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A subfamilial classification for the expanded asparagalean families Amaryllidaceae, Asparagaceae and Xanthorrhoeaceae

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We provide here a subfamilial scheme for the expanded asparagalean families Amaryllidaceae, Asparagaceae and Xanthorrhoeaceae. Our recommendation is that the first family has three subfamilies (Agapanthoideae, Allioideae and Amaryllidoideae), the second has seven (Agavoideae, Aphyllanthoideae, Asparagoideae, Brodiaeoideae, Lomandroideae, Nolinoideae and Scilloideae) and the last has three (Asphodeloideae, Hemerocallidoideae and Xanthorrhoeoideae). Tribal names are provided for the large subfamilies Allioideae, Amaryllidoideae and Scilloideae. The use of these subfamily names permits easier descriptions of characters by specialists for these well-supported subclades, but the use of the broader family limits greatly simplifies the taxonomy of Asparagales and thus makes the teaching of these families much easier. A new subfamilial name, Xanthorrhoeoideae, and a new tribal name, Oziroëeae, are proposed. *Botanical Journal of the Linnean Society*, 2009, **161**, 132–136.

ADDITIONAL KEYWORDS: APG classification – Asparagales classification – Asparagales system – molecular phylogenetics – monocot classification.

IINTRODUCTION

The classification of the lilioid monocots has long been problematic, with some authors largely treating them all as one family, Liliaceae *s.l.* (Cronquist, 1981), and others, such as Dahlgren, Clifford & Yeo (1985), splitting them into a number of orders, often composed of many small families. The strategy of Dahlgren *et al.* (1985) was an attempt to name as families groups in which they had some confidence of monophyly. In fact, this often turned out not to be the case (for example, Anthericaceae *sensu* Dahlgren *et al.*; Phormiaceae *sensu* Dahlgren *et al.*). Most researchers found the broad family limits of Liliaceae unacceptable from a descriptive standpoint and resorted to the use of subfamilies when working comparatively, but most were unwilling to take up the Dahlgrenian approach because of the use of so many small or poorly known families. Teaching plant taxonomy in the Dahlgrenian context was also difficult – there were simply too many families to teach any reasonable number of them. As a result, students continually came into contact with genera such as *Agapanthus* L'Hér., *Hemerocallis* L. and other cultivated genera that are in families not generally taught in plant taxonomy courses. Although not monophyletic, Liliaceae *s.l.* at least gave students and flora-writers a box, albeit large and highly heterogeneous, into which they could place such plants.

When the first molecular studies started to focus on the genera of Liliaceae *s.l.*, they used Dahlgren *et al.* (1985) as a guide to which taxa should be sampled. Dahlgren's justification (cited above) for the use of these narrowly defined families notwithstanding, it produced a legacy of his circumscriptions being used to label published DNA trees (for example, Chase *et al.*, 1995; Rudall *et al.*, 1997). When one of the families in Dahlgren's treatment was found to be polyphyletic (for example, Anthericaceae), there was a tendency not to lump the newly discovered clades into

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Table 1. Recognized subfamily names *sensu* APG III (2009) for bracketed families listed under Alliaceae, Asparagaceae and Xanthorrhoeaceae in APG II (2003)

APG II bracketed family	APG III family	APG III subfamily
Agapanthaceae	Amaryllidaceae*	Agapanthoideae
Agavaceae	Asparagaceae	Agavoideae
Alliaceae	Amaryllidaceae	Allioideae
Amaryllidaceae	Amaryllidaceae	Amaryllidoideae
Aphyllanthaceae	Asparagaceae	Aphyllanthoideae
Asparagaceae	Asparagaceae	Asparagoideae
Asphodelaceae	Xanthorrhoeaceae	Asphodeloideae
Hemerocallidaceae	Xanthorrhoeaceae	Hemerocallidoideae
Hesperocallidaceae	Asparagaceae	Agavoideae
Hyacinthaceae	Asparagaceae	Scilloideae
Laxmanniaceae	Asparagaceae	Lomandroideae
Ruscaceae	Asparagaceae	Nolinoideae
Themidaceae	Asparagaceae	Brodiaeoideae
Xanthorrhoeaceae	Xanthorrhoeaceae	Xanthorrhoeoideae subfam. nov.

*The name Amaryllidaceae has recently been conserved over Alliaceae, the older name (R. K. Brummitt, Kew, pers. comm.).

other, already recognized families, but rather to name each of these clades as a separate family, and so we ended up with Boryaceae and Laxmanniaceae as well as Anthericaceae *s.s*. Naturally, when APG (1998) was being planned, the narrow circumscriptions were inherited because the Angiosperm Phylogeny Group (APG) relied heavily on the DNA phylogenetic trees for support of the proposed classification.

One of the results of Dahlgren's legacy of many small families was observed in teaching; only a few families of the 26 in Asparagales *sensu* APG (1998) were routinely taught, leaving many common horticultural plants out of the classroom. As relationships were clarified within Asparagales, it became apparent that there were some larger clades composed of several families with reasonably obvious characters that could be named. The other orders into which lilioid taxa fell were much smaller and, because of the accidents of history, these were more readily condensed into larger families at an earlier stage. For example, *Uvularia* L. was moved into Colchicaceae early on rather than retained as Uvulariaceae *s.s*. when most of the genera previously allied to it were found to be unrelated. Clarification of higher level relationships in Asparagales took longer (and required more DNA regions) to work out, but we now have well-supported phylogenetic hypotheses for the order (Fay *et al.*, 2000; Pires *et al.*, 2006).

In APG II (2003), the compilers attempted to rectify this problem by naming the larger clades and then used brackets to indicate optional narrower circumscriptions. These optional circumscriptions were used to test the waters to see whether most users of APG had an interest in trading fewer, more broadly circumscribed families for the narrowly defined families that were Dahlgren's legacy to the APG process. Providing these options provoked a decidedly negative response, regardless of whether the person favoured the broader or narrower circumscriptions, and, in APG III (2009), brackets were abandoned in favour of the broader circumscriptions in Asparagales. Bracketed families *sensu* APG II and the recognized subfamilies *sensu* APG III are listed in Table 1.

Asparagales are the largest order of monocots (Chase *et al.*, 1995, 2000, 2006) and, in APG III (2009), the number of families recognized has fallen from 26 (APG, 1998) to 14, still a large number, but one that is more manageable for teaching purposes. These also have at least some characters that can be used to recognize them (see below). If anything, these broader circumscriptions are easier to identify for most users than the more narrowly circumscribed ones, but we admit that these broader family limits are also clearly more heterogeneous in morphological and cytological terms (Pires *et al.*, 2006).

Morphological synapomorphies, even for the Dahlgrenian (Dahlgren *et al.*, 1985) families, are problematic. Some genera that we now know belong in different major clades are indistinguishable in the field. *Trachyandra* Kunth and *Chlorophytum* Ker Gawl. are impossible to distinguish, for example, but the former is a member of Asphodeloideae (Xanthorrhoeaceae *sensu* APG III, 2009) and the latter a member of Agavoideae (Asparagaceae *sensu* APG III, 2009). However, for the two largest of the condensed families, Asparagaceae and Amaryllidaceae, recogni-

tion is relatively easy. Both are higher asparagoids (with successive microsporogenesis and mostly alkaloids). Asparagaceae have racemes (rarely umbels, for example Brodiaeoideae; Fay & Chase, 1996) and either three or more bracts subtending, but not enclosing, the inflorescence, or no bracts. Amaryllidaceae have umbels enclosed by two (sometimes fused) subtending bracts. Xanthorrhoeaceae *s.l.* have simultaneous microsporogenesis, xanthoquinones and, commonly, a strange form of thyrsoid inflorescence (for example, in *Hemerocallis* and *Phormium* J.R.Forst. & G.Forst.). If fewer flowers make up the inflorescence, this unusual branching type is less easily discerned but, given that *Trachyandra* (Xanthorrhoeaceae) and *Chlorophytum* (Agavaceae) are impossible to distinguish, these circumscriptions are no worse for students than any other circumscription used for these taxa. At least it is a simple, if morphologically difficult, system to use.

To allow specialists to communicate information about characters within these taxa more easily, given how heterogeneous these large families are, we provide below a system of subfamilies that should facilitate communication. It should be noted that, at present, the International Code of Botanical Nomenclature (McNeill *et al.*, 2006) governing plant names does not permit the conservation of names at the rank of subfamily. As a result, some names must be adopted presently that are unfortunate given the long-standing use of other well-known names (for example, Scilloideae instead of Hyacinthoideae or Nolinoideae instead of Ruscoideae). For Amaryllidaceae subfamily Amaryllidoideae and Asparagaceae subfamily Scilloideae, only tribes are listed (Meerow *et al.*, 2000), as these two subfamilies contain many genera and generic circumscription is in a state of flux, particularly in the latter (Pfosser & Speta, 1999; Manning, Goldblatt & Fay, 2004; Manning *et al.*, 2009). For Amaryllidaceae subfamily Allioideae, a tribal classification is presented but, in this case, the genera are also listed (Fay *et al.*, 2006).

Amaryllidaceae J.St.-Hil., Expos. Fam. Nat. 1: 134. Feb–Apr 1805, nom. cons.
Agapanthoideae Endl., Gen. Pl.: 141. Dec 1836.
Agapanthus L'Hér., nom. cons. (1789).
Allioideae Herb., Amaryllidaceae: 48. late Apr 1837.
Allieae Dumort., Fl. Belg.: 139. 1827.
Allium L. (1753 – including *Caloscordum* Herb., *Milula* Prain, *Nectaroscordum* Lindl.)
Gilliesieae Baker, J. Linn. Soc., Bot. 14: 509. 24 Apr 1875.
Ancrumia Harv. ex Baker (1877).
Erinna Phil. (1864).
Gethyum Phil. (1873).
Gilliesia Lindl. (1826).
Ipheion Raf. (1836).
Leucocoryne Lindl. (1830 – including *Pabellonia* Quezada & Martic. and *Stemmatium* Phil.)
Miersia Lindl. (1826).
Nothoscordum Kunth (1843).
Schickendantziella Speg. (1903).
Solaria Phil. (1858).
Speea Loes. (1927).
Trichlora Baker (1877).
Tristagma Poepp. (1833).
Tulbaghieae Endl. ex Meisn., Pl. Vasc. Gen.: Tab. Diagn. 397, 399, Comm. 302. 17–20 Dec 1842.
Tulbaghia L. corr. Giseke, 1792, nom. et orth. cons.
Amaryllidoideae Burnett, Outl. Bot.: 446. Feb 1835.
Amaryllideae Dumort., Anal. Fam. Pl.: 58. 1829.
Calostemmateae D.Müll.-Doblies & U.Müll.-Doblies, Feddes Repert. 107 (Short commun.): 7 Dec 1996.
Cyrtantheae Traub, Herbertia 5: 111. Nov 1938.
Eucharideae Hutch., Fam. Fl. Pl. 2: 130. 20 Jul 1934.
Eustephieae Hutch., Fam. Fl. Pl. 2: 130. 20 Jul 1934.
Galantheae Parl., Fl. Ital. 3: 75. 1858.
Gethyllideae Dumort., Anal. Fam. Pl.: 58. 1829.
Haemantheae Hutch. Fam. Fl. Pl. 2: 130. 20 Jul 1934.
Hippeastreae Herb. ex Sweet, Brit. Fl. Gard., ser. 2, 1: ad t. 14. 1 Sep 1829.
Hymenocallideae Small, Man. S.E. Fl.: 315. 30 Nov 1933.
Lycorideae Traub ex D.Müll.-Doblies & U.Müll.-Doblies, Feddes Repert. 107 (Short commun.): 6. Dec. 1996.
Narcisseae Lam. & DC., Syn. Pl. Fl. Gall.: 165. 30 Jun 1806.
Pancratieae Dumort., Anal. Fam. Pl.: 58. 1829.
Stenomesseae Traub, Pl. Life 19: 60. Jan 1963.

Asparagaceae Juss., Gen. Pl.: 40. 4 Aug 1789, nom. cons.
Agavoideae Herb., Amaryllidaceae: 48, 57, 67, 121. late Apr 1837.
Agave L. (1753).
Anemarrhena Bunge (1831).
Anthericum L. (1753).
Behnia Didr. (1855).
Beschorneria Kunth (1850).
Camassia Lindl., nom. cons. (1832).
Chlorogalum Lindl.) Kunth (1843).
Chlorophytum Ker Gawl. (1807).
Echeandia Ort. (1800).
Hastingsia S.Watson (1879).
Herreria Ruiz & Pav. (1794).
Herreriopsis Perrier (1934).
Hesperocallis A.Gray (1868).
Hosta Tratt. (1812).
Leucocrinum Nutt. ex A.Gray (1837).

Paradisea Mazzuc., nom. cons. (1811).
Schoenolirion Torr., nom. cons. (1855).
Yucca L. (1753).

Aphyllanthoideae Lindl., Veg. Kingd.: 202, 205. Jan-Mai 1846.
Aphyllanthes L. (1753).

Asparagoideae Burmeist., Handb. Naturgesch.: 224. 1837
Asparagus L. (1753).
Hemiphylacus S.Watson (1883).

Brodiaeoideae Traub, Pl. Life 28: 131. 22 Feb 1972.
Androstephium Torr. (1859).
Bessera Schult.f. (1829).
Bloomeria Kellogg (1863).
Brodiaea Sm., nom. cons. (1810).
Dandya H.E.Moore (1953).
Dichelostemma Kunth (1843)
Jaimehintonia B.L.Turner (1993).
Milla Cav. (1794).
Muilla S.Watson (1879).
Petronymphe H.E.Moore (1951).
Triteleia Douglas ex Lindl. (1830).
Triteleiopsis Hoover (1941).

Lomandroideae Thorne & Reveal, Bot. Rev. 73: 82. 29 Jun 2007.
Arthropodium R.Br. (1810).
Chamaescilla F.Muell. ex Benth. (1878).
Cordyline Comm. ex R.Br. (1810).
Eustrephus Cav. (1795).
Laxmannia R.Br. (1810).
Lomandra Labill. (1805).
Thysanotus R.Br., nom. cons. (1810).
Xerolirion A.S.George (1986).

Nolinoideae Burnett, Outl. Bot.: 985, 1095, 1106. Feb 1835.
Aspidistra Ker Gawl. (1822).
Calibanus Rose (1906).
Comospermum Rauschert (1982).
Convallaria L. (1753).
Danae Medik. (1787).
Dracaena Vand. ex L. (1767).
Eriospermum Jacq. ex Willd. (1799)
Maianthemum F.H.Wigg. (1780).
Nolina Michx. (1803).
Ophiopogon Ker Gawl. (1807).
Peliosanthes Andrews (1808).
Polygonatum Mill. (1754).
Ruscus L. (1753).
Semele Kunth (1842).
Speirantha Baker (1875).
Tupistra Ker Gawl. (1814).

Scilloideae Burnett, Outl. Bot.: 428. Feb 1835.
Hyacintheae Dumort., Fl. Belg.: 141. 1827.
Ornithogaleae Rouy, Fl. France 12: 330, 411. Nov 1910.
Oziroëeae M.W.Chase, Reveal & M.F.Fay, stat. et trib. nov. Basionym: Oziroëoideae Speta, *Phyton (Horn)* 38: 51. 14 Aug 1998.
Urgineeae Rouy, Fl. France 12: 330, 424. Nov 1910.

Xanthorrhoeaceae Dumort., Anal. Fam. Pl.: 60, 62, 103. 1829, nom. cons.

Asphodeloideae Burnett, Outl. Bot.: 427. Feb 1835.
Aloe L. (1753).
Asphodelus L. (1753).
Asphodeline Rchb. (1830).
Eremurus M.Bieb. (1810).
Haworthia Duval, nom. cons. (1809).
Kniphofia Moench (1794).

Hemerocallidoideae Lindl., Veg. Kingd.: 201, 205. Jan-Mai 1846
Eccremis Willd. ex Baker (1876).
Hemerocallis L. (1753).
Johnsonia R.Br. (1810).
Phormium J.R.Forst. & G.Forst. (1775).

Xanthorrhoeoideae M.W.Chase, Reveal & M.F.Fay, subfam. nov. Basionym: Xanthorrhoeaceae Dumort., Anal. Fam. Pl.: 60, 62, 103. 1829, nom. cons.
Xanthorrhoea Sm. (1798).

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