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Research Article

Molecular phylogenetics of subfamily Urgineoideae (Hyacinthaceae): Toward a coherent generic circumscription informed by molecular, morphological, and distributional data

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Abstract The taxonomy and systematics of Urgineoideae (Hyacinthaceae) have been controversial in recent decades, with contrasting taxonomic treatments proposed based on preliminary and partial studies that have focused on morphology and/or solely plastid DNA sequence data. Some authors have recognized only two genera, with a very broadly conceived *Drimia*, while others have accepted several genera that, although better defined morphologically, were doubtfully monophyletic. Here, we present phylogenetic analyses involving four plastid DNA regions (*trnL* intron, *trnL-F* spacer, *matK*, and the *trnCGCA-ycf6* intergenic region), a nuclear region (*Agt1*), and a selection of 40 morphological characters. Our study covers 293 samples and ca. 160 species of Urgineoideae (ca. 80% of its global diversity). Bayesian inference, maximum likelihood, and maximum parsimony analyses were performed to derive the phylogenetic patterns. The combination of data yielded phylogenetic trees with 31 well-defined clades or lineages, most corresponding to previously described genera, although some have required description or revised circumscription. As with other monocot families, a considerable degree of homoplasy was observed in morphological characters, especially in those groups with unspecialized flowers; nonetheless, consistent syndromes of traditional and novel characters are shown to support clade recognition at genus rank. The forthcoming revised classification of Urgineoideae is outlined here.

Key words: Asparagaceae, Hyacinthaceae, molecular systematics, morphology, Scilloideae, taxonomy, Urgineoideae.

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1 Introduction

Hyacinthaceae, *sensu* the Angiosperm Phylogeny Group (APG) (2003) (=Asparagaceae subfam. Scilloideae according to APG, 2009, 2016; Chase et al., 2009), includes about 1000 species of bulbous plants (Martínez-Azorín et al., 2018a). Based on studies of morphology, anatomy, and phytochemistry, and those involving DNA sequences (Speta, 1998a; Pfosser & Speta, 1999; Manning et al., 2004), four monophyletic subfamilies were recognized within Hyacinthaceae: Hyacinthoideae, Ornithogaloideae, Urgineoideae, and Oziroëoideae (=tribes Hyacintheae, Ornithogaleae, Urgineeae, and Oziroëeae *sensu* APG, 2016).

Urgineoideae is distributed in Africa, Europe, and southwestern Asia, reaching Thailand in the East, with two main centers of diversity—one in southern Africa and the other in the Mediterranean Basin (Buerki et al., 2012; Ali et al., 2013). This subfamily has earlier been considered to include about

100–110 species (see Stearn, 1978; Manning et al., 2004; Manning & Goldblatt, 2018), although we estimate the number of species in Urgineoideae to be at least double that figure, based on our fieldwork-informed taxonomic research that spans the last three decades. This expanded interpretation will reflect in our forthcoming monograph on the group (Martínez-Azorín et al., in prep.). The morphological variation in taxa of Urgineoideae has historically informed the description of several distinct genera in this subfamily, including *Drimia* Jacq. ex Willd., *Urginea* Steinh., *Tenicroa* Raf., *Fusifilum* Raf., *Litanthus* Harv., *Rhadamanthus* Salisb., *Bowiea* Harvey ex Hook. f., *Schizobasis* Baker, *Rhodocodon* Baker, *Thuranthos* C.H. Wright, *Urgineopsis* Compton, and *Rhadamanthopsis* (Oberm.) Speta (Fig. 1). These concepts have been accepted by most Hyacinthaceae workers based on clear apomorphies and/or unique syndromes of morphological traits (Jacquin, 1794; Willdenow, 1799; Steinheil, 1834; Rafinesque, 1837; Harvey, 1844; Salisbury, 1866; Hooker, 1867; Baker, 1897, 1898; Wright, 1916; Compton, 1930; Merxmüller, 1970; Jessop, 1977; Obermeyer, 1980a, 1980b, 1980c; van Jaarsveld, 1983, 1992; Snijman, 1985; Roessler, 1987; Stedje & Thulin, 1995; Speta, 1998a, 1998b; Snijman et al., 1999; Müller-Doblies et al., 2001; Manning et al., 2002; among others). However, other researchers have reflected on the difficulty of clearly circumscribing some genera, given what they interpret as a transition in the degree of tepal connation (Jessop, 1977; Stedje, 1987, 2001a, 2001b; Goldblatt & Manning, 2000; Manning & Goldblatt, 2018). Genera with distinctly connate tepals, such as *Drimia*, *Litanthus*, *Rhadamanthus*, *Rhadamanthopsis*, or *Rhodocodon*, are clearly recognized, and their subordinate taxa thus easily attributed. However, many other species from southern Africa presenting, for example, unspecialized flowers in which tepals vary from free to shortly connate, have been described as members of *Urginea* or *Drimia* s.l. (Baker, 1897; Adamson et al., 1944; Huber, 1969; Jessop, 1977; Hilliard & Burtt, 1985; Stedje, 1987). Such genera, in their broad sense, incorporate species with distant evolutionary relationships and diverse flower morphologies, to create artificial groups that obscure true relationships among species.

The taxonomy and systematics of Hyacinthaceae have been the focus of numerous studies in recent decades (Speta, 1998a, 1998b, 2001; Pfosser & Speta, 1999, 2001, 2004; Manning et al., 2004, 2009; Martínez-Azorín et al., 2011; Pfosser et al., 2012; Manning & Goldblatt, 2018; among others) that have generated considerable controversy regarding generic limits. The accounts of Speta (1998a, 1998b, 2001) and Pfosser & Speta (1999) combined morphological, anatomical, and molecular studies to substantiate the description of the monophyletic urgineoid genera *Boosia* Speta, *Charybdis* Speta, *Duthiea* Speta, *Ebertia* Speta, *Geschollia* Speta, *Indurgia* Speta, *Ledurgia* Speta, *Rhadamanthopsis* (Oberm.) Speta, *Sekanama* Speta, and *Urginavia* Speta, each showing a unique combination of morphological characters (Fig. 1), distribution, and evolutionary history. Shortly thereafter, Manning et al. (2004) extended the study to a second plastidial region (*rbcL* and *trnL-F*), but with limited sampling. These authors opted for a very broad *Drimia*, which was congruent with the whole subfamily Urgineoideae (except for *Bowiea* with one to two species) and accordingly synonymized all other urgineoid genera. In the process, extreme variation in morphology was included in *Drimia*, as reflected in the recent revision of the genus in southern Africa (Manning & Goldblatt, 2018), which delimited 20 sections. These sections generally align with earlier described urgineoid genera, with some sections circumscribed as para- or polyphyletic, as shown by prior phylogenetic accounts (Pfosser & Speta, 1999, 2001, 2004; Pfosser et al., 2012). This challenge in terms of delineation can be resolved through phylogenetic analyses, such as the present study, as when the clades resolved include taxa with a homogeneous morphology, they can be recognized as distinct genera. When both quantitative and qualitative characters of flower morphology are combined with those of fruits, seeds, and vegetative forms, clades or lineages can be accepted at genus rank, as shown earlier by Martínez-Azorín et al. (2011) for the sister subfamily Ornithogaloideae.

Here, we explore an alternative classification that leads to an improved and communicable understanding of generic boundaries in the Urgineoideae, based on the combination of molecular and morphological data sets. With substantially more comprehensive sampling than has previously been achieved, our intention here is to identify clades or lineages showing clear morphologies and distribution. Our taxonomic studies have informed the recent description of eight new genera in the subfamily based on their unique morphological syndromes (Martínez-Azorín et al., 2013d, 2017, 2018a, 2019b; Pinter et al., 2013, 2019; Speta, 2016; Crouch et al., 2018). A new classification that focuses on generic circumscription in the Urgineoideae is forthcoming.

2 Material and Methods

2.1 Taxon sampling

The phylogenetic analyses cover a total of 293 ingroup samples belonging to ca. 160 species from all previously recognized taxonomic groups in Urgineoideae (Table S1). Two samples of *Whiteheadia bifolia* (Jacq.) Baker (subfam. Hyacinthoideae) are used as an outgroup. Fresh material and herbarium specimens conserved at ABH, B, BLFU, BM, BOL, E, G, GRA, GZU, HAL, K, L, LINN, NU, NY, M, MO, NBG, P, PRE, S, SAM, TCD, UPS, W, WIND, WU, Z, ZSS, and ZT (acronyms follow Thiers, 2022) were used for morphological studies, including numerous samples currently kept in the living collection at the University of Alicante. These materials cover the full range of morphological and taxonomic variations of the Urgineoideae across its entire distribution range in Europe, Africa, and southwestern Asia. For a more detailed description of the materials and methods used for previous morphological studies undertaken on Hyacinthaceae, see Martínez-Azorín et al. (2007, 2009, 2011). Relative to data informing previous phylogenetic studies (e.g., Pfosser & Speta, 1999, 2001, 2004; Manning et al., 2004; Pfosser et al., 2012), the sampling has been extended in the present work by 140–270 samples and 120–140 taxa, now covering ca. 80% of the total accepted species for the subfamily. A total of 994 new DNA sequences were obtained for this study, which were combined with some other previously published sources and accessions available from the GenBank. Plant source information and GenBank accession numbers are

shown in Table S1. Author names of taxa cited in the text and tables align with IPNI (2022). Generic circumscription follows Crouch et al. (2018), Knirsch et al. (2015), Martínez-Azorín et al. (2013d, 2017, 2018a, 2019a, 2019b, 2019c, 2019d, 2022), and Pinter et al. (2013, 2019, 2020). Some species names used for BTU samples provided by U. Müller-Doblies & D. Müller-Doblies are inedited (ined.) and represent undescribed taxa. Other names used in this work (including the ones in the phylogenetic trees) correspond to inedited combinations, to accommodate particular taxa in the accepted taxonomic

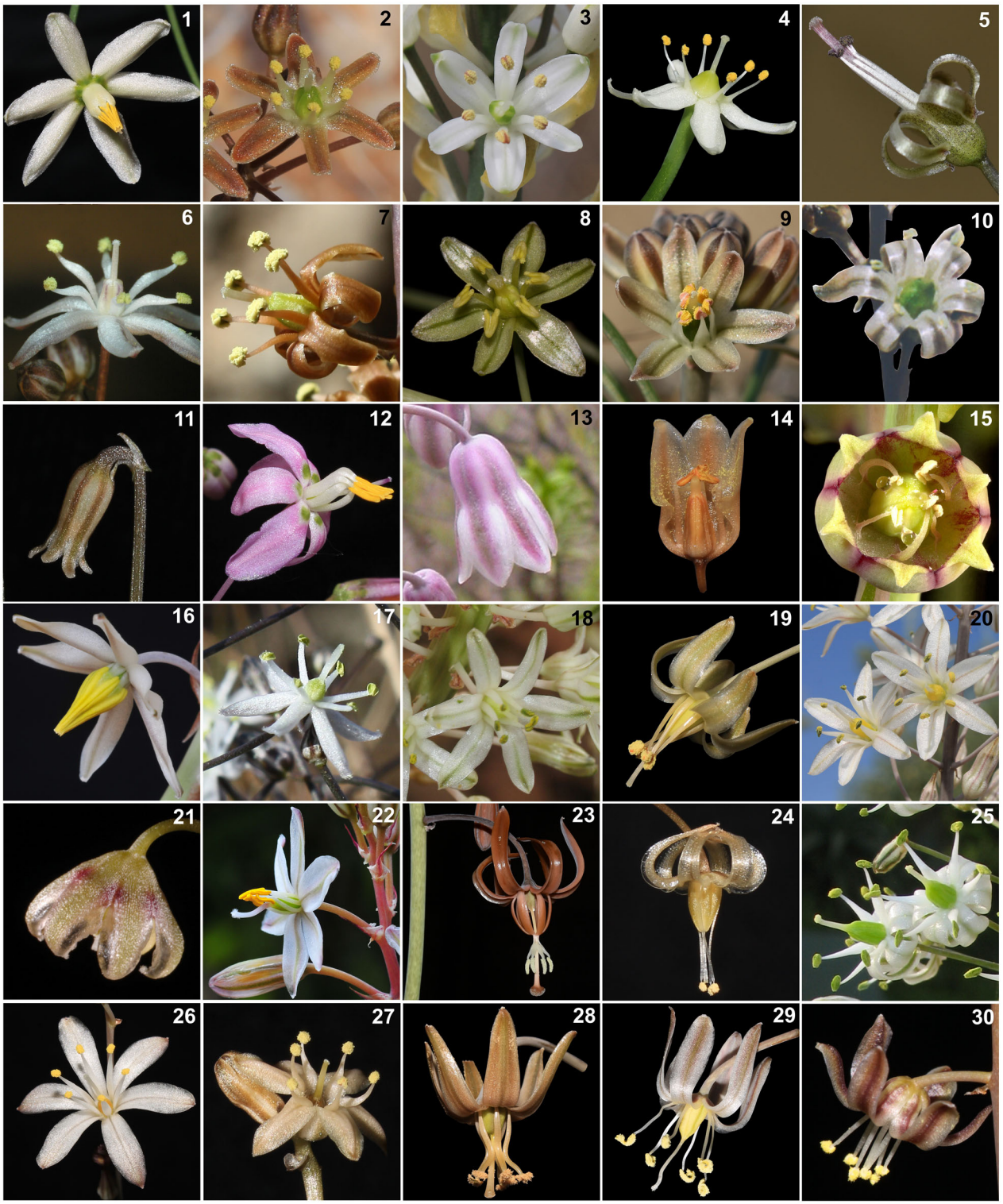

Fig. 1. Continued

treatment. Taxonomic equivalences and basionym information are detailed in Table S1. These unpublished combinations will be presented in a forthcoming monograph (Martínez-Azorín et al., in prep.). The nomenclature conventions and procedures follow the *Shenzhen Code* (ICN; Turland et al., 2018).

2.2 DNA amplification, extraction, and sequencing

Silica gel-dried material (Chase & Hills, 1991) collected during our fieldwork or fresh material from cultivated specimens of all described groups of Urgineoideae were used for total DNA extraction, using a modified 2× cetyltrimethylammonium bromide (CTAB) protocol (Doyle & Doyle, 1987). Additional DNA samples were obtained from the DNA bank collection from the Biocenter in Linz, Austria. Extracted total DNA was purified using MOBIO minicolumns and mostly kept in 0.1× TE buffer (10 mM Tris-HCl, 1 mM ethylenediaminetetraacetic acid [EDTA], pH 8.0). The present study is based on nucleotide sequences of four plastid regions (*trnL* intron plus the *trnL-F* spacer, *matK*, and *trnCGCA-ycf6* intergenic region) and a nuclear region (*Agt1*). The PCR amplifications were obtained using primers c (CGAAATCGGTAGACGCTACG), d (GGGGATAGAGGGACTTGAAC), e (GGTTCAAGTCCCTCTATCCC), and f (ATTTGAACTGGTGACACGAG) for the *trnL* intron and the *trnL-F* spacer (Taberlet et al., 1991); XF (TAATTTACGATCAATTCATTC) and 5R (GTTCTAGCACAAGAAAGTCG) for the *matK* region (see www.kew.org/barcoding); trnC^{GCA}F (CCAGTTCRAATCYGGGTG) and *ycf6R* (GCCCAAGCRAGACTTACTATATCCAT) for the *trnCGCA-ycf6* (*ycf*) region (Pfosser et al., 2012); and *Agt1*_fw (GATTTCCGHATGGATGANTGGGG) and *Agt*_rev (CCAYTCCTCCTTCTGHGTGCAGTT) for the *Agt1* region. The amplifications were performed on a reaction volume of 25 μL containing 22.5× ABGene, 1.1× Master Mix, 2.5 mM $MgCl_2$ (Thermo Scientific Waltham, MA, USA), 0.5 μL of 0.4% bovine serum albumin (BSA), 0.5 μL of each primer (10 pmol/μL), and 1 μL of template DNA with ca. 100 ng of DNA, on a 9700 GeneAmpl thermocycler (Applied Biosystems). The PCR program for the *trnL* intron and the *trnL-F* spacer was as follows: 2 min at 94 °C, followed by 28 cycles of 94 °C for 1 min, 50 °C for 1 min, 72 °C for 1 min, and a final extension at 72 °C for 7 min; for the *matK* region: 2 min at 94 °C, followed by 32 cycles of 94 °C for 1 min, 53 °C for 1 min, 72 °C for 1.5 min, and a final extension at 72 °C for 4 min; for the *trnCGCA-ycf6* region: 5 min at 95 °C, followed by 35 cycles of 94 °C for 20 sec, 50 °C for 30 sec, 72 °C for 1 min, and a final extension at 72 °C for 10 min; and the *Agt1* region: 5 min at 95 °C, followed by 35 cycles of 94 °C for 40 sec, 58 °C for 30 sec, 72 °C for 50 sec, and a final extension at 72 °C for 10 min.

The length of PCR fragments was verified on a 1% agarose gel by electrophoresis. Successful PCR products were analyzed at both the technical services of University of Alicante and the company Macrogen SPAIN.

2.3 Sequence alignment and data sets

Sequencher 4.1 (Gene Codes Corp., Ann Arbor, MI, USA) was used to assemble complementary strands and verify software base-calling. Sequence alignment was performed using MUSCLE (Edgar, 2004), conducted in MEGA X (v. 10.0.5) (Kumar et al., 2018) with minor manual adjustments to obtain the final aligned matrix (Material S10). The individual marker trees were studied for incongruence before combining data sets. The aligned matrix for the *ycf* region included 290 samples and 1475 bp, the *matK* matrix 294 samples and 908 bp, the *trnL-F* matrix 272 samples and 1200 bp, and the *Agt1* matrix 166 samples and 1090 bp, although some samples of the latter region showed a hypervariable central region including large polymorphic insertions that did not allow proper alignment. Therefore, this central region was removed for those samples in the phylogenetic analyses, leaving a common 486 bp (the first 266 bp and the last 220 bp).

Molecular data sets were produced for individual makers and their combination, corresponding, respectively, to (1) the concatenated plastid (four regions) data matrix and (2) the concatenated molecular (plastid plus nuclear) sequence data matrix.

2.4 Morphological data

A selection of 40 discrete morphological characters was used to explore relationships with the phylogenetic findings as follows: 1. Bulb scales (0. Compact; 1. Loose); 2. Cataphylls (0. Leaves lacking sheathing cataphylls with transversal dark or prominent ribs; 1. Leaves surrounded at the base by sheathing cataphylls with transversal dark or prominent ribs); 3. Leaf number (0. More than one per bulb; 1. One per bulb; 2. Absent in old plants); 4. Leaf curving (0. Straight or slightly curved; 1. Distinctly coiled distally); 5. Leaf section morphology around the middle portion (0. Flattened or canaliculate; 1. Round to hemicircular); 6. Leaf proportions (0. Clearly elongated, from three to many times longer than wide; 1. Suborbicular to ovate, up to two times longer than

Fig. 1. Floral variation in the genera of Urgineoideae: 1. *Aulostemon mzimvubuensis* (van Jaarsv.) Mart.-Azorín et al.; 2. *Austronea linearis* Mart.-Azorín et al.; 3. *Boosia macrocentra* (Baker) Speta; 4. *Bowiea gariepensis* van Jaarsv.; 5. *Drimia elata* Jacq. ex Willd.; 6. *Fusifilum montanum* (A.P. Dold & E. Brink) A.P. Dold et al.; 7. *Geschollia anomala* (Baker) Speta; 8. *Indurgia polyantha* (Blatt & McCann) Speta; 9. *Iosanthus toxicarius* (C. Archer & R.H. Archer) Mart.-Azorín et al.; 10. *Ledurgia guineensis* Speta; 11. *Litanthus stenocarpus* (J.C. Manning & J.M.J. Deacon) Mart.-Azorín et al.; 12. *Mucinaea nana* (Snijman) M. Pinter et al.; 13. *Rhadamanthopsis hyacinthoides* (Baker) Mart.-Azorín et al. (comb. nov. ined.); 14. *Rhadamanthus convallarioides* (L.f.) Salisb. ex Baker; 15. *Rhodocodon giganteus* ined.; 16. *Sagittanthera cyanelloides* (Baker) Mart.-Azorín et al.; 17. *Schizobasis macowanii* Baker; 18. *Sekanama sanguinea* (Schinz) Speta; 19. *Spirophyllos noctiflorus* (Batt. & Trab.) Mart.-Azorín et al. (comb. nov. ined.); 20. *Squilla maritima* (L.) Steinh.; 21. *Striatula platyphylla* (B. Nord.) M. Pinter et al.; 22. *Tenicroa exuviata* (Jacq.) Speta; 23. *Thuranthos nocturnale* R.A. Dyer; 24. *Triandra pellabergensis* Mart.-Azorín et al.; 25. *Urginavia epigea* (R.A. Dyer) Speta; 26. *Urginea fugax* (Moris) Steinh.; 27. *Urgineopsis barbata* (J.C. Manning & J.M.J. Deacon) Mart.-Azorín et al.; 28. *Vera-duthiea zebrina* Mart.-Azorín et al.; 29. *Zingela pooleyorum* N.R. Crouch et al.; 30. *Zulusia delagoensis* (Baker) Mart.-Azorín et al. (comb. nov. ined.).

wide); 7. Leaf keel presence (0. Lacking a distinct broad keel abaxially; 1. With a distinct broad keel abaxially); 8. Leaf adaxial furrows (0. Lacking longitudinal furrows; 1. With longitudinal furrows); 9. Leaf maculation (0. Immaculate; 1. With distinct maculae at base); 10. Co-occurrence of leaves and flowers (0. Hysteranthous or proteranthous leaves; 1. Synanthous or evergreen leaves); 11. Inflorescence type (0. Simple raceme; 1. Branched raceme or panicle); 12. Inflorescence consistency (0. Not succulent; 1. Succulent); 13. Inflorescence disposition (0. Not twining; 1. Twining); 14. Early developed inflorescence disposition (0. Erect; 1. Recurved and nodding); 15. Bract spur (0. Not spurred; 1. Spurred); 16. Bract persistence (0. Present in flower; 1. Caducous and absent in full flower); 17. Bracteoles (0. Absent; 1. Present); 18. Pedicel aging (0. Browning simultaneously with developing capsule, pedicel brown at dehiscence; 1. Remaining green as developing capsule browns, pedicel green at dehiscence); 19. Flower disposition (0. Patent to suberect; 1. Nodding); 20. Flowering time (0. Diurnal; 1. Nocturnal); 21. Connation of tepals (0. Free or nearly free (connate for less than 1 mm from base); 1. Connate from 1 mm to 2/5 of their length; 2. Connate from mid-length to most of their length); 22. Disposition of the free portion of tepals (0. Patently spreading to strongly reflexed; 1. Suberect); 23. Tepal basal marking (0. Lacking green basal markings adaxially; 1. With green basal markings adaxially); 24. Stamen number (0. Six; 1. Three); 25. Stamen disposition (0. Spreading and not approaching the style; 1. Connivent to the style, either anthers or filaments); 26. Filament orientation (0. Straight or somewhat arcuate, but never sigmoid or connivent to the style along the middle and spreading above; 1. Sigmoid and connivent to the style along the middle portion and spreading above); 27. Connation of filaments (0. Free above the perigone; 1. Distinctly connate above the perigone for most of their length to form a tube); 28. Filament indumentum (0. Smooth; 1. Papillate at base); 29. Dehisced anther morphology (0. Noncircinate; 1. Circinate); 30. Anther dehiscence (0. Dehiscing longitudinally along entire length; 1. Dehiscing by apical pores or slits extending up to the middle); 31. Connation of anthers (0. Free; 1. Connate); 32. Indehisced anther connective morphology (0. Not apically extended or overtopping anthers; 1. Extended apically into a membranous flap overtopping anthers); 33. Ovary color (0. Green, yellow, or orange, rarely combined with white portions; 1. Completely white, sometimes with a purple tinge); 34. Style disposition (0. Erect; 1. Declinate); 35. Stigma morphology (0. Indistinct to trigonus or capitate, but never six-toothed; 1. Extended into six, erect, minute teeth); 36. Withered tepal disposition when capsules unripe (1. Tepals cohering above to form a cap atop unripe capsule; 0. Tepals remain at the base of the unripe capsule); 37. Mature capsule disposition (0. Suberect to erect; 1. Patent to reflexed); 38. Capsule valves disposition (0. Suberect to somewhat spreading; 1. Reflexed from the base to expose seeds completely); 39. Seed size (0. Large [2.5–12 mm long]; 1. Small [0.5–2.4 mm long]); and 40. Seed morphology (0. Flattened and winged, mostly adapted to wind dispersal; 1. Polygonal or irregularly compressed; 2. Subellipsoid, usually heavier than the other types). A matrix with the 40 coded characters was constructed for the 295 samples included in the present work (Table S2, Materials S12). These data were incorporated into Mesquite v. 3.61 (Maddison & Maddison, 2022) to trace the morphological characters in relation to the obtained phylogenetic trees. The 40 characters were traced individually to evaluate apomorphies and ancestral characters for the obtained clades (Materials S13). Additionally, all characters were traced simultaneously on the phylogenetic trees (not shown).

2.5 Phylogenetic analyses

First, bayesian inference (BI) analyses were conducted using MrBayes v.3.2.7 (Ronquist et al., 2012) for individual markers and the combined data sets. To determine the best model of DNA substitutions for each independent region, jModelTest 2.1.10 (Darriba et al., 2012) was performed, using the Akaike Information Criterion (AIC; Akaike, 1974); models with the lowest BIC (Bayesian Information Criterion) score were considered to best describe the substitution pattern. The best models were the most-parameterized models, all with a Gamma distribution (*G* parameter). The best model for the *ycf* and *trnLF* markers was (T92) Tamura-nei (coded as nst = 6, rates = gamma), for *matK*, the (GTR) General Time Reversible model (coded as nst = 6, rates = gamma), and for the *Agt1* marker, the (HKY) Hasegawa–Kishino–Yano model (coded as nst = 2, rates = gamma). A partition was set to run each marker with the determined rates. For BI analysis, the Markov Chain Monte Carlo (MCMC) algorithm was run for 10×10^6 generations and sampled every 1000 generations for all individual analyses. Two runs were executed. The first 25% generations (burninfrac = 0.25) were excluded, and the remaining trees were used to compile a posterior probability (PP) distribution using a 50% majority-rule consensus. Additionally, two Bayesian analyses were performed combining the molecular (plastid and full molecular) data set with the 40 coded discrete morphological characters, indicating a mixed data type (DNA for the molecular and Standard for the morphological characters with a gamma rate), following the same criteria specified above for the molecular data. The results of the Bayesian analyses are shown for the concatenated plastid regions (Fig. S1) and the full molecular data set (plastid plus nuclear regions) (Fig. 2), indicating posterior probability (PP).

Second, phylogenetic analyses of the two molecular databases were obtained with maximum likelihood (ML) (Felsenstein, 1981) and maximum parsimony (MP) (Nei & Kumar, 2000), using the model indicated previously and applying, in all cases, partial deletion, as implemented in MEGA. ML analysis was conducted using the tree searching strategy based on the nearest neighbor interchange (NNI). MP analysis was performed using the Heuristic search options using the tree searching strategy based on the Subtree-Pruning-Regrafting (SPR) algorithm with search level 1 (Nei & Kumar, 2000), in which the initial trees were obtained by the random addition of sequences (10 replicates). For ML and MP methods, support was assessed by the bootstrap (Felsenstein, 1981), with 10 000 replicates holding ten trees per replicate. Clades showing bootstrap (BS) values of 50%–74% were considered as weakly supported, those with values of 75%–89% were considered as moderately supported, and those with values of 90%–100% were considered as strongly supported.

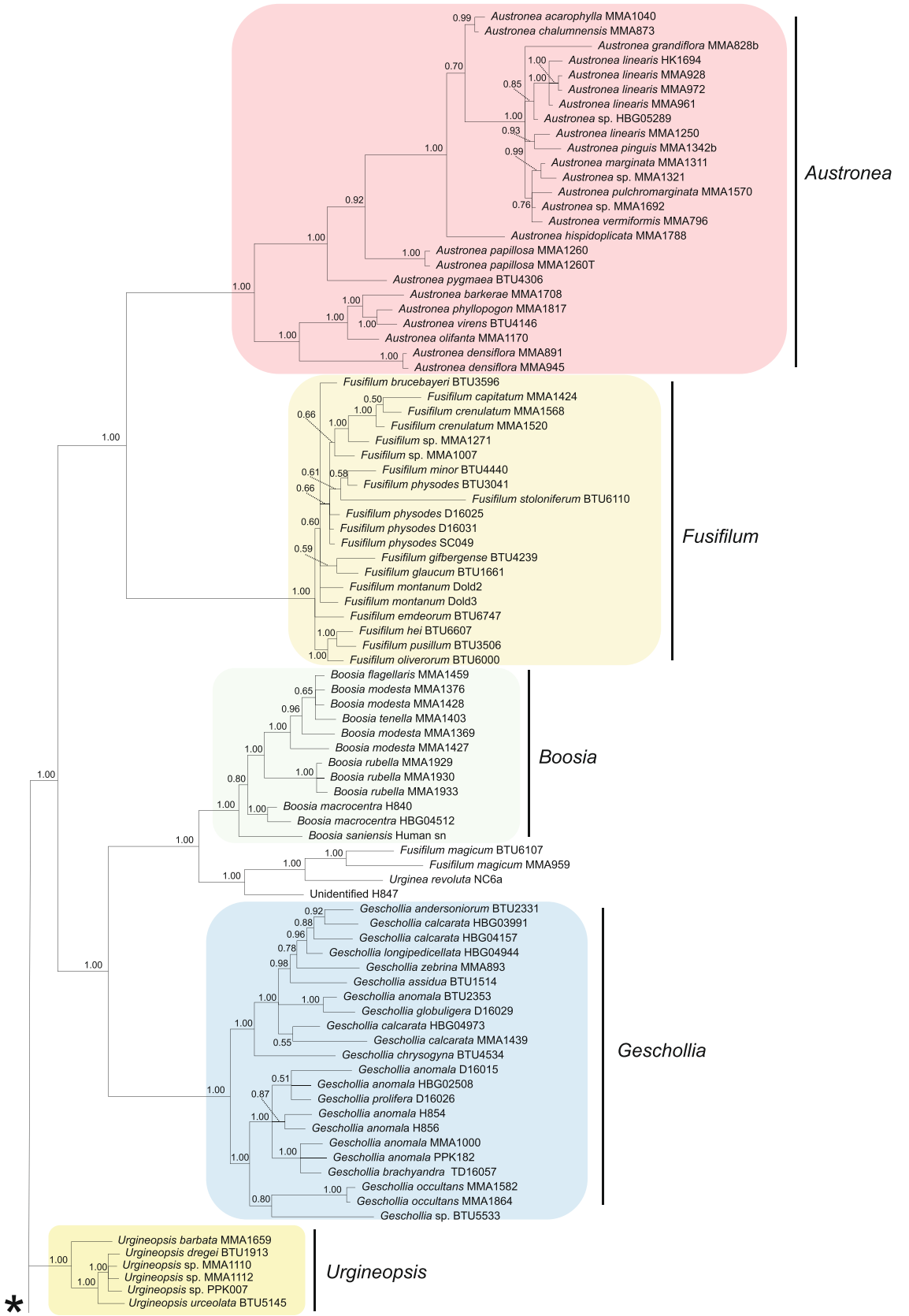

Fig. 2. Bayesian majority-rule consensus tree of the full combined chloroplast (*trnL* intron, *trnL-F* spacer, *matK*, and *trnCGCA-ycf6* intergenic region) and nuclear (*Agt1*) data sets for Urgineoideae; posterior probabilities (PP) are displayed at the nodes, and the proposed generic classification is indicated by shaded rectangles.

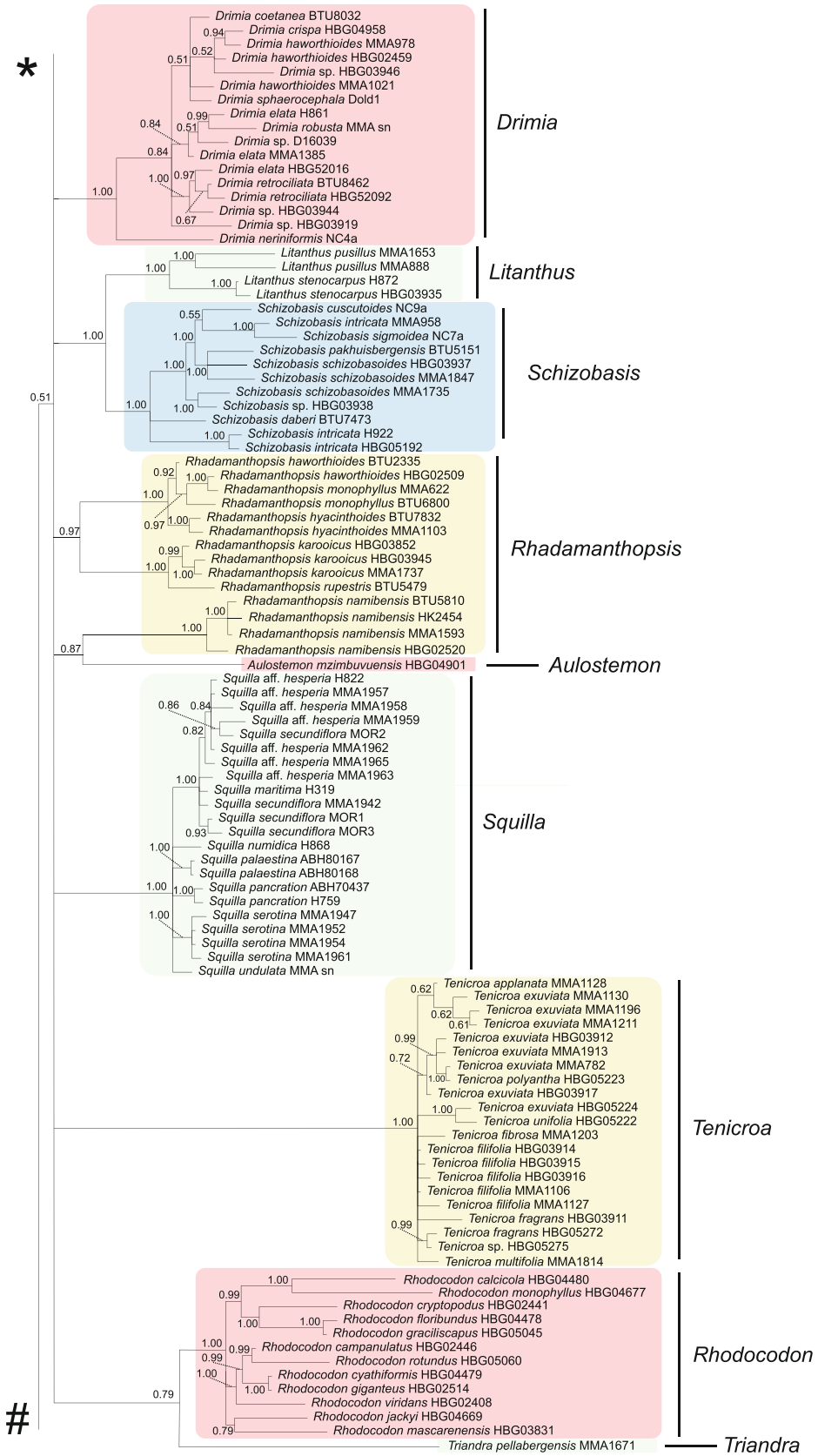

Fig. 2. Continued

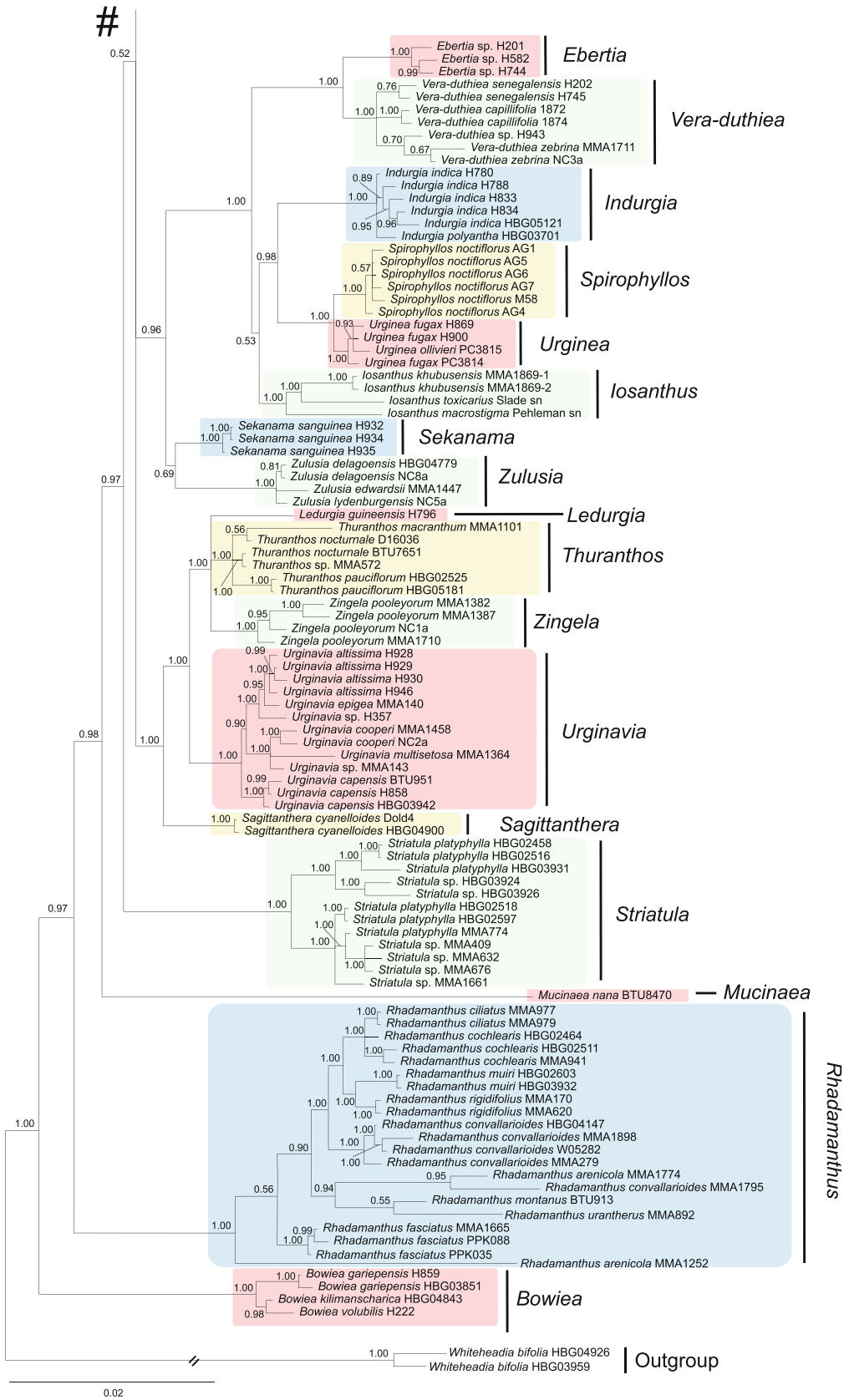

Fig. 2. Continued

2.6 Congruence between data sets

Topological incongruence between cpDNA (*trnL* intron, *trnL-F* spacer, *matK*, and the *trnCGCA-ycf6* intergenic region) and nDNA (*Agt1* region) data sets were checked using two methods. First, an incongruence length difference (ILD) test (Farris et al., 1994) was performed in PAUP v.4.0.b10 (Swofford, 2002) using heuristic search options, which included 100 random addition replicates and tree-bisection-reconnection (TBR) branch swapping with MulTrees in effect and keeping 10 trees per replicate. Second, comparison of the ML phylogenetic trees of individual cpDNA and nDNA data sets was performed using MEGA, with the substitution model T92 + G (Tamura, 1992) as selected in the jModelTest, and with 1000 fast bootstrap replicates. A tanglegram comparing the ML tree of each data set was computed in Dendroscope 3.7.5 (see Huson & Scornavacca, 2012) and checked for topological conflicts on the basis of BP support ≥85% (Norup et al., 2006), but also BP support ≥75% to detect further relationships. Comparison of the combined cpDNA tree and the nDNA tree was undertaken from a reduced matrix including only the 166 taxa for which both kinds of data were fully available.

2.7 Distribution patterns

We undertook a comparative study of the phytogeographic distribution patterns of the accepted genera, some of which are newly circumscribed, to further inform the delineation of genera in respect of sister or related clades (Fig. 3). To achieve this, we subdivided the original Sudano-Zambezian Region of Takhtajan (1986), applying his principle of subdivision into subregions, but with one notable exception, which is, further subdivision of the Zambezian Subregion into three informal "sections": northern (precipitation-rich, transitional toward the tropical regions of Central Africa), eastern (precipitation-rich, including a series of high-elevation mountain ranges), and southern (drier, home to arid and semi-arid savanna). The following resulting phytochoria were used to aid comparative analyses of the distribution maps of the genera: 1. the Cape Region; 2. the Karoo-Namib Region; 3. the Uzambara-Zululand Region; 4. the Madagascan Region; 5a: the southern section of the Zambezian Subregion; 5b. the northern section of the Zambezian Subregion; 5c. the eastern section of the Zambezian Subregion; 6a. the Erithraeo-Arabian Subregion; 6b. the Omano-Sindian Subregion; 7. the Guineo-Congolian Region; 8. the Sahelo-Sudanian Subregion; 9. the Saharo-Arabian Region; 10. the Mediterranean Region; 11. the Macaronesian Region; 12. the Indian Region; and 13. the Indochinese Region.

3 Results

Analyses of each individual matrix using BI, MP, and ML methods yielded trees with similar major topologies and support in most branches, resolving similar clades that are assimilated to genera in this work (see the Supplementary Material for BI Figs. S2, S3, S4, S6). However, early diverging relationships are sometimes collapsed or weakly supported in the individual DNA region trees. When the full cpDNA (Figs. S1, S5) and full molecular data sets (Figs. 2, S7) were analyzed, resolution improved considerably.

Use of the ILD test indicated the existence of slight incongruencies between plastid and nuclear data sets ($P = 0.01$), whereas comparison of individual ML trees of cpDNA and nDNA data sets yielded no remarkable conflicts (taking into account that most of the primary branches obtained in the nDNA analyses were weakly supported in unresolved positions). Consequently, as no major differences were found in the topologies of all obtained trees, and in view of the argument that combining heterogeneous data can also increase accuracy even if ILD analyses do not explicitly incorporate that heterogeneity (see Barker & Lutzoni, 2002), we accept that phylogenetic trees obtained from the combined molecular matrices (both the concatenated plastid regions and mostly the concatenated plastid plus nuclear regions) are good reconstructions of the evolutionary history of *Urgineoideae*. Further, our trees accord with previous partial phylogenetic analyses of the subfamily (Pfosser & Speta, 2001, 2004; Pfosser et al., 2012). Notably, some authors have long disregarded ILD as an appropriate tool for testing the suitability of data set concatenation (Yoder et al., 2001; Pirie, 2015).

3.1 Molecular phylogenetic trees

We obtained comprehensive data for the plastid regions *trnCGCA-ycf6* intergenic region, *matK*, and the *trnL* intron plus *trnL-F* spacer of the studied samples, with 290, 294, and 272 DNA sequences, respectively. The obtained phylogenetic trees, based on BI from each independent plastid region, provided several well-supported clades, although generally with inadequate support to explain their relationships (Figs. S2–S4). Concatenation of all plastid DNA regions generated an aligned matrix of 295 samples and 3583 characters. The Bayesian majority-rule consensus tree of the concatenated plastid regions is shown in Fig. S1.

MP and ML analyses from concatenation of all plastid DNA regions recovered a very similar general topology of the trees and generic relationships. However, the topology of the parsimony strict consensus tree (Fig. S5) resolved the polytomy of *Thuranthos, Ledurgia*, and *Zingela*, where the latter two genera form sister clades.

Amplification of the nuclear *Agt1* region produced 166 Urgineoideae sequences covering nearly all recognized genera in the subfamily (except for *Mucinaea* and *Triandra*) and yielded useful data for phylogenetic studies. The obtained phylogenetic tree based on BI for the final *Agt1* matrix (486 bp after removing the hypervariable central region) provided several well-supported clades, although generally with inadequate support to explain their relationships (Fig. S6). Concatenation of all plastid and nuclear DNA regions generated an aligned matrix of 295 samples and 4069 bp. The Bayesian majority-rule consensus tree of the concatenated plastid and nuclear regions is shown in Fig. 2. Two samples of *Whiteheadia bifolia* were used as outgroup, leaving Urgineoideae as a perfectly supported clade. Samples of *Bowiea* (1.00 PP) represent the earliest divergence lineage in Urgineoideae. The next diverging lineage is *Rhadamanthus* (1.00 PP) including a subclade comprising *Urginea ciliata* (L. f.) Baker, *Urginea muirii* N.E. Br., *Urginea rigidifolia* Baker, and *Drimia cochlearis* Mart.-Azorín et al. (these four species

are accepted as *Rhadamanthus* in this work, ined.). The remaining Urgineoideae form a clade (0.98 PP), where a sample of *Mucinaea nana* (Snijman) M. Pinter et al. appears sister. The rest of Urgineoideae form a clade (0.97 PP) in which samples of *Striatula* are monophyletic (1.00 PP). The additional Urgineoideae are included in two consecutive clades with very low support (0.52 PP and 0.51 PP), the latter also showing collapsed internal relationships. Within these clades, *Ledurgia* (1.00 PP), *Thuranthos* (1.00 PP), and *Zingela* (1.00 PP) form a polytomy, but with strong support in combination (1.00 PP). The next diverging lineage includes *Sagittanthera* (1.00 PP) and *Urginavia* (1.00 PP), all showing strongly supported relationships. Another clade with strong support (0.96 PP) includes two subclades. One, with weak support (0.69 PP), includes the sister *Zulusia* (1.00 PP) and *Sekanama* (1.00 PP). The other (1.00 PP) is divided into two subclades, one (0.53 PP) with *Iosanthus* (1.00 PP) being sister to a clade (0.98 PP) that includes the sister *Urginea* (1.00 PP) and *Spirophyllos* (1.00 PP), which, in combination, are sister to *Indurgia* (1.00 PP). The other subclade (1.00 PP) includes the sister *Ebertia* (1.00 PP) and *Vera-duthiea* (1.00 PP).

Within the large final polytomy, *Rhodocodon* (1.00 PP) is sister to a sample of *Triandra* that, in combination, form a clade with 0.79 PP. The genera *Tenicroa* (1.00 PP), *Squilla* (1.00 PP), *Drimia* (1.00 PP), and *Urgineopsis* (1.00 PP) form perfectly supported clades within a larger polytomy. *Litanthus* (1.00 PP) and *Schizobasis* (1.00 PP) are sister clades and constitute a strongly supported clade (1.00 PP). Samples of *Rhadamanthopsis* are polyphyletic and form three perfectly supported (1.00 PP) clades. Two of them are sister clades, being strongly supported in combination (0.97 PP). Samples of *Rhadamanthopsis namibensis* (Oberm.) Speta form a clade (1.00 PP) that is sister to a sample of *Aulostemon*, which, in combination, form a clade with moderate support (0.87 PP). The remaining samples form a clade (1.00 PP), with perfectly supported internal relationships. One subclade (1.00 PP) includes *Geschollia* (1.00 PP) being sister to a clade that combines *Boosia* (1.00 PP) and a clade (1.00 PP) including samples of *Fusifilum magicum* U. Müll.-Doblies et al., *Urginea revoluta* A.V. Duthie, and an unidentified taxon. The other subclade includes the sister *Fusifilum* (1.00 PP) and *Austronea* (1.00 PP).

MP and ML analyses from concatenation of all molecular data sets yielded a similar topology to the Bayesian tree. However, the Parsimony analysis recovers all studied samples of *Rhadamanthopsis* plus *Aulostemon* as monophyletic (86% BS), *Drimia* as sister to *Litanthus* plus *Schizobasis* (77% BS), and again resolves the polytomy of *Ledurgia*, *Thuranthos*, and *Zingela* (Fig. S7). Moreover, *Zulusia* and *Sekanama* are not related within the general polytomy, a sample of *Iosanthus* sp. from central Namibia is placed out from the other samples of the genus, although within very weakly supported relationships, and *Striatula* is sister to *Tenicroa*, albeit with very low support (60% BS) (Fig. S7).

3.2 Combined molecular and morphological data sets

The Bayesian analyses combining the molecular (plastid and full molecular) data sets with the 40 coded discrete morphological characters are shown in Figs. S8 and S9, respectively, and yielded similar general topologies to the plastid and full molecular data sets alone, although with improved resolution in some clades. When the plastid data set was combined with morphological characters (Fig. S8), *Rhadamanthopsis* in the sense of this work obtained full support (1.00 PP) relative to the studied sample of *Aulostemon*. However, this solution is not recovered when the full molecular data sets were combined with morphology (Fig. S9). In this latter analysis, *Drimia* (1.00 PP) and *Squilla* (1.00 PP) appear as sister clades with a combined support of 0.85 PP, and the polytomy of *Ledurgia*, *Thuranthos*, and *Zingela* (Fig. 2) is dissolved, with the latter two genera in combination forming a clade with moderate support (0.83 PP).

When tracing the selected 40 morphological characters (Tables S2 and S12) on the full molecular data set (Fig. 2) with Mesquite, several characters (numbered 2, 4, 7, 8, 9, 11, 12, 13, 14, 16, 18, 23, 24, 27, 31, 32, 33, 37, 38, 39, 40) (Materials S13) are shown as apomorphic for one to very few genera, indicating their usefulness in generic delineations. However, other characters (numbered 18, 20, 21, 25, 30, or 36) are distributed more commonly among the studied genera and reflect some degree of homoplasy (Materials S13). A selection of those characters is mapped in Fig. 3. Character 17 (bracteoles; character state: 1, present and distinct) appears to be the ancestral character of the fully supported clade (1.00 PP) combining *Ledurgia*, *Thuranthos*, *Zingela*, *Urginavia*, and *Sagittanthera* (Fig. 3). Character 25 (stamen disposition; character state 1: Connivent to the style, either anthers or filaments) is shown as the ancestral character of Urgineoideae when *Bowiea* is excluded (Fig. 3). Similarly, character 30 (anther dehiscence; character state 1: Dehiscing by apical pores or slits extending up to the middle) is also shown as ancestral for the oldest clades in the subfamily, except for *Bowiea* (Fig. 3). We indicate character number 17 in *Vera-duthiea* and character number 25 in *Schizobasis* in Fig. 3 as variable (character states 0/1) despite all our samples in Table S1 showing character state (0). This is because *Vera-duthiea macrocarpa* presents bracteoles and *Schizobasis macowanii* has spreading stamens (Fig. 1.17), with neither species included in the molecular genetic study.

4 Discussion

4.1 Previous phylogenetic studies and taxonomic treatments

Contrasting taxonomic arrangements have been inferred from the molecular data generated by several phylogenetic studies sampling Urgineoideae (Stedje, 1998, 2001a, 2001b; Speta, 1998a, 1998b, 2001; Pfosser & Speta, 1999, 2001, 2004; Manning et al., 2004; Pfosser et al., 2012). Pfosser & Speta (1999) used the plastidial region *trnL-F* and included 15 samples, placed into eight genera (*Charybdis*, *Urginea*, *Karoophila* [as *nomen nudum*], *Urginavia*, *Drimia*, *Rhadamanthus*, *Ebertia*, and *Thuranthos*), with most being monophyletic. Speta (1998a, 1998b, 2001) described the monophyletic genera *Boosia*, *Charybdis*, *Duthiea*, *Ebertia*, *Geschollia*, *Indurgia*, *Ledurgia*, *Rhadamanthopsis*, *Sekanama*, and *Urginavia*—each showing a unique combination of morphological characters (Fig. 1) and distribution. Pfosser & Speta (2001, 2004) extended the sampling to more than 140 samples of Urgineoideae based on the plastidial region *trnL-F* alone and confirmed that most genera accepted by Speta

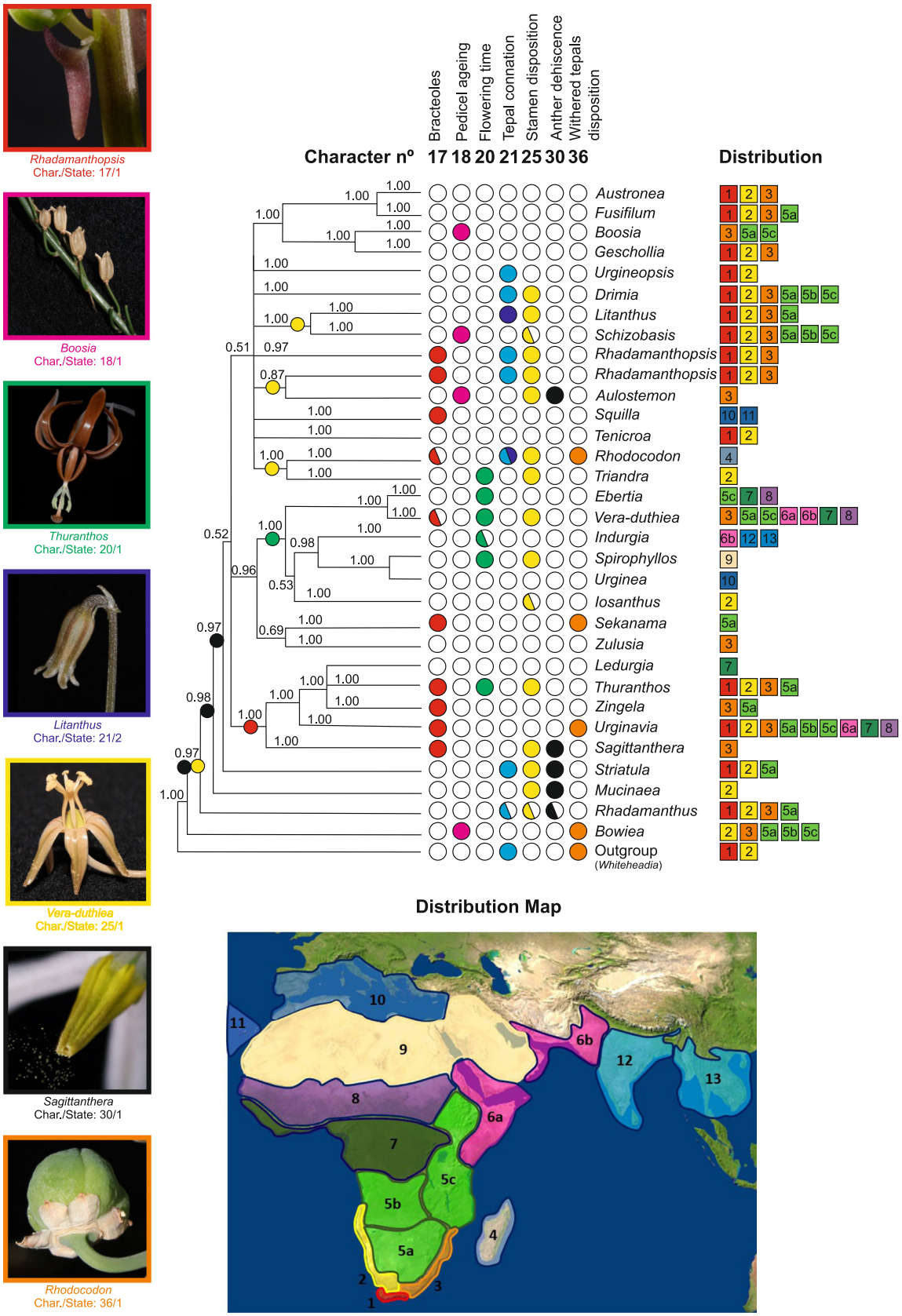

Fig. 3. Continued

(2001) formed well-supported clades. A contemporaneous study by Manning et al. (2004) combined two plastid regions (*rbcL* and *trnL-F*), but with only limited sampling (21 urgineoids), and identified few clades on the basis of morphological discontinuities. Despite the preliminary nature of their results, these authors opted to propose a very broadly conceived *Drimia* that was almost coincident with the whole subfamily Urgineoideae (excepting *Bowiea*). Their genus morphological characterization has been shown to be problematic for some of the included groups (Martínez-Azorín et al., 2013c). The phylogenetic tree of Manning et al. (2004) seemingly included 13 urgineoid genera (*Boosia*, *Bowiea*, *Charybdis*, *Drimia*, *Fusifilum*, *Litanthus*, *Rhadamanthus*, *Rhadamanthopsis*, *Schizobasis*, *Sekanama*, *Tenicroa*, *Thuranthos*, and *Urginavia*) and they argued the apparent paraphyly or polyphyly of some genera to justify their broad *Drimia* concept. Their arguments were that *Tenicroa* was paraphyletic unless *Tenicroa nana* Snijman is segregated, and *Fusifilum* was polyphyletic in their sense. Pinter et al. (2013) presented morphological evidence to separate *T. nana* from *Tenicroa* and to recognize the monotypic *Mucinaea* (Fig. 1.12). The four samples named by Manning et al. (2004) as "*Fusifilum calcarata*, *Fusifilum marginata*, *Fusifilum dregei* and *Fusifilum physodes*" were resolved in three distant clades in their phylogeny. Two of the four ("*Fusifilum calcarata*" and "*F. marginata*" *sensu* Manning et al., 2004) had not been previously accepted or combined in that genus and only *Fusifilum physodes* (Jacq.) Speta had been accepted in the earlier revision of *Fusifilum* by Müller-Doblies et al. (2001). *Urginea calcarata* (Baker) Hilliard & Burtt is a member of *Geschollia* (cf. Martínez-Azorín et al., 2019d), *Urginea marginata* (Thunb.) Baker belongs to *Austronea* (cf. Martínez-Azorín et al., 2018a), and *Urginea dregei* Baker is placed in *Urgineopsis* (cf. Martínez-Azorín et al., 2019a). All three taxa differ in morphology and distribution, and their misplacement by Manning et al. (2004) in *Fusifilum* accordingly led to their interpretation of that genus as polyphyletic (see Martínez-Azorín et al., 2019a).

Manning & Goldblatt (2018) presented a revision of *Drimia sensu lato* in southern Africa and accepted 20 sections that generally align with previously described urgineoid genera, with some circumscribed as para- or polyphyletic in view of previous phylogenetic findings (Pfosser & Speta, 1999, 2001, 2004; Pfosser et al., 2012). Our results confirm the polyphyly of their *Drimia* sect. *Macrocentrae* (including species of *Boosia* and *Sekanama*), sect. *Ledebouriopsis* (Baker) J.C. Manning & Goldblatt (merging species of *Boosia*, *Geschollia*, *Urginavia*, *Urgineopsis* and *Zulusia*), sect. *Thuranthos* (C.H. Wright) J.C. Manning & Goldblatt (including species of *Indurgia*, *Vera-duthiea, Zingela* and *Urginea revoluta* = *Drimia hesperantha*), sect. *Physodia* (Salisb.) J.C. Manning & Goldblatt (including a species of *Austronea*), and sect. *Rhadamanthus* (Salisb.) J.C. Manning & Goldblatt (including species of *Striatula*). Moreover, their sect. *Hyacinthoides* J.C. Manning & Goldblatt is included in *Rhadamanthopsis* in the sense of the present work and sect. *Juncifoliae* J.C. Manning & Goldblatt in *Tenicroa sensu* Pinter et al. (2020).

4.2 Phylogenetic relationships and morphology

Our phylogenetic results recover several well-supported clades or isolated lineages that correspond to 29 described genera in the Urgineoideae: *Aulostemon*, *Austronea*, *Boosia*, *Bowiea*, *Drimia*, *Ebertia*, *Fusifilum*, *Geschollia*, *Indurgia*, *Iosanthus*, *Ledurgia*, *Litanthus*, *Mucinaea*, *Rhadamanthopsis*, *Rhadamanthus*, *Rhodocodon*, *Sagittanthera*, *Schizobasis*, *Sekanama*, *Squilla*, *Striatula*, *Tenicroa*, *Thuranthos*, *Triandra*, *Urginavia*, *Urginea*, *Urgineopsis*, *Vera-duthiea*, and *Zingela*. Additionally, two new genera, *Spirophyllos* (for *Urginea noctiflora* Batt. & Trab.) and *Zulusia* (*Urginea delagoensis* Baker, *Urginea lydenburgensis* R.A. Dyer and *Drimia edwardsii* N.R. Crouch & Mart.-Azorín), would require a formal description and will be presented in a forthcoming monograph.

Bowiea is consistently retrieved as sister to the remaining Urgineoideae and is identified by its distinctly branched and fleshy inflorescence, long-lasting flowers with tepals that remain at the base of the mature capsule, the conical ovary with a semi-inferior appearance (Fig. 1.4), and green pedicels supporting dry dehisced capsules. Sister to the remaining Urgineoideae, the *Rhadamanthus* clade includes the species considered by Salisbury (1866), Dyer (1934), and Nordenstam (1970, with the exclusion of *Rhadamanthus platyphyllus* B. Nord. that belongs to *Striatula* and *Rhadamanthus cyanelloides* Baker that represents the monotypic *Sagittanthera*). These *Rhadamanthus* species share stamens connivent to the gynoecium, and anthers dehiscing by apical pore-like slits. Moreover, *Urginea ciliata*, *Urginea rigidifolia*, *Urginea muirii*, and *Drimia cochlearis* form a well-supported subclade that was recognized by Manning & Goldblatt (2018) as *Drimia* sect. *Sclerophyllae* J.C. Manning & Goldblatt, based on their nodding globular buds, patent to suberect stellate flowers, spreading filaments, and complete dehiscence of anthers. We suggest accepting them as *Rhadamanthus* based on the

Fig. 3. Molecular phylogenetic relationships of genera in Urgineoideae, simplified from Fig. 2. Some morphological characters and character states are shown, indicating the ancestral character states in color for some clades in the tree. Distribution ranges of genera are indicated by colored squares, and as outlined in the map (see Section 2.7 in the main text). Character numbers and character states: 17. Bracteoles (0 [white]. Absent; 1 [red]. Present); 18. Pedicel aging (0 [white]. Browning simultaneously with developing capsule, pedicel brown at dehiscence; 1 [pink]. Remaining green as developing capsule browns, pedicel green at dehiscence); 20. Flowering time (0 [white]. Diurnal; 1 [green]. Nocturnal); 21. Connation of tepals (0 [white]. Free or nearly free (connate for less than 1 mm from base); 1 [pale blue]. Connate from 1 mm to 2/5 of their length; 2 [dark blue]. Connate from mid-length to most of their length); 25. Stamen disposition (0 [white]. Spreading and not approaching the style; 1 [yellow]. Connivent to the style, either anthers or filaments); 30. Anther dehiscence (0 [white]. Dehiscing longitudinally along the entire length; 1 [black]. Dehiscing by apical pores or slits extending up to the middle); 36. Withered tepal disposition when capsules unripe (1 [white]. Tepals cohering above to form a cap atop unripe capsule; 0 [orange]. Tepals remain at the base of the unripe capsule); see also Table S2.

flower morphology transition observed in *Rhadamanthus albiflorus* B. Nord. or *Rhadamanthus fasciatus* B. Nord. (with an early diverging phylogenetic position in the genus) from subpatent flowers with nearly free and spreading tepals, to the nodding, urceolate flowers of *Rhadamanthus arenicola* B. Nord., *Rhadamanthus convallarioides* (L. f.) Salisb. ex Baker, *Rhadamanthus secundus* B. Nord. or *Rhadamanthus urantherus* R.A. Dyer, characterized by an increased degree of tepal connation (Fig. 3). However, further studies are required, including a complete sampling in the genus, to evaluate possible alternatives.

The monotypic *Mucinaea* consistently represents an independent lineage, supported by the unique combination of bright purplish-pink tepals with a basal green marking encircled by a white ring (Fig. 1.12); anthers opening as an apical pore or slit; a nonbarred, purple amplexicaul cataphyll; and the bulb structure (Pinter et al., 2013).

Although a species of *Striatula* in the sense of Pinter et al. (2019) (*R. platyphyllus*) was included in *Rhadamanthus* by Nordenstam (1970) based on the peculiar flower morphology and anther dehiscence, our phylogenetic results (Fig. 2) corroborate the findings of Pfosser et al. (2012) and Pinter et al. (2019) and place several samples of *Striatula* in a fully supported clade characterized by their ovate, flat, appressed, velutinous leaves with longitudinal furrows, a very rare and almost exclusive character in Urgineoideae.

Sagittanthera represents a fully supported clade to include samples of *R. cyanelloides* being easily identified by the large, connate anthers (unique in Hyacinthaceae) that dehisce by apical pores (Figs. 1.16, 3), presence of distinct bracteoles, and the leaves keeled abaxially, among other characters (Martínez-Azorín et al., 2013d).

Urginavia in the sense of Speta (1998b) and the present study includes species with bulbs composed of leathery scales (usually yellowish when dry), which are imbricate and produce white silky threads when broken, usually long racemose inflorescences, distinct bracteoles, withered tepals persisting below the developing capsule, and flattened black seeds. These species occur south of the Sahara Desert, and mostly fit sect. *Urginavia* (Speta) J.C. Manning & Goldblatt (Manning & Goldblatt, 2018). However, our phylogenetic results reveal that *Urginea multisetosa* Baker and *Urginavia echinostachya* Baker (placed in the polyphyletic sect. *Ledebouriopsis* by Manning & Goldblatt, 2018) also belong to *Urginavia* and share the diagnostic characters of that genus.

Samples of *Zingela* consistently form a well-supported clade characterized by loose bulb scales; hysteranthous, basally maculate, keeled leaves; multiflowered racemes; presence of bracteoles; diurnal flowers; and spreading stamens with circinnate dehisced anthers (Fig. 1.29) (Crouch et al., 2018), and are placed in a polytomy with *Thuranthos* and *Ledurgia* (Fig. 2), which is resolved in the parsimony analyses (Figs. S5, S7) where *Ledurgia* and *Zingela* form sister clades. *Thuranthos* differs from *Zingela* by the nonmaculate leaves; early caducous bracts and bracteoles; nodding, nocturnal flowers; basally expanded filaments that are sigmoid and connivent to the style along the middle portion and spreading above (Fig. 1.23); and noncircinnate anthers (Stirton, 1976). *Ledurgia* is a monotypic genus from Guinea, with compact bulb scales; a very short peduncle; few-flowered racemes; campanulate flowers (Fig. 1.10); and shortly connate tepals (Speta, 2001).

Sekanama sensu Speta (2001) includes *Urginea sanguinea* Schinz, *Urginea burkei* Baker, and *Urginea delagoensis* Baker. However, our results place samples of *U. sanguinea* in a well-supported clade and samples of *U. delagoensis, U. lydenburgensis*, and *Drimia edwardsii* in a clade that, in some analyses, is related to the former, but with very low support (Fig. 2). Important differences in distribution and morphology exist between the two groups. *Sekanama sanguinea* has a more northern and generally western distribution and shows hysteranthous leaves, elongated raceme with a much shorter peduncle, white stellate flowers (Fig. 1.18), withered tepals persisting at the base of the capsule, and flat and wide, elliptic seeds, whilst *U. delagoensis, U. lydenburgensis*, and *D. edwardsii* have a more southern distribution, and produce synanthous leaves; an elongated peduncle; subcampanulate, pale brown, or carneous to greenish flowers (Fig. 1.30); withered tepals persisting atop the capsule; narrowly ellipsoid capsules; and narrowly lanceolate seeds. Therefore, we suggest restricting *Sekanama* to include *S. sanguinea* and *S. burkei* and propose the new genus *Zulusia* Mart.-Azorín et al. (ined.) to accommodate *U. delagoensis, U. lydenburgensis*, and *D. edwardsii* (cf. Crouch & Martínez-Azorín, 2015), a solution also supported by their different chromosome counts (Goldblatt et al., 2012).

Our phylogenetic results consistently indicate a well-supported clade that includes *Iosanthus*, *Spirophyllos*, *Urginea*, *Indurgia*, *Vera-duthiea*, and *Ebertia*. Among those related clades, *Iosanthus sensu* Martínez-Azorín et al. (2019b) is monotypic and includes the small toxic plant *Ornithogalum toxicarium* C. Archer & R.H. Archer (Fig. 1.9). Our phylogenetic results consistently place a sample of this species as sister to two samples of *Drimia khubusensis* P.C. van Wyk & J.C. Manning. Moreover, our trees usually show all samples of those two taxa as sister to an undescribed species from central Namibia (Fig. 2). These three species characteristically share a relatively small plant size; hypogeal, compact bulbs; filiform leaves; lack of bracteoles; short and few-flowered inflorescence; free tepals; and capsule valves reflexed to completely expose the flattened, discoid, and winged seeds. Despite some morphological differences in flower structure (Manning & Goldblatt, 2018), we tentatively propose to expand *Iosanthus* to comprise those three latter species, to provide the most conservative solution.

Urginea, as typified by Adamson et al. (1944) in *Urginea fugax* Steinh., is narrowed to include the latter species and *Urginea ollivieri* Maire, being restricted to the western Mediterranean basin, where it forms a morphologically consistent group characterized by filiform leaves; diurnal, stellate, patent to suberect flowers with free tepals (Fig. 1.26); spreading filaments; and flattened, ellipsoid seeds. Our samples of *U. fugax* and *U. ollivieri* form a strongly supported clade that is sister to a clade comprising various samples of *U. noctiflora* from Morocco, a relationship reported earlier by Pfosser et al. (2006). The latter species differs from *Urginea* by the distinctly coiled leaves (a unique character in Urgineoideae); nocturnal nodding flowers with straight filaments that are connivent to the style and cross at their middle (Fig. 1.19); and patent capsules. We, therefore,

propose the description of a new genus named *Spirophyllos* Mart.-Azorín et al. (ined.) to accommodate *U. noctiflora*, based on the distinct differences noted above as well as its genetic divergence and different habitats and distributions.

The latter two genera are consistently shown in our trees as sister to samples of *Indurgia* in the sense of Yadav et al. (2019), who accommodated only southeast Asian members of Urgineoideae in their *Drimia* sect. *Indurgia* (Speta) J.C. Manning & Lekhak. *Indurgia* can be identified by the combination of caducous bracts; lack of bracteoles; nocturnal and nodding flowers or sometimes diurnal and spreading; suberect to spreading filaments; erect, usually thickened, subclavate style with truncate stigma (Fig. 1.8); apiculate capsule valves; and ellipsoid, flattened, and winged seeds.

Speta (2001) described the illegitimate *Duthiea* to include three species from Central to northwestern Africa: *Duthiea senegalensis* (Kunth) Speta, the type of the genus, *Duthiea macrocarpa* (Stedje) Speta, and *Duthiea noctiflora* (Batt. & Trab.) Speta. Speta (2016) subsequently published *Vera-duthiea* Speta as a *nom. nov*. to replace the illegitimate *Duthiea* (*sensu* Speta, non *Duthiea* Hack. ex Procop.-Procop., Poaceae). *Vera-duthiea* in the sense of Martínez-Azorín et al. (2018b, 2019a), Crouch et al. (2020), and Patzelt et al. (2021) include taxa from southern and central Africa and the southern Arabian Peninsula, characterized by maculate leaves (at least at their base); lack of bracteoles (rarely present); nodding, nocturnal flowers; tepals strongly reflexed; filaments incurved along the lower half, connivent to the style in the middle section and spreading distally (Fig. 1.28); style distinctly deflexed; and flattened subelliptic seeds. Our phylogenetic results agree with those of Pfosser and Speta (1999, 2001, 2004) in retrieving samples of this genus in a well-supported clade, being sister to *Ebertia*. Moreover, as reported earlier by Pfosser et al. (2006), *U. noctiflora* requires segregation from *Vera-duthiea sensu* Speta (2016) (as already noted under *Spirophyllos*), as this species does not present the typical leaf maculation of *Vera-duthiea*.

Ebertia Speta includes the tropical African taxa *Urginea pauciflora* Baker and *Urginea nana* Oyewole. This genus is characterized by filiform, proteranthous leaves; short peduncle and condensed few-flowered raceme; shortly spurred bracts; nocturnal, campanulate flowers; tepals shortly connate at the base; filaments shorter than tepals; pedicels of ripe capsules laterally recurved; and flattened black seeds. Our results recover three samples of *Ebertia* in a well-supported clade.

Triandra pellabergensis Mart.-Azorín et al. constitutes an isolated lineage supported by the presence of only three stamens per flower (unique in Hyacinthaceae) (Fig. 1.24), among other characters (cf. Martínez-Azorín et al., 2021). This genus approaches *Urginea revoluta* in flower morphology, although the latter produces the usual six stamens per flower and is only very distantly related in our phylogenetic studies. Further species and expanded genetic studies are required to elucidate the taxonomic placement of *U. revoluta*. Sister to *Triandra* appears a perfectly supported clade fitting with the Madagascan endemic *Rhodocodon* in the sense of Baker (1881) and Knirsch et al. (2015, 2016, 2019), characterized by urceolate to campanulate flowers (Fig. 1.15) (lasting for 3–7 days); tepals connate for most of their length and persisting at the base of capsules; adnate filaments; and seeds subellipsoidal and usually with a distinct raphe, or rarely compressed (Brudermann et al., 2018).

Tenicroa is a distinct genus accepted historically by most researchers, including by Pinter et al. (2020), in the latest revision of that genus, one easily characterized by mostly synanthous leaves with transversally striate-raised sheathing cataphylls; stellate flowers with free tepals; suberect stamens with subbasifixed anthers, and an elongate, deflexed, and curved-sigmoid style (Fig. 1.22). Our *Tenicroa* samples form a fully supported clade that is usually related to *Urgineopsis*.

Within the remaining clades, *Squilla* in the sense of Steinheil (1836) was treated in recent times as *Charybdis* Speta (1998b) nom. nov. to replace *Squilla*, a name considered by Speta to be an orthographic variant of both *Scilla* L. and *Skilla* Raf. However, typification by Rafinesque of *Scilla maritima* L. renders *Charybdis* illegitimate and unavailable for use (cf. Martínez-Azorín & Crespo, 2016a; Crespo et al., 2020; Martínez-Azorín et al., 2022). Martínez-Azorín & Crespo (2016b) have recently requested a binding decision on whether *Scilla* L. and *Squilla* Steinh. are sufficiently alike to be considered orthographic variants. It seems that most members of the Committee will accept *Squilla* as not being confusable with *Scilla* (W. Appelquist, pers. comm.), in which case the name *Squilla* would be available for the current concept of *Charybdis*, as already accepted by Martínez-Azorín et al. (2022). Previous phylogenetic analyses (Pfosser & Speta, 2001, 2004; Pfosser et al., 2012) place numerous samples of *Squilla* (as *Charybdis*) in a strongly supported clade, supporting acceptance of this group as an independent genus (Speta, 1998b; Pfosser & Speta, 2001, 2004; Conti et al., 2005; Jeanmonod & Gamisans, 2007; Bacchetta et al., 2012; Ali et al., 2013; Véla et al., 2016). We found our 22 samples of *Squilla* to form a strongly supported clade in an isolated position within Urgineoideae, and therefore, we recognize this genus based on the hysteranthous leaves; presence of distinct bracteoles; and flattened and winged seeds, together with their Mediterranean distribution (Martínez-Azorín et al., 2022).

A distinct group with nodding campanulate flowers was recognized as *Rhadamanthopsis* at the subgenus (Obermeyer, 1980a) or genus (Speta, 2001) level to include two species: *Rhadamanthopsis namibensis* and *Rhadamanthopsis karooicus* (Oberm.) Speta. These species are characterized by diurnal, nodding, and campanulate flowers; tepals connate for about 1/3 to 2/5 of their length and free, suberect, apical lobes (Fig. 1.13); stamens included and connivent to the style, with adnate filaments; loculicidal dehiscence of their anthers (instead of by apical pores or slits) and distinct bracteoles, differing substantially from *Rhadamanthus* (as interpreted in this paper). Other species agreeing morphologically with *Rhadamanthopsis* were described, including *Drimia hyacinthoides* Baker (1874), *Ornithogalum haworthioides* Baker (1878) (≡*Drimia bolusii* Baker 1897; not to be confused with *Drimia haworthioides* Baker 1875), and *Drimia monophylla* Oberm. ex J.C. Manning & Goldblatt. The phylogenetic analyses by Pfosser & Speta (1999, 2001, 2004) and Pfosser et al. (2012) found samples of *Rhadamanthopsis* to form a clade with moderate support, including samples of "*Karoophila bolusii*" (a genus name not formally published). Our phylogenetic results

consistently place samples morphologically fitting *Rhadamanthopsis* into three fully supported clades, which usually form a polytomy, where a sample of *Aulostemon* is also related. One clade includes samples of the namibian *R. namibensis*, another comprises the Namaqualand samples of *R. karooicus* and relatives, and the last clade accommodates the southeastern South African *D. hyacinthoides*, *D. monophylla*, and *O. haworthioides*. Although some morphological differences in vegetative characters exist among the taxa included in these three biogeographic subclades and their polyphyletic relationships are revealed in some analyses (Fig. 2), we propose to accept *Rhadamanthopsis* to include all species characterized by the distinct flower morphology detailed above. The placement of the *R. namibensis* clade is diverse in our analyses and sometimes it is recovered as an independent clade, although with its relationships very weakly supported or collapsed. However, when morphological data are included in the plastid phylogenetic analyses, *Rhadamanthopsis* recovers monophyly in the sense of this work (Fig. S8). Furthermore, the published chromosome numbers ($2n = 16$, 18) for this genus differ from common chromosome counts in the subfamily ($2n = 20$; $x = 10$) (Goldblatt et al., 2012). The required new combinations in the genus will be effected in a forthcoming monograph.

Aulostemon, although related to *Rhadamanthopsis* in the phylogenetic analyses, is readily differentiated by its stellate flowers; green pedicels supporting dry dehisced capsules, free tepals with a green basal macula; filaments connate to form a long tube above the perigone (Fig. 1.1) (a unique and diagnostic character in Hyacinthaceae); and free anthers, among other characters (Martínez-Azorín et al., 2017).

Another clade that consistently resolved in our phylogenetic analyses includes both *Litanthus* and *Schizobasis* as sister, fully supported lineages, corroborating the findings of Pfosser & Speta (2001, 2004) and Pfosser et al. (2012). This sister relationship, at first sight surprising based on their different flower and inflorescence morphologies, is supported by both the elongation of the anther connective into a small, translucent, membranous flap and the angled seeds (Manning & Goldblatt, 2018). However, *Litanthus* in the sense of Harvey (1844), Manning et al. (2013), and Martínez-Azorín et al. (2015b) is easily characterized by 1(2)-flowered inflorescence; two subopposite spurred bracts; nodding, tubular flowers with tepals connate into a long tube (Fig. 1.11); stamens with adnate very short filaments; trigonous, minute seeds; and most notably, stigma with six tiny, erect teeth (a unique character in Urgineoideae). *Schizobasis* is also highly distinctive on account of its slender, wiry, flexuose, branched inflorescences (Baker, 1873; Manning et al., 2014); it shares the latter character with *Bowiea*, although clearly differing in both sexual and vegetative morphology as noted above.

Another clade with full support, although with weakly supported relationships, includes the species of *Drimia* s.str. that constitute a morphologically compact group. The inclusion of numerous taxa in it after its original description by Willdenow (1799) blurred the morphological characterization of the genus and created considerable instability in generic circumscriptions in the Urgineoideae. This primarily stems from differing perceptions of the significance to be accorded to the extent of tepal connation, from nearly free to connate in a distinct tube (Huber, 1969; Jessop, 1977; Stedje, 1987, 2001a, 2001b; Deb & Dasgupta, 1982; Manning et al., 2004). However, when recovering its original sense, *Drimia* is easily recognized by the tepals connate in a cylindrical tube with linear, elongate, narrowly subspathulate, strongly reflexed lobes; adnate filaments that arise at the mouth of the tube; and stamens commonly curved and closely appressed to the style (Fig. 1.5), among other characters.

The originally monotypic *Urgineopsis* accommodated *Urgineopsis salteri* R.H. Compton (Compton, 1930), and although Speta (1980) intended to effect later the combination *Urgineopsis modesta* (Baker) Speta, our analyses place the latter species in *Boosia*. Our phylogenetic trees recover some species of *Urgineopsis* in the sense of Martínez-Azorín et al. (2019a) as monophyletic and well supported, based on their connate tepals forming a campanulate and usually widely open tube, and the spreading and slightly incurved filaments that arise at the apex of the tepal tube (Fig. 1.27). This genus is related to *Tenicroa* in some of our analyses (Fig. S1), with which it shares a general distribution. *Urgineopsis* was reduced to synonymy in *Drimia* by Jessop (1977), who argued that the degree of fusion of tepals is not a consistent character useful in defining genera in the Urgineoideae, as a continuum of connation degrees is observable. As noted above, we concur that this character alone should not be used for generic circumscription in the Urgineoideae due to a certain degree of homoplasy, but the correct combination of morphological characters and phylogenetic evidence supports the acceptance of several genera at that rank, including *Urgineopsis*.

Another clade with strong support includes two sister and fully supported genera, *Austronea sensu* Martínez-Azorín et al. (2018a, 2019c) and *Fusifilum sensu* Müller-Doblies et al. (2001), although with *Fusifilum magicum* being related to *Urginea revoluta* in our trees (Fig. 2). Both *Austronea* and *Fusifilum* share some general morphological characters, although their flower and inflorescence morphologies allow them to be readily distinguished. *Austronea* is characterized by its capitate to subcorymbose inflorescences that commonly nod at early development stages (one of the best diagnostic characters of the genus), the green to yellow-orange ovary (Fig. 1.2), and seeds trigonous in outline and tetrahedrally folded. On the other hand, *Fusifilum* differs in the white, fusiform filaments that are distinctly papillate basally; white flowers; white ovary, sometimes tinged with purple (Fig. 1.6) (one of the best diagnostic characters of the group); and ellipsoid flattened seeds.

Finally, the remaining samples constitute a fully supported clade where samples of *Geschollia* in the sense of Martínez-Azorín et al. (2019d) form a fully supported clade and share the main diagnostic characters of the genus, such as the single terete leaf (rarely 2) and comparatively small capsules with small polygonal or irregularly compressed, angled seeds, among other characters. The other samples are grouped in a clade with strong support with two fully supported subclades. One subclade includes *Urginea macrocentra* Baker (Fig. 1.3), corresponding to the monotypic *Boosia sensu* Speta (2001), plus other species distributed along southeastern South Africa and Lesotho, such as *Drimia flagellaris* T.J. Edwards et al., *Urginea modesta* Baker, *U.*

rubella Baker, *U. saniensis* Hilliard & B.L. Burtt, and *U. tenella* Baker. Despite *Boosia* being described originally as monotypic to accommodate a peculiar species with very long and colored bract spurs, and a single, terete, corky leaf, consideration of the morphological characters of these subclades reveals that they differ from the related *Geschollia* by a syndrome of morphological characters: multiple leaves per bulb (rarely one); often very long spurs on the basal bracts; pedicels that remain photosynthetic when capsules are completely ripe; and elongated, flattened seeds. We accordingly propose expanding *Boosia* to include several related species, the new combinations for which will be effected in a forthcoming monograph. Finally, the other subclade includes samples from western South Africa and comprises two samples of *F. magicum* (the only species of the genus *sensu* Müller-Doblies et al. (2001) that dissolves its monophyly), the sample "H847 *Boosia* sp." presented by Pfosser and Speta (2001, 2004) from Swellendam (which we were unable to study morphologically), and a sample of *Urginea revoluta*. The latter species is not a member of *Urginea* in the sense of the current work based on morphology, phylogenetic evidence, and distribution ranges and shows morphological affinities to *Triandra*. Further studies are needed to provide more insight into the relationships and statuses of taxa from western South Africa that resolve in the latter subclade.

4.3 Distribution patterns

Subfamily Urgineoideae is mostly restricted to Africa, Madagascar, the Mediterranean, and southwestern Asia, with two main centers of diversity—one in southern Africa, where Urgineoideae originated ca. 48 Ma ago, and the other in the Mediterranean Basin, representing a secondary center of diversity that was formed ca. 17–20 Mya by colonization from Africa (Buerki et al., 2012; Ali et al., 2013). This dispersal was facilitated by both low-elevation arid and high-elevation montane corridors linking the ancestral region of southern Africa and the Mediterranean, via East Africa (Martínez-Azorín et al., 2010; Buerki et al., 2012; Ali et al., 2013). The Ex-Africa scenario represented by *Indurgia* is indicative of the emergence of yet another secondary center of diversity in India and SE Asia.

Among the 31 clades or lineages accepted as genera in the present study, of which some are newly circumscribed here, several are restricted to the southern regions of Africa, thus reflecting their taxonomic independence (*Austronea*, *Aulostemon*, *Fusifilum*, *Geschollia*, *Iosanthus*, *Litanthus*, *Mucinaea*, *Rhadamanthopsis*, *Rhadamanthus*, *Sagittanthera*, *Sekanama*, *Striatula*, *Tenicroa*, *Thuranthos*, *Triandra*, and *Urgineopsis*) (regions 1, 2, 3, and 5a in Fig. 3). Among them, some are endemic to certain regions, such as *Iosanthus*, *Mucinaea*, and *Triandra* to the Karoo-Namib Region (region 2 in Fig. 3); *Aulostemon*, *Sagittanthera*, and *Zulusia* to the Uzambara-Zululand Region (region 3 in Fig. 3); *Rhodocodon* to the Madagascan Region (region 4 in Fig. 3); and *Sekanama* to the southern section of the Zambezian Subregion (region 5a in Fig. 3). *Tenicroa* and *Urgineopsis* are restricted to the Cape plus Karoo-Namib Regions (regions 1 and 2 in Fig. 3); *Austronea*, *Geschollia*, and *Rhadamanthopsis* share distribution with *Tenicroa* and *Urgineopsis* but also extend to the Uzambara-Zululand Region (region 3 in Fig. 3); and *Fusifilum*, *Litanthus*, *Rhadamanthus*, and *Thuranthos* also share the distribution of *Austronea*, *Geschollia*, and *Rhadamanthopsis* but spread further to the southern section of the Zambezian Subregion (region 5a in Fig. 3). *Striatula* grows in the Cape and Karoo-Namib Regions and the southern section of the Zambezian Subregion (regions 1, 2, and 5a in Fig. 3). *Zingela* is restricted to the Uzambara-Zululand Region and the southern section of the Zambezian Subregion (regions 3 and 5a in Fig. 3), and *Boosia* shares distribution with *Zingela* but also extends to the eastern section of the Zambezian Subregion (region 5c in Fig. 3). *Drimia*, *Bowiea*, and *Schizobasis* are also present in the southern regions of Africa but extend northwards to the Zambezian Subregion (regions 5a, 5b, and 5c in Fig. 3), although *Bowiea* is not present in the Cape Region. *Urginavia* widely occurs in the southern regions of Africa and extends to northern and eastern sections of the Zambezian Subregion, the Erithraeo-Arabian Subregion, the Guineo-Congolian Region, and the Sahelo-Sudanian Subregion (regions 5b, 5c, 6a, 7, and 8 in Fig. 3). *Vera-duthiea* is distributed along the Uzambara-Zululand Region, the southern and eastern sections of the Zambezian Subregion, the Guineo-Congolian Region, and the Sahelo-Sudanian Subregion, extending beyond Africa to the Erithraeo-Arabian and Omano-Sindian Subregions in southern Yemen and the Dhofar mountains in Oman (regions 3, 5a, 5c, 6a, 6b, 7, and 8 in Fig. 3), to share the latter Subregion with *Indurgia*.

Ledurgia is endemic to the Guineo-Congolian Region (region 7 in Fig. 3) and *Ebertia* occurs along the eastern section of the Zambezian Subregion, and the Guineo-Congolian and Sahelo-Sudanian Regions (regions 5c, 7, and 8 in Fig. 3) (Oyewole, 1989; Friis & Vollesen, 1999; Speta, 2001). *Urginea* is mostly restricted to the Mediterranean Region (region 10 in Fig. 3) and *Squilla* is widely distributed along the Mediterranean, extending to the Macaronesian Region (regions 10 and 11 in Fig. 3) (Pfosser & Speta, 2004; Martínez-Azorín et al., 2022). *Spirophyllos* is endemic to a narrow strip in desert habitats in northern Morocco and Algeria, south of the Atlas mountain range, included in the Saharo-Arabian Region (region 9 in Fig. 3). Finally, the only genus occurring in Asia is *Indurgia*, being mostly restricted to India and Thailand in the Indian and Indo-Chinese Regions and just entering the eastern part of the Omano-Sindian Subregion (regions 6b, 12, and 13 in Fig. 3).

Based on our phylogenetic findings, the genera *Ebertia*, *Indurgia*, *Iosanthus*, *Vera-duthiea*, *Spirophyllos*, and *Urginea* consistently place in a strongly supported clade, with the southern African lineages of *Vera-duthiea* and *Iosanthus* postulated to have given rise to the remaining northern hemisphere representatives of both the western Mediterranean and the southwestern Asian lineages. Our studies consistently place the Madagascan *Rhodocodon* as related to the northwestern South African *Triandra*. *Urginavia* and *Ledurgia*, both present in central Africa, are related to the southern African *Thuranthos* and *Zingela*.

4.4 Final general comments

Generic circumscription appears to be especially controversial in the Hyacinthaceae (Speta, 1998a, 1998b, 2001; Pfosser & Speta, 1999, 2001, 2004; Manning et al., 2004, 2009; Martínez-Azorín et al., 2011, 2013b, 2017, 2018a, 2019a, 2019b, 2019d). Bulbous plants are peculiarly problematic to research as they

are usually in flower for only a short period; leaves, flowers, and fruits and ripe seeds usually do not co-occur (especially in Urgineoideae); and several floral traits are not retained in herbarium vouchers. Numerous taxa have been described in the family, of which many were treated as synonyms in recent revisions based almost exclusively on the study of herbarium vouchers. As evidenced by some of our earlier studies (e.g., Martínez-Azorín et al., 2018a, 2019d), generic circumscriptions are crucially informed by the whole spectrum of qualitative characters in reproductive and vegetative organs. Special attention must be paid to flower morphology and characters such as the shape and disposition of filaments, color and shape of the ovary, and style morphology and disposition. Capsule and seed morphology assessments also contribute substantial evidence that informs the delimitation of certain genera.

Most of the petaloid monocot families show a basic trimerous flower pattern, as in the Hyacinthaceae. The major sources of variation are found in the degree of connation of tepals, adnation and/or connation of stamens, and morphology of the gynoecium and seeds, these being the primary historical basis for generic circumscriptions. Therefore, merging, for instance, *Litanthus*, *Rhadamanthus*, *Rhodocodon*, and *Thuranthos* (see flower morphology variation in Fig. 1), into *Drimia* or *Urginea* s.str. would be equivalent to merging *Muscari* Mill., *Eucomis* L′Hér., and *Hyacinthus* L., and ca. 30 other currently accepted Hyacinthoideae genera, into *Scilla*—a radical solution that has so far found no advocates. The same holds for lumping *Cathissa* Salisb., *Galtonia* Decne., *Neopatersonia* Schönland, and *Avonsera* Speta, among others, into *Ornithogalum* L. in the sister Ornithogaloideae (as proposed by Manning et al., 2009), to produce genera characterized by extreme variation in flower, fruit, and seed morphology. This is exemplified by the synonymizing of several other genera in *Albuca* L. (as proposed by Manning et al., 2009) despite their flowers strongly differing from the highly specialized flower morphology of *Albuca* s.str. (Johnson et al., 2012). A general application of very broad generic concepts would compromise recognition of most of the genera of flowering plants, and would effectively obscure the utility of taxonomy and systematics not only for taxonomists but also for general users (including horticulturists and conservationists).

The generic analytic treatment in Ornithogaloideae *sensu* Martínez-Azorín et al. (2011) has been broadly subscribed to (Garbari et al., 2003, 2007; Johnson et al., 2012; Martínez-Azorín & Crespo, 2012; Peruzzi et al., 2012; Pfosser et al., 2012; Ali et al., 2013; Martínez-Azorín et al., 2013a, 2013b, 2014, 2015a, 2015c; Mulholland et al., 2013; Brudermann et al., 2019; Riahi Rad et al., 2019; Heidarian et al., 2020; Bogdanovic et al., 2021). Nonetheless, the alternative system for a broad *Ornithogalum* and *Albuca* (as proposed by Manning et al., 2009) has to date been adopted by the influential "The Plant List" or "World Checklist of Selected Plant Families" (WCSP, 2022). The tendency of taxonomic lumping is motivated by an interest in reducing the number of families and genera (see, for instance, APG 2009, 2016). Proponents who have reflected on "too many of such taxa" have articulated that broader-conceived (lumped) taxa "would be more practicable for teaching purposes" (Chase et al., 2009), or that "a lower number makes the treatments more stable" (Manning et al., 2004, 2009). In our view, such arguments are unreasonably speculative and lack scientific substance.

In considering the consistency of subfamily treatments in Hyacinthaceae, we note that the number of genera accepted in our analytic treatment in Urgineoideae is similar to those widely accepted in the subfamily Hyacinthoideae. Manning et al. (2004), for example, accepted 11 genera of Hyacinthoideae for southern Africa, with ca. 20 more occurring in the Northern Hemisphere (Speta, 1998a, 1998b). Similarly, the treatment of Ornithogaloideae by Martínez-Azorín et al. (2011) accepts 20 genera (including *Igidia*).

Our resultant classification proposal upholds the primary principle of monophyly, and embodies the secondary principles of (1) providing stability, (2) conveying phylogenetic information, (3) integrating morphological and distributional traits, and (4) supporting identification. In this latter respect, we reveal (sometimes novel) qualitative characters that diagnostically define multiple stable genera that can be clearly communicated. A new taxonomic proposal for Urgineoideae at the genus and species level, as outlined here, will be published elsewhere, when an identification key and detailed descriptions of genera will be provided (Martínez-Azorín et al., in prep.).

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Conflict of Interest

The authors declare that they have no competing interests.

Author Contributions

MMA, MBC, and WW designed the study. MMA collected samples, performed most of the experiments, analyzed the data, and wrote the text. MBC, MAA, MPi, MPf, NC, APD, and LM assisted in collecting and processing samples. All authors discussed the results and contributed to the final version of the manuscript. MMA, https://orcid.org/0000-0002-2605-9575; MBC, https://orcid.org/0000-0002-3294-5637; MAA, https://orcid.org/0000-0003-3768-9203; MPi, https://orcid.org/0000-0002-6055-6989; NC, https://orcid.org/0000-0002-4938-5840; APD, https://orcid.org/0000-0002-9497-7503; LM, https://orcid.org/0000-0003-0317-8886; MPf, https://orcid.org/0000-0003-2050-4997; WW, https://orcid.org/0000-0002-9245-029X.

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Supplementary Material

The following supplementary material is available online for this article at http://onlinelibrary.wiley.com/doi/10.1111/jse.12905/suppinfo:

Fig. S1. Phylogram of the Bayesian majority-rule consensus tree of the concatenated plastid regions (*trnL* intron, *trnL-F* spacer, *matK*, *trnCGCA-ycf6*) data set for Urgineoideae displaying branch lengths; posterior probabilities (PP) are shown at the nodes; clade labels follow Fig. 2.

Fig. S2. Phylogram of the Bayesian majority-rule consensus tree of the plastid *trnCGCA-ycf6* region for Urgineoideae displaying branch lengths; posterior probabilities (PP) are shown at the nodes; clade labels follow Fig. 2.

Fig. S3. Phylogram of the Bayesian majority-rule consensus tree of the plastid *matK* region for Urgineoideae displaying branch lengths; posterior probabilities (PP) are shown at the nodes; clade labels follow Fig. 2.

Fig. S4. Phylogram of the Bayesian majority-rule consensus tree of the plastid *trnL* intron, *trnL-F* spacer region for

Urgineoideae displaying branch lengths; posterior probabilities (PP) are shown at the nodes; clade labels follow Fig. 2.

Fig. S5. Maximum Parsimony majority-rule consensus tree of the concatenated plastid regions (*trnL* intron, *trnL-F* spacer, *matK* and *trnCGCA-ycf6*) data set for Urgineoideae; bootstrap support (BS) values are shown at the nodes; clade labels follow Fig. 2.

Fig. S6. Phylogram of the Bayesian majority-rule consensus tree of the nuclear *Agt1* region for Urgineoideae displaying branch lengths; posterior probabilities (PP) are shown at the nodes; clade labels follow Fig. 2.

Fig. S7. Maximum Parsimony majority-rule consensus tree of the concatenated plastid (*trnL* intron, *trnL-F* spacer, *matK* and *trnCGCA-ycf6*) and nuclear (*Agt1*) data set for Urgineoideae; bootstrap support (BS) values are shown at the nodes; clade labels follow Fig. 2.

Fig. S8. Phylogram of the Bayesian majority-rule consensus tree of the concatenated plastid (*trnL* intron, *trnL-F* spacer, *matK*, and *trnCGCA-ycf6*) plus morpho (40 coded characters indicated in Table S2) data set for Urgineoideae displaying branch lengths; posterior probabilities (PP) are shown at the nodes; clade labels follow Fig. 2.

Fig. S9. Phylogram of the Bayesian majority-rule consensus tree of the concatenated plastid (*trnL* intron, *trnL-F* spacer, *matK*, and *trnCGCA-ycf6*), nuclear (*Agt1*) and morpho (40 coded characters indicated in Table S2) data set for Urgineoideae displaying branch lengths; posterior probabilities (PP) are shown at the nodes; clade labels follow Fig. 2.

Supplementary materials S10. Nexus file of the Bayesian analyses for the complete molecular data set for Urgineoideae.

Supplementary materials S11. Nexus file of the Bayesian analyses for the complete molecular and morphological data set for Urgineoideae.

Supplementary materials S12. Mesquite file where the studied 40 morphological characters are plotted onto the phylogenetic tree as in Figure 2.

Supplementary materials S13. File including the 40 plotted phylogenetic trees with the studied morphological characters using Mesquite.

Table S1. Data on the studied samples of Urgineoideae, including sample number, taxonomy, locality details, voucher codes, and Genbank numbers for each DNA sequence.

Table S2. Morphological matrix for the studied samples in Urgineoideae with 40 coded morphological characters, as follows: 1. Bulb scales (0. Compact; 1. Loose); 2. Cataphylls (0. Leaves lacking sheathing cataphylls with transversal dark or prominent ribs; 1. Leaves surrounded at base by sheathing cataphylls with transversal dark or prominent ribs); 3. Leaf number (0. More than one per bulb; 1. One per bulb; 2. Absent in old plants); 4. Leaf curving (0. Straight or slightly curved; 1. Distinctly coiled distally); 5. Leaf section morphology around the middle portion (0. Flattened or canaliculate; 1. Round to hemicircular); 6. Leaf proportions (0. Clearly elongated, from 3 to many times longer than wide; 1. Suborbicular to ovate, up to 2 times longer than wide); 7. Leaf keel presence (0. Lacking a distinct broad keel abaxially; 1. With a distinct broad keel abaxially); 8. Leaf adaxial furrows (0. Lacking longitudinal furrows; 1. With longitudinal furrows); 9. Leaf maculation (0. Immaculate; 1. With distinct maculae at base); 10. Co-occurrence of leaves and flowers (0. Hysteranthous or proteranthous leaves; 1. Synanthous or evergreen leaves); 11. Inflorescence type (0. Simple raceme; 1. Branched raceme or panicle); 12. Inflorescence consistency (0. Not succulent; 1. Succulent); 13. Inflorescence disposition (0. Not twining; 1. Twining); 14. Early developed inflorescence disposition (0. Erect; 1. Recurved and nodding); 15. Bract spur (0. Not spurred; 1. Spurred); 16. Bract persistence (0. Present in flower; 1. Caducous and absent in full flower); 17. Bracteoles (0. Absent; 1. Present); 18. Pedicel aging (0. Browning simultaneously with developing capsule, pedicel brown at dehiscence; 1. Remaining green as developing capsule browns, pedicel green at dehiscence); 19. Flower disposition (0. Patent to suberect; 1. Nodding); 20. Flowering time (0. Diurnal; 1. Nocturnal); 21. Connation of tepals (0. Free or nearly free (connate for less than 1 mm from base); 1. Connate from 1 mm to 2/5 of their length; 2. Connate from mid-length to most of their length); 22. Disposition of the free portion of tepals (0. Patently-spreading to strongly reflexed; 1. Suberect); 23. Tepal basal marking (0. Lacking green basal markings adaxially; 1. With green basal markings adaxially); 24. Stamen number (0. Six; 1. Three); 25. Stamen disposition (0. Spreading and not approaching the style; 1. Connivent to the style, either anthers or filaments); 26. Filament orientation (0. Straight or somewhat arcuate but never sigmoid or connivent to the style along the middle and spreading above; 1. Sigmoid and connivent to the style along the middle portion and spreading above); 27. Connation of filaments (0. Free above the perigone; 1. Distinctly connate above the perigone for most of their length to form a tube); 28. Filament indumentum (0. Smooth; 1. Papillate at base); 29. Dehisced anther morphology (0. Non-circinate; 1. Circinate); 30. Anther dehiscence (0. Dehiscing longitudinally along entire length; 1. Dehiscing by apical pores or slits extending up to the middle); 31. Connation of anthers (0. Free; 1. Connate); 32. Indehisced anther connective morphology (0. Not apically extended or overtopping anthers; 1. Extended apically into a membranous flap overtopping anthers); 33. Ovary color (0. Green, yellow, or orange, rarely combined with white portions; 1. Completely white, sometimes with purple tinge); 34. Style disposition (0. Erect; 1. Declinate); 35. Stigma morphology (0. Indistinct to trigonus or capitate, but never six-toothed; 1. Extended into six, erect, minute teeth); 36. Withered tepal disposition when capsules unripe (1. Tepals cohering above to form a cap atop unripe capsule; 0. Tepals remain at the base of the unripe capsule); 37. Mature capsule disposition (0. Suberect to erect; 1. Patent to reflexed); 38. Capsule valve disposition (0. Suberect to somewhat spreading; 1. Reflexed from the base to expose seeds completely); 39. Seed size (0. Large (2.5–12 mm long); 1. Small (0.5–2.4 mm long)); 40. Seed morphology (0. Flattened and winged, mostly adapted to wind dispersal; 1. Polygonal or irregularly compressed; 2. Subellipsoid, usually heavier than the other types).