bercht. & J. Presl (1820)

- Anacardiaceae R.Br. (1818), nom. cons.
- Biebersteiniaceae Schnizl. (1856)
- Burseraceae Kunth (1824), nom. cons.
- Kirkiaceae Takht. (1967)
- Meliaceae Juss. (1789), nom. cons.
- §Nitrariaceae Lindl. (1835), nom. cons. (including Peganaceae Tiegh. ex Takht., Tetradiclidaceae Takht.)
- Rutaceae Juss. (1789), nom. cons.
- Sapindaceae Juss. (1789), nom. cons.
- Simaroubaceae DC. (1811), nom. cons.

We circumscribe Nitrariaceae broadly. The four genera included show considerable variation, although their basic morphology, anatomy and chemistry are poorly known.

†Berberidopsidales Doweld (2001)

- Aextoxicaceae Engl. & Gilg (1920), nom. cons.
- Berberidopsidaceae Takht. (1985)

The morphologically distinct Aextoxicaceae and Berberidopsidaceae are strongly supported as sister taxa, and recent work (Moore *et al.*, in press) placed them with strong support as sister to (Santalales (Caryophyllales + asterids)); thus, ordinal status is appropriate.

Santalales R.Br. ex Bercht. & J. Presl (1820)

- *Balanophoraceae Rich. (1822), nom. cons.
- Loranthaceae Juss. (1808), nom. cons.
- Misodendraceae J. Agardh (1858), nom. cons.
- Santalaceae R.Br. (1810), nom. cons.
- Olaceae R.Br. (1818), nom. cons.
- Opiliaceae Valetton (1886), nom. cons.
- *Schoepfiaceae Blume (1850)

The genera included in Schoepfiaceae used to be included in Olacaceae *s.l.*, but they are exclusively related. They are well supported as being in a clade with Misodendraceae, but that family is morphologically so distinct that combination of the two families is inappropriate. The paraphyletic Olacaceae are being resolved into a number of clades (Malécot & Nickrent, 2008), but relationships between these clades are uncertain and so new families/family limits

are not proposed here. Santalaceae are kept with their previous circumscription. That they can be divided into clades (Der & Nickrent, 2008), one of which is the morphologically distinct Viscaceae, is of itself insufficient reason for their dismemberment (see Introduction, also Dipsacales below). Balanophoraceae are to be included in Santalales (Nickrent, Der & Anderson, 2005; Barkman *et al.*, 2007), and there is some evidence that Cynomoriaceae might also belong here (see comments under Saxifragales, above).

Caryophyllales Juss. ex Bercht. & J. Presl (1820)

- Achatocarpaceae Heimerl (1934), nom. cons.
- Aizoaceae Martinov (1820), nom. cons.
- Amaranthaceae Juss. (1789), nom. cons.
- *Anacampserotaceae Eggli & Nyffeler (2010, in press)
- Ancistrocladaceae Planch. ex Walp. (1851), nom. cons.
- Asteropeiaceae Takht. ex Reveal & Hoogland (1990)
- Barbeuiaceae Nakai (1942)
- Basellaceae Raf. (1837), nom. cons.
- Cactaceae Juss. (1789), nom. cons.
- Caryophyllaceae Juss. (1789), nom. cons.
- §Didiereaceae Radlk. (1896), nom. cons.
- Dioncophyllaceae Airy Shaw (1952), nom. cons.
- Droseraceae Salisb. (1808), nom. cons.
- Drosophyllaceae Chrtek, Slavíková & Studnička (1989)
- Frankeniaceae Desv. (1817), nom. cons.
- Gisekiaceae Nakai (1942)
- Halophytaceae A. Soriano (1984)
- *Limeaceae Shipunov ex Reveal (2005)
- *Lophiocarpaceae Doweld & Reveal (2008)
- §Molluginaceae Bartl. (1825), nom. cons.
- *Montiaceae Raf. (1820)
- Nepenthaceae Dumort. (1829), nom. cons.
- Nyctaginaceae Juss. (1789), nom. cons.
- Physenaceae Takht. (1985)
- Phytolaccaceae R.Br. (1818), nom. cons.
- Plumbaginaceae Juss. (1789), nom. cons.
- Polygonaceae Juss. (1789), nom. cons.
- §Portulacaceae Juss. (1789), nom. cons.
- Rhabdodendraceae Prance (1968)
- Sarcobataceae Behnke (1997)
- Simmondsiaceae Tiegh. (1900)
- Stegnospermataceae Nakai (1942)
- *Talinaceae Doweld (2001)
- Tamaricaceae Link (1821), nom. cons.

The recognition of a number of new but small families is necessitated by recent phylogenetic work on core Caryophyllales. Anacampserotaceae, Portulacaceae *s.s.*, Montiaceae and Talinaceae are all clades near Cactaceae that are for the most part well supported as distinct (e.g. Applequist & Wallace, 2001; Nyffeler, 2007; Nyffeler & Eggli, in press; Brockington

et al., in press). Expansion of Cactaceae to include all or some of these small clades cannot, however, be justified. Not only have the limits of Cactaceae been stable over the years, but inclusion of *Anacampseros* and relatives (Anacampserotaceae) and Portulacaceae s.s. in Cactaceae (compatible with the best phylogenetic hypotheses) would yield a clade characterized solely by multicellular axillary hairs. Similarly, inclusion of these two groups and Talinaceae in Cactaceae would yield a clade characterized by parallelocytic stomata (probably) and fruit characters, but the latter have been subsequently lost in Cactaceae (Ogburn & Edwards, 2009). Anacampserotaceae has only recently been described (Nyffeler & Eggli, in press), recognition is compatible with their phylogenetic position.

It has long been recognized that the limits of Molluginaceae *s.l.* are unclear (e.g. Endress & Bittrich, 1993). Limeaceae and Lophiocarpaceae are segregates necessitated by recent phylogenetic findings (Cuénoud *et al.*, 2002). Molluginaceae *s.l.* are yet another group much in need of basic anatomical, developmental and phytochemical study. We still know little about relationships of Phytolaccaceae, almost certainly not a monophyletic family as currently circumscribed. However, its division, as in Judd *et al.* (2007), is premature.

ASTERIDS

Cornales Link. (1829)

- Cornaceae Bercht. & J.Presl (1825), nom. cons. (including Nyssaceae Juss. ex Dumort.)
- Curtisiaceae Takht. (1987)
- Grubbiaceae Endl. ex Meisn., (1841), nom. cons.
- Hydrangeaceae Dumort. (1829), nom. cons.
- Hydrostachyaceae Engl. (1894), nom. cons.
- Loasaceae Juss. (1804), nom. cons.

Ericales Bercht. & J.Presl (1820)

- Actinidiaceae Engl. & Gilg. (1824), nom. cons.
- Balsaminaceae A.Rich. (1824), nom. cons.
- Clethraceae Klotzsch (1851), nom. cons.
- Cyrillaceae Lindl. (1846), nom. cons.
- Diapensiaceae Lindl. (1836), nom. cons.
- Ebenaceae Gürke (1891), nom. cons.
- Ericaceae Juss. (1789), nom. cons.
- Fouquieriaceae DC. (1828), nom. cons.
- Lecythidaceae A.Rich. (1825), nom. cons.
- Marcgraviaceae Bercht. & J.Presl (1820), nom. cons.
- *Mitrastemonaceae Makino (1911), nom. cons.
- §Pentaphylacaceae Engl. (1897), nom. cons. (including Ternstroemiaceae Mirb. ex DC.)
- Polemoniaceae Juss. (1789), nom. cons.
- §Primulaceae Batsch ex Borkh. (1797), nom. cons. (including Maesaceae Anderb., B.Ståhl & Källersjö, Myrsinaceae R.Br., nom. cons., Theophrastaceae G.Don, nom. cons.)

- Roridulaceae Martinov (1820), nom. cons.
- Sapotaceae Juss. (1789), nom. cons.
- Sarraceniaceae Dumort. (1829), nom. cons.
- \$\$\$Sladeniaceae Airy Shaw (1965)
- Styracaceae DC. & Spreng. (1821), nom. cons.
- Symplocaceae Desf. (1820), nom. cons.
- §Tetrameristaceae Hutch. (1959) (including Pellicieraceae L.Beauvis.)
- Theaceae Mirb. ex Ker Gawl. (1816), nom. cons.

It was clear in APG II that Theaceae *s.l.* could not be maintained. Subsequent work on the potential segregates has clarified the morphological pattern of variation (Stevens, 2001, for a summary). Sladeniaceae are recognized as distinct from Pentaphylacaceae; although the two are sister taxa, they share few obvious characters, and little would be gained by uniting them. However, Ternstroemiaceae have much in common with Pentaphylacaceae and so the former are included in the latter. Theaceae *s.s.* are not immediately related to these families.

The monogeneric Pellicieraceae are included in Tetrameristaceae; the resulting family, with three genera, is moderately well characterized. Mitrastemonaceae is a morphologically distinctive holoparasitic family that is well embedded in Ericales.

The biggest problem for APG III was the question of how to treat Primulaceae and their immediate relatives, a closely related group that in the past has often been recognized as a separate order. Although Primulaceae and relatives are clearly in Ericales, taxon limits in this group have been problematic. Maesaceae are a monogeneric family necessitated by the break-up of Myrsinaceae, as are a monogeneric Samolaceae Raf. by the break-up of Primulaceae (or Theophrastaceae would have to be extended, so becoming less recognizable; see Källersjö, Bergqvist & Anderberg, 2000; Ståhl & Anderberg, 2004, for information). The limits of Myrsinaceae were extended, and those of Primulaceae correspondingly restricted. Given that the limits of the two best-known families in the group, Myrsinaceae and Primulaceae, have been substantially changed, apomorphies are hard to recognize (less so for Maesaceae and Primulaceae *s.s.*), and the group as a whole has numerous synapomorphies and is easy to recognize so we extend the limits of Primulaceae (see also Mabberley, 2008), although we know that this move will not be universally welcomed.

LAMIIDS

- §*Boraginaceae Juss. (1789), nom. cons. (including Hoplestigmataceae Gilg, nom. cons.)
- Vahliaceae Dandy (1959)
- Icacinaceae Miers (1851), nom. cons.

Metteniusaceae H.Karst. ex Schnizl. (1860–1870)
 Oncothecaceae Kobuski ex Airy Shaw (1965)

The limits of Boraginaceae are drawn broadly. Not only are the phylogenetic relationships within the family still unclear, but as we know more about relationships within its component clades, they become less easy to distinguish (e.g. Gottschling *et al.*, 2005 for Cordioideae A.Gray). Molecular data suggest that Hoplestigmataceae are to be included in Boraginaceae *s.l.*, being placed in or near Cordioideae (K. Wurdack, pers. comm.; V. Savolainen and M. Powell, pers. comm.); *Hoplestigma* Pierre is similar in inflorescence, ovary, pollen, etc. to Boraginaceae. Relationships of Boraginaceae *s.l.* and Vahliaceae remain unclear, in the former case despite the sequencing of the whole plastid genome (Moore *et al.*, in press). Three families, Icacinaceae, Metteniusaceae and Oncothecaceae, are to be placed in this general area of the tree. Furthermore, genera that used to be included in Icacinaceae *s.l.* are also to be found here, although they do not group with Icacinaceae *s.s.* (Kårehed, 2001); these include *Apodytes* Arn., *Cassinopsis* Sond. and *Emmotum* Ham. (= Emmota-ceae Tiegh.). All these taxa show similarities to Garryales, and circumscription of that order could easily be expanded to include them if phylogenetic relationships warranted it. Revised family limits depend on further phylogenetic work.

Garryales Lindl. (1835)

Eucommiaceae Engl. (1907), nom. cons.
 §Garryaceae Lindl. (1834), nom. cons. (including Aucubaceae Bercht. & J.Presl)

Although Aucubaceae and Garryaceae (both monogeneric) appear distinct, there are several apomorphies for the combined group.

Gentianales Juss. ex Bercht. & J.Presl (1820)

Apocynaceae Juss. (1789), nom. cons.
 Gelsemiaceae Struwe & V.A.Albert (1995)
 Gentianaceae Juss. (1789), nom. cons.
 Loganiaceae R.Br. ex Mart. (1827), nom. cons.
 Rubiaceae Juss. (1789), nom. cons.

Lamiales Bromhead (1838)

§Acanthaceae Juss. (1789), nom. cons.
 Bignoniaceae Juss. (1789), nom. cons.
 Byblidaceae Domin (1922), nom. cons.
 Calceolariaceae Olmstead (2001)
 Carlemanniaceae Airy Shaw (1965)
 Gesneriaceae Rich. & Juss. (1816), nom. cons.
 Lamiaceae Martinov (1820), nom. cons.
 *Linderniaceae Borsch, K.Müll., & Eb.Fisch. (2005)
 Lentibulariaceae Rich. (1808), nom. cons.
 Martyniaceae Horan. (1847), nom. cons.
 Oleaceae Hoffmanns. & Link (1809), nom. cons.

Orobanchaceae Vent. (1799), nom. cons.
 Paulowniaceae Nakai (1949)
 Pedaliaceae R.Br. (1810), nom. cons.
 Phrymaceae Schauer (1847), nom. cons.
 §Plantaginaceae Juss. (1789), nom. cons.
 Plocospermataceae Hutch. (1973)
 Schlegeliaceae Reveal (1996)
 Scrophulariaceae Juss. (1789), nom. cons.
 Stilbaceae Kunth (1831), nom. cons.
 Tetrachondraceae Wettst. (1924)
 *Thomandersiaceae Sreem. (1977)
 Verbenaceae J.St.-Hil. (1805), nom. cons.

Note that relationships among many families in Lamiales, and to a certain extent also their limits, are still unclear. Some of us would prefer a vastly expanded circumscription of Scrophulariaceae, far beyond what it has ever included, whereas others are not so inclined. The limits of Plantaginaceae have been further restricted since APG II by the recognition of the family of small herbs with rather distinctive stem anatomy and floral morphology (e.g. Linderniaceae), and *Thomandersia* has been removed from Acanthaceae as the monogeneric Thomandersiaceae (Wortley, Harris & Scotland, 2007).

Solanales Juss. ex Bercht. & J.Presl (1820)

Convolvulaceae Juss. (1789), nom. cons.
 Hydroleaceae R.Br. ex Edwards (1821)
 Montiniaceae Nakai (1943), nom. cons.
 Solanaceae Juss. (1789), nom. cons.
 Sphenocleaceae T.Baskerv. (1839), nom. cons.

CAMPANULIDS

Aquifoliales Senft (1856)

Aquifoliaceae Bercht. & J.Presl (1820), nom. cons.
 §Cardiopteridaceae Blume (1847), nom. cons. (including Leptaulaceae Tiegh.)
 Helwingiaceae Decne. (1836)
 Phyllonomaceae Small (1905)
 Stemonuraceae Kårehed (2001)

Leptaulus Benth., previously unplaced, is assigned to Cardiopteridaceae (Kårehed, 2001).

Asterales Link (1829)

Alseuosmiaceae Airy Shaw (1965)
 Argophyllaceae Takht. (1987)
 Asteraceae Bercht. & J.Presl (1820), nom. cons.
 Calyceraceae R.Br. ex Rich. (1820), nom. cons.
 §Campanulaceae Juss. (1789), nom. cons. (including Lobeliaceae Juss., nom. cons.)
 Goodeniaceae R.Br. (1810), nom. cons.
 Menyanthaceae Dumort. (1829), nom. cons.
 Pentaphragmataceae J.Agardh (1858), nom. cons.

Phellinaceae Takht. (1967)
 Rouseaceae DC. (1839)
 §Stylidiaceae R.Br. (1810), nom. cons. (including
 Donatiaceae B.Chandler, nom. cons.)

Expansion of Stylidiaceae to include the monogeneric Donatiaceae is supported by morphology and geography, and the expanded Campanulaceae have strong support in molecular studies and are well characterized morphologically. Relationships within Campanulaceae *s.l.* are still unclear (Tank & Donoghue, in press), and a future attempt to recognize Lobeliaceae might either result in a clade poorly supported morphologically or entail the recognition of yet other families in this complex.

†Escalloniales R.Br. (1835)
 §Escalloniaceae R.Br. ex Dumort. (1829), nom. cons.
 (including Eremosynaceae Dandy, Polyosmaceae
 Blume, Tribelaceae Airy Shaw)

This is a heterogeneous group of genera that forms a well-supported clade, but one of uncertain position and within which relationships are poorly supported (Tank & Donoghue, in press). It is likely to be sister to Asterales or, more probably, to all campanulids apart from Asterales and Aquifoliales. Even if sister to Asterales, inclusion in that order would make the latter distinctly more heterogeneous; separate ordinal status is needed.

†Bruniales Dumort. (1829)
 Bruniaceae R.Br. ex DC. (1825), nom. cons.
 §Columelliaceae D.Don (1828), nom. cons. (including
 Desfontainiaceae Endl., nom. cons.)

An order is needed for the two families above. Winkworth, Lundberg & Donoghue (2008) found some support for a position sister to Asterales and Tank & Donoghue (in press) found stronger support for a position sister to the Paracryphiales–Dipsacales–Apiales clade; ordinal status is appropriate. Columelliaceae are broadly circumscribed because Desfontainiaceae have much in common with them; both families are Andean and monogeneric.

†Paracryphiales Takht. ex Reveal (1992)
 §Paracryphiaceae Airy Shaw (1965) (including
 *Quintiniaceae Doweld, Sphenostemonaceae
 P.Royen & Airy Shaw (1972))

Although these three families are at first sight strikingly different, they have several characters in common and form a strongly supported clade (Tank & Donoghue, in press); all are monogeneric and from the southwestern Pacific. Combination is in order (see also Myrtales, Crossosomatales). Tank & Donoghue (in press) found 100% bootstrap support for a position of Paracryphiales as sister to Dipsacales.

Dipsacales Juss. ex Bercht. & J.Presl (1820)
 Adoxaceae E.Mey. (1839), nom. cons.
 §Caprifoliaceae Juss. (1789), nom. cons. [including
 Diervillaceae Pyck, Dipsacaceae Juss., nom.
 cons., Linnaeaceae Backlund, Morinaceae Raf.,
 Valerianaceae Batsch, nom. cons.]

A broad circumscription of Caprifoliaceae is adopted here as it is widely preferred (Judd *et al.*, 2007; Mabberley, 2008). The expanded family is well characterized, but half the clades it includes are poorly characterized morphologically.

Apiales Nakai (1930)
 Apiaceae Lindl. (1836), nom. cons.
 Araliaceae Juss. (1789), nom. cons.
 Griseliniaceae J.R.Forst. & G.Forst. ex A.Cunn.
 (1839)
 Myodocarpaceae Doweld (2001)
 Pennantiaceae J.Agardh (1858)
 Pittosporaceae R.Br. (1814), nom. cons.
 §Torricelliaceae Hu (1934) (including Aralidiaceae
 Philipson & B.C.Stone, Melanophyllaceae Takht.
 ex Airy Shaw)

Expansion of Torricelliaceae to include Aralidiaceae and Melanophyllaceae is reasonable. All three are monogeneric and poorly known. Nevertheless, they form a strongly supported clade (e.g. Lundberg, 2001; Plunkett, 2001; Kårehed, 2002, 2003), and that they were kept separate before was a simple oversight. The recognition of Myodocarpaceae results from our improved understanding of relationships of members included formerly in Araliaceae.

TAXA OF UNCERTAIN POSITION

Apodanthaceae Takhtajan [three genera]
 Cynomoriaceae Endl. ex Lindl. (1833), nom. cons.
Gumillea Ruiz & Pav.
Petenaea Lundell (possibly Malvales)
Nicobariodendron (see Simmons, 2004; possibly
 Celastraceae).

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