

A phylogenetic classification of the land plants to accompany APG III

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A formal classification of the land plants that is compatible with the APG III classification is proposed. Previous classifications inflated taxonomic ranks, particularly of the angiosperms. If the major clades of green algae are recognized as classes, then all land plants, the embryophytes, should be included in a single class, here recognized as Equisitopsida. Accordingly, the 16 major clades of land plants, including the angiosperms, should all be recognized as subclasses, the angiosperms as Magnoliidae. Major clades within the angiosperms are then recognized as superorders. This classification still uses a few informal categories (e.g. eudicots, lamiids, etc.) within the angiosperms because this is convenient. Two new names are established: Amborellanae and Austrobaileya-nae. © 2009 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2009, **161**, 122–127.

ADDITIONAL KEYWORDS: APG system – land plant classification – land plant system.

INTRODUCTION

The Angiosperm Phylogeny Group (APG) classification (APG, 1998; APG II, 2003; APG III, 2009) is not a complete formal classification of the angiosperms and recognizes only families and orders, leaving many major nodes unnamed or giving these only informal names (magnoliids, monocots, lamiids, etc.). Partly this was done for practical reasons; the deeper nodes in many cases were weakly supported or unresolved and it was unwise to name these until they were better supported. Since the time of the first APG classification (APG, 1998), many of the unclear relationships in the angiosperm tree have been robustly resolved and it is now possible to provide a system of formally named higher taxa.

The biggest issue facing a higher-level phylogenetic classification of the angiosperms is that of the appropriate rank for the clade as a whole. Nearly all previous systems of classification recognized the angiosperms as comprising many subclasses (e.g.

Cronquist, 1981). Takhtajan's most recent classification (2009) was even more inflated and recognized the angiosperms as a class, Magnoliopsida, with 11 extant and one extinct subclasses. If the angiosperms as a whole are treated as a class, then by the tenets of phylogenetic classification the other major clades of land plants must be treated as at least at the rank of class, which necessitates that the major groups of algae be treated at an even higher ranks (see Lewis & McCourt, 2004, who classified the green plants as a whole as Kingdom Chlorobionta). This results in a classification in which ranks have been inflated beyond what is reasonable. If any concept of age enters into consideration, then the angiosperms must be treated at the same rank as extant clades of gymnosperms, which then permits other major clades of land plants to be given this same rank. In the Lewis & McCourt (2004) classification of green plants, it is clear that land plants should be given equal rank to the major groups of green algae, which they recognized as classes. If Charales are a class, then all land plants (embryophytes) should be placed in a single class (Table 1), which leaves only the rank of subclass available for each of the 16 major clades of

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Table 1. A working classification of class Equisetopsida [embryophytes] (Fig. 1)

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- Class Equisetopsida C.Agardh, *Classes Pl.*: 7. 20 May 1825
 Subclass Anthocerotidae Engl., in H.G.A. Engler & K.A.E. Prantl, *Nat. Pflanzenfam. I*, 3: 1, 6. 10 Oct 1893.
 Subclass Bryidae Engl., *Syllabus*: 47. Apr 1892.
 Subclass Marchantiidae Engl., in H.G.A. Engler & K.A.E. Prantl, *Nat. Pflanzenfam. I*, 3: 1, 5. 10 Oct 1893.
 Subclass Lycopodiidae Beketov, *Kurs Bot.* 1: 115. 1863.
- [monilophytes]
 Subclass Equisetidae Warm., *Osnov. Bot.*: 221. 22–28 Apr 1883.
 Subclass Marattiidae Klinge, *Fl. Est-Liv-Churland* 1: 93. 22–28 Jun 1882
 Subclass Ophioglossidae Klinge, *Fl. Est-Liv-Churland* 1: 94. 22–28 Jun 1882.
 Subclass Polypodiidae Cronquist, Takht. & Zimmerm., *Taxon* 15: 133. Apr 1966.
 Subclass Psilotidae Reveal, *Phytologia* 79: 70. 29 Apr 1996.
- [gymnosperms]
 Subclass Ginkgooidae Engl., in H.G.A. Engler & K.A.E. Prantl, *Nat. Pflanzenfam. Nacht.* 1: 341. Dec 1897.
 Subclass Cycadidae Pax, in K.A.E. Prantl, *Lehrb. Bot.*, ed. 9: 203. 5 Apr 1894.
 Subclass Pinidae Cronquist, Takht. & Zimmerm., *Taxon* 15: 134. Apr 1966.
 Subclass Gnetidae Pax, in K.A.E. Prantl, *Lehrb. Bot.*, ed. 9: 203. 5 Apr 1894.
- [angiosperms]
 Subclass Magnoliidae Novák ex Takht., *Sist. Filog. Cvetk. Rast.*: 51. 4 Feb 1967.
 Superorder Amborellanae M.W.Chase & Reveal, *stat. et superord. nov.* Basionym: Amborellaceae Pichon, *Bull. Mus. Hist. Nat. (Paris)*, ser. 2, 20: 384. 25 Oct 1948, *nom. cons.*
 Superorder Nymphaeanae Thorne ex Reveal, *Novon* 2: 236. 13 Oct 1992.
 Superorder Austrobaileyanae Doweld ex M.W.Chase & Reveal, *stat. et superord. nov.* Basionym: Austrobaileyoideae Croizat, *J. Arnold Arbor.* 21: 404. 24 Jul 1940.
- [core angiosperms – mesangiosperms]
 Unplaced order: Chloranthales Mart., *Consp. Regn. Veg.*: 12. Sep–Oct 1835. If assigned to a superorder not recognized here, the name, Chloranthanae Doweld, *Tent. Syst. Pl. Vasc.*: xxiv. 23 Dec 2001, is available.
- Superorder Magnolianaes Takht., *Sist. Filog. Cvetk. Rast.*: 51. 4 Feb 1967.
 Order Canellales Cronquist, *Bull. Jard. Bot. Bruxelles* 27: 17. 31 Mar 1957.
 Order Laurales Juss. ex Bercht. & J.Presl, *Přir. Rostlin*: 235. Jan–Apr 1820.
 Order Magnoliales Juss. ex Bercht. & J.Presl, *Přir. Rostlin*: 223. Jan–Apr 1820.
 Order Piperales Bercht. & J.Presl, *Přir. Rostlin*: 261. Jan–Apr 1820.
- Superorder Lillianaes Takht., *Sist. Filog. Cvetk. Rast.*: 473. 4 Feb 1967. [monocots]
 Order Acorales Mart., *Consp. Regn. Veg.*: 6. Sep–Oct 1835.
 Order Alismatales R.Br. ex Bercht. & J.Presl, *Přir. Rostlin*: 271. Jan–Apr 1820.
 Order Asparagales Link, *Handbuch* 1: 272. 4–11 Jul 1829.
 Order Dioscoreales Mart., *Consp. Regn. Veg.*: 9. Sep–Oct 1835.
 Order Liliales Perleb, *Lehrb. Naturgesch. Pflanzenr.*: 129. Sep–Oct 1826.
 Order Pandanales R.Br. ex Bercht. & J.Presl, *Přir. Rostlin*: 262. Jan–Apr 1820.
 Order Petrosaviales Takht., *Divers. Classif. Fl. Pl.*: 577. 24 Apr 1997.
- [commelinids]
 Unplaced family: Dasygongonaceae Dumort., *Anal. Fam. Pl.*: 54, 55. 1829. If assigned to an order not recognized here, the name, Dasygongonales Doweld, *Tent. Syst. Pl. Vasc.*: lxi. 23 Dec 2001, is available.
 Order Arecales Bromhead, *Mag. Nat. Hist.*, n.s., 4: 333. Jul 1840.
 Order Commelinales Mart., *Consp. Regn. Veg.*: 27. Sep–Oct 1835.
 Order Poales Small, *Fl. S.E. U.S.*: 48. 22 Jul 1903.
 Order Zingiberales Griseb., *Grundr. Syst. Bot.*: 167. 1–2 Jun 1854.
- Superorder Ceratophyllanaes Takht. ex Reveal & Doweld, *Novon* 9: 549. 30 Dec 1999.
 Order Ceratophyllales Link, *Handbuch* 2: 406. 4–11 Jul 1829.
- [eudicots]
 Superorder Buxanaes Takht. ex Reveal & Doweld, *Novon* 9: 549. 30 Dec 1999.
 Buxales Takht. ex Reveal (1996)
 Superorder Proteanaes Takht., *Sist. Filog. Cvetk. Rast.*: 401. 4 Feb 1967.
 Proteales Juss. ex Bercht. & J.Presl (1820)
 Superorder Ranunculanaes Takht. ex Reveal, *Novon* 2: 236. 13 Oct 1992.
 Ranunculales Juss. ex Bercht. & J.Presl (1820)
- [core eudicots]
 Superorder Myrothamnanaes Takht., *Divers. Classif. Fl. Pl.*: 134. 24 Apr 1997.
 Order Gunnerales Takht. ex Reveal, *Novon* 2: 239. 13 Oct 1992.

Table 1. *Continued*

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- Unplaced family: Dilleniaceae Salisb., *Parad. Lond.* 2: ad t. 73. 1 Jun 1807, *nom. cons.* If assigned to an order not recognized here, the name, Dilleniales DC. ex Bercht. & J. Presl, *Přir. Rostlin*: 223. Jan–Apr 1820, is available; if considered to be assigned to the rank of superorder, the name, Dilleniaceae Takht. ex Doweld, *Tent. Syst. Pl. Vasc.*: xxviii. 23 Dec 2001, is available.
- Unplaced order: Saxifragales Bercht. & J. Presl, *Přir. Rostlin*: 259. Jan–Apr 1820. If assigned to a superorder not recognized here, the name, Saxifraganae Reveal in *Phytologia* 76: 4. 2 May 1994, is available.
- Superorder Rosanae Takht., *Sist. Filog. Cvetk. Rast.*: 264. 4 Feb 1967.
- Order Vitales Juss. ex Bercht. & J. Presl, *Přir. Rostlin*: 225. Jan–Apr 1820.
- [fabids: eurosid I]
- Order Celastrales Link, *Handbuch* 2: 115. 4–11 Jul 1829.
- Order Cucurbitales Juss. ex Bercht. & J. Presl, *Přir. Rostlin*: 236. Jan–Apr 1820.
- Order Fabales Bromhead, *Edinburgh New Philos. J.* 25: 126. Jul 1838.
- Order Fagales Engl., *Syllabus*, ed. 1: 94. Apr 1892.
- Order Malpighiales Juss. ex Bercht. & J. Presl, *Přir. Rostlin*: 225. Jan–Apr 1820.
- Order Oxalidales Bercht. & J. Presl, *Přir. Rostlin*: 221. Jan–Apr 1820.
- Order Rafflesiales Mart., *Consp. Regn. Veg.*: 18. Sep–Oct 1835.
- Order Rosales Bercht. & J. Presl, *Přir. Rostlin*: 231. Jan–Apr 1820.
- Order Zygothylales Link, *Handbuch* 2: 228. 4–11 Jul 1829.
- [malvids: eurosid II]
- Order Brassicales Bromhead, *Edinburgh New Philos. J.* 24: 416. Apr 1838.
- Order Crossosomatales Takht. ex Reveal, *Phytologia* 74: 174. 25 Mar 1993.
- Order Geraniales Juss. ex Bercht. & J. Presl, *Přir. Rostlin*: 221. Jan–Apr 1820.
- Order Huerteales Doweld, *Tent. Syst. Pl. Vasc.*: xxxv. 23 Dec 2001.
- Order Malvales Juss. ex Bercht. & J. Presl, *Přir. Rostlin*: 221. Jan–Apr 1820.
- Order Myrtales Juss. ex Bercht. & J. Presl, *Přir. Rostlin*: 233. Jan–Apr 1820.
- Order Picramniales Doweld, *Tent. Syst. Pl. Vasc.*: xxxviii. 23 Dec 2001.
- Order Sapindales Juss. ex Bercht. & J. Presl, *Přir. Rostlin*: 224. Jan–Apr 1820.
- Superorder Berberidopsidanae Thorne & Reveal, *Bot. Rev.* 73: 93. 29 Jun 2007.
- Order Berberidopsidales Doweld, *Tent. Syst. Pl. Vasc.*: xxviii. 23 Dec 2001.
- Superorder Caryophyllanae Takht., *Sist. Filog. Cvetk. Rast.*: 144. 4 Feb 1967.
- Order Caryophyllales Takht., *Sist. Filog. Cvetk. Rast.*: 144. 4 Feb 1967.
- Superorder Santalanae Thorne ex Reveal, *Novon* 2: 236. 13 Oct 1992.
- Order Santalales R.Br. ex Bercht. & J. Presl, *Přir. Rostlin*: 234. Jan–Apr 1820.
- Superorder Asteranae Takht., *Sist. Filog. Cvetk. Rast.*: 451. 4 Feb 1967.
- Order Cornales Link, *Handbuch* 2: 2. 4–11 Jul 1829.
- Order Ericales Bercht. & J. Presl, *Přir. Rostlin*: 251. Jan–Apr 1820.
- [lamiids: euasterid I]
- Unplaced families: Boraginaceae Juss., *Gen. Pl.*: 128. 4 Aug 1789, *nom. cons.*; Icacinaceae Miers, *Ann. Mag. Nat. Hist.*, ser. 2, 8: 174. Sep 1851, *nom. cons.*; Metteniusaceae H.Karst. ex Schnizl., *Iconogr. Fam. Regni Veg.* 2: ad t. 142*. 1860–1870; Oncothecaceae Kobuski ex Airy Shaw, *Kew Bull.* 18: 264. 8 Dec 1965; and Vahliaaceae Dandy, *J. Hutchinson, Fam. Fl. Pl.*, ed. 2: 461. 4 Jun 1959. If assigned to an order not otherwise recognized here, the following names are available: Boraginales Juss. ex Bercht. & J. Presl, *Přir. Rostlin*: 244. Jan–Apr 1820; Icacinales Tiegh., *Bot. Jahresber. (Just)* 25(2): 406. 19 Jan 1900; Metteniusales Takht., *Divers. Classif. Fl. Pl.*: 352. 24 Apr 1997; Oncothecales Doweld, *Tent. Syst. Pl. Vasc.*: li. 23 Dec 2001; and Vahliales Doweld, *Tent. Syst. Pl. Vasc.*: xlvi. 23 Dec 2001.
- Order Garryales Mart., *Consp. Regn. Veg.*: 16. Sep–Oct 1835.
- Order Gentianales Juss. ex Bercht. & J. Presl, *Přir. Rostlin*: 248. Jan–Apr 1820.
- Order Lamiales Bromhead, *Mag. Nat. Hist.*, ser. 2, 2: 210. Apr 1838.
- Order Solanales Juss. ex Bercht. & J. Presl, *Přir. Rostlin*: 243. Jan–Apr 1820.
- [campanulids: euasterid II]
- Order Apiales Nakai, *Hisi-Shokubutsu*: 58. 1930.
- Order Aquifoliales Senft, *Lehrb. Forstl. Bot.*: 2: 118. 1856.
- Order Asterales Link, *Handbuch* 1: 731. 4–11 Jul 1829.
- Order Bruniales Dumort., *Anal. Fam. Pl.*: 34. 1829.
- Order Dipsacales Juss. ex Bercht. & J. Presl, *Přir. Rostlin*: 255. Jan–Apr 1820.
- Order Escalloniales Link, *Handbuch* 2: 339. 4–11 Jul 1829.
- Order Paracryphiales Takht. ex Reveal, *Novon* 2: 239. 13 Oct 1992.
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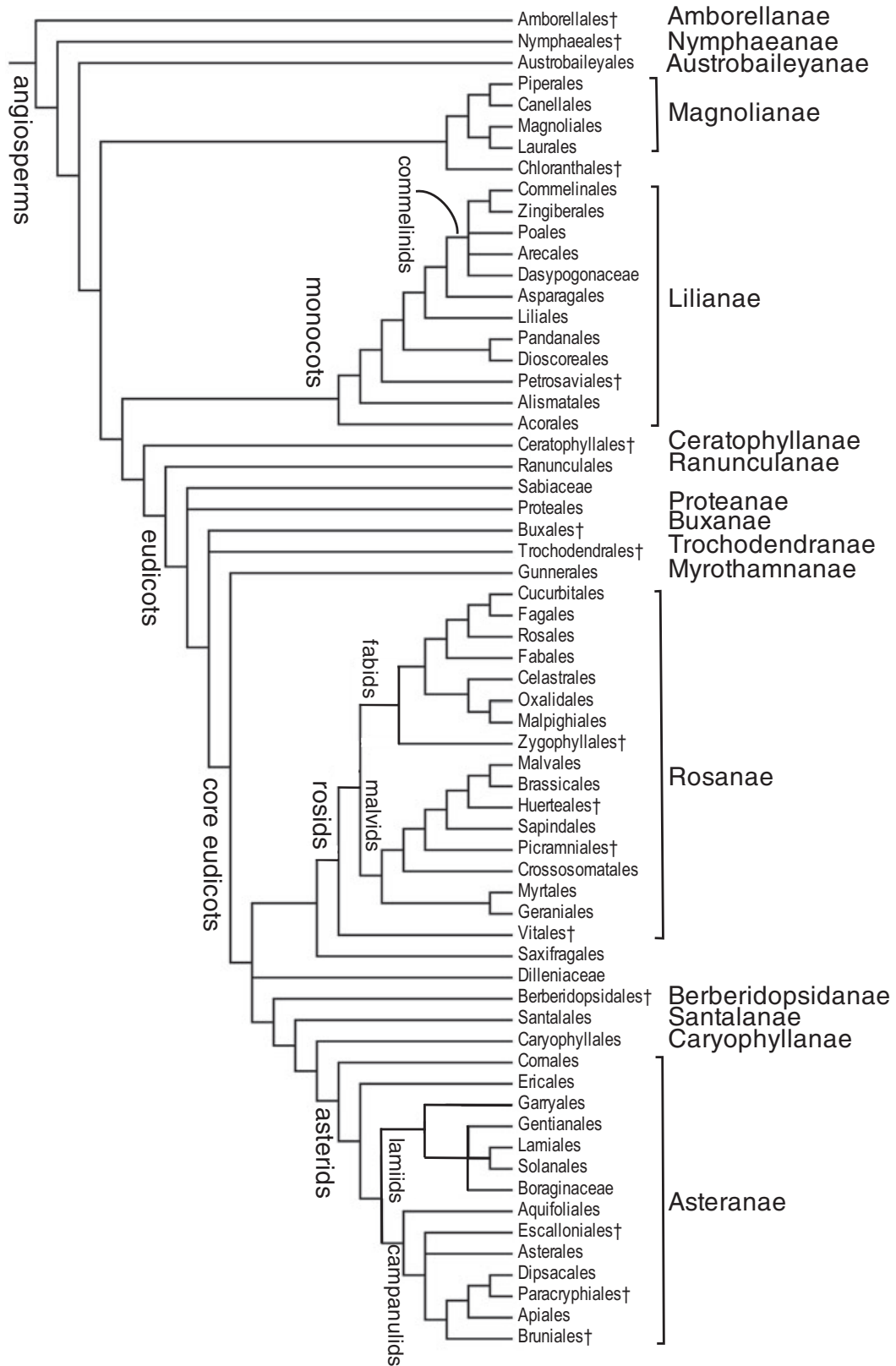


Figure 1. The APG III (2009) tree showing relationships of the orders of the angiosperms overlaid with the classification proposed here. The other groups of land plants are not shown.

land plants: mosses, hornworts, liverworts, lycophytes, whisk ferns, ophioglossoid ferns, marattioid ferns, osmundoid ferns and leptosporangiate ferns, cycads, conifers, *Ginkgo*, Gnetales and angiosperms. It would also be possible to recognize the extant gymnosperms as a single subclass. We have not chosen to do this because, by naming each of the gymnosperm groups as subclasses, it permits assignment of this rank to many of the fossil groups of gymnosperms, which are numerous and highly diverse and have unclear relationships to the extant gymnosperms. The Lewis & McCourt (2004) classification of green plants treated the land plants as a class, Embryophyceae, but this is not a legitimate name because it is not based on a taxonomic name; here we use Equisetopsida (Table 1).

Another alternative would be to treat each of the major groups of angiosperms as a subclass, which would result in seven subclasses being recognized, several presently without available, validly published names: a subclass each for Amborellales, Austrobaileyales, Ceratophyllales, eudicots, magnoliids, monocots and Nymphaeales. However, recognition of these seven entities as subclasses contains little grouping information because four of them contain only a single order (Amborellales, Austrobaileyales, Ceratophyllales and Nymphaeales). Also in the monocots and magnoliids, only orders would then be recognized, with no intermediate categories, whereas in eudicots it seems important to recognize superorders to capture more of their phylogenetic structure. This sort of unbalanced system would be confusing for some users.

If the angiosperms are considered to be a single subclass, then one is faced with what ranks should be applied to their major clades. Dahlgren (1980), Dahlgren, Clifford & Yeo (1985), Thorne (1992) and Thorne & Reveal (2007) used the category of superorder, and this seems an appropriate rank to use for major clades within the angiosperms. If too few clades are named, then the classification hampers communication because much detail is lost. If too many are adopted, then the classification becomes too complicated for most to remember. It is desirable to limit the number of higher taxa so they are easy to remember both as names and as concepts. We have therefore opted for an intermediate solution and have thus not given formal rank to the larger clades such as eudicots, mesangiosperms (Moore *et al.*, 2007) or smaller clades such as fabids (eurosoid I), malvids (eurosoid II), lamiids (euasterid I) and campanulids (eurosoid II) used in the APG III (2009) classification.

With the exception of Saxifragales, the way to name the rosids seems clear: one superorder with two informally named subgroups, fabids and malvids. At present, it is not clear to which informal subgroup Vitales should be assigned, but by naming the whole

clade Rosanae, the placement of Vitales, so far as formally recognized higher categories is concerned, is not a problem. Saxifragales could either be recognized as a superorder (as Saxifraganae), should they turn out to be sister to both rosids and asterid/Caryophyllales/Santalales/Berberidopsidales clades, or included in Rosanae if they are found to be exclusively related to the rosids. If sister to the larger clade in which the asterids are embedded, then they should also be recognized as a superorder.

The problem in the remaining angiosperms, the larger asterid clade in which the asterids *sensu* APG III are embedded, is not as simple, and there appear to be two options. It seems to be clear that Berberidopsidales, Santalales and Caryophyllales are related to the asterids (Tank & Donoghue, in press), and there are morphological similarities that could prove to be synapomorphic for this larger clade (Nandi, Chase & Endress, 1998). The simplest solution, and one that parallels the treatment given to the rosids, their sister clade, is to name the larger assemblage Asteranae. The drawback to this solution is that these groups have never been treated as asterids, but then before APG (1998) Cornales and Ericales had never been considered asterids either, so this just expands the definition of what is considered an asterid. Dilleniaceae could be recognized as a superorder (as Dilleniaceae) should they be found to be sister to both Rosanae and Asteranae or included in one or the other, depending on where they eventually are placed.

The other equally acceptable solution is to give the name Asteranae to the group considered to be asterids in APG and then to recognize each of these orders as monordinal superorders. It might have been preferable not to recognize superorders for the other major clades of eudicots, but this would have meant assigning all eudicots to a single superorder (Rosanae). However, this would have made the classification too simple and with so many clades left unnamed that the resulting classification would not be useful for communication.

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