Classification and phylogeny of Amaryllidaceae, the modern synthesis and the road ahead: a review

Clasificación y filogenia de Amaryllidaceae, la síntesis moderna y el camino por recorrer: una revisión

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Resumen

La clasificación y la historia filogenética de las Amaryllidaceae se revisa desde el amanecer de la sistemática molecular en la década de 1990. Actualmente, se reconoce que la familia comprende tres subfamilias: Agapanthoideae, Allioideae y Amaryllidoideae, de las cuales la última es la más grande. La familia probablemente se originó en Gondwana, en lo que ahora es África. Agapanthoideae es monotípica, endémica de Sudáfrica y la primera rama del árbol genealógico de la vida de la familia; Allioidieae es hermana de Amaryllidoideae. Se reconocen cuatro tribus en Allioideae: Allieae (monotípica, con casi 1000 especies de *Allium* en el hemisferio norte), Gilliesieae (5-7 géneros del sur de América del Sur), Leucocoryneae (seis géneros principalmente en el sur de América del Sur) y Tulbaghieae (monotípica, con unas 30 especies endémicas de Sudáfrica). Amaryllidoideae es cosmopolita, pero en su mayoría pantropical, y consta de 13 tribus. Los centros de diversidad se encuentran en Sudáfrica, América del Sur y la región del Mediterráneo. El clado americano es hermano del clado euroasiático (tribus Galantheae, Lycorideae, Narcisseae y Pancratieae) de la subfamilia. Las Amaryllidoideae americanas se resuelven en dos grupos monofiléticos, 1) el clado hippeastroide (tribus Griffineae e Hippeastreae) y 2) el clado tetraploide andino (tribus Clinantheae, Eucharideae, Eustephieae e Hymenocallideae). Se revisan los análisis moleculares para cada clado principal de la familia, junto con los cambios taxonómicos resultantes. Se discuten brevemente las direcciones para futuros estudios.

Palabras clave

Geófitos, monocotiledóneas, sistemática, secuencias de ADN, taxonomía.

Summary

The classification and phylogenetic history of the Amaryllidaceae is reviewed since the dawn of molecular systematics in the 1990's. The family is now recognized as comprising three subfamilies: Agapanthoideae, Allioideae, and Amaryllidoideae, of which the latter is the largest. The family likely had a Gondwanaland origin in what is now Africa. Agapanthoideae is monotypic, endemic to South Africa, and the first branch in the family tree of life; Allioidieae is sister to Amaryllidoideae. Four tribes are recognized in Allioideae: Allieae (monotypic, with nearly 1000 species of *Allium* across the Northern Hemisphere), Gilliesieae (5-7 genera in southern South America), Leucocoryneae (six genera mostly in southern South America), and Tulbaghieae (monotypic, with ca. 30 species endemic to South Africa). Amaryllidoideae is cosmopolitan, but mostly pantropical, consisting of 13 tribes. Centers of diversity occur in South Africa, South America and the Mediterranean region. The American clade is sister to the Eurasian clade (tribes Galantheae, Lycorideae, Narcisseae and Pancratieae) of the subfamily. The American Amaryllidoideae resolves as two monophyletic groups, 1) the hippeastroid clade (tribes Griffineae and Hippeastreae) and 2) the Andean tetraploid clade (tribes Clinantheae, Eucharideae, Eustephieae, and Hymenocallideae). Molecular analyses are reviewed for each main clade of the family, along with the resultant taxonomic changes. Directions for future studies are briefly discussed.

Key words

DNA sequences, geophytes, monocots, systematics, taxonomy.

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INTRODUCTION

Our understanding of angiosperm phylogeny has undergone a revolution over the past three decades, largely due to two spectacular advances in the science of systematic botany (Judd *et al.,* 2015). With the advent of polymerase chain reaction (PCR) technology (Saiki *et al*., 1988), direct comparison of the nucleotide sequences of organismal DNA became possible. Secondly, phylogenetic analysis has become the standard methodology for testing hypotheses of phylogeny among organisms in systematic biology (Wiley, 1981; Felsenstein, 2004) based upon principles formally enumerated by Hennig (1966). To the parsimony method (Kitching *et al*., 1998) has been added both maximum likelihood (Huelsenbeck & Crandall, 1995) and Bayesian analysis (Beaumont, 2010), which have proven valuable in dealing with large DNA sequence datasets.

The precise relationship of Amaryllidaceae J.St.-Hil. to other Asparagales remained elusive until Fay & Chase (1996) used the plastid gene rubisco (*rbcL*) to argue that *Agapanthus* L'Hér., Alliaceae Borkh., and Amaryllidaceae form a monophyletic group (also evident in Chase *et al*., 1995a, b), and that together they are related most closely to Hyacinthaceae Batsch ex Borkh. s.s. and the resurrected family Themidaceae Salisb. (the former tribe Brodiaeeae of Alliaceae), both now classified as subfamilies within a broad circumscription of Asparagaceae Juss. (APG, 2009). They recircumscribed Amaryllidaceae to include *Agapanthus*, previously included in Alliaceae, as subfamily Agapanthoideae Endl. Subsequent analyses of multiple DNA sequences from both the chloroplast and nuclear genomes have shown quite strongly that *Agapanthus*, Amaryllidaceae, and Alliaceae represent a distinct lineage within the monocot order Asparagales Link (Meerow *et al*., 1999; Fay *et al*., 2000), but the exact relationships among the three groups have been difficult to resolve with finality (Graham *et al*., 2006); APG II (APG, 2003) recommended treating all three as a single family, Alliaceae (which had nomenclatural priority at that time), and more emphatically in APG III (APG, 2009), but as Amaryllidaceae, reflecting the successful proposal for superconservation of the name (Meerow *et al*., 2007). Current consensus has Allioideae Herb. and Amaryllidoideae Burnett as sister groups, and Agapanthoideae sister to both (Baker *et al*., 2022).

Based on the cladistic relationships of chloroplast DNA sequences (Ito *et al*., 1999; Meerow *et al*., 1999) all three subfamilies originated in Africa (Gondwanaland) and infrafamilial relationships are resolved along biogeographic lines (Fig. 1). Subfamily Amaryllidoideae, the largest in number of genera, has colonized all continents except Antarctica. Janssen & Bremer (2004) estimated the age of the family at 87 million years before present (MYBP). The only fossil for the family is from early Eocene western North America and was diagnosed as allied to Allioideae (Pigg *et al*., 2018); contested by Friesen (2022). A leaf fossil from Colombia assigned by Wing *et al*. (2018) to Amaryllidaceae is at best ambiguous.

Agapanthoideae

The genus *Agapanthus* (subfamily Agapanthoideae) is restricted to South Africa and consists of six to 10 species of rhizomatous, evergreen or deciduous perennials, most with blue flowers (Snoeijer, 2004). The flowers have superior ovaries, and the genus contains saponins. To date, no molecular studies have been conducted to estimate the species phylogeny of this relatively small genus.

Allioideae

Allioideae is represented in Africa by the South African endemic genus *Tulbaghia* L., and a single species of *Allium* L., but is most diverse generically in southern South America (Chile and Argentina). Three tribes were recognized by some (Chase *et al.,* 2009; Escobar *et al.,* 2020): Allieae Dumort., Gilliesieae Baker and Tulbaghieae Endl. ex Meisn. Leucocoryneae Ravenna is now accepted as a fourth distinct tribe (Sassone *et al*., 2018), of which the first and third consist of only a single genus, *Allium* and *Tulbaghia* (the monotypic genus *Prototulbaghia* Vosa appears nested within *Tulbaghia* (Stafford *et al*., 2016)).

The subfamily is characterized by solid styles, superior ovaries and the unique allyl sulfide chemistry that gives many members their characteristic garlic odor. Monotypic Allieae is the largest tribe, entirely due to the speciose genus *Allium* (Friesen, 2022; Li *et al*., 2010).

Tulbaghieae

The South African endemic genus *Tulbaghia* consists of 20-30 species and is badly in need of a thorough taxonomic revision. Vosa (2007) recognized a monotypic segregate genus *Prototulbaghia* that in a recent molecular study resolved as sister to one subclade of *Tulbaghia* spp. (Stafford *et al.*, 2016). Vosa (2009) presented a synoptic classification for the genus, distinguishing species groups (sections) primarily on the basis of the morphology of the staminal corona, recognizing 23 species, but Stafford *et al.* (2016) suggest that there may be as many as 30. *Tulbaghieae* is endemic to South Africa and is sister to the South American tribes Gilliesieae (Costa *et al.,* 2020; Escobar *et al.,* 2020) and Leucocoryneae (ca. six genera Sassone & Giussani, 2018).

Allieae

Allium contains over 900 species (Herden *et al.,* 2016) and is one of the largest genera of monocots known. More than 50 species are used as edible, medicinal and ornamental crops. Variable morphologically as well as ecologically, it has spread across the Holarctic region, inhabiting dry subtropics to boreal vegetation. Only a single species of *Allium* occurs outside the Holartic zone, *A. synnotia* G.Don (syn. *A. dregeanum* Kunth), native to South Africa (de Wilde-Duyfjes, 1976; de Sarker *et al.,* 1997), though Friesen (2022) suggests that it may have been introduced by early European colonists. An Old World center of diversity encompasses the Mediterranean Basin to Central and Eastern Asia, with a second smaller one in western North America. Friesen (2022), Friesen *et al.* (2006) and Li *et al.* (2010) review the infrageneric taxonomic history of this complex genus. Molecular studies have either addressed the phylogenetic relationships of the entire genus (Mes *et al.,* 1997; Dubouzet & Shinoda, 1999; He *et al.,* 2000; Fritsch & Friesen, 2002; Friesen *et al.,* 2006; Li *et al.,* 2010, 2016b; Xie *et al.,* 2020) or specific subgenera and sections *Amerallium* Traub: Samoylov *et al.,* 1995, 1999; *Cyathophora* (R.M.Fritsch) R.M.Fritsch: Li *et al.*, 2016a *Melanocrommyum* (Webb & Berth.) Rouy: Dubouzet & Shinoda, 1998; Mes *et al.*, 1999; Gurushidze *et al.*, 2008, 2010; Fritsch *et al.*, 2010, *Rhizirideum* (G. Don ex Koch) Wendelbo: Dubouzet *et al.*, 1997, section *Cepa* (Mill.) Prokh: Gurushidze *et al.*, 2007, origins of *A. ampeloprasum* L. horticultural races and section *Allium*: Hirschegger *et al.*, 2010). Other molecular phylogenetic investigations have been concerned with the origins of economically important *Allium* crops (e.g. Friesen & Klaas, 1998; Friesen *et al.*, 1999; Blattner & Friesen, 2006; Friesen, 2022). Nguyen *et al.* (2008) examined the phylogeny of the western North American species and their adaptation to serpentine soils.

Friesen *et al.*'s (2006) analysis of 195 species of *Allium* using the ITS region of nrDNA presented a new subgeneric classification consisting of 15 monophyletic subgenera, and this is still mostly accepted. Earlier, Friesen *et al.* (2000) showed that the anomalous *Milula* Prain with a spicate inflorescence was nested within the Himalayan species of *Allium*. *Nectaroscordum* Lindl. and *Caloscordum* Herb. are also retained within *Allium*. Li *et al.* (2010) used ITS sequences along with the intron of the plastid gene *rps16* across over 300 *Allium* taxa and included a biogeographical analysis of the genus. Three major clades are consistently resolved (Fritsch, 2001; Fritsch & Friesen, 2002; Friesen *et al.*, 2006; Li *et al.*, 2010), which Xie *et al.*'s (2020) whole plastome phylogeny supports as well. Subgenera *Amerallium*, *Anguinum* G.Don ex W.D.J.Koch) N.Friesen, *Vvedenskya* (Kamelin) R.M.Fritsch, *Porphyroprason* (Ekberg) R.M.Fritsch and *Melanocrommyum* originated in eastern Asia. The putatively oldest lineage consists of only bulbous plants (subgenera *Nectaroscordum*, *Microscordum* (Maxim.) N.Friesen and *Amerallium*) that only rarely produce a rhizome (Fritsch & Friesen, 2002). The second clade includes subgenera *Caloscordum*, *Anguinum*, *Vvedenskya*, *Porphyroprason* and *Melanocrommyum*, and the third subgenera *Butomissa* (Salisb.) N. Friesen, *Cyathophora*, *Rhizirideum*, *Allium*, *Cepa*, *Reticulatobulbosa* (Kamelin) N. Friesen and *Polyprason* Radić. The latter two contain both rhizomatous and bulbous species. The third clade was the most poorly resolved in these analyses and includes a number of non-monophyletic subgenera (Li *et al.*, 2010), but resolution and levels of support were greatly increased with analysis of whole plastomes (Xie *et al.*, 2020). A scenario of rapid radiation was proposed for this clade. The first two clades contain both Old and New World species; almost all of the western North American species are classified in subgenus *Amerallium* (Nguyen *et al*., 2008), which has sparingly extended to central and eastern North America. The only other North American species are members of subg. *Anguinum* (Li *et al*., 2010; Xie *et al*., 2020).

Costa *et al*. (2020) estimated the age of Allioideae as ca. 63 million years and hypothesized that the Indian plate rafted Allieae to the northern hemisphere from which the genus *Allium* (ca. 52 MYBP) diversified via polyploidy and geographic spread throughout the Northern Hemisphere. Friesen (2022) supported this hypothesis.

Gilliesieae and Leucocoryneae

The tribes Gilliesieae and Leucocoryneae are entirely restricted to the American continents and are most diverse in southern South America, especially Argentina and Chile, and includes such established ornamental bulb crops as *Ipheion* Raf. and *Leucocoryne* Lindl. Only one species of *Nothoscordum* Kunth extends outside of that region, and may be adventive. The sister relationship of these tribes to Tulbaghieae (Fay & Chase, 1996; Fay *et al*., 2006) suggests an austral entry into South America, perhaps via Antarctica, as has been suggested for many groups showing a similar biogeographic scenario (Raven & Axelrod, 1974). Unfortunately, generic limits within the group remain problematic, with many species having been variously treated as members of diverse genera (Rahn, 1998; Zöllner & Arriagada, 1998; Rudall *et al*., 2002; Fay *et al*., 2006).

The two tribes are immediately separable by the symmetry of the flowers; all Gilliesieae are zygomorphic, and all Leucocoryneae are actinomorphic. The latter also alone possess septal nectaries (Rudall *et al*., 2002). Both tribes show greater variability in karyotype than either *Allium* or *Tulbaghia* (Costa *et al*., 2020). A combination of plastid and ribosomal DNA sequences robustly supports the two floral morphological clades (Fay *et al*., 2006; Pellicer *et al*., 2017; Sassone & Giussani, 2018). Interestingly, the zygomorphic flowers of *Gilliesia* Lindl. are hypothesized to be insect mimics with a pseudocopulatory pollination syndrome (Rudall *et al*., 2002).

Escobar *et al*. (2020) applied ITS and plastid *rbcL* and *trnL-F* sequences to explore generic limits in the Gilliesieae. Two major clades were well-supported: Clade I comprises the genera *Gilliesia*, *Gethyum* Phil. and *Solaria* Phil., and Clade II, *Miersia* Lindl. and *Speea* Loes. However, *Gilliesia, Gethyum* and *Miersia* were all found to be paraphyletic, resulting in the recognition of the monotypic genus *Ancrumia* Harv. ex Baker. *Schickendantziella* Speg. and *Trichlora* Baker were not represented in the sampling. García *et al*. (2022a) resolved the same phylogenetic tree, and published two novel species of *Miersia*.

Sassone and colleagues have studied Leucocoryneae extensively (Sassone & Arroyo-Leuenberger, 2018; Sassone & Giussani, 2018; Sassone *et al*., 2013; Sassone *et al*., 2018), and the taxonomic history of the tribe is summarized in Sassone & Giussani (2018).

This tribe consists of six South American genera with ca. 100 species (Sassone *et al*., 2014a): *Beauverdia* Herter (four spp., Sassone *et al*., 2014b), *Ipheion* (three spp., Sassone *et al*., 2014a), *Latace* Phil. (two spp., Sassone *et al*., 2015), *Leucocoryne* (15 spp., Muñoz & Moreira, 2000), *Nothoscordum* (20-80 spp.), and *Tristagma* Poepp. (12 spp.; Arroyo-Leuenberger & Sassone, 2016). However, both *Tristagma* and *Nothoscordum* resolve as biphyletic (Pellicer *et al*., 2017; Sassone & Giussani, 2018), and *Beauverdia*, with both white and yellow uniflorous species, is nested within the latter. For this reason, Pellicer *et al.* (2017) argued that *Beauverdia* should be placed into synonomy with *Nothoscordum*. Most recently García *et al.* (2022b) described a new monotypic genus in the Leucocoryneae, *Atacamallium* Nic.García, which resolved as sister to the genus *Leucocoryne*.

Amaryllidoideae

The largest subfamily of Amaryllidaceae in number of genera is Amaryllidoideae (Fig. 1). This subfamily is also economically important, albeit for its large number of ornamental bulbs rather than any food value. It is characterized by an inferior ovary, a unique group of alkaloidal compounds, many with bioactive properties (Meerow & Snijman, 1998; He *et al*., 2015), and base chromosome number of $x = 11$ (Meerow & Snijman, 1998).

Tribe Amaryllideae, entirely southern African with the exception of pantropical *Crinum* L., is sister to the rest of Amaryllidaceae with very high bootstrap support in Meerow *et al.*'s (1999) analysis of plastid genes (Fig. 1). The remaining two African tribes of the family, Haemantheae Hutch. (including subtr. Gethyllidinae Dumort) and Cyrtantheae Traub (consisting of only *Cyrtanthus* Ait.), were well supported, but their position relative to the Australasian Calostemmateae D.Müll.-Doblies & U.Müll.Doblies and a large clade comprising the Eurasian and American genera, was not clear. Most surprising, the Eurasian and American elements of the family were each monophyletic sister clades. Ito *et al*. (1999) resolved a very similar topology for a more limited sampling of Amaryllidaceae and related asparagoids using plastid *matK* sequences. Plastid *ndhF* sequences (Meerow & Snijman, 2006) resolved Cyrtantheae as sister to a clade of Calostemmataeae and Haemantheae.

Amaryllideae

Almost all of the generic diversity of the tribe Amaryllideae is confined to South Africa (Snijman & Linder, 1996). Compared to other tribes in Amaryllidaceae, Amaryllideae is marked by a large number of synapomorphies (Snijman & Linder, 1996; Meerow & Snijman, 1998): extensible fibers in the bulb tunics, bisulculate pollen with spinulose exine, scapes with a sclerenchymatous sheath, unitegmic or ategmic ovules, and nondormant, water-rich, nonphytomelaninous seeds with chlorophyllous embryos. A few of the genera extend outside of South Africa proper, but only *Crinum*, with seeds well suited to oceanic dispersal (Koshimizu, 1930), ranges through Asia, Australia, and America. The tribe is the first branch within the subfamily (Ito *et al*., 1999; Meerow, 2010; Meerow *et al*., 2000; Meerow & Snijman, 2006). Snijman and Linder's (1996) phylogenetic analysis of the tribe based on morphological, floral and seed anatomical, and cytological data resulted in recognition of two monophyletic subtribes: Crininae Baker (*Boophone* Herb., *Crinum*, *Ammocharis* Herb., and *Cybistetes* Milne-Redh. & Schweick., the latter now transferred to *Ammocharis* (Snijman & Williamson, 1994) and Amaryllidinae Walp. (*Amaryllis* L., *Nerine* Herb., *Brunsvigia* Heist., *Crossyne* Salisb., *Hessea* Herb., *Strumaria* Jacq., and *Carpolyza* Salisb. *Carpolyza* has been transferred to *Strumaria* (Meerow & Snijman, 2001). Meerow *et al*.'s (1999) incomplete sampling of this tribe for three plastid sequences resolved *Amaryllis* as sister to the rest of the tribe. Weichhardt-Kulessa *et al*. (2000) presented an analysis of internal transcribed spacer (ITS) sequences for a part of the tribe (subtribe Strumariinae sensu D. & U. Müller-Doblies [1985, 1996]). Meerow & Snijman (2001) analyzed morphology and ITS sequences across the entire tribe. *Amaryllis* is sister to the remaining genera, followed by *Boophone*. All other genera were included in two clades conforming to Snijman & Linder's (1996) subtribes Amaryllidinae (less *Amaryllis*, thus now Strumariinae) and Crininae (less *Boophone*), and *Carpolyza* was transferred into *Strumaria* (Meerow & Snijman, 2001).

Meerow et al. (2003) presented phylogenetic and biogeographical analyses of nrDNA ITS and plastid *trnL-F* sequences for all continental groups of the large, pantropical genus *Crinum* and related genera. Their results indicated that *C. baumii* Harms is more closely related to *Ammocharis* than to *Crinum sensu stricto* (s.s.). Three clades are resolved in *Crinum* s.s. The first one unites a monophyletic American group with tropical and North African species. Meerow *et al*. (2003) hypothesized that emergent aquatic tropical African species with actinomorphic perianths were likely the sister group to the American species, which was shown to be the case by Kwembeya *et al*. (2007). The second clade included all southern African species and the Australian endemic *C. flaccidum* Herb. The third includes monophyletic Madagascar, Australasian and Sino-Himalayan clades, with southern African species. The salverform, actinomorphic perianths of subg. *Crinum* appear to have evolved several times in the genus from ancestors with zygomorphic perianths (subg. *Codonocrinum* Willd. ex Schult.f.), thus neither subgenus is monophyletic. Biogeographical analyses place the origin of *Crinum* in southern Africa. The genus underwent three major waves of radiation corresponding to the three main clades resolved in the trees. Two entries into Australia of the genus were indicated, as were separate Sino-Himalayan and Australasian dispersal events. These results were confirmed by Kwembeya *et al*. (2007), including the origin of the endemic American species from tropical west African spp.

Calostemmateae, Cyrtantheae and Haemantheae

The three tribes Calostemmateae, Cyrtantheae and Haemantheae form a clade that is sister to the American and Eurasian tribes of the subfamily (Fig. 1; Meerow *et al*., 1999; Meerow & Snijman, 2006), though their exact relationships to each other remain ambiguous (Meerow & Snijman, 2006; Bay-Schmidt *et al*., 2010).

Calostemmateae consists of two Australasian genera (*Proiphys* Herb., pseudopetiolate forest understory herbs of Malaysia, Indonesia, the Philippines and tropical Australia; and *Calostemma* R. Br., endemic to Australia). The indehiscent capsules of both genera are similar in appearance to the unripe berry-fruits of *Scadoxus* Raf. and *Haemanthus* L. (Haemantheae), but early in the development of the seed, the embryo germinates precociously, and a bulbil forms within the capsule and functions as the mature propagule (Rendle, 1901). A reasonable hypothesis is that the lineage represents an early entry into Australia directly from Africa.

Cyrtantheae consists of a single genus. *Cyrtanthus* is endemic to sub-Saharan Africa, with well over 90% of its species concentrated in South Africa (Dyer, 1939; Reid & Dyer, 1984). With about 55 species it is the largest genus of southern Africa's Amaryllidaceae (Snijman & Archer, 2003) and one of the largest in the family overall (Snijman & Meerow, 2010). The genus exhibits a high level of floral morphological diversity which is unparalleled in any other genus of the family. Conversely, the genus shows great consistency in chromosome number, with $2n = 16$ characteristic of most, if not all, of the species (Wilsenach, 1963; Ising, 1970; Strydom *et al*., 2007). It is also the only African genus with the flattened, winged, phytomelaninous seed, so common in the American clade of the family (Meerow & Snijman, 1998). Snijman & Meerow (2010) explored the phylogeny of the genus in the context of floral and ecological adaptation using plastid *ndhF* and nuclear ribosomal DNA.

Haemantheae is the only group of Amaryllidaceae that have evolved a baccate fruit (Meerow *et al*., 1999; Meerow & Clayton, 2004). It is entirely African, and like *Cyrtanthus*, most of its diversity is in South Africa (Meerow & Snijman, 1998). Meerow & Clayton (2004) analyzed plastid *trnL-F* and nrDNA ITS sequences across the tribe. Two main clades are resolved, one comprising the monophyletic rhizomatous genera *Clivia* Lindl. and *Cryptostephanus* Welw. ex Baker, and a larger clade that unites *Haemanthus* and *Scadoxus* as sister to an *Apodolirion* Baker/*Gethyllis* L. subclade.

The Eurasian clade (Lycorideae, Galantheae, Narcisseae, and Pancratieae)

The Eurasian clade of the Amaryllidaceae (Fig. 1) contains the members of the family that have adapted to the highest latitudes in the Northern Hemisphere, and also those with the greatest economic value as spring flowering temperate zone garden plants (*Narcissus* L., *Galanthus* L., *Leucojum* L.). The clade was only recently recognized as a monophyletic group, resolved as sister to the endemic American genera by plastid DNA sequences (Ito *et al*., 1999; Meerow *et al*., 1999). The Eurasian clade encompasses four tribes that were previously recognized (Meerow & Snijman, 1998): Galantheae Parl., Lycorideae Herb., Narcisseae Lam. & DC., and Pancratieae Dumort., the overall relationships of which were obscured by their diversity of chromosome number and morphology (Traub, 1963). Müller-Doblies & Müller-Doblies (1978a) earlier observed similarities between the internal bulb morphology of *Ungernia* Bunge (Lycorideae) and *Sternbergia* Waldst. & Kit. (Narcisseae). With the exception of the Central and East Asian Lycorideae, the clade is centered within the Mediterranean region (Meerow & Snijman, 1998; Lledó *et al*., 2004). There are 11 genera in the clade, comprising ca. 120 spp., with *Lycoris* Herb. (ca. 20 spp.) and *Narcissus* L. (40 spp.) the largest genera (Meerow & Snijman, 1998).

Lledó *et al*. (2004) presented a cladistic analysis of the clade that focused on the relationships of *Leucojum* and *Galanthus* using plastid *matK*, nuclear ribosomal ITS sequences, and morphology. *Leucojum* was revealed as paraphyletic, and the genus *Acis* Salisb. was resurrected to accommodate the linear-leaved Mediterranean *Leucojum* species with solid scapes. While their sampling within these three genera was extensive, only a single species each of the genera *Pancratium* L., *Sternbergia*, *Narcissus*, and *Vagaria* Herb., along with the monotypic *Lapiedra* Lag., were used as outgroups. *Hannonia* Braun-Blanq. & Maire was not included. Consequently, the phylogenetic relationships of the entire clade were not explicitly examined in their analyses. A similar case holds for Graham & Barrett's (2004) study of floral evolution in *Narcissus* using plastid *ndhF* and *trnL-F* sequences, which included only *Lapiedra* and one species each of *Galanthus*, *Leucojum*, and *Sternbergia* as outgroups in their analyses.

Meerow *et al.* (2006) analyzed the clade using plastid *ndhF* and rDNA ITS sequences for 33 and 29 taxa, respectively; all genera were represented by at least one species. Both sequence matrices resolve the Central and East Asian tribe Lycorideae as sister to the Mediterranean-centered genera of the clade, and two large subclades were recognized within the greater Mediterranean region: Galantheae, consisting of *Acis*, *Galanthus* and *Leucojum*; and Narcisseae (sister genera *Narcissus* and *Sternbergia*, and *Pancratium*). However, there were areas of incongruence between the two markers, which disappeared when three predominantly monotypic genera, *Hannonia*, *Lapiedra*, and *Vagaria*, centered in North Africa, were removed from the alignments. The authors hypothesized that incomplete lineage sorting took place after the divergence of Galantheae and Narcisseae/*Pancratium* from a common ancestor, with the three small or monotypic genera retaining a mosaic of the ancestral haplotypes. After the vicariant divergence of the Asian Lycorideae, North Africa and the Iberian Peninsula are the most likely areas of origin for the rest of the clade (Meerow *et al.*, 2006). A new genus, *Shoubiaonia* W.H.Qin, W.Q.Meng & Kun Liu, was recently described in Lycorideae and is sister to *Lycoris* and *Ungernia* (Qin *et al.*, 2021).

Narcissus is the most important genus of temperate zone spring flowering bulbs in the Amaryllidaceae. The genus is taxonomically very complex (Fernandes, 1968a; Webb, 1980; Mathew, 2002), no doubt in part due to its propensity to hybridize in nature (Marques, 2010), and the many horticultural hybrids and selections (Mathew, 2002). Consequently, the number of species varies considerably in different studies. For example, Webb (1980) recognized 26 species; Fernandes (1968a) accepted 63. Blanchard (1990) favored Fernandes' (1968a) treatment. The genus is most speciose in the Western Mediterranean area, particularly the Iberian Peninsula and NW Africa. This group is also fascinating biologically due to the occurrence of all four major classes of heterostyly, from stylar monomorphism, stigma-height dimorphism, distyly, to tristyly (reviewed in Barrett & Harder, 2005). It is the only heterostylous genus of Amaryllidaceae.

Fernandes (1968a) divided *Narcissus* into two subgenera, *Hermione* (Salisb. ex Haw.) Spach with base chromosome number $x = 5$, and *Narcissus* with $x = 7$. He recognized 10 sections (*Apodanthae* [as *Apodanthi*] A. Fernandes*,* *Aurelia* (J. Gay) Baker*,* *Bulbocodii* DC.*,* *Ganymedes* (Haw.) Schult f., *Jonquilla* DC., *Narcissus*, *Pseudonarcissus* DC., *Serotini* Parl., *Tapeinanthus* (Herb.) Traub and *Tazettae* DC.) based on his decades of karyotypic studies in the genus (summarized in Fernandes, 1967, 1968a, b, 1975). Pérez-Barrales *et al.*, (2003) used the short plastid intergenic spacer between *trnL* and *trnF* across a small sampling of *Narcissus* species and did not get much resolution beyond the two recognized subgenera. Graham & Barrett (2004) provided phylogenetic analyses of the plastid *trnL-F* and *ndhF* regions sequenced from 32 *Narcissus* species representing all 10 sections recognized by Fernandes (1975) and Blanchard (1990). This report strongly supported monophyletic subgenera *Hermione* and *Narcissus*, but not of all sections. Only section *Apodanthae* was clearly monophyletic, but several clades corresponded approximately to recognized sections (Graham & Barrett, 2004). The most robust study is that of Marques *et al.* (2017) who utilized plastid, mitochondrial and nrDNA (ITS) across a large sampling of species with multiple accessions. She uncovered striking incongruence between trees supported by the cytoplasmic versus the nuclear sequences, which she attributed to widescale hybridization throughout the evolutionary history of the genus. Tests for recombination in the ITS alignments supported this hypothesis. Again, only few of Fernandes' (1968a) sections were found to be monophyletic. Könyves *et al.* (2019) concluded much the same in their study of *Narcissus* section *Bulbocodii*.

The sister genus to *Narcissus* is *Sternbergia* (Meerow *et al.*, 2006), a small genus of ca. eight dwarf white or yellow cup-shaped flowered species, generally appearing in autumn. The scapes are uniflorous. It is distributed around the Mediterranean basin, with diversity and endemism highest from Greece to Israel. Two species flower in spring: *S. vernalis* (Mill.) Gorer & J.H.Harvey and *S. candida* B.Mathew. & T.Baytop, the latter the sole white-flowered species. *S. lutea* (L.) Ker Gawl. ex. Spreng. has been in cultivation for millennia and has naturalized in areas of northern Europe (Mathew, 1983).

Gage *et al.* (2011) published the most recent phylogeny of the genus and concluded that it forms two main clades: 1) *S. colchiciflora* Waldst. & Kit. sister to *S. vernalis, S. candida* and *S. clusiana* Boiss., and 2) *S. lutea* and its allies. The two spring flowering species are closely related. In the *S. lutea* complex, there was insufficient resolution, supporting arguments that *S. sicula* Tineo ex Guss. and *S. greuteriana* Kamari & R.Artelari are conspecific with *S. lutea*.

The relationship between *Galanthus* and *Leucojum sensu lato* (s.l.) has long been recognized, as has their relationship to *Narcissus* and *Sternbergia* (Müller-Doblies & Müller-Doblies, 1978b; Davis, 1999; 2001). Both genera share pendulous, predominantly white flowers, similar internal bulb morphology and poricidal anthers (Müller-Doblies & Müller-Doblies, 1978b). Unlike *Narcissus*, both lack a floral tube or a paraperigone (corona). *Galanthus* is marked by the striking length differences between the inner and outer tepal series, which are only subequal in *Leucojum* and *Acis* (Meerow & Snijman, 1998).

Galanthus consists of 18 species, mostly distributed in Europe, Asia Minor and the Near East (Davis, 1999, 2001). Stern (1956) recognized three series in *Galanthus*, erected primarily by leaf vernation: *Nivales* Beck (leaves flat), *Plicati* Beck (leaves plicate) and *Latifolii* Stern (leaves convolute). Davis (1999) combined series *Nivales* and *Plicati* into series *Galanthus*, and divided series *Latifolii* into two subseries: *Glaucaefolii* (Kem.-Nath.) A. P. Davis and *Viridifolii* (Kem.-Nath.) A.P.Davis. Molecular phylogenetic studies (Lledó *et al*., 2004; Larsen *et al*., 2010; Rønsted *et al*., 2013) indicate that the two subseries are not monophyletic.

Leucojum s.l. originally contained 10 species (Stern, 1956), mostly occurring in the western Mediterranean area, from the Atlantic coast of Portugal and Morocco to the northern Balkans and Crimea, but today the genus comprises only two: *L. vernum* L. and *L. aestivum* L. (Lledó *et al*., 2004; Meerow *et al*., 2006; Larsen *et al*., 2010), both broadly distributed in central and northern Europe, Turkey and the Caucasus. *Leucojum* is characterized by hollow scapes, broad leaves and clavate styles. Both species have a base chromosome number of $x = 11$. *L. vernum*, the type of the genus, is widespread in central and northern Europe. Its seeds have a pale outer testa and elaiosomes. *L. aestivum* is found throughout the Mediterranean and central Europe to Turkey and eastern Caucasus. It differs from *L. vernum* by its water-dispersed seed with a dark testa and lack of elaiosomes.

The remaining *Leucojum* species are now classified in the genus *Acis*, divided into subgenus *Acis* or *Ruminia* Parl. (Lledó *et al*., 2004; Meerow *et al*., 2006, Larsen *et al*., 2010), characterized by solid scapes, narrow leaves and filiform styles. The subgenera *Acis* and *Ruminia* are differentiated by the morphology of the epigynous staminal disc, six-lobed in *A*. subgenus *Ruminia*, and unlobed in *A*. subgenus *Acis*. *Acis* subg. *Acis* is the larger of the two subgenera with five species.

The American clade

In the American clade, the relationships of the endemic American genera (the entry of *Crinum* onto the continent is considered a separate event) were well resolved using the spacer regions of nuclear ribosomal DNA (Meerow *et al*., 2000a), and the major relationships have also been supported by plastid genes and introns (Meerow *et al*., 1999; 2000b; Meerow & Snijman, 2006; Meerow, 2010). The American genera of the family form two major subclades (Fig. 1). The first, or hippeastroid clade, are diploid ($2n = 22$), primarily the extra-Andean element of the family (though several of the genera do have Andean representatives), comprising the Brazilian endemic tribe Griffinieae Ravenna (*Cearanthes* Ravenna, *Griffinia* Ker Gawl. and *Worsleya* (Watson ex Traub) Traub) sister to genera treated as tribe Hippeastreae Herb. ex Sweet in most recent classifications (Dahlgren *et al*. 1985; Muller-Doblies & Muller-Doblies, 1996; Meerow & Snijman, 1998; García *et al*., 2019). ITS resolved monotypic *Worsleya* as the first branch in the tribe, and monotypic *Cearanthes* and *Griffinia* (16 species) as sister genera (Campos-Rocha *et al*., 2022b). A monograph of the tribe is underway (Campos-Rocha *et al*., 2018, 2019a, b).

Several genera within the hippeastroid clade resolved as polyphyletic (*Rhodophiala* C. Presl., *Zephyranthes* Herb.) and the possibility of reticulate evolution (i.e., early hybridization) in these lineages was hypothesized (Meerow *et al*., 2000; Meerow, 2010). This was confirmed with further analyses of plastome and multiple nuclear gene sequences (García *et al*., 2014, 2017). Hippeastreae constitutes two main clades, the subtribe Hippeastrinae Walp. and the mostly Chilean endemic subtribe Traubiinae D. Müll.-Doblies & U. Müll.-Doblies (García *et al*., 2014, 2017). In contrast to the Hippeastrinae, the Traubiinae exhibit a mostly tree-like pattern of evolution (García *et al*., 2017). García *et al*. (2019) presented a new classification scheme for Hippeastreae that reflects its reticulate phylogeny. Within Hippeastriinae, only two genera are recognized, *Hippeastrum* Herb. (two subgenera, *H*. subg. *Hippeastrum* and *H*. subg. *Tocantinia* (Ravenna) Nic.García) and *Zephyranthes* (five subgenera, *Z*. subg. *Eithea* (Ravenna) Nic.García, *Z*. subg. *Habranthus* (Herb.) Nic.García, *Z*. subg. *Myostemma* (Salisb.) Nic. García (= core *Rhodophiala* clade), *Z*. subg. *Neorhodophiala* Nic.García & Meerow subg. nov., and *Z*. subg. *Zephyranthes*). One species, *Z. pedunculosa* (Herb.) Nic.García & S.C.Arroyo, was designated as *incertae sedis*.

In the second subtribe, Traubiinae, García *et al*. (2019) and García & Meerow (2020) recognized four genera, the first two monotypic *Traubia* Moldenke and *Paposoa* Nic.García, *Phycella* Lindl. (including *Placea* Miers), 12 or more species all but one endemic to Chile, and the alpine *Rhodolirium* Phil. with two spp., both found in Chile and adjacent Argentina. There has been a great deal of cytogenetic work for the subtribe (Baeza & Macaya, 2020; Baeza *et al*., 2009a, 2009b, 2012, 2017).

The economically most important genus of American Amaryllidaceae subfam. Amaryllidoideae, *Hippeastrum*, is still not very well understood taxonomically. *Hippeastrum* consists of 70-100 entirely New World species, though one species, *H. reginae* Herb. appears to have been introduced to Africa. No modern revision of the genus has appeared since that of Traub & Moldenke (1949). The species are concentrated in two main areas of diversity, one in eastern Brazil, and the other in the central southern Andes of Peru, Bolivia, and Argentina, on the eastern slopes and adjacent foothills. A few species extend north to Mexico and the West Indies. Meerow *et al*. (2000a) included seven species in their molecular phylogenetic analysis of the American genera of subfam. Amaryllidoideae, representative of the biogeographic range of the genus. Their results suggested that the genus is robustly monophyletic and originated in Brazil. Campos-Rocha *et al*. (2022b), using 20 spp., further supported these results. García *et al*. (2014; 2017), using whole plastomes and multiple nuclear genes on a larger sampling of species, confirmed this. *Hippeastrum reticulatum* Herb., with unusual fruit and seed morphology was sister to all other species of subg. *Hippeastrum*, recently displaced by the morphologically unusual *H. velloziflorum* Campos-Rocha & Meerow (Campos-Rocha *et al*., 2022b). The low rates of base substitution in both plastid and nrDNA sequences, and the consistent interfertility of species -well-mined by bulb breeders (Meerow, 2009)- suggest that the genus underwent a relatively recent radiation (Oliveira, 2012). Many of the species seem to intergrade with one another. Traub & Moldenke (1949) attempted a formal subgeneric classification of the genus (as *Amaryllis*) based on floral morphology, but most of their infrageneric taxa do not appear to be monophyletic (Meerow & Snijman, 1998). The newly described *H. velloziflorum* resolves with ITS as sister to the rest of subgenus *Hippeastrum*. Lara *et al*. (2021) presented a revision of the Bolivian species, recognizing 34 native to that country, but there was no attempt to place the taxa into a phylogenetic context. Oliveira (2012) recognized 27 species (now 35) as occurring in Brazil and documented with sequence data and network analysis significant reticulation. New Brazilian species continue to be described (Oliveira *et al*., 2013, 2017; Campos-Rocha *et al*., 2022a, 2022b).

The second clade of the American Amaryllidoideae constitutes the tetraploid-derived (x = 23) Andean-centered tribes (Fig. 1). All, or at least some, members of each tribe have $2n$ = 46 chromosomes. The Andean clade is characterized by three consistent deletions, two in the ITS1 and one in the ITS2 regions (Meerow *et al*., 2000a), with the exception of Eustephieae Hutch. which lacks the indel in ITS2. The first branch of the clade is the tribe Eustephieae. The tribes Hymenocallideae Small and its sister tribe Clinantheae Meerow were recognized. A petiolate-leafed Andean subclade, containing elements of both Eucharideae Hutch. and Stenomesseae Traub (tribe Eucharideae) was also resolved. Interestingly, in both of the American subclades there is a small but diverse tribe that is sister to the rest of the group, the Eustephieae in the Andean clade, and the Griffinieae in the hippeastroid clade (Fig. 1). These two small tribes likely represent very isolated elements of their respective clades. Meerow (2010) concluded that the genus *Pyrolirion* Herb. was the first branch of the Eustephieae, rather than allied with *Zephyranthes*. Most recently, Meerow *et al.* (2020) performed a phylogenomic analysis of the clade and applied a curated suite of 524 nuclear genes and a partial plastome, which yielded well-supported, fully resolved trees, with much improved species resolution. All of Meerow *et al.* (2000)'s tribes were robustly supported as were most genera, and their generic composition is as follows: Clinantheae: *Clinanthus* Herb., *Pamianthe* Stapf, *Paramongaia* Velarde); Eucharideae: *Eucrosia* Ker Gawl., *Phaedranassa* Herb., *Plagiolirion* Baker, *Rauhia* Traub, *Stenomesson* Herb. and *Urceolina* Reichb. (including *Eucharis* Planch. & Lind., *Caliphruria* Herb. and *Eucrosia dodsonii* Meerow & Dehgan); Eustephieae: *Chlidanthus* Herb., *Eustephia* Cav., *Hieronymiella* Pax, *Pyrolirion*); and Hymenocallideae (*Hymenocallis* Salisb., *Ismene* Salisb., *Leptochiton* Sealy).

The Eustephieae, with a southerly bias in distribution, is always resolved as sister to the rest of the clade. The monotypic genus *Androstephanos* Fern.Casas, placed under synonomy of *Hieronymiella argentina* (Pax) Hunz. & S.C.Arroyo, appears more closely related to *Eustephia* with ITS sequences (unpubl. data). *Clinantheae* and *Hymenocallideae* are sister tribes, in turn sister to the *Eucharideae* (Fig. 1).

Unlike the Hippeastreae, the Andean clade does not appear to have experienced much reticulate evolution at the generic level (Meerow *et al.*, 2020), but interspecific hybridization was evident within *Hymenocallis* especially, and within the rain forest understory subclade of the pseudo-petiolate leafed tribe Eucharideae. As a result, Traub's (1971) transfer of *Eucharis* and *Caliphruria* into *Urceolina* was accepted (Meerow *et al*., 2020). *Stenomesson* is its sister genus. The Peruvian endemic *Caliphruria korsakoffii* was transferred into *Stenomesson*, and *Eucrosia dodsonii* to *Urceolina* (Meerow *et al*., 2023).

The Road Ahead

The past quarter century has resulted in the most resolute and accurate understanding of phylogenetic relationships in Amaryllidaceae to date. However, despite such progress, there are still many questions that remain to be answered. Surprisingly, outside of García *et al.* (2017) and Meerow *et al.* (2020), there has been no other application of next generation DNA technology such as sequence capture using anchored hybrid enrichment, also known as Hyb-Seq (Cronn *et al*., 2012; Lemmon *et al*., 2012; Lemmon & Lemmon, 2013; Weitemier *et al*., 2014) applied to the family. Sassone *et al.* (2021) did apply genotyping by sequencing (GBS) to study the diversification of genus *Ipheion* in the Pampean region as well as to investigate the domestication history of *Iphieon uniflorum* (Graham) Raf. (Sassone *et al*., 2022). Hyb-Seq is clearly the future for developing more robust phylogenetic data sets at the species and generic levels.

There has been interest in whole plastome data recently (Cheng *et al*., 2022; Dennehy *et al*., 2021; Jimenez *et al*., 2020; Xie *et al*., 2020). Whole plastome sequence data has been applied to recognize new species and estimate phylogeny in *Lycoris* (Lou *et al*., 2022; Zhang *et al*., 2021; Zhang *et al*., 2022) without any nuclear sequence data for tree comparison. There is frequently sizable cytonuclear discordance between phylogeny estimates from plastome versus nuclear data in the family (Marques *et al*., 2017; García *et al*., 2017; Meerow *et al*., 2020), which can at times signify reticulation. To that end, one must exercise some caution in formalizing taxonomic inferences from plastomes alone, without corresponding trees from the nuclear genome, especially in genera where hybridization has been documented.

Evolutionary development (evo-devo) compares the developmental processes of different organisms to infer how such evolved, using molecular data generally of candidate genes that are integral to developmental pathways (Goodman & Coughlin, 2000) or via transcriptome data (Roux *et al.*, 2015). Very few evo-devo studies have been conducted in Amaryllidaceae (see Waters *et al*., 2013). Given the degree of canalized and convergent morphological characters in the family (Meerow, 2010), it is an approach that will hopefully see greater application in the future.

A final classification for the genera of tribes Gilliesiae and Leucocoryneae seems within reach, and just requires acceptance of only monophyletic genera, which will then require either taxonomic lumping or splitting.

The large genera *Hippeastrum* and *Zephyranthes* would benefit from a next generation sequencing approach combined with whole plastome sequences to unwind the obvious history of hybridization, aneuploidy and polyploidy. In the Andean clade, wider sampling within Eustephieae would be helpful. Among the Eurasian genera, the broadly distributed *Pancratium* is badly in need of a comprehensive revision as well as a well-sampled molecular phylogeny. New species have recently been described from India (Sasikala & Kumari, 2013; Sadasivaiah, 2018).

Many amaryllids are relatively rare in nature and may not flower every year. New exploration will undoubtedly continue to uncover new species. I look forward to seeing the next generation of systematists working on the family.

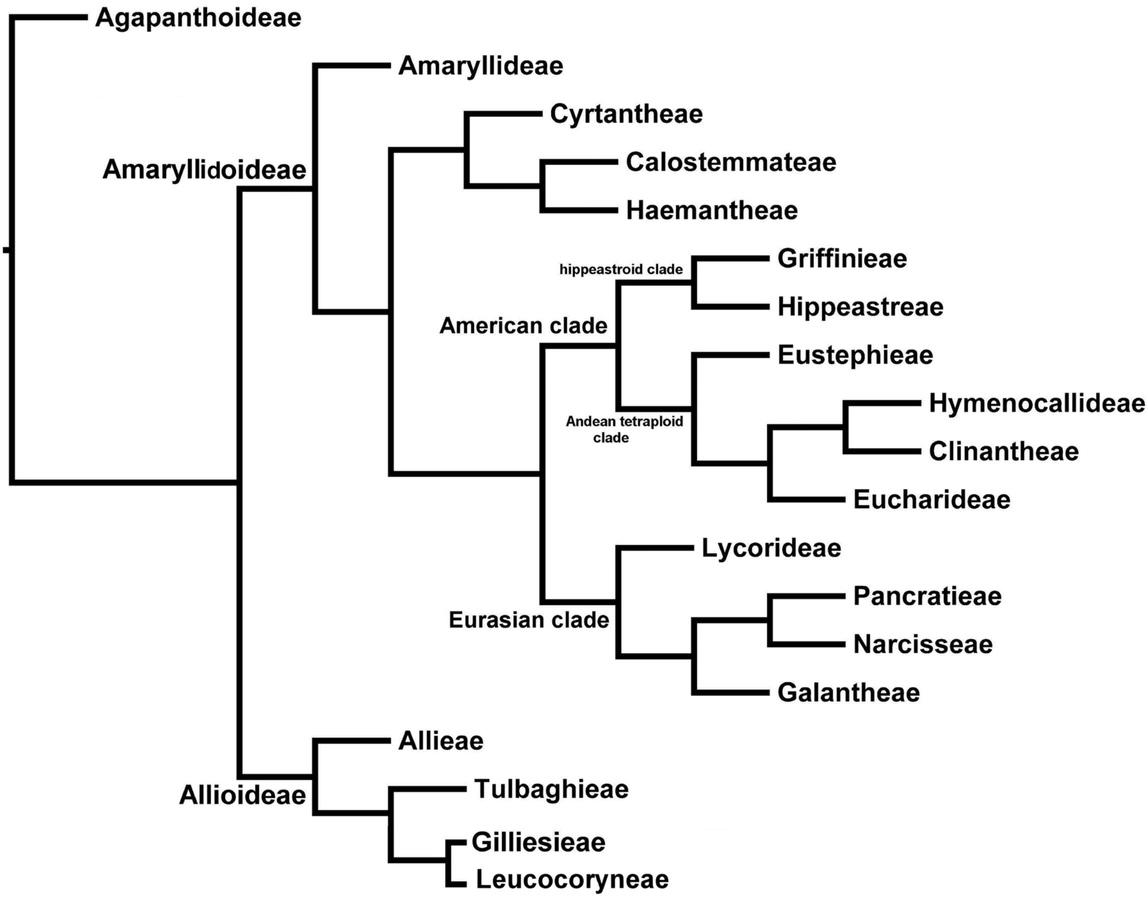

Fig. 1. Subfamilial and tribal level phylogeny of the Amaryllidaceae, based on García *et al.* 2014, 2017, 2019, 2022a), Meerow (2010), Meerow & Snijman (2006), Meerow *et al.* (1999, 2000a, b, 2006, 2020), and Sassone & Giussani (2018).

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