

SYSTEMATICS AND PHYLOGENY

Generic classification of Amaryllidaceae tribe Hippeastreae

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Abstract A robust generic classification for Amaryllidaceae has remained elusive mainly due to the lack of unequivocal diagnostic characters, a consequence of highly canalized variation and a deeply reticulated evolutionary history. A consensus classification is proposed here, based on recent molecular phylogenetic studies, morphological and cytogenetic variation, and accounting for secondary criteria of classification, such as nomenclatural stability. Using the latest sutribal classification of Hippeastreae (Hippeastrinae and Traubiinae) as a foundation, we propose the recognition of six genera, namely *Eremolirion* gen. nov., *Hippeastrum*, *Phycella* s.l., *Rhodolirium* s.str., *Traubia*, and *Zephyranthes* s.l. A subgeneric classification is suggested for *Hippeastrum* and *Zephyranthes* to denote putative subclades. In *Hippeastrum*, we recognize *H.* subg. *Hippeastrum* and *H.* subg. *Tocantinia*. In *Zephyranthes*, *Z.* subg. *Eithea*, *Z.* subg. *Habranthus*, *Z.* subg. *Myostemma* (= core *Rhodophiala* clade), *Z.* subg. *Neorhodophiala* subg. nov., and *Z.* subg. *Zephyranthes* are recognized. Descriptions, synonymy, taxonomic keys, and new combinations are provided for each genus and subgenus.

Keywords Amaryllidaceae; angiosperms; Asparagales; classification; generic circumscription; plant taxonomy

INTRODUCTION

A classificatory framework of biological diversity that accounts for reticulate evolution seems necessary to confront the increasing evidence for network-like evolutionary patterns in angiosperms (Vriesendorp & Bakker, 2005; García & al., 2014; Sun & al., 2015). Tribe Hippeastreae (of Amaryllidaceae) is an appropriate system in which to address the above-mentioned challenge because generic limits are still elusive and controversial in this clade, and ancient hybridizations at the diploid level appear to have been involved in its early radiation (Meerow & al., 2000; Meerow, 2010; García & al., 2014, 2017).

Recent advances in phylogenetics of Hippeastreae. — Genera of Hippeastreae were traditionally placed in different subgroups of Liliaceae or Amaryllidaceae (Herbert, 1837; Pax, 1888; Hutchinson, 1959). A review of their classification during the second half of the 20th century is provided by Meerow & al. (1999), in which the treatments of traditional genera as proposed by Traub (1963), Dahlgren & al. (1985), Müller-Doblies & Müller-Doblies (1996), and Meerow & Snijman (1998) are compared (Table 1). More recently, Ravenna (2000, 2002, 2003b) described several new Neotropical genera, including *Tocantinia* Ravenna, *Eithea* Ravenna, and *Aidema* Ravenna, and proposed a major

taxonomic treatment of Chilean genera (Ravenna, 2003a). Relevant contributions of the latter work include: (1) the suggestion that *Rhodophiala* C.Presl. had been illegitimately used and that *Myostemma* Salisb. was the correct name for Chilean-Argentine taxa; and (2) the recognition of groups with a capitate stigma (i.e., *Rhodolirium* Phil.) as different from those with trilobed or trifid stigma (i.e., *Myostemma*) (Ravenna, 2003a).

The molecular era of plant systematics has altered our understanding of relationships within Hippeastreae and brought significant changes to the classification of Amaryllidaceae sensu stricto (s.str.), including the recognition of: (1) an American clade of Amaryllidaceae that is divided into the hippeastroid clade and the Andean tetraploid clade (including tribes Eustephieae, Hymenocallideae, Clinantheae, and Eucharideae) (Meerow & al., 1999, 2000); (2) tribe Griffinieae within the hippeastroids, including *Griffinia* Ker Gawl. and *Worsleya* (W. Watson ex Traub) Traub, which is sister to Hippeastreae (Meerow & al., 2000); and (3) *Pyrolirion* Herb. as the first branch in Eustephieae rather than being closely related to *Habranthus* Herb. and *Zephyranthes* Herb. (Meerow, 2010). Traditionally, *Pyrolirion* had been considered close to the latter genera due to morphological similarities (i.e., tubular spathe valve, single-flowered scape).

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Phylogenetic analyses of nrDNA ITS sequences (Meerow & al., 2000; Meerow, 2010) were the first molecular-based studies to elucidate relationships within Hippeastreae and showed that some genera—*Myostemma* (as *Rhodophiala*), *Habranthus*, and *Zephyranthes*—are polyphyletic. Meerow (2010) also suggested that ancient reticulation event(s) had occurred in Hippeastreae, with subsequent diversification of daughter clades. However, these studies lacked good representation of Chilean-Argentinean endemic groups, such as *Famatina* Ravenna, *Phycella* Lindl., *Placea* Miers, *Rhodolirium*, and *Traubia* Moldenke. An increased taxon sampling for ITS and a well-resolved chloroplast DNA (cpDNA) tree provided strong support for two major clades within Hippeastreae and these were formalized by García & al. (2014) as subtribes: Traubiinae and Hippeastrinae. Supporting Meerow's hypothesis of deep reticulation, widespread cytonuclear discordance was detected in Hippeastrinae, while Traubiinae showed a tree-like pattern of evolution, consistent with an apparent lack of allopolyploidy.

Consequences of deep reticulation in the tribe. —

Given the available phylogenetic framework and the distribution of basic chromosome numbers within Hippeastreae, García & al. (2014) hypothesized that the putative deep reticulation event(s) that preceded the radiation of Hippeastrinae most likely consisted of homoploid hybridization(s) at the diploid level and that allopolyploidization was likely involved in the diversification of the *Habranthus-Zephyranthes-Sprekelia* Heist. complex, as suggested by polyploid series based mostly on $n = 6$ and cytogenetic evidence (Naranjo, 1974; Flory, 1977; Greizerstein & Naranjo, 1987). Recent analyses based on nuclear markers and complete chloroplast genomes (García, 2015; García & al., 2017) suggest (1) two major subclades within diploid Hippeastrinae, the first composed of *Hippeastrum* and *Tocantinia*, characterized by $2n = 22$, and the second by *Eithea*, *Habranthus*, *Myostemma*, and *Zephyranthes* with $2n = 12, 14, \text{ or } 18$, (2) ancient diploid hybridizations and incomplete lineage sorting were likely involved in the early

Table 1. Comparison of the present proposal with the four most recent classifications of Amaryllidaceae tribe Hippeastreae.

Traub (1963)	Dahlgren & al. (1985)*	Müller-Doblies & Müller-Doblies (1996)	Meerow (1995), Meerow & Snijman (1998)	This classification
Amarylleae	Hippeastreae	Hippeastreae	Hippeastreae	Hippeastreae
		subtr. Hippeastrinae		subtr. Hippeastrinae
<i>Hippeastrum</i> Herb. (as <i>Amaryllis</i> L.)	<i>Hippeastrum</i>	<i>Hippeastrum</i> (incl. <i>Phycella</i> , <i>Worsleya</i>)	<i>Hippeastrum</i>	<i>Hippeastrum</i> (incl. <i>Tocantinia</i> Ravenna)
<i>Worsleya</i> Traub	<i>Worsleya</i>		<i>Worsleya</i>	
<i>Placea</i> Miers	<i>Placea</i>	<i>Placea</i>	<i>Placea</i>	
		<i>Rhodophiala</i> Presl.		
Zephyrantheae		subtr. Zephyranthinae		
<i>Zephyranthes</i> Herb.	<i>Zephyranthes</i>	<i>Zephyranthes</i>	<i>Zephyranthes</i> (incl. <i>Haylockia</i>)	<i>Zephyranthes</i> (incl. <i>Haylockia</i> , <i>Habranthus</i> , <i>Sprekelia</i> , <i>Eithea</i> Ravenna, <i>Myostemma</i> Salisb.)
<i>Habranthus</i> Herb.	<i>Habranthus</i>	<i>Habranthus</i>	<i>Habranthus</i>	
<i>Sprekelia</i> Heist.	<i>Sprekelia</i>	<i>Sprekelia</i>	<i>Sprekelia</i>	
<i>Haylockia</i> Herb.		<i>Haylockia</i>		
<i>Pyrolirion</i> Herb.	<i>Pyrolirion</i>	<i>Pyrolirion</i>	<i>Pyrolirion</i>	
<i>Rhodophiala</i> Presl.	<i>Rhodophiala</i>		<i>Rhodophiala</i>	
		subtr. Griffiniinae		
		<i>Griffinia</i> Ker Gawl.	<i>Griffinia</i>	
Traubieae		subtr. Traubiinae		subtr. Traubiinae
<i>Traubia</i> Moldenke		<i>Traubia</i>	<i>Traubia</i>	<i>Traubia</i>
				<i>Eremolirion</i> Nic. García
				<i>Rhodolirium</i> Phil.
Eustephieae				
<i>Phycella</i> Lindl.			<i>Phycella</i>	<i>Phycella</i> (incl. <i>Placea</i>)
<i>Lepidopharynx</i> Rusby (= <i>Hippeastrum</i>)				

Pyrolirion Herb. was shown by Meerow (2010) to properly belong to the Eustephieae. *Griffinia* and *Worsleya* are now in the tribe Griffiniinae. *As Dahlgren & al. (1985) did not consistently list the component genera in their tribal concepts, their exact generic composition is inferred. Most of their delimitations are presumed to have followed Traub (1963).

diversification of Hippeastrinae, and (3) the *Habranthus-Zephyranthes-Sprekelia* polyploid complex originated within ancestral lineages with $2n = 12-14$.

Our current knowledge of the phylogeny of Hippeastreae suggests that it is better represented as a network rather than a bifurcating tree, even at the diploid level (García & al., 2017). Current theory and methods consider bifurcating trees as a model for morphological evolution (e.g., Hennig, 1950, 1965, 1966; Wiley & Lieberman, 2011; Cornwell & Nakagawa, 2017), and no such methods have as yet been developed to infer ancestral states over phylogenetic networks. In the same way, there currently are no clear rules to classify a group based on a network of relationships. Even though a few authors have defended the use of the concept of monophyly in the context of a network (e.g., Schander, 1998; Schmidt-Lebuhn, 2011), this theoretical framework is still incomplete. Therefore, the most likely tree based on our current knowledge has been selected as the basis of a generic classification of Hippeastreae (Fig. 1). This corresponds to the nuclear species tree of García & al. (2017), which was based on 18 nuclear markers. The nuclear topology was preferred over the chloroplast tree because the latter seems to be widely affected by chloroplast capture events in Hippeastrinae at the diploid level. The widespread occurrence of allopolyploidy, especially in *Zephyranthes* subg. *Zephyranthes* (Flory, 1977), makes the phylogeny of Hippeastrinae even more tangled and difficult to translate into a classification at a finer scale.

Taxonomic approach and concepts. — The classification proposed here for tribe Hippeastreae follows a rank-based scheme, as has been traditionally applied to the Amaryllidaceae (e.g., Meerow & Snijman, 1998). The term *rank* is used in a nomenclatural sense, equivalent by designation; ranks have only a relative function, which is to inform the user regarding the phylogenetic/hierarchic structure of the taxonomic system (Potter & Freudenstein, 2005; Dubois, 2007, 2008; Dubois & Raffaëlli, 2012). All named supraspecific taxa correspond to hypothesized clades with the highest statistical, cytogenetic, and/or morphological support based on species tree estimation analyses that considered various nuclear sequence markers (García & al., 2014, 2017).

This generic classification is based solely on extant organisms; hence, a synchronic definition of monophyly is adopted (Hennig, 1966; Nelson, 1971; Mishler, 2010). Podani (2009, 2010) proposed the term *monocladistic* for a group of contemporaneous organisms derived from a common ancestor (i.e., definition adopted here) and suggested use of the term *monophyletic* only for groups that include the hypothesized ancestors and/or extinct taxa. In this study, the term *monophyly* (or its adjectival form, monophyletic) will be used and considered equivalent to *monocladistic*. This approach seems appropriate in this case because there are no unequivocal fossils for Amaryllidaceae (Meerow & al., 2000).

We believe that classifications, to be most useful, should simultaneously serve multiple purposes (Nickrent & al., 2010),

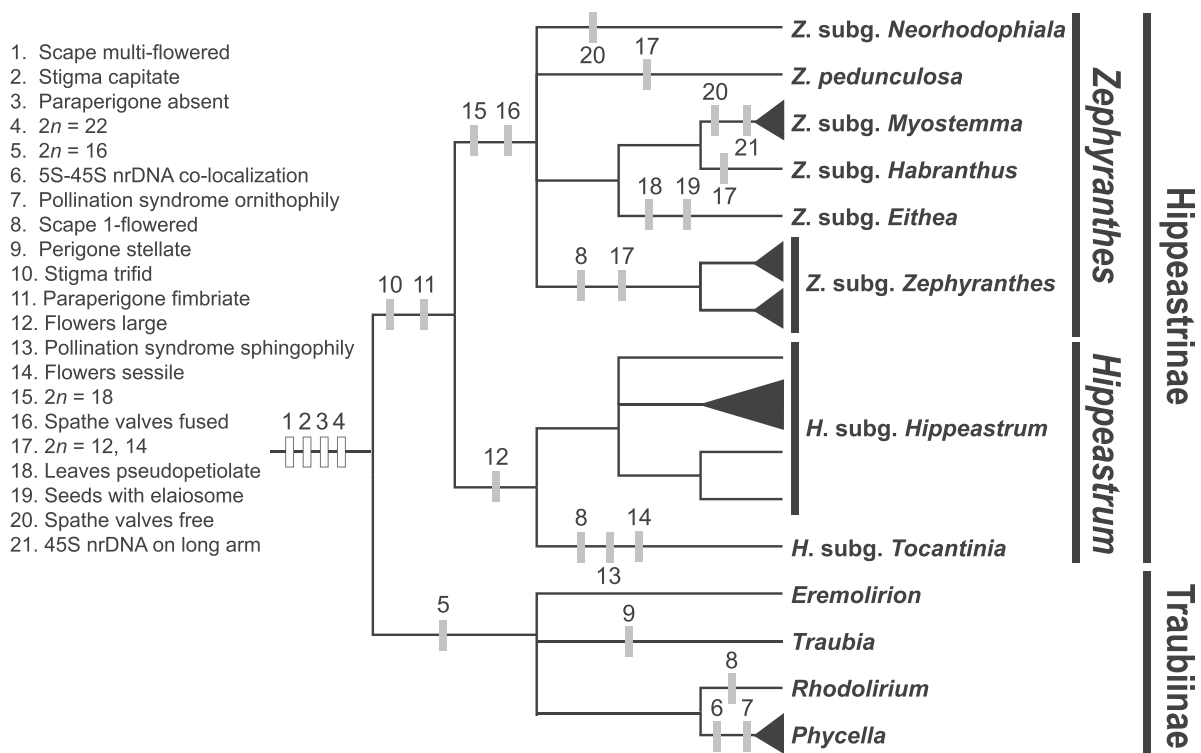


Fig. 1. Major clades of Amaryllidaceae tribe Hippeastreae based on García & al. (2017). White bars correspond to putative plesiomorphic character states for the tribe. Grey bars indicate putative apomorphic character states. These are not based on an explicit ancestral reconstruction.

such as representing the phylogenetic structure of a particular group, aiding in organizing and retrieving information (e.g., databases, collections, Floras), and in teaching/communicating information regarding biological diversity. In addition to the primary principle of monophyly, Backlund & Bremer (1998) list four secondary principles that involve maximizing (1) nomenclatural stability, (2) phylogenetic information (= size and redundancy), (3) support for monophyly, and (4) diagnosability (= ease of identification) (also see Judd & al., 2016). We have attempted to follow these secondary principles to aid taxon circumscriptions in the proposed classification.

A genus is here defined as the most inclusive clade subordinate to the subtribal level, as proposed by García & al. (2014) for tribe Hippeastreae. Each genus and/or subgenus is treated in terms of nomenclature, morphological variation, cytogenetics, and geographic distribution based on various literature sources and the authors' observations. Nomenclatural changes and taxonomic novelties are proposed when appropriate; all taxa are named according to the recommendations of Turland & al. (2018). Dichotomous keys to the genera and subgenera are also provided. Morphological descriptions are based on relevant botanical literature (e.g., Traub, 1963; Fabris, 1968; Ravenna, 1969, 1972, 1974, 1981, 2000, 2002, 2003a,b,c; Arroyo & Cutler, 1984; Meerow & Snijman, 1998; Flagg & al., 2002; Arroyo-Leuenberger, 2009; Oliveira, 2012) and were complemented with observations of herbarium specimens and living plants. These descriptions reflect the range of variation in each clade; hence, values given for certain characters should be interpreted as extreme points in the pattern of variation, especially when in parentheses and/or in species-rich groups.

Classification of Traubiinae. — One approach to generic delimitation in Traubiinae would be to combine the former *Rhodolirium laetum* (Phil.) Ravenna with *Traubia*, as some nuclear gene trees would support (García & al., 2017). Species tree analyses, however, do not show strong support for this relationship, and neither is it indicated by morphology; thus, combining both into a single genus could potentially violate the primary principle of monophyly. The same can be said about lumping *Rhodolirium* s.str. into *Phycella*, especially when each clade is better characterized when considered separately. Thus, we describe the new genus *Eremolirion* (for *Rhodolirium laetum*) and maintain *Rhodolirium* s.str. as distinct from *Phycella* sensu lato (s.l.). On the other hand, current molecular and cytogenetic data do not support keeping *Placea* separate from *Phycella* s.str., because that would make *Phycella* paraphyletic (García & al., 2014, 2017). Hence, *Placea* cannot be maintained as distinct from *Phycella*, given a phylogenetic perspective and available data; a better resolution of relationships within *Phycella* would help to clarify character evolution and thus allow recognition of major lineages in this clade.

Classification of Hippeastrinae. — Considering the adopted phylogenetic hypothesis for Hippeastreae (Fig. 1) and putative character evolution, Hippeastrinae represent a challenge to classify at the generic level because of

uncertainties in their relationships and canalization of morphological variation (Meerow, 2010). A splitting approach to classify this group could consider each minor subclade as a genus. This scheme would define more easily diagnosable taxa and maximize nomenclatural stability in most cases; however, the lack of phylogenetic resolution and complexities brought about by reticulate evolution in this part of the phylogeny could render such a classification still open to nomenclatural instability at the generic level. This means that each early-diverging lineage allied to *Zephyranthes* could be considered at the generic level, such as *Z. pedunculosa* comb. nov. (= *Habranthus pedunculatus* Herb.), *Z. andina* (R.E.Fr.) Traub., *Z. americana* (Hoffmanns.) Ravenna, *Sprekelia*, and probably also others, as more species are included in analyses and higher resolution is attained for relationships in this group.

An alternative approach, therefore, should possibly be considered, at least from a phylogenetic perspective, and this would be to recognize only a single genus in Hippeastrinae. This choice would result in a morphologically heterogeneous assemblage, thus making this broadly circumscribed genus very difficult to diagnose. The genus would, however, be defined by two clear morphological synapomorphies: (1) a trilobed stigma and (2) a fimbriate paraperigone (perianth corona sensu Waters & al., 2013). This option would also add redundancy to the classification, as the subtribe would be equivalent to the genus, and this approach would contribute to nomenclatural instability, considering all the combinations involved, for instance from *Zephyranthes* and *Habranthus* to *Hippeastrum* (~150 spp.) or from *Hippeastrum* to *Zephyranthes* (~100 spp.). *Hippeastrum* and *Zephyranthes* have the same priority given that Herbert described them in the same publication, and both genera have been extensively used in the taxonomic and horticultural literature (e.g., Huxley & al., 1992; Brickell & Zuk, 1997).

The above-mentioned option is the one adopted by Christenhusz & al. (2018), but in an even more extreme version because their circumscription of *Hippeastrum* includes the entire tribe. Christenhusz and associates ignored the latest literature on Hippeastreae phylogenetics (Meerow, 2010; García & al., 2014, 2017) and, therefore, have overlooked subtribal limits. Overall, we consider their classification of Hippeastreae inappropriate because it oversimplifies this tribe's phylogenetic complexity (García & al., 2014, 2017). Unfortunately, it has in our opinion already generated nomenclatural noise within a group that is already nomenclaturally overloaded (as a result of its complex and intricate taxonomic history). Of the 178 new combinations or new names proposed by Christenhusz & al. (2018) in *Hippeastrum*, we will only use in the present classification those three corresponding to former species of *Tocantinia* (here proposed as *Hippeastrum* subg. *Tocantinia* comb. & stat. nov.; Büneker & al., 2016).

A compromise approach that divides Hippeastrinae into two genera, *Hippeastrum* and *Zephyranthes* s.l., seems to us to be the most reasonable alternative. This choice would also comply better with the definition of a genus, as given previously, i.e., the most inclusive clade subordinate to the subtribal

level. Even though there are no clear synapomorphies for each subclade, multiples of 6, 7, and 10 chromosomes and fused spathe valves characterize most species of *Zephyranthes*, while multiples of 11 chromosomes, free spathe valves, and generally larger flowers are most frequent in *Hippeastrum* (García, 2015). A division into subgenera would be informative regarding relationships within each genus, notwithstanding that this subgeneric classification is open to further considerations as their phylogenetic structures are better resolved. The refinement of the subgeneric taxonomy, however, would not require additional changes in species names (as subgeneric names are not part of the binomial). Therefore, this scheme is likely to lead to more robust nomenclatural stability in this traditionally contentious group.

Of the 92 new combinations or new names at the species level resulting from this proposal, most of them (63) involve the transfer of *Habranthus* basionyms into *Zephyranthes*, especially within *Z.* subg. *Zephyranthes*. Considering that the species taxonomy of this subgenus is still unclear, we have considered Arroyo-Leuenberger & Dutilh (2008) and The Plant List (2013) as references to ensure that each currently accepted *Habranthus* species has a corresponding name in *Zephyranthes*. Morphological conditions traditionally used to separate *Habranthus* from *Zephyranthes*, that is, zygomorphy, 4-seriate stamens, anther morphology, and nodding flowers (e.g., Traub, 1963; Fabris, 1968; Meerow & Snijman, 1998; Arroyo-Leuenberger, 2009; Flagg & al., 2010), are probably plesiomorphic within *Zephyranthes* s.l., and diploid species showing these suites of character states are clearly paraphyletic (García & al., 2014).

The genera and subgenera proposed here cannot be easily identified by a single character, but rather are diagnosed by a combination of character states. The most complicated case in terms of diagnosability is the differentiation of *Zephyranthes* subg. *Myostemma* comb. & stat. nov. and *Z.* subg. *Neorhodophiala* subg. nov., both of which were formerly recognized at the generic level as *Rhodophiala*. In particular, the red-flowered species of *Z.* subg. *Myostemma* can appear almost identical to some phenotypes of *Z. bifida* comb. nov.; within multi-flowered *Zephyranthes*, yellow species occur only in *Z.* subg. *Myostemma*, as far as known. Similar examples of poorly diagnosable taxa include *Sequencia* Givnish (Bromeliaceae), which owes its name to its initial recognition based on molecular sequences (Givnish & al., 2007); also, *Parapolystichum* (Keiserl.) Ching (Dryopteridaceae) and *Sarcomphalus* P.Browne (Rhamnaceae), which cannot be distinguished morphologically from *Lastreopsis* Ching (Labiak & al., 2014a,b) and *Ziziphus* Mill. (Hauenschild & al., 2016), respectively. The best characters to use in distinguishing a red-flowered species of *Z.* subg. *Myostemma* from subgenus *Neorhodophiala* include chromosome numbers (i.e., $2n = 16$ is only present in subg. *Neorhodophiala*; Naranjo & Poggio, 2000), NOR (nucleolar organizer region) position in the karyotype (Baeza & al., 2006; García, 2015), and DNA sequences for specified marker(s) (Meerow, 2010; García & al., 2014, 2017). The reliance on cryptic or molecular characters to diagnose

clades that were initially only recognized by DNA sequences is a common and necessary practice in modern plant systematics (for many examples see Judd & al., 2016; Soltis & al., 2018), due to the frequent homoplasy of most macroscopic characters, as has been inferred throughout flowering plants in general.

■ FORMAL TAXONOMY

Hippeastreae Herb. ex Sweet, Brit. Fl. Gard., ser. 2, 1: ad t. 14. 1829 ('Hippeastriformes') – Type: *Hippeastrum* Herb., nom. cons.

= Hippeastroideae Herb. ex Sweet, Brit. Fl. Gard., ser. 2, 2: ad t. 107. 1831.

Bulbous geophytes, bulb tunicate, generally prolonged into a pseudoneck. Leaves lorate or linear, sometimes terete, rarely pseudopetiolate with a broadened lamina. Scape fistulose or solid, usually terete, sometimes flattened laterally, terminated by two spathe bracts enclosing the flowers before anthesis, if connate then tubular and frequently bifid apically. Perigone tubular to funnelliform, weakly to strongly zygomorphic, tepals basally connate, paraperigone often present at the throat, most frequently consisting of fimbriae. Filaments in unequal lengths, with the longest opposite the petals, usually declinate. Capsule globose-tricocous, seeds generally flattened and winged, sometimes wedge-shaped, rarely globose and turgid, phytomelan present, rarely bearing an elaiosome.

Key to the subtribes and genera of Amaryllidaceae tribe Hippeastreae

1. Stigma capitate (obscurely trilobed in *Rhodolirium andicola*, but then scape single-flowered and perigone dark pink with a purplish-black central spot); paraperigone usually absent or consisting of a tube or free subulate appendages alternating the filaments; chromosome number usually $2n = 16$ (rarely $2n = 32$) 2 (Traubiinae)
1. Stigma trifid to obscurely trilobed (exceptionally capitate in *Zephyranthes capitata*, but then perigone red and tubular, and *Hippeastrum mirum*, but then scape with a single sessile flower); paraperigone usually a ring of fimbriae, but sometimes absent; chromosome number usually $2n = 12, 18, 22$ (exceptionally $2n = 16$ in some populations of *Zephyranthes bifida*) and polyploid variations of these numbers, most frequently multiples of 6 5 (Hippeastrinae)
2. Scapes usually single-flowered (very rarely 2-flowered in *R. montanum*); perigone infundibuliform to campanulate; paraperigone absent; plants exclusively in high-Andean habitats of Chile and Argentina ***Rhodolirium***
2. Scapes multi-flowered (incidentally single-flowered in *Phycella*, but then perigone red, and in *Traubia*, but then perigone stellate); perigone infundibuliform, stellate, or tubular; paraperigone present or absent; plants almost exclusively restricted to central Chile, growing mostly in

- coastal desert, sclerophyllous scrub, temperate forest, or high-Andean habitats 3
3. Paraperigone usually present, either as subulate and/or bifid appendages alternating the filaments and free from base or connate basally forming a tube, variously dissected; if paraperigone absent, then the perigone is tubular and red **Phycella**
3. Paraperigone absent; perigone star-shaped and white, or infundibuliform and rose 4
4. Perigone stellate, white, with a magenta longitudinal stripe abaxially; tepals linear-oblong, 3–4 mm wide; floral tube obsolete (1–2 mm long); plants in coastal scrubs or savannahs of *Acacia caven* in central Chile, between Coquimbo and Lib. B. O'Higgins Regions (31°S–34°S) **Traubia**
4. Perigone infundibuliform, rose; tepals oblanceolate, 8–15 mm wide; floral tube ca. 1 cm long; plants in loma habitats (fog oasis) of the coastal desert in northern Chile, between Antofagasta and Atacama Regions (23°S–26°S) **Eremolirion**
5. Tepals usually more than 6 cm long; spathe valves free from the base; chromosome number $2n = 22$ and multiples of 11 **Hippeastrum**
5. Tepals usually less than 6 cm long; spathe valves either fused into a tube or free from the base; chromosome number $2n = 12, 18$ (rarely $2n = 14, 16$) and multiples of 6 and 9 **Zephyranthes**

Hippeastrinae Walp

For a general description, see García & al. (2014).

- Hippeastrum** Herb., Appendix [in Bot. Reg. 6]: 31. 1821, nom. cons. \equiv *Aschamia* Salisb., Gen. Pl.: 134. 1866 – Type: *Amaryllis reginae* L. \equiv *Hippeastrum reginae* (L.) Herb., typ. cons.
- \equiv *Callicore* Link, Handbuch 1: 193. 1829 – **Type (designated here):** *Callicore reticulata* (L'Hér.) Link \equiv *Amaryllis reticulata* L'Hér. \equiv *Hippeastrum reticulatum* (L'Hér.) Herb.
- \equiv *Aulica* Raf., Fl. Tellur. 4: 10. 1838 (“1836”) – **Type (designated here):** *Aulica latifolia* Raf. \equiv *Amaryllis aulica* Ker Gawl. \equiv *Hippeastrum aulicum* (Ker Gawl.) Herb.
- \equiv *Eusarcops* Raf., Fl. Tellur. 4: 11. 1838 (“1836”) – Type: *Eusarcops reticulata* (L'Hér.) Raf. \equiv *Amaryllis reticulata* L'Hér. \equiv *Hippeastrum reticulatum* (L'Hér.) Herb.
- \equiv *Trisacarpis* Raf., Fl. Tellur. 4: 11. 1838 (“1836”) – **Type (designated here):** *Trisacarpis falcata* Raf. \equiv *Amaryllis calypttrata* Ker Gawl. \equiv *Hippeastrum calypttratum* (Ker Gawl.) Herb.
- \equiv *Lais* Salisb., Gen. Pl.: 134. 1866 – Type (designated by Traub & Moldenke, Amaryllidaceae Trib. Amaryllieae: 111. 1949): *Amaryllis striata* Lam. \equiv *Hippeastrum striatum* (Lam.) H.E.Moore.
- \equiv *Omphalissa* Salisb., Gen. Pl.: 134. 1866 – Type (designated by Traub & Moldenke, Amaryllidaceae Trib. Amaryllieae: 126. 1949): *Amaryllis aulica* Ker Gawl. \equiv *Hippeastrum aulicum* (Ker Gawl.) Herb.

- \equiv *Chonais* Salisb., Gen. Pl.: 135. 1866 – Type: *Amaryllis vittata* L'Hér. \equiv *Hippeastrum vittatum* (L'Hér.) Herb.
- \equiv *Lepidopharynx* Rusby in Mem. New York Bot. Gard. 7: 214. 1927 – Type: *Lepidopharynx deflexa* Rusby (\equiv *Hippeastrum cybister* (Herb.) Benth. ex Baker).
- \equiv *Tocantinia* Ravenna in Onira 5(3): 9. 2000 – Type: *Tocantinia mira* Ravenna \equiv *Hippeastrum mirum* (Ravenna) Christenh. & Byng.

Key to the subgenera of *Hippeastrum*

1. Scape single-flowered; flower sessile; perigone white, sweet-scented nocturnally; paraperigone absent; plants in Cerrado habitats from central Brazil (Bahia, Minas Gerais, Tocantins) **Hippeastrum** subg. **Tocantinia**
1. Scape multi-flowered; flowers pedicellate; perigone variously colored, mostly without fragrance; paraperigone fimbriate, in plaques, or absent; plants in various Neotropical vegetation types and habitats, mostly from Argentina to Colombia, occasional in Mesoamerica and the Caribbean, very diverse in eastern Brazil (Mata Atlantica, Cerrado) and central Andes of Peru and Bolivia **Hippeastrum** subg. **Hippeastrum**

Hippeastrum subg. *Hippeastrum*

Description. – Plants (15–)30–100 cm high. Bulb globose. Leaves usually annual, mostly hysteranthous, sometimes persistent, usually lorate to falcate, less frequently lanceolate or linear, canaliculate or flat, rarely semicylindrical, sometimes fleshy, various shades of green, venation parallel (rarely with transverse veinlets), (4–)40–80 cm long, (1–)15–65 mm wide, apex acute to obtuse or rounded. Scape fistulose, 2–30 cm long, 1–6 mm wide below the spathe. Spathe bivalved, valves free to base, membranous, marcescent, 0.8–3(–5.5) cm long. Inflorescence (1–)2–4(–8)-flowered, each flower subtended by a lanceolate to filiform bracteole. Flowers slightly to strongly zygomorphic, nodding to patent, always pedicellate, pedicel (1.5–)2–7 cm long. Perigone usually infundibuliform to salverform, less frequently campanulate, rarely appearing labiate by three upper tepals reflexed and the three lower declinate and convolute proximally, forming a pseudolabellum that encloses the stamens and style; tepals oblanceolate or obovate to elliptical, rarely narrow and lanceolate or falcate, white, red to pink, yellow, or green, can be variously striped or with a basal light to dark region, (3–)6–15 cm long, (0.5–)1.5–4.5(–7) mm wide, almost free to the base to connate forming a tube (0.2–)1–4(–12) cm long, thus obsolete to representing more than ½ of the flower's length, apex reflexed to straight. Paraperigone, if present, a fimbriate ring that can be continuous to discontinuous or as broad scales (i.e., callose ridge in Meerow & Snijman, 1998; “plaques” in Oliveira, 2012). Filaments filiform, declinate-ascending, 4-seriate. Stigma capitate or obscurely trilobed (i.e., capitate-trilobed) to trifid, each lobe (1–)2–4(–10) mm long. Capsule globose-tricoccus, sometimes apically depressed. Seeds semielliptical and flat,

papyraceous, obliquely winged or irregularly discoid, rarely turgid and globose or subglobose, black or brown. $2n = 22, 33, 44, 55, 66, 77$.

Diversity and distribution. – A complex nomenclatural and taxonomic history and our current knowledge about species limits prevent us from providing a full list of accepted species for *Hippeastrum* subg. *Hippeastrum*; however, we estimate that this large clade is composed of ca. 100 species. This group is found widely in South America, from central Argentina to Colombia, but the regions of highest diversity are in eastern Brazil and the Andes of Peru and Bolivia. This subgenus also has been introduced in Central America, Mexico, the West Indies, and Africa (e.g., Correll & Correll, 1982; Meerow, 2003).

Comments. – Latest research on the phylogeny of *Hippeastrum* subg. *Hippeastrum* indicates that there are at least three major lineages, of yet unresolved relationship: (1) *H. reticulatum* Herb., (2) *H. brasilianum* (Traub & L.J.Doran) Dutilh and *H. idimae* Dutilh & R.S.Oliveira, and (3) the remaining species, also known as the core *Hippeastrum* clade (García & al., 2014, 2017); however, the phylogenetic pattern could be more complex given a complete sampling of Brazilian taxa, as suggested by Oliveira (2012). The core *Hippeastrum* clade contains most of the species in the subgenus (except 3–5 species) and is yet largely unresolved, probably as a consequence of rapid radiation and hybridization (Oliveira, 2012; García & al., 2014).

Hippeastrum lavrense (Ravenna) R.S.Oliveira & Dutilh, **comb. nov.** \equiv *Amaryllis lavrensis* Ravenna in *Onira* 9(2): 12. 2003.

Hippeastrum stapfianum (Kraenzl.) R.S.Oliveira & Dutilh, **comb. nov.** \equiv *Crinum stapfianum* Kraenzl. in *Bull. Misc. Inform. Kew* 1913(5): 191. 1913.

Hippeastrum subg. *Tocantinia* (Ravenna) Nic.García, **comb. & stat. nov.** \equiv *Tocantinia* Ravenna in *Onira* 5(3): 9. 2000.

Description. – Plants 30–70 cm tall. Bulb globose. Leaves annual, proteranthous, 3–8 when flowering, linear to linear-lorate, canaliculate, green, parallel venation, 7–50 cm long, 3–21 mm wide, apex acute to rounded. Scape fistulous (solid in *H. mirum*, according to Büneker & al., 2016), 15–70 cm long, 2–7 mm wide below the spathe. Spathe with 2–3 valves (single valve with margins free to base in *H. mirum*, according to Ravenna, 2000), covering the ovary, valves free to the base, lanceolate, 3–8 cm long. Inflorescence single-flowered. Flowers slightly zygomorphic, erect to patent, sessile to subsessile, scented. Perigone narrowly infundibuliform, mostly white; tepals oblanceolate, 11–20 cm long, 10–30 mm wide, connate forming a pale green tube (5–)8–12 cm long; the upper half spreading and wider, white, apically reflexed. Paraperigone absent. Filaments declinate-ascending, 4-seriate, apex incurved. Stigma capitate or trifid. Ovules 13–16 in each locule, clavate-capitate to suborbicular (with a round chalazal protuberance that possibly develops into an aril in seed in *H. mirum*, according to

Ravenna, 2000). Capsule globose-tricoccus. Seeds unknown. $2n = 22$ (García, 2015).

Diversity and distribution. – This small group of three species formerly in *Tocantinia* (Büneker & al., 2016) was combined into *Hippeastrum* by Christenhusz & al. (2018), a decision with which we agree. *Hippeastrum* subg. *Tocantinia* inhabits the Cerrado ecoregion in the Brazilian states of Bahia, Minas Gerais, and Tocantins. The plants grow in sandy soils, within semideciduous dry forests.

Comments. – The monophyly of *Hippeastrum* subg. *Tocantinia* has not been tested with molecular data; *H. mirum* (Ravenna) Christenh. & Byng is known only from the type collection and has not been found in the wild since 1991. The recently described *H. stigmatovittatum* (Büneker & al.) Christenh. & Byng is also known from a single population, whereas *H. dutilhianum* (Büneker & al.) Christenh. & Byng is known from only two locations (Büneker & al., 2016). However, the monophyly of this subgenus is suggested by a combination of shared morphological characters that is not found elsewhere within the tribe, including the spathe valve(s) with margins free to the base, single-flowered scape, and sessile white flower with a long, scented tube.

Subgenus *Tocantinia* (represented in García & al., 2017 by *H. dutilhianum* as *Tocantinia dutilhiana* Büneker & al.) is sister to subgenus *Hippeastrum*, perhaps an ancient offshoot of the ancestral $2n = 22$ lineage. A single sessile flower in contrast to multiple pedicellate flowers in *H.* subg. *Hippeastrum* can be used to distinguish *H.* subg. *Tocantinia*.

Zephyranthes Herb., Appendix [in *Bot. Reg.* 6]: 36. 1821, nom. cons. \equiv *Atamosco* Adans., *Fam. Pl.* 2: 57, 522. 1763, nom. rej. – Type: *Zephyranthes atamasco* (L.) Herb. \equiv *Amaryllis atamasco* L.

\equiv *Sprekelia* Heist., *Beschr. Neu. Geschl.*: 15, 19. 1755 – Type: *Sprekelia formosissima* (L.) Herb. \equiv *Amaryllis formosissima* L., **syn. nov.**

\equiv *Habranthus* Herb. in *Bot. Mag.* 51: t. 2464. 1824 – Type: *Habranthus gracilifolius* Herb. \equiv *Zephyranthes gracilifolia* (Herb.) G.Nicholson.

\equiv *Haylockia* Herb. in Edwards's *Bot. Reg.* 16: t. 1371. 1830 – Type: *Haylockia pusilla* Herb. (= *Zephyranthes americana* (Hoffmanns.) Ravenna).

\equiv *Cooperia* Herb. in Edwards's *Bot. Reg.* 22: t. 1835. 1836 – Type: *Cooperia drummondii* Herb. (= *Zephyranthes chlorosolen* (Herb.) D.Dietr.).

\equiv *Sceptranthes* Graham in *Edinburgh New Philos. J.* 20: 413. 1836 – Type: *Sceptranthes drummondii* (D.Don) Graham \equiv *Zephyranthes drummondii* D.Don.

\equiv *Plectronema* Raf., *Fl. Tellur.* 4: 10. 1838 (“1836”) \equiv *Argyropsis* M.Roem., *Fam. Nat. Syn. Monogr.* 4: 125. 1847 – Type: *Plectronema candida* (Lindl.) Raf. \equiv *Amaryllis candida* Lindl. \equiv *Argyropsis candida* (Lindl.) M.Roem. \equiv *Zephyranthes candida* (Lindl.) Herb.

\equiv *Pogonema* Raf., *Fl. Tellur.* 4: 10. 1838 (“1836”) – Type: *Pogonema carinata* (Herb.) Raf. \equiv *Zephyranthes carinata* Herb.

- = *Mesochloa* Raf., Fl. Tellur. 4: 11. 1838 (“1836”) – Type: *Mesochloa canaliculata* Raf. ≡ *Zephyranthes mesochloa* Herb. ex Lindl.
- = *Arviela* Salisb., Gen. Pl.: 135. 1866 – Type: *Amaryllis tubispatha* L’Hér. ≡ *Zephyranthes tubispatha* (L’Hér.) Herb.
- = *Myostemma* Salisb., Gen. Pl.: 135. 1866 – Type: *Myostemma advena* (Ker Gawl.) Ravenna ≡ *Amaryllis advena* Ker Gawl. ≡ *Zephyranthes advena* (Ker Gawl.) Nic.García, **syn. nov.**
- = *Hippeastrum* subg. *Zephyranthella* Pax in Bot. Jahrb. Syst. 11: 329. 1890 ≡ *Zephyranthella* (Pax) Pax in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 15a: 416. 1930 – Type: *Zephyranthella tubispatha* (Pax) Pax ≡ *Hippeastrum tubispathum* Pax (= *Zephyranthes pedunculosa* (Herb.) Nic.García & S.C.Arroyo).
- = *Famatina* Ravenna in Pl. Life 48: 56. 1972 – Type: *Famatina saxatilis* Ravenna (= *Zephyranthes capitata* Nic.García), **syn. nov.**
- = *Eithea* Ravenna in Bot. Australis 1: 2. 2002 – Type: *Eithea blumenavia* (K.Koch & C.D.Bouché ex Carrière) Ravenna ≡ *Griffinia blumenavia* K.Koch & C.D.Bouché ex Carrière ≡ *Zephyranthes blumenavia* (K.Koch & C.D.Bouché ex Carrière) Nic.García & Dutilh, **syn. nov.**
- = *Aidema* Ravenna in Onira 8(1): 2. 2003 – Type: *Aidema cearensis* (Herb.) Ravenna ≡ *Habranthus cearensis* Herb. ≡ *Zephyranthes cearensis* (Herb.) Baker.
- = *Bathya* Ravenna in Bot. Australis 2: 11–12. 2003 – Type: *Bathya andina* (Phil.) Ravenna ≡ *Rhodophiala andina* Phil. ≡ *Zephyranthes philippiana* Nic.García, **syn. nov.**

Key to the subgenera and incertae sedis of *Zephyranthes*

1. Leaves differentiated into a blade and a pseudopetiole; seeds rounded on the back and with an elaiosome on the chalazal extreme *Zephyranthes* subg. *Eithea*
1. Leaves linear, lorate, lanceolate, or falcate, not differentiated into blade and pseudopetiole; seeds usually flat, papery, lacking an elaiosome 2
2. Spathe bracts fused into a tube; chromosome number most frequently $2n = 12, 14$, or multiples of 6 ($2n > 18$) 3
2. Spathe bracts free from the base (rarely fused in *Zephyranthes bifida*, but then scape multi-flowered and perigone infundibuliform, red to lavender); chromosome number $2n = 16, 18$, or multiples of 9 5
3. Scape single-flowered (if multi-flowered, then $2n > 14$); flowers actinomorphic or zygomorphic *Zephyranthes* subg. *Zephyranthes*
3. Scape multi-flowered (if single-flowered, then $2n = 12$ or 14); flowers zygomorphic 4
4. Leaves flat or canalicate *Zephyranthes* subg. *Habranthus*
4. Leaves terete and fistulous ... *Zephyranthes pedunculosa*
5. Perigone always infundibuliform, red to lavender, rarely white; chromosome number $2n = 16$ or 18; 45S nrDNA (NOR) terminal on short arm of a subtelocentric chromosome; plants mostly in Pampa grassland habitats from

- northern Argentina, Uruguay, Paraguay, and southern Brazil (Rio Grande do Sul) *Zephyranthes* subg. *Neorhodophiala*
5. Perigone infundibuliform to tubular, red to pink or yellow, rarely white; chromosome number usually $2n = 18$, polyploidy also present; 45S nrDNA (NOR) terminal on long arm of a submetacentric to subtelocentric chromosome; plants in various vegetation types from Chile (Antofagasta to Valdivia, 23°S–40°S), also in high-Andean habitats in Chile and central-southwestern Argentina *Zephyranthes* subg. *Myostemma*

Nomenclatural note. – This recircumscription implies acceptance of a formal proposal to conserve the name *Zephyranthes* (Herbert, 1821) against *Sprekelia* (Heister, 1755) to the General Committee of Nomenclature as required under Arts. 14.12 and 56.2 of the ICN (in this volume). *Sprekelia* has been traditionally allied to *Habranthus* and *Zephyranthes* due to their single-flowered scapes and fused spathe valves, but also considered a distinct genus, mainly due to its ultra-zygomorphic perigone with the three lower tepals forming a pseudolabellum (e.g., Herbert, 1837; Kunth, 1850; Baker, 1888; Pax, 1888; Pax & Hoffmann, 1930; Traub, 1963; Müller-Doblies & Müller-Doblies, 1996; Meerow & Snijman, 1998). The latter floral morphology is also found in two species of *Hippeastrum* (i.e., *H. angustifolium* Pax, *H. cybister* (Herb.) Benth. ex Baker), but these two species have names under *Sprekelia*; therefore, its occurrence in *Zephyranthes* is considered here a convergence due to the high canalization and deep reticulations within Hippeastrinae (Meerow, 2010; García & al., 2014). Phylogenetic analyses of DNA sequences (Meerow & al., 2000; Meerow, 2010; García & al., 2014; García, 2015) strongly suggest that *Sprekelia* is deeply embedded in *Zephyranthes*. The origin of Mexican *Sprekelia* is still unclear and potentially could represent a series of ancient polyploid events due to their chromosome number $2n = 60$ (also $2n = 120, 150, 180$ in cultivated specimens; Bose & Flory, 1965; Flory, 1977; García & al., 2014; García, 2015). The conservation of *Zephyranthes* against *Sprekelia* would provide nomenclatural stability because the former has been widely used in taxonomic and horticultural literature (e.g., Huxley & al., 1992; Brickell & Zuk, 1997), while the latter is currently composed of only two species. Hence, adopting the older name would imply performing ca. 100 new combinations, versus transferring two names (*Sprekelia formosissima*, *S. howardii* Lehmiller) to *Zephyranthes*. In consequence, the transfer of *Sprekelia formosissima* (L.) Herb. (≡ *Amaryllis formosissima* L.) into *Zephyranthes* will be pending until the proposal to conserve the latter name over *Sprekelia* is accepted by the General Committee of Nomenclature.

Zephyranthes subg. *Zephyranthes*

Description. – Plants 4–50 cm tall. Bulb globose or ovoid, sometimes oblong-pyriform. Leaves usually annual,

sometimes persistent, usually linear, rarely lorate, canaliculated or flat, sometimes fleshy, various tones of green, sometimes glaucous or pruinose, parallel venation, 10–30(–60) cm long, (1–)2–9(–13) mm wide, apex attenuate-acute to obtuse or rounded. Scape fistulose, cylindrical to filiform, 2–30 cm long, sometimes completely underground at anthesis and included in the bulb pseudoneck, 1–6 mm wide below the spathe, sometimes pruinose. Spathe valves 2 with margins fused from the base into a tube of various lengths, membranous, marcescent, bifid or fenestrate towards the apex, sometimes entire, 0.8–3(–5.5) cm long. Inflorescence single-flowered, rarely 2-flowered, flowers subtended by a filiform-lanceolate bracteole. Flowers slightly to strongly zygomorphic or actinomorphic, nodding to patent, usually pedicellate, pedicel up to 6 cm long, sometimes sessile. Perigone broadly infundibuliform to salverform or campanulate to rotaceous, rarely appearing labiate by three upper tepals reflexed and the three lower declinate and convolute proximally, forming a pseudolabellum that encloses the stamens and style; tepals oblanceolate to elliptic or ovate, rarely narrow and lanceolate or falcate, usually white to pink, less frequently yellow or red, rarely lilaceous, sometimes striped or with a basal light to dark spot, (0.6–)2–5(–7) cm long, (2–)4–13(–16) mm wide, almost free to the base to connate forming a tube commonly 2–4 mm long but up to 13 cm long, thus obsolete to representing more than $\frac{3}{4}$ of the flower's length, apex reflexed to straight. Paraperigone, if present, a fimbriate ring 0.3–2 mm long. Filaments usually filiform, declinate-ascending and 4-seriate, or straight and 2-seriate, sometimes both series of the same length. Stigma obscurely trilobed (i.e., capitate-trilobed) to trifid, each lobe <0.5–4(–7) mm long. Capsule globose-tricocccous, sometimes laterally or apically depressed. Seeds semielliptical to almost triangular, flat, sometimes obliquely winged, papyraceous, black. $2n = 12, 14, 20, 24, 28, 30, 32, 36, 38, 48, 54, 60, 72, 110$, and other variants.

Diversity and distribution. – A complex nomenclatural and taxonomic history and our current knowledge about species limits prevent us from providing a full list of accepted species for *Zephyranthes* subg. *Zephyranthes*; however, we estimate that this large clade is composed of ca. 150 species. Subgenus *Zephyranthes* is distributed widely in the Neotropics, but also occurs in subtropical to temperate regions, from central Argentina to the southern United States, also in the Caribbean islands.

Comments. – The closed tubular spathe valve is a likely synapomorphy for *Zephyranthes* s.l., and this condition is stable throughout *Z.* subg. *Zephyranthes*. Many species have 4-seriate stamens, slightly zygomorphic and nodding flowers (former *Habranthus*), whereas others have biseriate stamens, actinomorphic and patent flowers (former definition of *Zephyranthes*). A few species have an underground scape due to elongation suppression (i.e., *Haylockia*), including *Z. americana* from Argentina and Uruguay, *Z. andina* from the central Andean plateau of Peru, Bolivia, and northern Argentina, and *Z. verecunda* Herb. from Mexico. Two Mexican species, formerly considered in *Sprekelia*, have an ultra-zygomorphic perigone consisting of

the three upper tepals reflexed and the three lower declinate and convolute proximally, forming a pseudolabellum that encloses the stamens and style; this floral morphology is convergent with two *Hippeastrum* species. Ravenna (2003b) does not clearly state the defining characters for *Aidema*, but certain species combined under this genus clearly belong in *Zephyranthes* according to DNA sequences (García & al., 2014) and their tubular spathe valves. There is some variation in leaf anatomy (see Arroyo & Cutler, 1984), flower size and shape, fimbriate paraperigone (i.e., absent from most North American taxa), stigma, and chromosome numbers. This subgenus urgently needs a critical evaluation of species limits that considers molecular, chromosomal, and morphological variation.

Overall, the diversification of *Z.* subg. *Zephyranthes* is very complex and seems to have been deeply affected by reticulate evolution. Hybridization and polyploidy have been traditionally invoked as major forces in the group's evolution (e.g., Flagg & Flory, 1976; Flory, 1977; Greizerstein & Naranjo, 1987). Additionally, apomixis has been documented in North American polyploid taxa (Flory, 1939; Brown, 1951), and the consequences of this have not been addressed critically in relation to the group's diversification. Self-compatibility has been reported in several species and is probably more common than currently known (Meerow & Snijman, 1998; N. García, pers. obs.). The phylogeny of *Z.* subg. *Zephyranthes* is still unclear and pending future studies that consider a broader sampling, while addressing methodological issues encountered in previous studies (García, 2015).

Zephyranthes amambaica (Ravenna) Nic.García & Meerow, **comb. nov.** \equiv *Habranthus amambaicus* Ravenna in *Onira* 9(2): 14. 2003.

Zephyranthes andalgalensis (Ravenna) S.C.Arroyo, **comb. nov.** \equiv *Habranthus andalgalensis* Ravenna in *Sellowia* 19: 30. 1967.

Zephyranthes araguaiensis (Ravenna) R.S.Oliveira & Dutilh, **comb. nov.** \equiv *Habranthus araguaiensis* Ravenna in *Onira* 6(5): 41. 2001.

Zephyranthes aurata (Ravenna) Nic.García & Meerow, **comb. nov.** \equiv *Habranthus auratus* Ravenna in *Onira* 9(2): 15. 2003.

Zephyranthes bahiensis (Ravenna) R.S.Oliveira & Dutilh, **comb. nov.** \equiv *Habranthus bahiensis* Ravenna in *Onira* 1(8): 53. 1988.

Zephyranthes barrosiana (Hunz. & DiFulvio) S.C.Arroyo, **comb. nov.** \equiv *Habranthus barrosianus* Hunz. & DiFulvio in *Kurtziana* 7: 255. 1973.

Zephyranthes botumirimensis (R.S.Oliveira) R.S.Oliveira & Dutilh, **comb. nov.** \equiv *Habranthus botumirimensis* R.S. Oliveira in *Kew Bull.* 64: 538–539, fig. 1. 2009.

Zephyranthes caaguazuensis (Ravenna) Nic.García & Meerow, **comb. nov.** \equiv *Habranthus caaguazuensis* Ravenna in *Onira* 9(2): 15. 2003.

Zephyranthes calderensis (Ravenna) Nic.García & S.C.Arroyo, **comb. nov.** \equiv *Habranthus calderensis* Ravenna in *Onira* 9(2): 13. 2003.

- Zephyranthes carminea* (Ravenna) S.C.Arroyo, **comb. nov.** ≡ *Habranthus carmineus* Ravenna in Not. Mens. Mus. Nac. Hist. Nat. 15(173): 5. 1970.
- Zephyranthes chacoensis* (Ravenna) S.C.Arroyo, **comb. nov.** ≡ *Habranthus chacoensis* Ravenna in Not. Mens. Mus. Nac. Hist. Nat. 15(173): 5. 1970.
- Zephyranthes concinna* (Ravenna) R.S.Oliveira & Dutilh, **comb. nov.** ≡ *Habranthus concinnus* Ravenna in Onira 3(17): 63. 1999.
- Zephyranthes contermina* (Ravenna) R.S.Oliveira & Dutilh, **comb. nov.** ≡ *Habranthus conterminus* Ravenna in Onira 3(17): 57. 1999.
- Zephyranthes correntina* (Roitman, J.A.Castillo & M.R.Barrios) Nic.García & S.C.Arroyo, **comb. nov.** ≡ *Habranthus correntinus* Roitman, J.A.Castillo & M.R.Barrios in Bol. Soc. Argent. Bot. 43(1–2): 153–155, fig. 1. 2008.
- Zephyranthes crassibulba* (Ravenna) S.C.Arroyo, **comb. nov.** ≡ *Habranthus crassibulbus* Ravenna in Onira 3(17): 63. 1999.
- Zephyranthes datensis* (Ravenna) R.S.Oliveira & Dutilh, **comb. nov.** ≡ *Habranthus datensis* Ravenna in Onira 3(16): 58. 1999.
- Zephyranthes duarteana* (Ravenna) R.S.Oliveira & Dutilh, **comb. nov.** ≡ *Habranthus duarteanus* Ravenna in Pl. Life 30: 45. 1974.
- Zephyranthes gameleirensis* (Ravenna) R.S.Oliveira & Dutilh, **comb. nov.** ≡ *Habranthus gameleirensis* Ravenna in Onira 3(16): 57. 1999.
- Zephyranthes goiana* (Ravenna) R.S.Oliveira & Dutilh, **comb. nov.** ≡ *Habranthus goianus* Ravenna in Pl. Life 30: 45. 1974.
- Zephyranthes guachipensis* (Ravenna) S.C.Arroyo, **comb. nov.** ≡ *Habranthus guachipensis* Ravenna in Pl. Life 30: 43. 1974.
- Zephyranthes immaculata* (Traub & Clint) Nic.García & Meerow, **comb. nov.** ≡ *Habranthus immaculatus* Traub & Clint in Pl. Life 13: 68. 1957.
- Zephyranthes irwiniana* (Ravenna) Nic.García, **comb. nov.** ≡ *Habranthus irwinianus* Ravenna in Pl. Life 26: 97. 1970.
- Zephyranthes ischihualasta* (Ravenna) S.C.Arroyo, **comb. nov.** ≡ *Habranthus ischihualastus* Ravenna in Onira 3(17): 63. 1999.
- Zephyranthes itaobina* (Ravenna) Nic.García, **comb. nov.** ≡ *Habranthus itaobinus* Ravenna in Onira 3(16): 56. 1999.
- Zephyranthes lehmilleri* Nic.García & Meerow, **nom. nov.** ≡ *Sprekelia howardii* Lehmillier in Herbertia 54: 230. 2000 (“1999”), non *Zephyranthes howardii* Traub 1963.
Etymology. – Dedicated to David J. Lehmillier M.D. (1940–), a devoted student of the genus *Crinum*, both botanically and horticulturally.
- Zephyranthes leonensis* (Ravenna) S.C.Arroyo, **comb. nov.** ≡ *Habranthus leonensis* Ravenna in Onira 3(16): 56. 1999.
- Zephyranthes leptandra* (Ravenna) Nic.García, **comb. nov.** ≡ *Habranthus leptandrus* Ravenna in Pl. Life 34: 87–89. 1978.
- Zephyranthes lucida* (R.S.Oliveira) R.S.Oliveira & Dutilh, **comb. nov.** ≡ *Habranthus lucidus* R.S.Oliveira in Kew Bull. 64(3): 538–541, fig. 2. 2009.
- Zephyranthes magnoi* (Ravenna) S.C.Arroyo, **comb. nov.** ≡ *Habranthus magnoi* Ravenna in Sellowia 19: 31. 1967.
- Zephyranthes martinezii* (Ravenna) Nic.García, **comb. nov.** ≡ *Habranthus martinezii* Ravenna in Not. Mens. Mus. Nac. Hist. Nat. 15(173): 3. 1970.
- Zephyranthes mataca* (Ravenna) S.C.Arroyo, **comb. nov.** ≡ *Habranthus matacus* Ravenna in Onira 3(17): 66. 1999.
- Zephyranthes matogrossensis* (Ravenna) R.S.Oliveira & Dutilh, **comb. nov.** ≡ *Aidema matogrossensis* Ravenna in Onira 8(1): 3. 2003.
- Zephyranthes medinae* (L.O.Alvarado & García-Mendoza) Nic.García & Meerow, **comb. nov.** ≡ *Habranthus medinae* L.O.Alvarado & García-Mendoza in Novon 18(3): 283–286, fig. 1, 2. 2008.
- Zephyranthes mexicana* (T.M.Howard) Nic.García & Meerow, **comb. nov.** ≡ *Habranthus mexicanus* T.M.Howard in Herbertia 51: 42–43. 1996.
- Zephyranthes microcarpa* (Rusby) S.C.Arroyo, **comb. nov.** ≡ *Atamosco microcarpa* Rusby in Mem. New York Bot. Gard. 7: 213. 1927.
- Zephyranthes millarensis* (Ravenna) Nic.García, **comb. nov.** ≡ *Habranthus millarensis* Ravenna in Pl. Life 37: 66. 1981.
- Zephyranthes minor* (Ravenna) R.S.Oliveira & Dutilh, **comb. nov.** ≡ *Habranthus minor* Ravenna in Onira 9(2): 13. 2003.
- Zephyranthes neumannii* (Roitman, J.A.Castillo & Maza) Nic.García & S.C.Arroyo, **comb. nov.** ≡ *Habranthus neumannii* Roitman, J.A.Castillo & Maza in Darwiniana 46(1): 67–68, fig. 1. 2008.
- Zephyranthes nivea* (Ravenna) S.C.Arroyo, **comb. nov.** ≡ *Habranthus niveus* Ravenna in Pl. Life 26: 95. 1970.
- Zephyranthes oranensis* (Ravenna) S.C.Arroyo, **comb. nov.** ≡ *Habranthus oranensis* Ravenna in Onira 3(17): 64. 1999.
- Zephyranthes pantanalensis* (Ravenna) R.S.Oliveira & Dutilh, **comb. nov.** ≡ *Habranthus pantanalensis* Ravenna in Onira 3(16): 59. 1999.
- Zephyranthes philadelphica* (Ravenna) Nic.García & Meerow, **comb. nov.** ≡ *Habranthus philadelphicus* Ravenna in Onira 9(2): 16. 2003.
- Zephyranthes picta* (Ravenna) S.C.Arroyo, **comb. nov.** ≡ *Habranthus pictus* Ravenna in Onira 3(16): 59. 1999.
- Zephyranthes riojana* (Ravenna) S.C.Arroyo, **comb. nov.** ≡ *Habranthus riojanus* Ravenna in Pl. Life 26: 96. 1970.
- Zephyranthes rubra* (Ravenna) R.S.Oliveira & Dutilh, **comb. nov.** ≡ *Habranthus ruber* Ravenna in Pl. Life 26: 94, fig. 24. 1970.
- Zephyranthes ruizlealii* (Ravenna) S.C.Arroyo, **comb. nov.** ≡ *Habranthus ruizlealii* Ravenna in Pl. Life 30: 44. 1974.

- Zephyranthes saipinensis* (Ravenna) Nic.García, **comb. nov.** ≡ *Habranthus saipinensis* Ravenna in *Onira* 10(3): 10. 2005.
- Zephyranthes salinarum* (Ravenna) S.C.Arroyo, **comb. nov.** ≡ *Habranthus salinarum* Ravenna in *Not. Mens. Mus. Nac. Hist. Nat.* 15(173): 3. 1970.
- Zephyranthes saltensis* (Ravenna) S.C.Arroyo, **comb. nov.** ≡ *Habranthus saltensis* Ravenna in *Not. Mens. Mus. Nac. Hist. Nat.* 15(173): 6. 1970.
- Zephyranthes sanavirone* (Roitman, J.A.Castillo, G.M.Tourn & Uria) Nic.García & S.C.Arroyo, **comb. nov.** ≡ *Habranthus sanavirone* Roitman, J.A.Castillo, G.M.Tourn & Uria in *Novon* 17(3): 393–394. 2007.
- Zephyranthes schulziana* (Ravenna) S.C.Arroyo, **comb. nov.** ≡ *Habranthus schulzianus* Ravenna in *Not. Mens. Mus. Nac. Hist. Nat.* 15(173): 8. 1970.
- Zephyranthes spectabilis* (Ravenna) S.C.Arroyo, **comb. nov.** ≡ *Habranthus spectabilis* Ravenna in *Not. Mens. Mus. Nac. Hist. Nat.* 15(173): 28. 1970.
- Zephyranthes steyermarkii* (Ravenna) S.C.Arroyo, **comb. nov.** ≡ *Habranthus steyermarkii* Ravenna in *Pl. Life* 34: 85. 1978.
- Zephyranthes tepicensis* (Greenm. ex Flagg & G.Lom.Sm.) Flagg & G.Lom.Sm., **comb. nov.** ≡ *Habranthus tepicensis* Greenm. ex Flagg & G.Lom.Sm. in *Herbertia* 63: 175–176, fig. 1. 2010 (“2009”).
- Zephyranthes venturiana* (Ravenna) S.C.Arroyo, **comb. nov.** ≡ *Habranthus venturianus* Ravenna in *Onira* 3(17): 65. 1999.
- Zephyranthes vittata* (T.M.Howard) Nic.García & Meerow, **comb. nov.** ≡ *Habranthus vittatus* T.M.Howard in *Herbertia* 46(1–2): 115, fig. 1–4. 1991 (“1990”).
- Zephyranthes zapotecana* Nic.García & Meerow, **nom. nov.** ≡ *Habranthus oaxacanus* T.M.Howard in *Herbertia* 51: 43. 1996, non *Zephyranthes oaxacana* Ravenna 2005.

Etymology. – Named after the Zapotec culture, original of the State of Oaxaca, Mexico.

- Zephyranthes* subg. *Habranthus* (Herb.) Nic.García, **comb. & stat. nov.** ≡ *Habranthus* Herb. in *Bot. Mag.* 51: t. 2464. 1824.

Description. – Plants 10–30 cm tall. Bulb globose to oblong. Leaves annual, usually absent when flowering, linear to almost filiform, canaliculated, green, parallel venation, 15–30 cm long, 3–10 mm wide, apex attenuate-acute to obtuse. Scape fistulose, cylindrical, 6–20 cm long, 2–3 mm wide below the spathe, somewhat pruinose. Spathe valves 2 with margins fused from the base into a tube up to a half of its length, membranous, marcescent, 25–60 cm long. Inflorescence 1–4-flowered, flowers subtended by a filiform-lanceolate bracteole. Flowers slightly zygomorphic, nodding, pedicellate, pedicel 0.6–6 cm long. Perigone infundibuliform; tepals oblanceolate to elliptical, white to pink, sometimes with dark pink stripes, with greenish pigmentation near the base, 4.0–5.5 cm long, 8–15 mm wide, connate basally forming a tube 1.5–3.5 mm long, apex reflexed, apiculate. Paraperigone a fimbriate ring

0.3–2.0 mm long. Filaments filiform, declinate-ascending and 4-seriate. Stigma trifold, each lobe 2–4 mm long. Capsule globose-tricocous. Seeds semielliptical, flat, papyraceous, black. $2n = 12, 14$.

Diversity and distribution. – The group is currently composed of only three species, found in northern Argentina, Uruguay, and southern Brazil (Rio Grande do Sul). In Argentina, *Zephyranthes jamesonii* inhabits sand dunes at sea level to high-Andean scrubs at 3000 m a.s.l.

Comments. – *Zephyranthes* subg. *Habranthus* is sister to *Z.* subg. *Myostemma* according to nuclear-based phylogenies (García & al., 2017). Both clades share having multi-flowered scapes with funnellform flowers, a combination of characters that is probably plesiomorphic within Hippeastrinae; however, species in subgenus *Habranthus* have fused spathe valves (vs. free in *Z.* subg. *Myostemma*). In turn, the clade formed by these two subgenera seems to be sister to *Z.* subg. *Eithea* (García & al., 2017); no putative synapomorphies are known for that comprehensive clade.

The number of species in this group is rather uncertain. The wide environmental range displayed by *Zephyranthes jamesonii* deserves more in-depth studies of its morphological and genetic variation to explore the possible existence of cryptic species. This matter should be tested with morphological and genetic studies, as should the extent of *Z. gracilifolia* into southeastern Brazil (e.g., Amaral-Lopes & Cavalcanti, 2015).

- Zephyranthes estensis* (Ravenna) Nic.García & S.C.Arroyo, **comb. nov.** ≡ *Habranthus estensis* Ravenna in *Pl. Life* 30: 46. 1974.

- Zephyranthes jamesonii* (Baker) Nic.García & S.C.Arroyo, **comb. nov.** ≡ *Hippeastrum jamesonii* Baker in *J. Bot.* 16: 83. 1878.

- Zephyranthes* subg. *Eithea* (Ravenna) Nic.García, **comb. & stat. nov.** ≡ *Eithea* Ravenna in *Bot. Australis* 1: 2. 2002.

Description. – Plants 12–50 cm tall. Bulb ovoid. Leaves annual or evergreen, present when plant flowers or not, 1–8, pseudopetiolate; petioles subtrigonus, with reddish to brownish pigmentation abaxially, 2–9 cm long; blade dark to light green, elliptical, lanceolate or oblanceolate to slightly falcate, apex acute, base attenuate into pseudopetiole, texture herbaceous, often slightly plaited (shiny), with distinct transverse reticulate veinlets, 8–21 cm long, 1–6 cm wide. Scape fully fistulose or solid in the lower fifth, slightly compressed laterally, 8–30 cm long, 2–6 mm wide. Spathe bivalved, valves free or fused for more than the lower half, narrowly lanceolate, marcescent, 17–43 mm long. Inflorescence pseudo-umbellate, 1–6-flowered, each flower subtended by a linear-attenuate bracteole. Flowers slightly zygomorphic, patent or slightly nodding, pedicels 0.5–2.4 cm long, elongating with fructification up to 7 cm long. Perigone infundibuliform to campanulate, mostly white; tepals oblanceolate, white, sometimes with variably faint magenta stripes, except on the lower inner tepal, with greenish pigmentation near the base, 2–6 cm long, 5–24 mm wide, connate basally forming a tube 0.2–0.5 cm long, apically reflexed.

Paraperigone a fimbriate ring. Filaments declinate-ascending, 4-seriate, apex incurved. Stigma trilobed, each lobe 1.0–4.5 mm long. Capsule globose-tricocous. Seeds ellipsoid, irregular, angular, smooth, with a wrinkled elaiosome on the chalazal extreme, black. $2n = 18$ (García, 2015).

Diversity and distribution. – This is a small clade of only two species (Campos-Rocha & al., 2017; García & al., 2017). *Zephyranthes blumenavia* inhabits the Brazilian Atlantic forest (i.e., Mata Atlântica) in the states of São Paulo, Parana, and Santa Catarina, while *Z. lagopaivae* is known from only two semideciduous forest fragments within areas with well-defined seasonality in the state of São Paulo. According to Ravenna (2002), *Z. blumenavia* is found in very humid conditions within the forest, such as along rocky banks of small rivers or among large plants.

Comments. – There are very few known populations of species of *Zephyranthes* subg. *Eithea*, and they usually consist of few individuals (Ravenna, 2002; Campos-Rocha & al., 2017). Both species are likely bordering on extinction due to the destruction of the native forest; as a consequence, *Z. blumenavia* is considered an Endangered species (Ministério do Meio Ambiente, 2014) and *Z. lagopaivae* has been proposed as Critically Endangered (Campos-Rocha & al., 2017). For leaf anatomical details and comparison of both species, see Campos-Rocha & al. (2017).

Zephyranthes blumenavia (K.Koch & C.D.Bouché ex Carrière) Nic.García & Dutilh, **comb. nov.** \equiv *Griffinia blumenavia* K.Koch & C.D.Bouché ex Carrière in Rev. Hort. (Paris) 1867: 32. 1867.

Zephyranthes lagopaivae (Campos-Rocha & Dutilh) Nic. García & Dutilh, **comb. nov.** \equiv *Eithea lagopaivae* Campos-Rocha & Dutilh in PhytoKeys 85: 48, fig. 1A–M, 2A–H. 2017.

Zephyranthes subg. *Neorhodophiala* Nic.García & Meerow, **subg. nov.** – Type: *Zephyranthes bifida* (Herb.) Nic. García & Meerow, **comb. nov.** \equiv *Habranthus bifidus* Herb. in Bot. Mag. 52: t. 2597. 1825.

Diagnosis. – Similar to *Myostemma* Salisb., but flowers always infundibuliform and never yellow; nucleolar organizing region on the short arm of a subtelocentric chromosome; DNA sequence synapomorphies in nuclear ribosomal ITS region.

Etymology. – *Neo* means new, *rhodo* means red, and *phiala* is a bowl or saucer. The new genus used to be considered part of *Rhodophiala* due to its morphological similarity to Chilean species traditionally treated under this genus. As a way to document its taxonomic history, *Neorhodophiala* is intended to mean “new *Rhodophiala*” due to the long-standing view that former Chilean *Rhodophiala* (now *Zephyranthes* subg. *Myostemma*) belonged in the same genus as *R. bifida*.

Description. – Plants 15–40 cm tall. Bulb globose to ovoid. Leaves annual, usually hysteranthous, linear, green, sometimes pruinose, canaliculate, parallel venation, 15–30 cm

long, 3–7 mm wide, apex obtuse. Scape fistulose, 10–30 cm long, 4–6 mm wide below the spathe, somewhat pruinose. Spathe bivalved, valves free from base, exceptionally fused into a tube (Fabris, 1968), lanceolate, membranous, 3–6 cm long. Inflorescence pseudo-umbellate, 2–7(–8)-flowered, each flower subtended by a lanceolate bracteole. Flowers slightly zygomorphic, nodding to patent, pedicels 1–7 cm long. Perigone narrowly infundibuliform to well open; tepals oblanceolate to elliptical, light to dark red (carmine-vermilion), also light to dark pink or lavender, rarely white, usually with a white-greenish stripe along the center of each tepal, 3–5.5 cm long, 6–13 mm wide, connate basally forming a short tube 0.2–0.4 cm long, apically reflexed. Paraperigone a fimbriate ring, ca. 2 mm long (Fabris, 1968). Filaments filiform, declined, ascending 4-seriate, apex incurved. Style trilobed, each lobe 1–3 mm long. Capsule globose-tricocous. Seeds semielliptical to almost triangular, flat, papyraceous, black. $2n = 16, 18$.

Diversity and distribution. – *Zephyranthes* subg. *Neorhodophiala* consists of a single polymorphic species that is widely distributed throughout Uruguay, northeastern Argentina (Buenos Aires, Corrientes, Entre Ríos, Misiones), southern Brazil (Río Grande do Sul), and Paraguay (Itapúa). It is a component of the Pampas ecoregion, inhabiting open environments such as grasslands, savannahs, and between rocks in low hilly areas.

Comments. – A focused study of this species would be desirable to explore its variation across geographic range, phenotypes, and cytotypes; the known variation suggests that it may represent a species complex.

Zephyranthes subg. *Myostemma* (Salisb.) Nic.García, **comb. & stat. nov.** \equiv *Myostemma* Salisb., Gen. Pl.: 135. 1866. = *Famatina* Ravenna in Pl. Life 48: 56. 1972. = *Bathya* Ravenna in Bot. Australis 2: 11. 2003.

Description. – Plants 5–50 cm tall. Bulb globose to ovoid. Leaves annual, proteranthous to hysteranthous, linear to lorate, green, sometimes glaucous, canaliculate, parallel venation, 20–40 cm long, (2–)3.5–9(–14) mm wide, apex obtuse. Scape fistulose, 1–30(–50) cm long, 2–6(–10) mm wide below the spathe. Spathe bivalved, valves mostly free to base, lanceolate to linear-lanceolate, membranous, 3–6 cm long. Inflorescence pseudo-umbellate, 1–8-flowered, each flower subtended by a linear-attenuate to filiform bracteole. Flowers slightly to strongly zygomorphic, nodding to patent, pedicels 3–4 cm long. Perigone infundibuliform to tubular, sometimes slightly bilabiate; tepals oblanceolate to elliptical, various tones of red, also pink, orange, or yellow, rarely white, usually with a white-greenish zone near the base of each tepal, 3–6 cm long, 4–9 mm wide, connate basally forming a short tube 0.3–0.6 cm long, apically reflexed. Paraperigone a fimbriate ring, 1–2 mm long. Filaments declined, ascending 4-seriate, apex incurved. Style obscurely trilobed to trifid, each lobe 0.4–2 mm long, rarely capitate. Capsule globose-tricocous. Seeds semielliptical, flat, papyraceous, black. $2n = 18, 36, 54, 72$.

Diversity and distribution. – This group of ca. 17 species was previously treated as *Rhodophiala* and/or *Myostemma*. They grow in Chile and Argentina between 24°S and 42°S, inhabiting a range of habitats including desert, sclerophyllous mediterranean-type scrub, deciduous *Nothofagus* forests, and high-Andean scrubs, rarely in Patagonian steppe.

Comments. – Species limits should be reassessed in this group with morphological and molecular approaches; the exact number of species is uncertain. Plants with red, funnelliform flowers can be easily confused with *Zephyranthes bifida* if the origin is unknown. However, subgenera *Myostemma* and *Neorhodophiala* have non-overlapping distributions in nature; the safest way to tell them apart is by the karyotype and molecular markers.

Regarding the group's phylogeny, *Zephyranthes capitata* (formerly *Phycella herbertiana* Lindl. ≡ *Famatina herbertiana* (Lindl.) Ravenna) seems to be sister to the rest and is different from other species in *Z.* subg. *Myostemma* and most Hippeastrinae by having a capitate stigma. The lack of sufficient information regarding this taxon, such as chromosome number, prevented us from erecting it as a monotypic subgenus of *Zephyranthes*, despite its sister relationship to the rest of *Z.* subg. *Myostemma* being a robust result in latest phylogenetic studies of the tribe (García & al., 2014, 2017). The remaining species in the subgenus form a well-supported clade (i.e., core *Rhodophiala* clade sensu García & al., 2014, 2017) characterized by $2n = 18$, 45S nrDNA (NOR) terminal on the long arm of a submetacentric to subtelocentric chromosome, multi-flowered scapes, free spathe valves, and trifold stigma (García, 2015).

Zephyranthes advena (Ker Gawl.) Nic.García, **comb. nov.** ≡ *Amaryllis advena* Ker Gawl. in Bot. Mag. 28: t. 1125. 1808.

Zephyranthes ananuca (Phil.) Nic.García, **comb. nov.** ≡ *Hippeastrum ananuca* Phil. in Anales Univ. Chile, I, Mem. Ci. Lit. 93: 150. 1896.

Zephyranthes araucana (Phil.) Nic.García, **comb. nov.** ≡ *Hippeastrum araucanum* Phil. in Anales Univ. Chile, I, Mem. Ci. Lit. 93: 152. 1896.

Zephyranthes bagnoldii (Herb.) Nic.García, **comb. nov.** ≡ *Habranthus bagnoldii* Herb. in Edwards's Bot. Reg. 17: t. 1396. 1831.

Zephyranthes berteroaana (Phil.) Nic.García, **comb. nov.** ≡ *Habranthus berteroaanus* Phil. in Linnaea 29: 66. 1858.

Zephyranthes capitata Nic.García, **nom. nov.** ≡ *Phycella herbertiana* Lindl. in Edwards's Bot. Reg. 16: t. 1341. 1830, non *Zephyranthes herbertiana* D.Dietr. 1840.

Etymology. – Named for its capitate stigma, a characteristic that is almost unique within Hippeastrinae.

Zephyranthes cisandina (Ravenna) Nic.García, **comb. nov.** ≡ *Famatina cisandina* Ravenna in Bot. Australis 2: 16. 2003.

Zephyranthes cuyana Nic.García, **nom. nov.** ≡ *Habranthus mendocinus* Phil. in Anales Univ. Chile 1862: 406. 1862, non *Zephyranthes mendocensis* Baker 1888.

Etymology. – Named for its distribution within the geographic and historic region of Cuyo in western Argentina.

Zephyranthes laeta (Phil.) Nic.García, **comb. nov.** ≡ *Hippeastrum laetum* Phil. in Anales Univ. Chile, I, Mem. Ci. Lit. 93: 157. 1890 ≡ *Amaryllis tiltiensis* Traub & Moldenke, Amaryllidaceae Trib. Amaryllaceae: 88. 1949.

Zephyranthes maculata (L'Hér.) Nic.García, **comb. nov.** ≡ *Amaryllis maculata* L'Hér., Sert. Angl.: 7. 1789.

Zephyranthes moelleri (Phil.) Nic.García, **comb. nov.** ≡ *Hippeastrum moelleri* Phil. in Anales Univ. Chile, I, Mem. Ci. Lit. 93: 154. 1896.

Zephyranthes monantha (Ravenna) Nic.García, **comb. nov.** ≡ *Myostemma monantha* Ravenna in Onira 10(5): 15–16. 2005.

Zephyranthes montana (Phil.) Nic.García, **comb. nov.** ≡ *Habranthus montanus* Phil. in Anales Univ. Chile, I, Mem. Ci. Lit. 43: 66. 1873.

Zephyranthes philippiana Nic.García, **nom. nov.** ≡ *Rhodophiala andina* Phil. in Anales Univ. Chile, I, Mem. Ci. Lit. 43: 543. 1873, non *Zephyranthes andina* (R.E.Fr.) Traub 1951.

Etymology. – Dedicated to Rudolph Amandus Philipp (1808–1904), German naturalist, who made major contributions to Chilean botany and natural history.

Zephyranthes phycelloides (Herb.) Nic.García, **comb. nov.** ≡ *Habranthus phycelloides* Herb. in Edwards's Bot. Reg. 17: t. 1417. 1831.

Zephyranthes splendens (Renjifo) Nic.García, **comb. nov.** ≡ *Habranthus splendens* Renjifo in Anales Univ. Chile, I, Mem. Ci. Lit. 65: 300. 1884.

Zephyranthes elwesii (C.H.Wright) Nic.García, **comb. nov.** ≡ *Hippeastrum elwesii* C.H.Wright in Kew Bull. 1914: 330. 1914.

Incertae sedis at the subgeneric level

Zephyranthes pedunculosa (Herb.) Nic.García & S.C.Arroyo, **comb. nov.** ≡ *Habranthus pedunculatus* Herb., Amaryllidaceae: 161, t. 26., fig. 1. 1837 ≡ *Hippeastrum pedunculatum* (Herb.) E.Holmb. in Anales Mus. Nac. Buenos Aires, ser. 3, 5: 146. 1905.

= *Hippeastrum tubispathum* Pax in Bot. Jahrb. Syst. 11: 329. 1889, nom. illeg. ≡ *Zephyranthella tubispatha* (Pax) Pax in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 15a: 416. 1930.

= *Zephyranthes unifolia* Arechav. in Anales Mus. Nac. Montevideo 2: 290. 1900 ≡ *Habranthus unifolius* (Arechav.) Traub in Pl. Life 7: 42. 1951.

= *Hippeastrum teretifolium* C.H.Wright in Bull. Misc. Inform. Kew 1901: 144. 1901 ≡ *Habranthus teretifolius* (C.H.

- Wright) Traub & Moldenke, Amaryllidaceae Trib. Amaryllaceae: 145. 1949.
 = *Hippeastrum tubispathum* var. *grandiflorum* Hicken in Anales Soc. Ci. Argent. 55: 234–235. 1903.
 = *Hippeastrum holmbergii* Hicken in Anales Soc. Ci. Argent. 55: 235–237. 1903.
 = *Habranthus juncifolius* Traub & Hayward in *Herbertia* 12: 40. 1947.
 = *Habranthus holmbergii* Traub in *Pl. Life* 7: 42. 1951.
 = *Habranthus paxii* Traub in *Pl. Life* 22: 62. 1966.
 = *Habranthus concordiae* Ravenna in *Pl. Life* 26: 98. 1970.

Distribution. – This species inhabits the Pampas and Chaco ecoregions in northeastern Argentina (Buenos Aires, Chaco, Corrientes, Entre Ríos, Misiones, Santa Fé), western Uruguay, southeastern Paraguay, and Río Grande do Sul in Brazil.

Comments. – Morphological descriptions of this species can be found in Ravenna (2003c; as *Habranthus teretifolius*), Hurrel (2009), and Amaral-Lopes & Cavalcanti (2015). Phylogenetic analyses of molecular data suggest that *Zephyranthes pedunculosa* might be sister to *Z.* subg. *Zephyranthes* or an early offshoot of its ancestral $2n = 12/14$ lineage (García, 2015; García & al., 2017). This species is peculiar in having terete leaves, fused spathe valves, and scapes with at least two large flowers (up to six), in contrast to species of *Z.* subg. *Zephyranthes* that usually have a single-flowered scape. Other South American *Zephyranthes* taxa that characteristically have fused spathe valves and multi-flowered scapes (but can also have a single flower) include species in *Z.* subg. *Habranthus*, although anomalous 2-flowered scapes have been reported in North American *Sprekelia formosissima* and *Z. drummondii* (Flagg & al., 2002), both in *Z.* subg. *Zephyranthes*. Its cylindrical and rigid leaves are unique in *Zephyranthes* and, apparently, in the entire tribe (Arroyo & Cutler, 1984).

Traubiinae D.Müll.-Doblies & U.Müll.-Doblies

For a general description, see García & al. (2014).

Traubia Moldenke in *Pl. Life* 19: 55. 1963 – Type: *Traubia chilensis* (F.Phil. ex Phil.) Moldenke \equiv *Lapidra chilensis* F.Phil. ex Phil. (= *Traubia modesta* (Phil.) Ravenna).

Description. – Plant usually less than 10 cm tall, on exposed soils, but taller when shaded. Bulb ovoid. Leaves annual, hysteranthous, appearing during winter, linear, parallel venation, 30–35 cm long, 1.5–2 mm wide, somewhat fleshy, moderately canaliculate, with thin edges, apex obtuse. Scape narrowly fistulose, flushed by diminutive purple-brown lines, (2–)4–8(–22) cm long, 0.5–1.3 mm wide below the spathe. Spathe bivalved, valves free to the base (rarely connate to the top by one of their margins and splitting on one side according to Ravenna, 1974, 2003a), lanceolate, 1.1–2.4 cm long, 1–2 mm wide, membranous, marcescent. Inflorescence pseudo-umbellate, 1–5(–8)-flowered, each flower subtended by a filiform-lanceolate bracteole. Flowers slightly zygomorphic, patent to nodding, pedicel 0.3–2.3 cm long. Perigone well expanded, stellate; tepals linear-oblong, white, often magenta-

tinged internally at the center, with 3–5 magenta central veins marked longitudinally on abaxial side (rarely lacking), 1.5–2.5 cm long, 3–4 mm wide, very shortly connate at the base from 0.1–0.2 cm, and then spreading horizontally. Paraperigone lacking. Filaments filiform, closely fasciculate, straightly ascending, almost imperceptibly 4-seriate, apex slightly incurved. Style filiform, slightly declined, ascending obliquely below the stamen fascicle. Stigma capitate-punctate. Capsule depressed globose-tricocous. Seeds flat, semiovalate or semielliptical, shiny, with membranous edges, black. $2n = 16$.

Diversity and distribution. – A single species, *Traubia modesta*, inhabits hilly areas close to the coast of central Chile, between the localities of Huentelauquén and Salamanca (Coquimbo Region; $\sim 31^\circ\text{S}$), and Rapel (Metropolitan Region; $\sim 34^\circ\text{S}$) (Ravenna, 2003a).

Comments. – *Traubia modesta* represents an isolated lineage, probably a relict of the ancestral Traubiinae (see comments under *Eremolirion*). Historically this species was very common on coastal hills of central Chile, but currently it is known from only a few populations. It is considered an endangered species due to habitat loss and its restricted distribution.

Eremolirion Nic.García, **gen. nov.** – Type: *Eremolirion laetum* (Phil.) Nic.García, **comb. nov.** \equiv *Rhodophiala laeta* Phil., Fl. Atacam.: 51. 1860.

Diagnosis. – Similar to *Rhodolirium* Phil., but leaves usually wider than 5 mm; scape 2–5-flowered; pedicels longer than 1 cm; tepals dark pink, sometimes with a whitish longitudinal stripe and lighter towards the base.

Etymology. – Derived from the Greek words *eremos* meaning desert and *lirion* which is a general designation for lilies; hence, *Eremolirion* translates to “desert lily”. The name refers to its habitat in the coastal desert of northern Chile.

Description. – Plant usually over 10 cm tall. Bulb ovoid. Leaves annual, present while blooming, lorate, 30–60 cm long, 5–9 mm wide, flat and slightly fistulose, round edges, apex obtuse. Scape fistulose, 10–30 cm long, 2–4 mm wide below the spathe. Spathe bivalved, valves free to the base, lanceolate, parallel venation, 2.5–6 cm long, 4–10 mm wide, membranous, marcescent. Inflorescence pseudo-umbellate, 2–5-flowered, each flower subtended by a lanceolate bracteole. Flowers slightly zygomorphic, nodding, pedicel 1–5 cm long. Perigone infundibuliform, tepals oblanceolate, dark pink, usually with a white longitudinal stripe and lighter towards the base, 4–7 cm long, (8–)10–15 mm wide, connate basally forming a tube ca. 1 cm long, apically reflexed. Paraperigone lacking. Filaments filiform, closely fasciculate, straightly ascending, 4-seriate, apex slightly incurved. Style filiform, slightly declined, ascending obliquely and incurved apically. Stigma capitate-punctate. Capsule globose-tricocous. Seeds flat, semielliptical, black, shiny, with membranous edges. $2n = 16$.

Diversity and distribution. – *Eremolirion laetum*, the single species within this new genus, inhabits fog oases or loma vegetation in the coastal desert of northern Chile, between the Antofagasta ($\sim 23^\circ\text{N}$) and Atacama ($\sim 26^\circ\text{N}$) Regions.

Comments. – As mentioned for *Traubia*, *Eremolirion* represents an isolated lineage, likely a relict of the ancestral Traubiinae. The plesiomorphic status of *Traubia* and *Eremolirion* within Traubiinae is also supported by their low karyotype asymmetry in relation to the more derived and asymmetrical karyotype of *Phycella* (Baeza & al., 2009; García, 2015). *Eremolirion laetum* is a species of conservation concern due to its restricted habitat and distribution.

Rhodolirium Phil. in *Linnaea* 29: 65. 1858 – **Type (designated here):** *Rhodolirium montanum* Phil.

Description. – Plant usually 15 to 25 cm tall. Bulb ovoid. Leaves annual, absent or emerging while flowering, linear, parallel venation, 15–30 cm long, 2–5 mm wide, flat, canaliculate, sometimes pruinose, apex obtuse. Scape fistulose, 10–20 cm long, 3 mm wide below the spathe. Spathe bivalved, valves free to the base, lanceolate, 2–4 cm long, 2–5 mm wide, membranous, marcescent. Inflorescence single-flowered, rarely 2 flowers, with or without a linear bracteole subtending the flower. Flowers slightly zygomorphic, patent to nodding, and almost sessile to shortly pedicellate, pedicel 0.1–0.9 cm long. Perigone infundibuliform, tepals oblanceolate, dark pink to white, with a black-purplish basal spot or multiple longitudinal magenta stripes, these continuous-linear or dotted, sometimes the base green-yellowish, 2–6 cm long, 6–10 mm wide, connate basally forming a tube 1–2 cm long, apically reflexed. Paraperigone lacking. Filaments filiform, closely fasciculate, straightly ascending, 4-seriate, sometimes appearing biseriate, apex incurved or straight. Style filiform, declinate-ascending, incurved apically. Stigma capitate-punctate to obscurely trilobed. Capsule globose-tricocccous. Seeds flat, semielliptical, black, shiny, with membranous edges. $2n = 16$.

Diversity and distribution. – This small clade, represented by only two species (*Rhodolirium andicola* (Poepp.) Ravenna, *R. montanum*), inhabits high-Andean to Patagonian steppe habitats from central-southern Chile and adjacent Argentina.

Comments. – The monophyly of this genus is strongly supported by ITS and plastid sequence data, and by their apomorphic single-flowered scapes. Both species in this group were traditionally allied to *Myostemma* (e.g., Traub & Moldenke, 1949; Ravenna, 1969), but can be easily differentiated by their single-flowered scape, capitate to obscurely trilobed stigma, chromosome number $2n = 16$, and high-Andean habitat (Naranjo & Poggio, 2000; Ravenna, 2003a; García & al., 2014).

Phycella Lindl. in *Bot. Reg.* 11: sub t. 928. 1825 – **Type (designated here):** *Phycella cyrtanthoides* (Sims) Lindl. = *Amaryllis cyrtanthoides* Sims.

= *Placea* Miers in Edwards's *Bot. Reg.* 27: t. 50. 1841 – Type: *Placea ornata* Miers = *Phycella ornata* (Miers) Nic.García, **syn. nov.**

= *Rhodophiala* C.Presl. in *Abh. Königl. Böhm. Ges. Wiss.*, ser. 5, 3: 545. 1845 – Type: *Rhodophiala amarylloides* C.Presl (= *Phycella cyrtanthoides*).

= *Miltinea* Ravenna in *Bot. Australis* 2: 8. 2003 – Type: *Miltinea maulensis* (Ravenna) Ravenna = *Famatina maulensis* Ravenna = *Phycella maulensis* (Ravenna) Nic. García & J.M.Watson, **syn. nov.**

Description. – Plant 20–100 cm tall. Bulb ovoid. Leaves annual, proteranthous to hysteranthous, sometimes already withered at anthesis, linear, linear-lanceolate, or lorate, parallel venation, 30–60 cm long, (3–)4–15(–30) mm wide, flat or terete and fistulose, with lamellous or spongy parenchyma within, round to angled edges, apex acute to obtuse. Scape fistulose, 20–30 cm long, 2–9 mm wide below the spathe. Spathe bivalved, valves free to the base, lanceolate, 3–7 cm long, 4–10 mm wide, marcescent. Inflorescence usually pseudo-umbellate, 1–9-flowered, each flower subtended by a linear-lanceolate bracteole. Flowers slightly to strongly zygomorphic, nodding or patent, pedicel 1–7 cm long. Perigone infundibuliform or tubular, tepals oblanceolate, various tones of red, dark pink, white, cream, or rarely yellow, either with red to magenta longitudinal stripes or the basal half green-yellowish, 3–7 cm long, (4–)8–15 mm wide, connate basally forming a tube (0.3–)1–2 cm long, apically reflexed. Paraperigone, if present, formed by oblong-subulate or cultriform appendages alternate to the filaments, well developed or inconspicuous, or these crenate apically, bifid or trifid, or connate into a tube that can be entire or 3–6 lobed, usually red or dark pink throughout (rarely white-greenish or magenta) or with green-yellowish basal half. Filaments filiform, closely fasciculate, ascending or straight, 4-seriate, apex straight or slightly to strongly incurved. Style filiform, straight or declined, then ascending obliquely and incurved apically. Stigma capitate-punctate. Capsule globose-tricocccous. Seeds flat, semielliptical, black, shiny, with membranous edges. $2n = 16, 32$.

Diversity and distribution. – *Phycella* is a clade composed of ca. 13 species and mostly restricted to central Chile between 29°S and 38°S. Besides the species transferred here into *Phycella*, we also accept the following species: *Phycella angustifolia* Phil., *P. australis* Ravenna, *P. cyrtanthoides*, and *P. scarlatina* Ravenna. These plants inhabit various habitat types such as desert scrub, sclerophyllous scrub and forest, high-Andean vegetation, including bogs and creeks. There is a single population known from Neuquén, Argentina (J. Watson, pers. comm.).

Comments. – This circumscription of *Phycella* includes *Placea*, which used to be differentiated by the conspicuous tubular paraperigone of the latter (e.g., Traub & Moldenke, 1949; Hutchinson, 1959; Traub, 1963; Meerow & Snijman, 1998). However, *Placea* is embedded within *Phycella* according to all molecular markers tested so far, and its recognition would make the latter paraphyletic. In addition to an apparent shift towards hummingbird-pollinated flowers, a putative synapomorphy for this clade is the co-localization of 45S and 5S rDNA loci on the short arm of a medium submetacentric chromosome (Baeza & Schrader, 2004; García, 2015). This clade is likely the result of a rapid radiation, and its topology is largely unresolved; hence, faster-evolving

markers and a broader sampling should be used to clarify relationships within this group.

There is significant variation in paraperigone morphology as suggested by character-state reconstructions, including species that lack a paraperigone and others with free appendages or a tubular paraperigone (García, 2015). Variation in paraperigone morphology should be studied in detail to evaluate its diagnostic utility. Species limits within this clade are currently being reassessed by the first author of the present article using molecular and morphological approaches.

Phycella amoena (Phil.) Nic.García, **comb. nov.** ≡ *Placea amoena* Phil. in *Anales Univ. Chile*, I, Mem. Ci. Lit. 93: 145. 1896.

Phycella arzae (Phil.) Nic.García, **comb. nov.** ≡ *Placea arzae* Phil. in *Anales Univ. Chile*, I, Mem. Ci. Lit. 43: 541. 1873.

Phycella chilensis (L'Hér.) Grau ex Nic.García, **comb. nov.** ≡ *Amaryllis chilensis* L'Hér., *Sert. Angl.*: t. 7. 1789.
= *Amaryllis pratensis* Poepp., *Fragm. Syn. Pl.*: 5. 1833, **syn. nov.**

= *Habranthus speciosus* Herb. in *Amaryllidaceae*: 158. 1837, **syn. nov.**

= *Rhodophiala biflora* Phil. in *Linnaea* 29: 66. 1858, **syn. nov.**

= *Rhodophiala volckmannii* Phil. in *Linnaea* 33: 259. 1864, **syn. nov.**

Phycella davidii (Ravenna) Nic.García, **comb. nov.** ≡ *Placea davidii* Ravenna in *Pl. Life* 37: 73–75. 1981.

Phycella fulgens (Hook.f.) Nic.García, **comb. nov.** ≡ *Habranthus fulgens* Hook.f. in *Bot. Mag.* 92: t. 5563. 1866.

Phycella germainii (Phil.) Nic.García, **comb. nov.** ≡ *Placea germainii* Phil. in *Linnaea* 29: 67. 1858.

Phycella lutea (Phil.) Nic.García, **comb. nov.** ≡ *Placea lutea* Phil. in *Linnaea* 33: 259–260. 1864.

Phycella maulensis (Ravenna) Nic.García & J.M.Watson, **comb. nov.** ≡ *Famatina maulensis* Ravenna in *Pl. Life* 28: 58–59, fig. 19. 1972.

Phycella ornata (Miers) Nic.García, **comb. nov.** ≡ *Placea ornata* Miers in *Edwards's Bot. Reg.* 27: t. 50. 1841.

■ AUTHOR CONTRIBUTIONS

Conceptualization: NG & WSJ. Investigation (taxonomy and nomenclature): NG, AWM, SAL, RSO & JHD. Writing (original draft): NG. Writing (review and editing): NG, AWM, SAL, RSO, JHD, PSS & WSJ. Literature cited: NG & RSO. Supervision: NG & AWM. — NG, <https://orcid.org/0000-0001-9003-1510>; AWM, <https://orcid.org/0000-0003-1882-8327>; SAL, <https://orcid.org/0000-0002-8670-496X>; RSO, <https://orcid.org/0000-0002-6944-1547>; JHD, <https://orcid.org/0000-0003-4353-0899>; PSS, <https://orcid.org/0000-0001-9310-8659>

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