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Molecular phylogenetics of subfamily Ornithogaloideae (Hyacinthaceae) based on nuclear and plastid DNA regions, including a new taxonomic arrangement

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• *Background and Aims* The taxonomic arrangement within subfamily Ornithogaloideae (Hyacinthaceae) has been a matter of controversy in recent decades: several new taxonomic treatments have been proposed, based exclusively on plastid DNA sequences, and these have resulted in classifications which are to a great extent contradictory. Some authors have recognized only a single genus *Ornithogalum* for the whole subfamily, including 250–300 species of variable morphology, whereas others have recognized many genera. In the latter case, the genera are inevitably much smaller and they are better defined morphologically. However, some are not monophyletic as circumscribed.
• *Methods* Phylogenetic analyses of Ornithogaloideae were based on nucleotide sequences of four plastid regions (*trnL* intron, *trnL-F* spacer, *rbcL* and *matK*) and a nuclear region (ITS). Eighty species covering all relevant taxonomic groups previously recognized in the subfamily were sampled. Parsimony and Bayesian analyses were performed. The molecular data were compared with a matrix of 34 morphological characters.
• *Key Results* Combinations of plastid and nuclear data yielded phylogenetic trees which are better resolved than those obtained with any plastid region alone or plastid regions in combination. Three main clades are found, corresponding to the previously recognized tribes *Albuceae*, *Dipcadieae* and *Ornithogaleae*. In these, up to 19 clades are described which are definable by morphology and biogeography. These mostly correspond to previously described taxa, though some need recircumscription. Morphological characters are assessed for their diagnostic value for taxonomy in the subfamily.
• *Conclusions* On the basis of the phylogenetic analyses, 19 monophyletic genera are accepted within Ornithogaloideae: *Albuca*, *Avonsera*, *Battandiera*, *Cathissa*, *Coilonox*, *Dipcadi*, *Eliokarmos*, *Elsiea*, *Ethesia*, *Galtonia*, *Honorius*, *Loncomelos*, *Melomphis*, *Neopatersonia*, *Nicipe*, *Ornithogalum*, *Pseudogaltonia*, *Stellarioides* and *Trimelopter*. Each of these has a particular syndrome of morphological characters. As a result, 105 new combinations are made and two new names are proposed to accommodate the taxa studied in the new arrangement. A short morphological diagnosis, synonymy, details of distribution and an identification key are presented.

Key words: Ornithogaloideae, Hyacinthaceae, Asparagaceae, Scilloideae, molecular systematics, taxonomy.

INTRODUCTION

Hyacinthaceae include about 700–900 species of bulbous plants which are mainly distributed through Europe, Africa and south-west Asia, with a single small genus in South America (APG II, 2002). Following the molecular studies of Pfosser and Speta (1999) and Manning *et al.* (2004), four monophyletic subfamilies can be clearly recognized within Hyacinthaceae: Hyacinthoideae, Ornithogaloideae, Urgineoideae and Oziroëoideae. Alternatively, Hyacinthaceae can be treated as subfamily Scilloideae of Asparagaceae, and the subfamilies above are then treated as tribes Hyacintheae, Ornithogaleae, Oziroëeae and Urgineeae (e.g. APG III, 2009; Chase *et al.*, 2009). Hyacinthaceae are monophyletic within Asparagaceae (*sensu lato*), and here the former system is followed (although M.F.F. prefers the latter).

Ornithogaloideae are distributed through Europe, south-west Asia and Africa and include about 280 species (Speta, 1998*a*). The definition of genera and the assignment of species to

genera within this subfamily have troubled taxonomists since Linnaeus (Stedje, 2001*a*, *b*), and there has been a great controversy concerning generic treatments. At least three taxonomic arrangements at generic level have been proposed within Ornithogaloideae in recent times (Speta, 1998*a*; Manning *et al.*, 2004, 2009*a*), all based exclusively on plastid DNA regions. Furthermore, those proposals are to a great extent contradictory.

Speta (1998*a*) in a study of Ornithogaloideae recognized 13 genera: *Stellarioides* Medik., *Coilonox* Raf., *Albuca* L., *Pseudogaltonia* Kuntze, *Dipcadi* Medik., *Galtonia* Decne., *Zahariadia* Speta, *Melomphis* Raf., *Cathissa* Salisb., *Eliokarmos* Raf., *Loncomelos* Raf., *Honorius* Gray and *Ornithogalum* L. He also considered *Neopatersonia* Schönland as a possible member of the subfamily. However, Pfosser and Speta (1999) in a phylogenetic analysis based on 30 species and one plastid DNA region (*trnL-F*) showed that some of the genera recognized by Speta (1998*a*) were polyphyletic.

Manning *et al.* (2004) extended the phylogenetic study to 40 taxa within Ornithogaloideae and a second plastid DNA region (*rbcL*) was added. These authors opted for accepting just a single genus, *Ornithogalum*, in Ornithogaloideae, thus expanding *Ornithogalum* to include *Albuca*, *Dipcadi*, *Galtonia*, *Neopatersonia* and *Pseudogaltonia*, together with the other genera accepted by Speta (1998a). This treatment was justified by the complete collapse at the base of the phylogenetic tree, and the apparent lack of monophyly of these genera as previously circumscribed.

This recognition of *Ornithogalum* (*sensu lato*) proved to be somewhat unpopular (e.g. Van Jaarsveld *et al.*, 2007; Manning *et al.*, 2009a), and recently Manning *et al.* (2009a) continued the study of the generic circumscription in Ornithogaloideae. They added a third plastid region (*matK*) and extended their previous study to 70 species (Manning *et al.*, 2009a), obtaining higher resolution by combining sequences from the different plastid regions, as previously suggested for other groups by for instance Barfuss *et al.* (2005). Manning *et al.* (2009a) obtained a combined tree with four strongly supported main clades. They discussed extensively three possible taxonomic arrangements in Ornithogaloideae on the basis of their plastid molecular data, and finally favoured three tribes (Albuceae, Dipcadieae and Ornithogaleae), with only four genera (*Dipcadi*, *Pseudogaltonia*, *Ornithogalum* and *Albuca*). Among these, *Ornithogalum* and *Albuca* were still defined in a broad sense and, as a result, are highly heterogeneous in morphology. Both genera were, however, divided into many subgenera, sections and series, some of which were monophyletic and well characterized from a morphological point of view.

Plastid sequences have constituted an important source of characters for the phylogenetic reconstruction in plant groups (Palmer *et al.*, 1988; Clegg and Zurawski, 1992; Cameron, 2004). However, due to the cytoplasmic inheritance of that DNA, it can have a tendency to show significant errors due to hybridization, introgression or irregular distribution of lineages (Rieseberg and Soltis, 1991; Doyle, 1992). Fortunately, these problems may to some degree be identified by comparing phylogenetic trees from plastid and nuclear DNA sequences (Smith and Sytsma, 1990; Rieseberg, 1991; Wendel *et al.*, 1991; Peterson *et al.*, 2004, 2009; Alzate *et al.*, 2009; Zarrei *et al.*, 2009), and by checking the relationships among the species (Sytsma and Schaal, 1985; Rieseberg *et al.*, 1988; Wallace and Jansen, 1990). As the combination of *trnL-F*, *rbcL* and *atpB* plastid sequences has been relatively unfruitful in resolving taxonomic questions in Hyacinthaceae (Lebatha *et al.*, 2006), the nuclear ribosomal ITS region appears to be a good candidate, though few data have been generated for this family to date (cf. Pires and Sytsma, 2002). The presence of multiple alleles has been detected (Pfosser in Lebatha *et al.*, 2006), making sequencing difficult. Moreover, Herrmann (2002) pointed out that the ITS region is not a useful molecular marker with which to study the phylogenetics of *Ornithogalum*, due to difficulties in amplification.

The aims of the present contribution are: (*a*) to explore phylogenetic relationships in Ornithogaloideae by combining plastid (*rbcL*, *trnL-F* and *matK*) and nuclear (ITS) DNA sequences; (*b*) to evaluate generic limits and circumscriptions after consideration of molecular data, morphological traits and/or biogeographical distribution of each group obtained; and (*c*) to generate and justify a new taxonomic arrangement with regard to other options discussed by previous authors.

MATERIALS AND METHODS

Taxon sampling

Eighty ingroup taxa were selected, including representatives from all previously recognized taxonomic groups in Ornithogaloideae [Table 1; acronyms of herbaria follow Thiers (2009), whereas plant names and authorities follow IPNI (2010)], which cover the full range of morphological and taxonomic variation. With regard to previous studies (Manning *et al.*, 2009a), sampling has been extended by nine taxa, mostly corresponding to Eurasian and north African representatives of *Ornithogalum sensu stricto*. Nearly 25 % of the total accepted species for the subfamily are included in the present study. Five taxa from other subfamilies of Hyacinthaceae were chosen as outgroups: *Bowiea volubilis* Harv. ex Hook.f. and *Rhadamanthus convallarioides* Salisb. (both Urgineoideae), *Massonia echinata* L.f. and *Muscari neglectum* Guss. ex Ten. (both Hyacinthoideae) and *Oziroë biflora* (Ruiz & Pav.) Speta (Oziroëoideae) (Table 1).

Laboratory procedures

Total genomic DNA was extracted from fresh or silica-gel dried material using the $2\times$ CTAB method of Doyle and Doyle (1987) with minor modifications. Total DNA was purified by MOBIO minicolums and mostly kept in $0.1\times$ TE buffer (10 mM Tris–HCl, 1 mM EDTA, pH 8.0). Some samples were purified on $CsCl_2$/ethidium bromide (1.55 g mL^{-1}) density gradients (Creeth and Denborough, 1970).

Some samples, especially those from southern Africa, were obtained from the DNA banks of the Royal Botanic Gardens, Kew (www.rbgkew.org.uk/data/dnaBank/homepage.html) and National Botanic Gardens, Kirstenbosch (NBG) (www.nbi.ac.za/frames/researchfram.htm) (Table 1). The DNA for the remainder of samples was isolated and deposited at the DNA banks of Alicante University and the Royal Botanic Gardens, Kew (Table 1).

The *trnL* intron and *trnL-F* spacer (the *trnL-F* region; hereafter *trnL-F*) were amplified, mostly in one piece, using primers c and f (Taberlet *et al.*, 1991), though some taxa required the use of the internal primers d and e (Taberlet *et al.*, 1991). Amplification of the *rbcL* gene was performed using the primers 1F and 1360R, though some taxa required the use of internal primers, 427F and 724R (Lledó *et al.*, 1998). ITS was amplified using the 18Z and AB102 primers (Douzery *et al.*, 1999; Pires, 2000). When the sequences were not obtained in one reaction, the internal primers ITS2 and ITS3 (White *et al.*, 1990) were also used.

A total volume of 25 μL was used in the PCR amplification process as follows: 21 μL of Abgene PCR mastermix (1.25 U Thermoprime Plus DNA polymerase, 75 mM Tris–HCl, 20 mM $(NH_4)_2SO_4$, 2.5 mM $MgCl_2$, 0.01 % Tween® 20, 0.2 mM each dNTP); 0.5 μL of bovine serum albumin (BSA; 0.4 %); 10 mM of each primer; 0.5 μL of water; and approx. 40 ng of DNA template. The ITS amplifications were done using

TABLE 1. *Samples included in the phylogenetic analyses of the Hyacinthaceae, mainly the subfamily Ornithogaloideae*

DNA bank code	Species	Locality	Voucher
K 1784	*Albuca abyssinica* Jacq.	South Africa, 20 km E of Nelspruit	Manning 2687 (NBG), Chase 1784 (K)
LH 504	*Albuca amboensis* (Schinz) Oberm.	Botswana	Beaumont 568 (NBG)
K 1845	*Albuca aff. chaetopoda* Chiov.	ex hort, Kew 1981–1086	Chase 1845 (K)
K 24814	*Albuca cooperi* Baker	South Africa, Namaqualand, Knersvlakte, Douse-the-Glim	Chase 24814 (K)
K 8252	*Albuca fragrans* Jacq.	South Africa, Darling	Manning 2184 (NBG)
K 12563	*Albuca glandulosa* Baker	Without locality	Goldblatt & Manning 11528 (NBG)
K 1776	*Albuca pendula* B.Mathew	ex hort., Kew 1991–846	Chase 1776 (K)
K 8253	*Albuca rupestris* Hilliard & B.L.Burtt	South Africa, KwaZulu-Natal, near Bulmer	Not found (K)
K 12514	*Albuca setosa* Jacq.	South Africa, Kaapmuiden	Manning 2689 (NBG)
K 1012	*Albuca shawii* Baker	ex hort., Kew 1983–8300	Chase 1012 (K)
K 1736	*Albuca tortuosa* Baker	ex hort., Kew 1993–1849	Chase 1736 (K)
K 1843	*Albuca wakefieldii* Baker	ex hort., Kew 1977–5233	Chase 1843 (K)
LH s.n.	*Avonsera convallarioides* (H.Perrier) Speta	Madagascar, Ankarafantsika Plateau	Lavranos s.n. (NBG)
ABH 416	*Battandiera amoena* (Batt.) Maire	Morocco, Erfoud, antes del puesto de fósiles	SALA 135875
LH 1493 K 26930	*Battandiera pulchra* (Schinz) Mart.-Azorín, M.B.Crespo & Juan	Namibia, Windhoek	Mannheimer CM2506 (NBG, WIND)
LH 819	*Battandiera seineri* (Engl. & Krause) Mart.-Azorín, M.B.Crespo & Juan	South Africa, Kgalaghadi Transfrontier Park	Snijman s.n. (no voucher)
LH 138 K 28300	*Battandiera stapffii* (Schinz) Mart.-Azorín, M.B.Crespo & Juan	Namibia, Farm Keitzaub	Mannheimer 1747 (WIND)
K 176	*Bowiea volubilis* Harv. ex Hook.f.	Without locality	Chase 176 (NCU, K)
ABH 233	*Cathissa cocinna* (Salisb.) Speta	Spain, Zamora, Torregamones	ABH 47140
ABH 206 K 20985	*Cathissa reverchonii* (Lange ex Willk.) Speta	Spain, Cádiz, Grazalema, Tajo de los Pajaritos	ABH 47138
ABH 208 K 20987	*Cathissa unifolia* (L.) Mart.-Azorín, M.B.Crespo & Juan	Spain, Huelva, La Nava	ABH 50131
K 12561	*Coilonox concordianum* (Baker) Speta	South Africa, Loeriesfontein	Goldblatt, Manning & Savolainen 11527 (MO, NBG)
K 12520	*Coilonox polyphyllum* (Jacq.) Speta	South Africa, Namaqualand, Grootvlei	Goldblat, Manning & Savolainen 11510 (MO, NBG)
LH 626	*Coilonox secundum* (Jacq.) Speta	South Africa	Manning s.n. (no voucher)
K 12499	*Coilonox suaveolens* (Jacq.) Speta	South Africa, Anenous Flats	Goldblat, Manning & Savolainen 11493 (NBG)
K 1783	*Dipcadi filifolium* Baker	Yemen, North Yemen, NW side of Jebel Thallanlan, above Hadia Raymah	Chase 1783 (K)
LH 197 K 26640	*Dipcadi glaucum* (Burch. ex Kew Gawl.) Baker	South Africa, 42 km NE from Strydenburg	Manning 2237 (NBG)
LH 345 K 26740	*Dipcadi gracillimum* Baker	South Africa, 20 km N from Amsterdam	Manning 2682 (NBG)
K 16972	*Dipcadi longifolium* (Ker Gawl.) Baker	Malawi, Mulanje	Chase 16972 (K)
K 1824	*Dipcadi serotinum* (L.) Medik.	Portugal, between Ourique and Castro Verde	Chase 1824 (K)
K 8254	*Dipcadi viride* (L.) Moench	South Africa, Inchanga	Manning s.n. (no voucher)
LH 195	*Eliokarmos bicornutus* (F.M.Leight.) Mart.-Azorín, M.B.Crespo & Juan	South Africa, Ratelpoort N de Springbok	Goldblatt & Manning 11503 (NBG)
LH 3043	*Eliokarmos ceresianus* (F.M.Leight.) Mart.-Azorín, M.B.Crespo & Juan	South Africa, Ceres	ABH 49975
ABH 267	*Eliokarmos conicus* (Jacq.) Mart.-Azorín, M.B.Crespo & Juan	South Africa, Cape Peninsula, Camps Bay	Manning 2993 (NBG)
LH 375 K 26763	*Eliokarmos constrictus* (F.M.Leight.) Mart.-Azorín, M.B.Crespo & Juan	South Africa, Addo	Manning s.n. (NBG)
LH 3054	*Eliokarmos corticatus* (Mart.-Azorín) Mart.-Azorín, M.B.Crespo & Juan	South Africa, Northern Cape, Sutherland, Klein Roggeveld	ABH 51609; Martínez-Azorín & Manning 96 (K, MO, NBG)
LH 3045	*Eliokarmos dubius* (Houtt.) Mart.-Azorín, M.B.Crespo & Juan *sensu stricto*	South Africa, Hottentots Kloof	Martínez-Azorín & Manning 6 (NBG)
LH 3046	*Eliokarmos dubius* (=*Ornithogalum fimbrimarginatum* F.M.Leight.)	South Africa, Hottentots Kloof	Martínez-Azorín & Manning 8 (NBG)
K 12467	*Eliokarmos neomaculatus* Mart.-Azorín, M.B.Crespo & Juan	South Africa, Nieuwoudtville	Manning s.n. (no voucher)
LH 349 K 26743	*Eliokarmos pilosus* (Jacq.) Mart.-Azorín, M.B.Crespo & Juan	South Africa, Gordon's Bay	Manning 2696 (NBG)
LH 156 K 26605	*Eliokarmos pruinosus* (F.M.Leight.) Mart.-Azorín, M.B.Crespo & Juan	South Africa, Loeriesfontein	Goldblatt, Manning & Savolainen 11526 (NBG)
LH s.n.	*Eliokarmos rupestris* (L.f.) Mart.-Azorín, M.B.Crespo & Juan	South Africa, Langebaan	Manning s.n. (no voucher)
LH 3044	*Eliokarmos strictus* (L.Bolus) Mart.-Azorín, M.B.Crespo & Juan	South Africa, Cape, near Ceres	ABH 49977; Manning & Martínez-Azorín 3 (NBG)

TABLE 1. *Continued*

DNA bank code	Species	Locality	Voucher
LH 3042	*Eliokarmos thyrsoides* (Jacq.) Raf.	South Africa, Western Cape, Elandskloof Farm	ABH 50035; Martínez-Azorín & Manning 13 (NBG)
LH 1464 K 28846	*Elsiea corymbosa* F.M.Leight.	South Africa, Worcester, Milner Peak	Helme 2850 (NBG)
LH 1824 K 28638	*Ethesia haalenbergensis* (U.Müll.-Doblies & D.Müll.-Doblies) Mart.-Azorín, M.B.Crespo & Juan	Namibia, Klinghadtsberge	Mannheimer 2443 (WIND)
K 12466	*Ethesia xanthochlora* (Baker) Mart.-Azorín, M.B.Crespo & Juan	South Africa, foot of Anenous Pass	Goldblatt, Manning & Savolainen 11491 (NBG)
K 2024	*Galtonia candicans* (Baker) Decne.	South Africa, ex hort. Kew 1969–19589	Chase 2024 (K)
ABH 175	*Galtonia saundersiae* (Baker) Mart.-Azorín, M.B.Crespo & Juan	South Africa, in culture	ABH 50132
K 17517	*Galtonia viridiflora* Verdoorn	Lesotho, Blue Mtn. Pass	Chase 17517 (K)
ABH 381	*Honorius nutans* (L.) Gray	Comercial origin, Kew Gardens	Martínez-Azorín s.n. (no voucher)
ABH 211 K 20990	*Loncomelos narbonense* (L.) Speta	Spain, Alicante, Benissa	ABH 50146
ABH 203 K 20982	*Loncomelos pyrenaicus* (L.) L.D.Hrouda ex Holub	Spain, Huelva, Puebla de Guzmán	ABH 50135
K 9182	*Massonia echinata* L.f.	Without locality	Goldblatt & Manning 10961 (NBG)
ABH 214 K 20993	*Melomphis arabica* (L.) Raf.	Spain, Cadiz, Tarifa cementery	ABH 50134
K 3540	*Muscari neglectum* Guss. ex. Ten.	ex hort., Kew 1987–1738	Chase 3540 (K)
K 12469	*Neopatersonia namaquensis* G.J.Lewis	South Africa, 40 km S of Springbok	Goldblatt & Manning 11369 (NBG)
K 12519	*Neopatersonia rotata* (U.Müll.-Doblies & D.Müll.-Doblies) Mart.-Azorín, M.B.Crespo & Juan	South Africa, Anenous Flats	Manning 2275 (NBG)
K 5639	*Neopatersonia uitenhagensis* Schönland	South Africa, lime works near Robertson	Goldblatt & Manning 10723 (MO, NBG)
K 1863	*Nicipe gracillima* (R.E.Fr.) Mart.-Azorín, M.B.Crespo & Juan	Kenya	Chase 1863 (K)
LH 3056	*Nicipe graminifolia* (Thunb.) Mart.-Azorín, M.B.Crespo & Juan	South Africa, Western Cape, Hottentots Kloof, near Ceres	ABH 49981; Martínez-Azorín & Manning 7 (NBG)
LH 377 K 26765	*Nicipe juncifolia* (Jacq.) Mart.-Azorín, M.B.Crespo & Juan	South Africa, Grahamstown	Manning 2699 (NBG)
LH 377	*Nicipe paludosa* (Baker) Mart.-Azorín, M.B. Crespo & Juan	South Africa, Witzieshoek	Manning 3149 (NBG)
LH 3079	*Nicipe sephtonii* (Hilliard & B.L.Burtt) Mart.-Azorín, M.B.Crespo & Juan	Lesotho, 25 km from Semonkong towards Roma	Snijman 2036 (NBG)
K 1682-B	*Ornithogalum armeniacum* Baker	Turkey, SW of Turkey, Mugla, Koycegiz, Sandras Dag, road from Agla to Gokceova	Chase 1682.B (K)
ABH 184 K 20963	*Ornithogalum baeticum* Boiss.	Spain, Cádiz, Grazalema, Llanos del Republicano	ABH 47137
ABH 187 K 20966	*Ornithogalum bourgaeanum* Jord. & Fourr.	Spain, Alicante, Sª Aitana, Font del Arbre	ABH 47142
K 20637	*Ornithogalum chionophilum* Holmboe	Cyprus, Troodos Mts.	Not found (K)
ABH 387	*Ornithogalum kochii* Parl.	Slovenia, Istria, Lipica	Peruzzi s.n. (no voucher)
K 21432	*Ornithogalum lanceolatum* Labill.	Lebanon, road from Beirut to Zamble Dab	Not found (K)
ABH 228 K 31122	*Ornithogalum montanum* Ten.	Turkye, División II, Estanbul, Prince Islands	ABH 50139
ABH 383	*Ornithogalum monticolum* Jord. & Fourr.	France, Massif Central, Coiran	Peruzzi s.n. (no voucher)
K 20631	*Ornithogalum oligophyllum* E.D.Clarke	Greece, Mount Vermion, near to Naussa	Chase 28108 (K)
ABH 393	*Ornithogalum orthophyllum* Ten.	Italy, Basilicata, Baltarno	Peruzzi s.n. (no voucher)
K 20634	*Ornithogalum pedicellare* Boiss. & Kotschy	Cyprus, Area 4, Ayos Antonios, approx. 1·6 km. E of Sotira	No voucher
K 20632	*Ornithogalum refractum* Willd.	Yugoslavia, Macedonia, Mount Sinjaciko	Chase 20632 (K)
K 20636	*Ornithogalum sintenisi* Freyn	Iran, Elburz Mts. E of Gorgan 13 km S of Aliabad towards Qalieh Now	Chase 20636 (K)
K 793	*Oziroë biflora* (Ruiz & Pav.) Speta	ex hort., Kew 1977–2343	Chase 793 (K)
K 2255	*Pseudogaltonia clavata* (Mast.) Phillips	Namibia, 9 miles E of Windhoek	Codd sub Chase 2255 (K)
K 5951	*Rhadamanthus convallarioides* Salisb.	Without locality	Goldblatt 10852 A
K 1507	*Stellarioides longebracteata* (Jacq.) Speta	South Africa, ex hort, Kew, 1994–2325	Chase 1507 (K)
K 1846	*Stellarioides sordida* (Baker) Speta	ex hort Kew 1981–1010	Chase 1846 (K)
LH 344 K 26739	*Stellarioides tenuifolia* (Redoute) Speta	South Africa, Drummond	Manning 2667 (NBG)
LH 196 K 12516	*Trimelopter etesiogaripense* (U.Müll.-Doblies & D.Müll.-Doblies) Mart.-Azorín, M.B.Crespo & Juan	Namibia, Spitzkop to Rosh Pinah	Goldblatt & Manning 11352 (NBG)
LH 134	*Trimelopter unifolium* (Retz.) Mart.-Azorín, M.B.Crespo & Juan	South Africa, Pieter Meintjies Siding	Manning 2270b (NBG)

Abbreviations: ABH: University of Alicante, Spain; K: Royal Botanic Gardens, Kew, UK; MO: Missouri Botanical Garden, USA; NBG: Compton Herbarium, Kirstenbosch, South Africa; SALA: University of Salamanca, Spain; WIND: National Botanical Research Institute, Windhoek, Namibia. GenBank accession numbers are given in Supplementary Data Table S3, available online.

1·5 mM MgCl$_2$ Abgene PCR mastermix and 1 μL of dimethyl sulphoxide (DMSO). Amplifications were performed on a 9700 GeneAmp thermocycler (Applied Biosystems), with the following programme: 4 min at 94 °C, followed by 28 cycles of 94 °C for 1 min, 48 °C for 30 s for *rbcL*, or 50 °C for 1 min for *trnL-F*, 72 °C for 1 min, and a final extension 72 °C for 7 min. For ITS, a touchdown programme was used with a initial 94 °C for 5 min, following by 12 cycles of 94 °C for 30 s, 59 °C for 1 min decreasing 1 °C in each cycle plus 18 cycles at 48 °C for 1 min, 72 °C 1 min, and a final extension 72 °C for 7 min. PCR products were purified with MOBIO minicolumns following the manufacturer's protocol. Sequencing data were obtained using ABI Prism Big Dye Terminator Cycle Sequencing Kits (Applied Biosystems) and run on an ABI 3700 Genetic Analyser according to manufacturer's protocols.

All ITS sequences are original (Table 1), whereas some of those for *trnL-F* and *rbcL* (mostly from southern African taxa) and the *matK* matrix were obtained from John Manning (South African National Biodiversity Institute, Kirstenbosch) and Félix Forest (Royal Botanic Gardens, Kew). The plastid (except *matK*) sequences of the Eurasian species are all original. All new sequences were deposited in GenBank (see Table 1).

Data analyses

Sequencer 4·1 (Gene Codes Corp., Ann Arbor, MI, USA) was used to assemble complementary strands and verify software base-calling. All DNA regions were aligned by eye in PAUP version 4·0b10 (Swofford, 2002). Maximum parsimony (MP) trees were obtained from the resulting matrices using heuristic search options, using PAUP. Searches included 1000 random addition replicates and tree–bisection–reconnection (TBR) branch swapping, with MULTREES in effect (keeping multiple most-parsimonious trees). All characters had equal weight. Gaps were treated as missing. The shortest trees held in the initial heuristic search were used as initial trees for a final heuristic analysis, using all the cited options. MP support was assessed using 1000 bootstrap (BS) replicates, TBR branch swapping, simple addition sequence and MULTREES on, but keeping only ten trees per replicate following Salamin *et al.* (2003). Clades with BS values of 50–74 % were described as weakly supported, 75–89 % moderately supported and 90–100 % strongly supported.

A Bayesian analysis was conducted with MrBayes 3·1 (Ronquist and Huelsenbeck, 2003). The software MrModeltest (ver. 2; Nylander, 2004) was used to determine the best model of DNA substitution for each partition, using the Akaike Information Criterion (Akaike, 1974). The Markov Chain Monte Carlo chains were run for 1×10^6 generations and sampled every 100 generations. The chains reached stationarity and the average standard deviation of the split frequencies stabilized in <250 000 generations. Thus the first 750 trees were excluded ('burn-in') and the remaining trees were used to compile a posterior probability (PP) distribution using a 50 % majority-rule consensus. One of these remaining trees was drawn using PAUP software. Clades with PP equal to or higher than 0·95 are regarded as strongly supported.

The MP analyses were performed using all five outgroup taxa, which in all cases were external to the fully supported, monophyletic ingroup. In the Bayesian approaches only one outgroup taxon (*Bowiea volubilis*) was included.

Evaluation of morphological character state distribution patterns were mapped on the Bayesian tree using MacClade version 4·08 (Maddison and Maddison, 2005) with the default settings. Thirty-four characters (Tables S1 and S2 in Supplementary data, available online) were traced using ACCTRAN optimization and assuming Fitch parsimony, equal weighting of all characters, transitions among all states equally probable, and characters as unordered. Character states were determined from literature and personal observation.

RESULTS

Plastid trees

Combination of all three plastid DNA regions (*rbcL, matK* and *trnL-F*) generated a matrix of 3382 characters. Of these, 754 were variable and 341 (45·2 %) were potentially phylogenetically informative. A total of 7100 MP trees was obtained [1243 steps, consistency index (CI) = 0·70, retention index (RI) = 0·82]. Bayesian analysis yielded trees based on a General Time Reversible + Gamma + Proportion invariant distribution (GTR + I + G) with topologies that are consistent with those retrieved with the MP analysis. These data yielded trees (not shown) fully congruent with those obtained by Manning *et al.* (2009*a*).

ITS trees

Amplification of the ITS region was successful for most species and yielded useful data for phylogenetic studies in Ornithogaloideae. However, it was not possible to sequence *Pseudogaltonia*, the position of which is thus unknown. The ITS matrix contained 959 characters, of which 500 were variable and 337 (67·4 %) were potentially phylogenetically informative.

A total of 5590 MP trees was obtained (1539 steps, CI = 0·52, RI = 0·76). The topology of the parsimony strict consensus tree (not shown) is similar to the Bayesian tree. Therefore, only one of the post-burn-in trees obtained from a Bayesian analysis under the GTR + I + G model is shown (Fig. 1). Bayesian PP and parsimony BS values are well correlated, the Bayesian being consistently higher (Fig. 1).

Several main clades can be distinguished (Fig. 1). One formed by *Neopatersonia* plus *O. rotatum* U. Müll.-Doblies & D. Müll.-Doblies (0·97 PP; 99 % BS) is sister to a large clade including the remainder of the subfamily (0·97 PP; 56 % BS).

Successively sister groups appear in that large group. First, there is a well-supported clade (1·00 PP; 93 % BS) that can be divided into two subclades. One (1·00 PP; 80 % BS) comprises the *Dipcadi* clade (0·99 PP; 76 % BS) sister to the *Battandiera* clade (0·89 PP; 77 % BS). The other (0·87 PP; 68 % BS) includes *Stellarioides*, *Trimelopter*, *Albuca* and *Coilonox* species, and is divided into two groups. One includes *Albuca* plus *Coilonox* (1·0 PP; 66 % BS) and shows little

internal resolution, though *Coilonox* (*O. polyphyllum* Jacq.-*O. suaveolens* Jacq.) appears as a clade (1·00 PP; 60 % BS). The other comprises *Stellarioides* plus *Trimelopter* (0·80 PP; 53 % BS), in which the monophyly of both subclades is strongly supported (1·00 PP, 98 % BS and 1·00 PP, 100 % BS, respectively).

Secondly, a large clade not fully resolved includes two sub-clades. The first one includes the Madagascan endemic *O. convallarioides* H.Perrier (=*Avonsera* Speta) and a clade comprising *Eliokarmos*, *Ethesia* and *Galtonia* (1·00 PP; 58 % BS); however, their phylogenetic relationships are not resolved. In this latter clade, two groups are identified. One (0·95 PP; 96 % BS) includes *Galtonia*, *O. saundersiae* (= *Zahariadia* Speta) and two species of *O.* subgenus *Urophyllon* (*sensu* Obermeyer, 1978): *O. haalenbergense* U.Müll.-Doblies & D.Müll.-Doblies and *O. xanthochlorum* Baker (0·95 PP; 96 % BS). The other is highly supported (1·00 PP; 100 % BS) and corresponds to *Eliokarmos* (= *O.* subgenus *Aspasia* groups Aspasiae and Hispidae, *sensu* Obermeyer, 1978), with several internally well-supported groups. Finally, the second subclade includes all Eurasian and north African taxa of *Ornithogalum* (including *Honorius*, *Loncomelos*, *Melomphis* and *Cathissa*) plus the southern and eastern African *O.* subgenus *Aspasia* group Angustifoliati (*sensu* Obermeyer, 1978) that corresponds to *Nicipe* Raf. and *Elsiea* F.M.Leight. This clade is strongly supported (1·00 PP; 95 % BS) though the internal relationships are not fully resolved. Only some clades are well supported, namely those corresponding to *Ornithogalum* plus *Honorius* (1·00 PP; 99 % BS), *Loncomelos* (1·00 PP; 97 % BS) and *Nicipe* (1·00 PP; 81 % BS).

Combined trees

Combination of *trnL-F*, *rbcL*, *matK* and ITS regions generated a total matrix with 4242 characters, of which 1198 were variable and 653 (54·5 %) were potentially phylogenetically informative. A total of 1761 MP trees was obtained (2713 steps, CI = 0·58, RI = 0·78). The topology of the parsimony strict consensus tree (not shown) is quite similar to the Bayesian consensus tree obtained under the GTR + I + G model. Phylogenetic relationships are shown by one of the post-burn-in topologies (Fig. 2). Bayesian PP and parsimony BS values are well correlated, the Bayesian being consistently higher (Fig. 2).

The trees in Figs 1 and 2 generally have a similar topology, but clade support is substantially higher in the latter. However, the combined tree (Fig. 2) shows two clades placed in quite different positions compared with the ITS tree (Fig. 1). Firstly, the *Neopatersonia* plus *O. rotatum* clade (1·00 PP; 100 % BS) is in the Bayesian combined tree (Fig. 2) nested within Ornithogaleae (Clade C), sister to the group including the Eurasian and North African species plus *Nicipe* and *Elsiea* (0·98 PP). That clade is, however, placed as sister to the rest of Ornithogaleae in the MP combined tree (not shown), with moderate support (88 % BS). Secondly, the *Trimelopter* clade (*O. unifolium* Retz. plus *O. etesiogaripense* U.Müll.-Doblies & D.Müll.-Doblies) is in the combined tree (by both MP and Bayesian analyses) sister to the clade comprising *Stellarioides*, *Coilonox* and *Albuca*.

Two main clades can be identified in Fig. 2. The first main clade (Clade A + B), which corresponds to Albuceae plus Dipcadieae (*sensu* Manning *et al.*, 2009a), receives moderate support (0·71 PP; 75 % BS) and includes the genera *Pseudogaltonia*, *Dipcadi*, *Battandiera, Trimelopter, Albuca, Coilonox* and *Stellarioides* as recognized here. It can be divided into two subclades. *Pseudogaltonia* and *Dipcadi* species form a strongly supported group (1·0 PP; 94 % BS). In the *Dipcadi* clade, segregation of the Mediterranean *D. serotinum* Medik. from the South African representatives is strongly supported (1·0 PP; 100 % BS). A second clade (1·00 PP; 65 % BS) comprises *Battandiera*, *Trimelopter*, *Stellarioides*, *Albuca* and *Coilonox*. Within that clade, as sister to the rest, is a well-supported group (1·0 PP; 99 % BS) including *O. seineri* (Engl. & K.Krause) Oberm., *O. pulchrum* Schinz, *O. stapffii* Schinz and *O. amoenum* Batt., which are here included in *Battandiera*. The next branch groups *O. etesiogaripense* and *O. unifolium* (*Trimelopter* clade) (1·0 PP; 100 % BS) together, sister to *Albuca*, *Coilonox* and *Stellarioides* (1·0 PP; 88 % BS). The *Stellarioides* species (*O. longebracteatum* Jacq., *O. sordidum* Baker and *O. tenuifolium* Redouté) constitute a fully supported subclade (1·0 PP; 100 % BS), sister to *Albuca* plus *Coilonox* (1·0 PP; 99 % BS). Although *Albuca* was not supported as monophyletic in the heuristic MP analysis, the Bayesian one yielded two fully supported monophyletic groups: *Coilonox* (1·00 PP) and *Albuca* (1·00 PP). In *Albuca* two main clades appear, one of which matches the former *Pallastema* Salisb (0·99 PP; 55 % BS).

The second main clade in the combined tree (Clade C), which corresponds to Ornithogaleae (*sensu* Manning *et al.*, 2009a), is well supported (1·0 PP; 88 % BS). However, relationships of the principal lineages are not well resolved. First, a large clade (1·0 PP; 69 % BS) comprises the species of the here-accepted genera *Galtonia*, *Ethesia* and *Eliokarmos*. Each of these three genera form a well-supported clade. Species of *Galtonia sensu stricto* plus *O. saundersiae* Baker form a strongly supported subclade (1·0 PP; 97 % BS), and therefore we consider all of them as members of *Galtonia*. This group is sister to the one formed by *O. haalenbergense* U.Müll.-Doblies & D.Müll.-Doblies and *O. xanthochlorum* Baker (1·0 PP; 100 % BS), here segregated as *Ethesia*. Sister to these two genera is a strongly supported subclade (1·0 PP; 100 % BS), which we accept as *Eliokarmos*, that includes species of *O.* subgenus *Aspasia* groups Aspasiae and Hispidae (*sensu* Obermeyer, 1978). Moreover, in *Eliokarmos* two strongly supported subgroups (each one 1·0 PP; 100 % BS) are identified which show morphological peculiarities as discussed below: one comprising *O. maculatum* Jacq. and *O. rupestre* L.f., and the other the rest of the species of *Eliokarmos*.

The position of the Madagascan *O. convallarioides* (=*Avonsera*) is not resolved, as it constitutes a separate clade in an unresolved position in Ornithogaleae. As said before, the *Neopatersonia* clade falls sister to a well-supported third main clade (1·0 PP; 99 % BS) that comprises the rest of representatives from Europe, Middle East and North Africa. This latter clade includes all samples of *Ornithogalum*, *Honorius*, *Loncomelos*, *Melomphis* and *Cathissa*, plus some species from southern and eastern Africa belonging to *Elsiea* and *Nicipe*. Within this wide group, *O. esterhuyseniae*
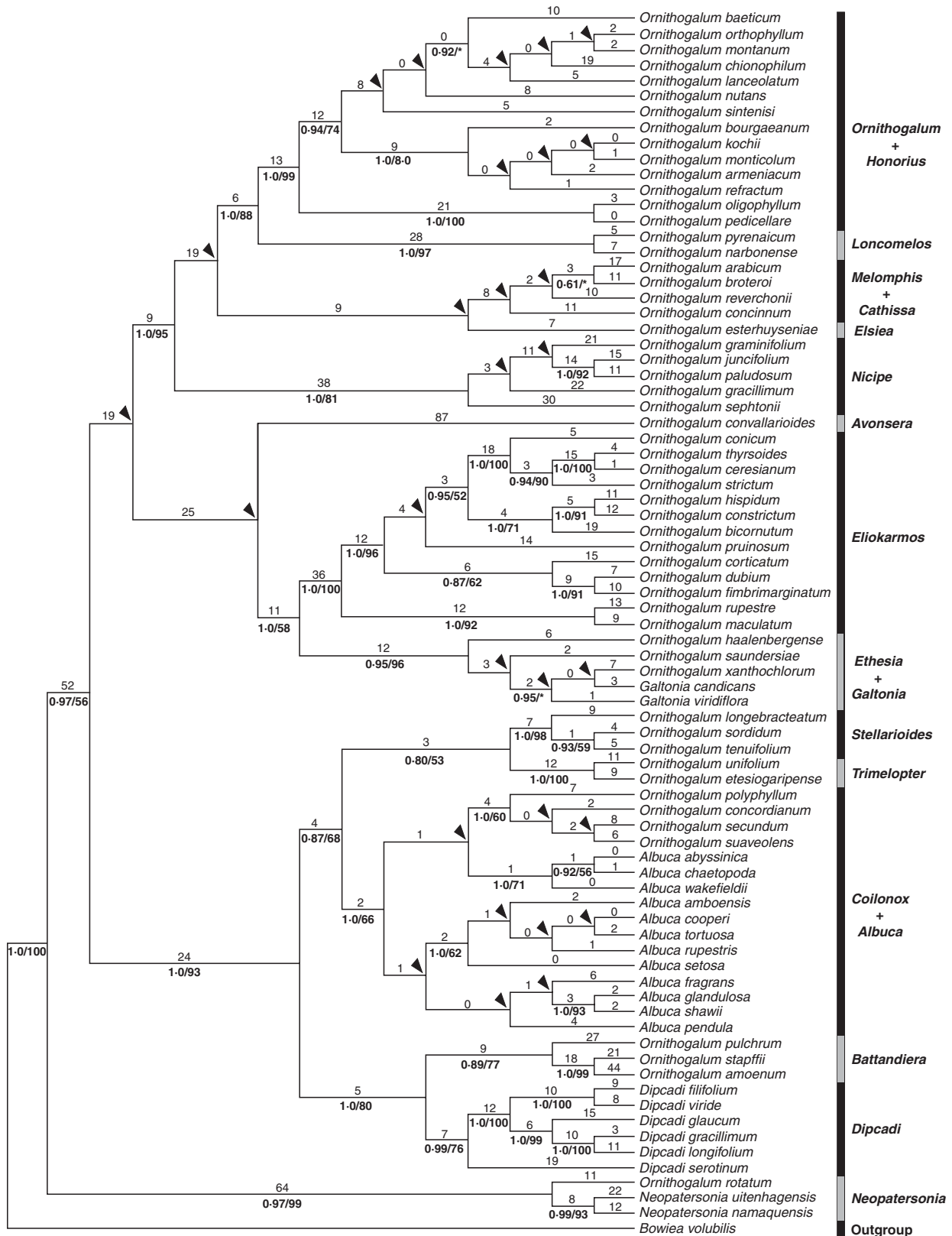
FIG. 1. Bayesian inference analysis obtained from ITS sequences in the phylogenetic analysis of Ornithogaloideae. Phylogenetic relationships shown by one of the post-burn-in topologies. Taxa are identified following the traditional treatment of *Ornithogalum* and other related genera (cf. Obermeyer, 1978; Zahariadi, 1980; Müller-Doblies and Müller-Doblies, 1996). The new proposed generic circumscription of the present study is shown on the right side. Branch lengths are shown above branches, and posterior probabilities and bootstrap percentages are shown below. Arrows indicate branches that collapse in the 50 % majority rule consensus tree obtained by Bayesian analysis.
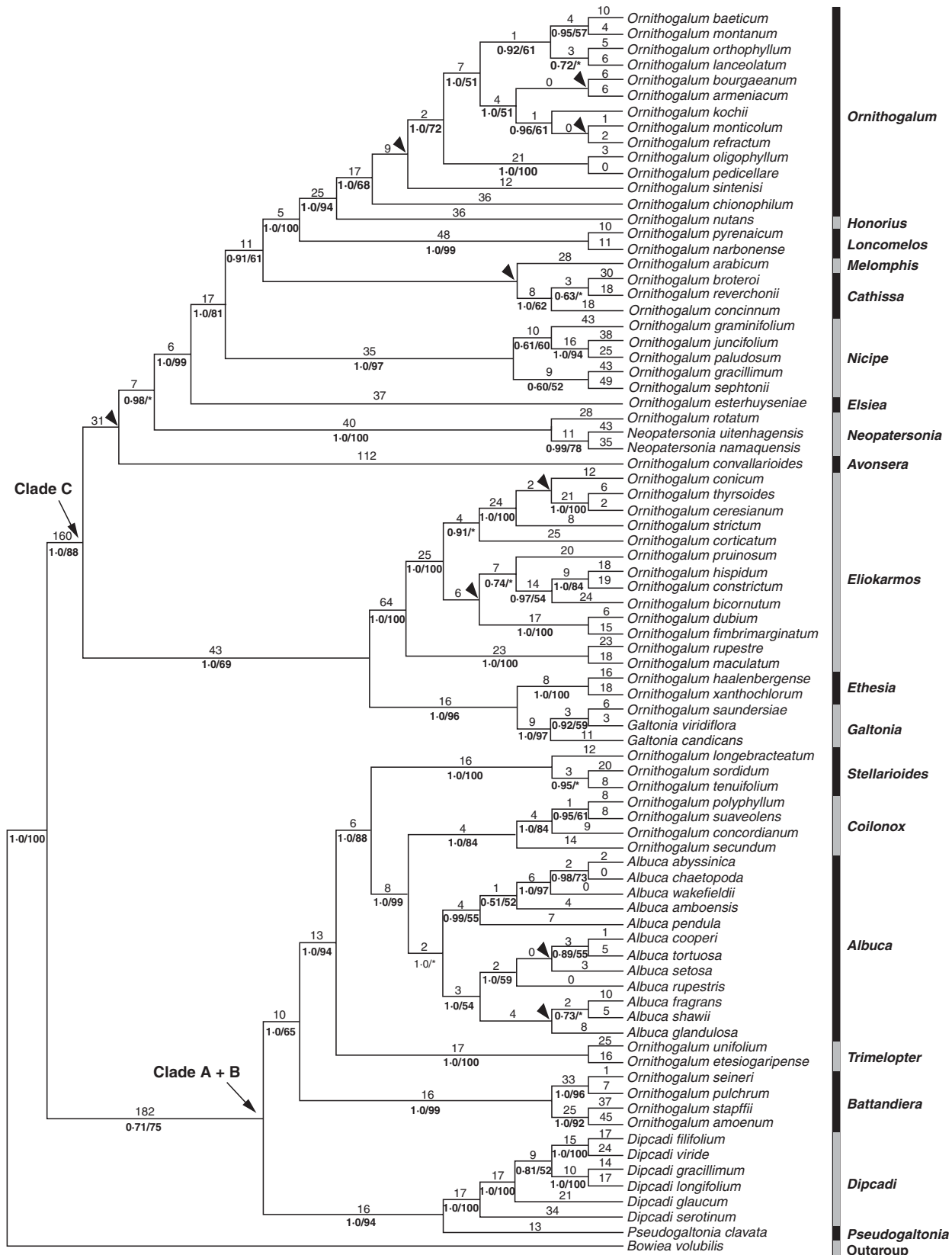
FIG. 2. Bayesian inference analysis of the combination of *rbcL*, *trnL-F*, *matK* and ITS sequences in the phylogenetic analysis of Ornithogaloideae. Phylogenetic relationships shown by one of the post-burn-in topologies. Taxa are identified following the traditional treatment of *Ornithogalum* and other related genera (cf. Obermeyer, 1978; Zahariadi, 1980; Müller-Doblies and Müller-Doblies, 1996). The new proposed generic circumscription of the present study is shown on the right side. Branch lengths are shown above branches, and posterior probabilities and bootstrap percentages are shown below. Arrows indicate branches that collapse in the 50 % majority rule consensus tree obtained by Bayesian analysis.

Oberm. (=*Elsiea*) is strongly supported (1·0 PP; 99 % BS) as sister to the rest of taxa. The species of *Nicipe* form a strongly supported subclade (1·0 PP; 97 % BS), sister to the rest of the Eurasian and North African taxa (0·91 PP; 61 % BS). The species of *Cathissa* form a clade (1·0 PP; 62 % BS). Relationships of *Melomphis*, which is represented here only by *O. arabicum* L., are not resolved. Finally, the species of *Loncomelos* form a strongly supported subclade (1·0 PP; 99 % BS), which is sister to *Honorius* plus *Ornithogalum* (1·0 PP; 94 % BS), with *Ornithogalum* being rather well supported (1·0 PP; 68 %BS).

Evaluation of morphological characters

Only some of the 34 morphological characters studied (Table S1 in Supplementary data) were shown to be important for the taxonomy of the subfamily, as commented on below.

Central longitudinal white band on leaves (character 9) The reconstruction of character states reveals the concolour leaves as plesiomorphic in the subfamily, and the white-banded leaves are thus synapomorphic for some species of *Ornithogalum* (*sensu stricto*).

Inflorescence structure (character 11) Most species of Ornithogaloideae have helicoidally disposed flowers, a character state that appears to be plesiomorphic. Therefore, according to our analysis, the usually unilateral inflorescence of *Dipcadi* is an autapomorphy of this genus, with a high discriminant taxonomic value.

Flower disposition (character 12) In most species the flowers are patent to erect, which is the plesiomorphic state. Conversely, some species of *Albuca*, *Dipcadi*, *Galtonia*, *Honorius* and *Pseudogaltonia* have nodding flowers, an apomorphy which has evolved independently in several linages of the subfamily.

Main colour of tepals (disregarding the central band) (character 14, Fig. 3A) Whereas most of the Eurasian representatives of the subfamily have white flowers, this state is an apomorphy that was acquired secondarily in many of the clades of Ornithogaloideae. Coloured flowers are thus a plesiomorphic state in the subfamily that is more common in the species from southern Africa.

Darker central band on tepals (character 16, Fig. 3B) Species of clade A + B (tribes Dipcadieae plus Albuceae, *sensu* Manning *et al.*, 2009*a*) have tepals with a usually evident and well-defined wide darker central band on both sides of the tepals, rarely somewhat difused on the adaxial face. In contrast, clade C (tribe Ornithogaleae) has unmarked tepals or tepals with a central band only visible on the abaxial side, as in *Ornithogalum sensu stricto* or some species of *Nicipe*, *Eliokarmos* and *Neopatersonia*. Therefore, tepals banded on both sides are a symplesiomorphy in clade A + B, whereas in clade C, the unmarked tepals (such in *Melomphis*, *Cathissa*, *Elsiea*, *Avonsera* and some *Eliokarmos* and *Nicipe*) are plesiomorphic, though in some other clades the banded abaxial side of tepals is an apomorphy that appeared independently several times.

Inner tepal disposition (character 17) Most representatives of the subfamily show spreading, not connivent, inner tepals as a symplesiomorphy. However, in some groups such as *Albuca* and *Dipcadi* connivent inner tepals are an apomorphy.
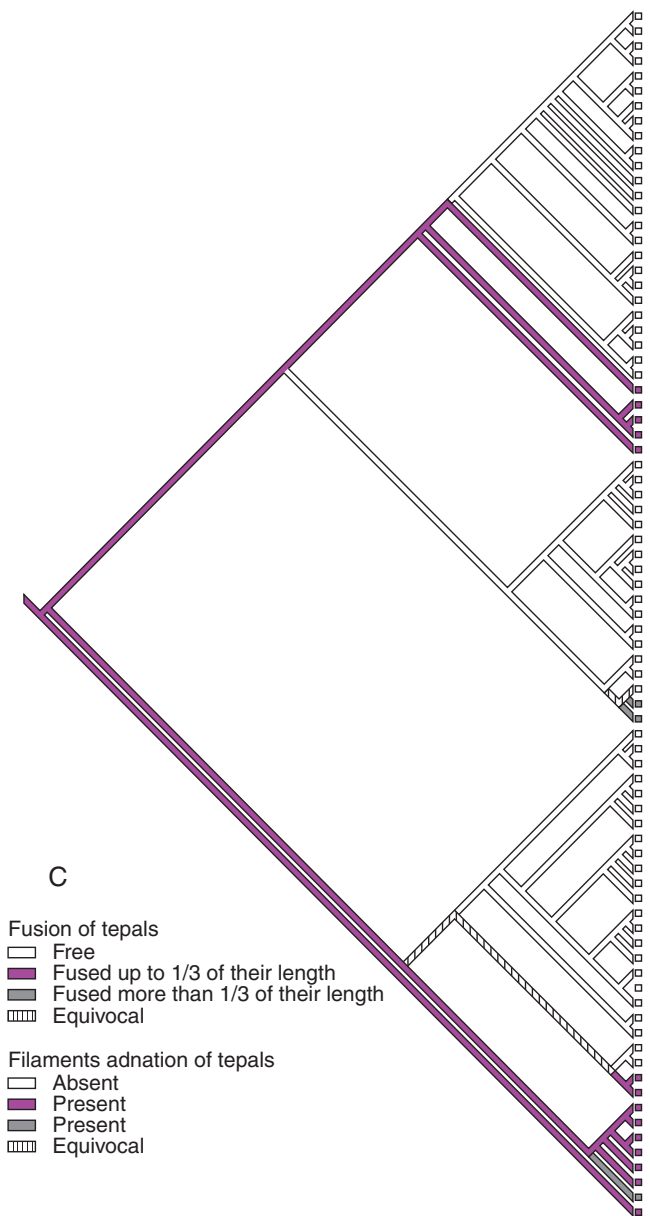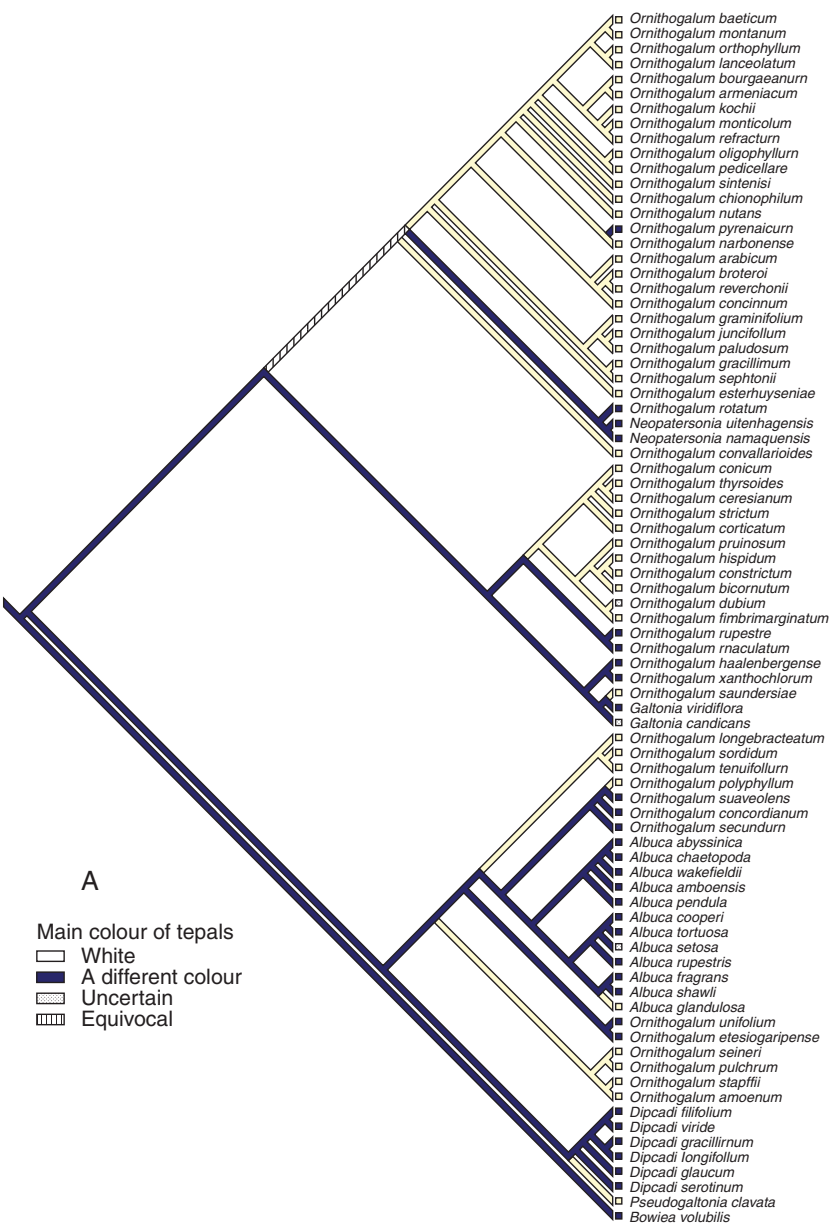
Fusion of tepals and filament adnation (characters 19 and 21, Fig. 3C) The character state reconstruction shows fusion of tepals and adnation of filaments to the perigone as plesiomorphic states in the subfamily, as it occurs in the other subfamilies of Hyacinthaceae, the free tepals and filaments being apomorphic and having evolved independently in different clades. Most genera with all or some of their species with a fused perigone and adnate filaments (e.g. *Pseudogaltonia*, *Dipcadi*, *Battandiera*, *Galtonia*, *Avonsera*, *Neopatersonia*, *Elsiea* and *Nicipe*) are mostly distributed in the southern hemisphere. Conversely, the number of species with free tepals and filaments is dominant in the subfamily and are common among the Eurasian taxa, with few exceptions (e.g. *Dipcadi serotinum*).

Capsule section (character 27) Trilobate cross-section of capsule (including those 6-lobed by further furrowing of individual lobes) is the apomorphic state, which has evolved independently several times in Ornithogaloideae. Capsules with rounded or trigonous section appear to be plesiomorphic. This character in combination with other reproductive features has proved to be important in the taxonomy of the genera.

Position of the dry perianth with respect to the capsule (character 29) In some clades of Ornithogaleae, the perianth withers and remains appressed, concealing the fruit. This is an apomorphy which characterizes some genera such as *Cathissa*, *Eliokarmos* or *Nicipe*. The plesiomorphic state of this character is present in most of the remaining genera, the fruits being totally or mostly exposed, never hidden.

Seed morphology (character 30, Fig. 3D) This feature appears to be useful in the classification of the subfamily. Species of clade A + B (tribes Dipcadieae plus Albuceae, *sensu* Manning *et al.*, 2009*a*) produce mostly flattened and subdiscoid seeds, this character being plesiomorphic. In clade C (tribe Ornithogaleae, *sensu* Manning *et al.*, 2009*a*), the irregularly compressed or polygonal seeds are common and also plesiomorphic, whereas globose seeds are rare and exclusive apomorphies of some genera, such as *Avonsera*, *Honorius*, *Neopatersonia* and *Ornithogalum*.

Testa morphology (character 31) Puzzle-like testas are widespread and plesiomorphic in the subfamily, whereas those verruculose and reticulate are apomorphic. Most species of clade A + B (tribes Dipcadieae plus Albuceae, *sensu* Manning *et al.*, 2009*a*) show puzzle-like testas, excepting a few taxa of *Albuca* (e.g. *A. echinosperma* U. Müll.-Doblies) and species of *Trimelopter*. Similarly, this pattern is also common in taxa of clade C (tribe Ornithogaleae, *sensu* Manning *et al.*, 2009*a*), and it is the basis on which two additional secondary morphologies can arise that constitute apomorphies for some groups. On the one hand, *Ornithogalum* plus *Honorius* have a coarsely reticulate testa, in which the anticlinal walls of cells are prominent and undulate, with the central part sunken. On the other hand, some taxa of *Eliokarmos*, *Neopatersonia*, *Nicipe* and *Cathissa* produce seeds with a
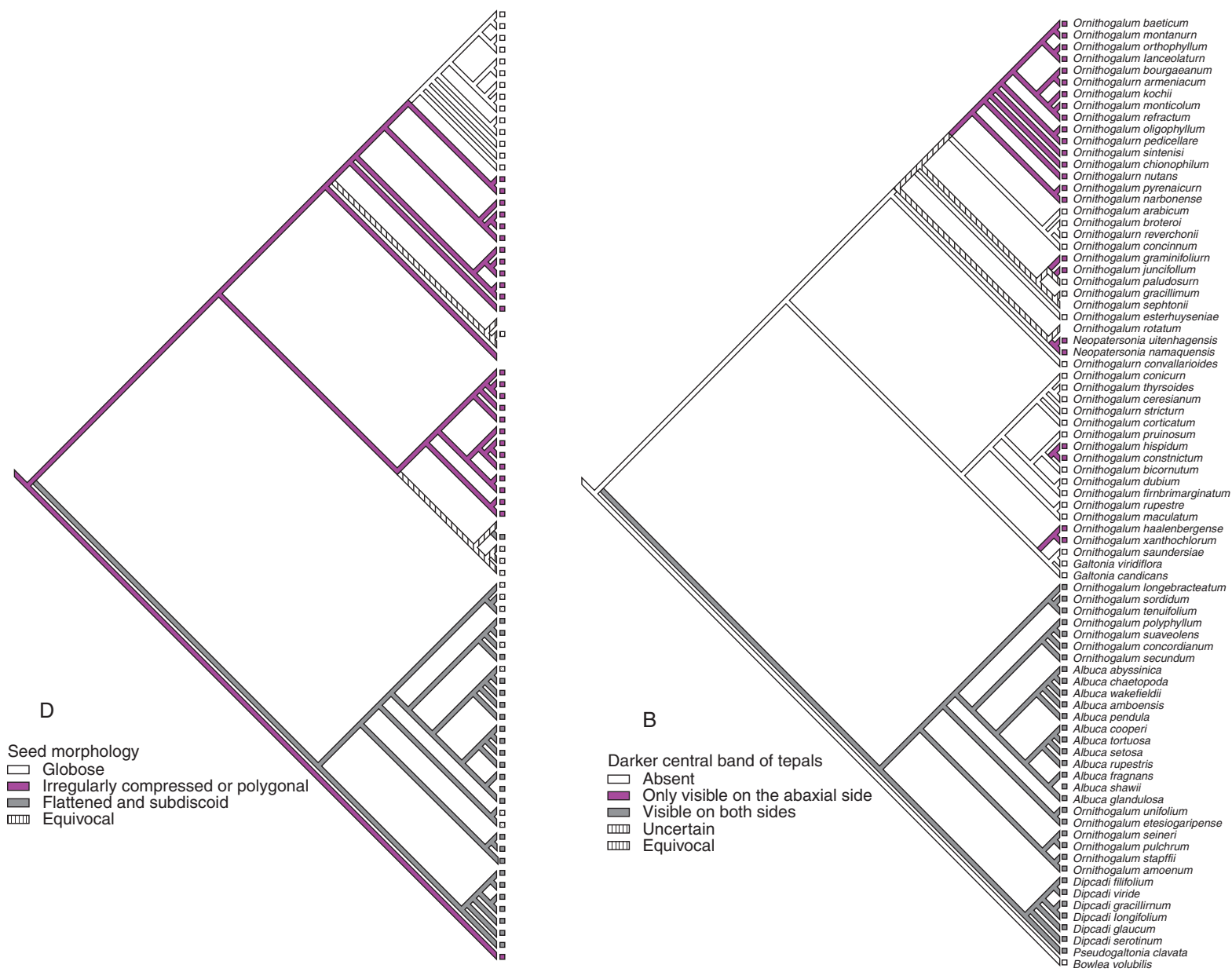
A

Ornithogalum baeticum
Ornithogalum montanum
Ornithogalum orthophyllum
Ornithogalum lanceolatum
Ornithogalum bourgaeanurn
Ornithogalum armeniacum
Ornithogalum kochii
Ornithogalum monticolum
Ornithogalum refracturn
Ornithogalum oligophyllurn
Ornithogalum pedicellare
Ornithogalum sintenisi
Ornithogalum chionophilum
Ornithogalum nutans
Ornithogalum pyrenaicurn
Ornithogalum narbonense
Ornithogalum arabicum
Ornithogalum broteroi
Ornithogalum reverchonii
Ornithogalum concinnum
Ornithogalum graminifolium
Ornithogalum juncifollum
Ornithogalum paludosum
Ornithogalum gracillimum
Ornithogalum sephtonii
Ornithogalum esterhuyseniae
Ornithogalum rotatum
Neopatersonia uitenhagensis
Neopatersonia namaquensis
Ornithogalum convallarioides
Ornithogalum conicum
Ornithogalum thyrsoides
Ornithogalum ceresianum
Ornithogalum strictum
Ornithogalum corticatum
Ornithogalum pruinosum
Ornithogalum hispidum
Ornithogalum constrictum
Ornithogalum bicornutum
Ornithogalum dubium
Ornithogalum fimbrimarginatum
Ornithogalum rupestre
Ornithogalum rnaculatum
Ornithogalum haalenbergense
Ornithogalum xanthochlorum
Ornithogalum saundersiae
Galtonia viridiflora
Galtonia candicans
Ornithogalum longebracteatum
Ornithogalum sordidum
Ornithogalum tenuifollurn
Ornithogalum polyphyllum
Ornithogalum suaveolens
Ornithogalum concordianum
Ornithogalum secundurn
Albuca abyssinica
Albuca chaetopoda
Albuca wakefieldii
Albuca amboensis
Albuca pendula
Albuca cooperi
Albuca tortuosa
Albuca setosa
Albuca rupestris
Albuca fragrans
Albuca shawli
Albuca glandulosa
Ornithogalum unifolium
Ornithogalum etesiogaripense
Ornithogalum seineri
Ornithogalum pulchrum
Ornithogalum stapffii
Ornithogalum amoenum
Dipcadi filifolium
Dipcadi viride
Dipcadi gracillirnum
Dipcadi longifollum
Dipcadi glaucum
Dipcadi serotinum
Pseudogaltonia clavata
Bowiea volubilis

C

Fusion of tepals
☐ Free
☐ Fused up to 1/3 of their length
☐ Fused more than 1/3 of their length
☐ Equivocal

Filaments adnation of tepals
☐ Absent
☐ Present
☐ Present
☐ Equivocal

Main colour of tepals
☐ White
☐ A different colour
☐ Uncertain
☐ Equivocal

D

Seed morphology
☐ Globose
█ Irregularly compressed or polygonal
▨ Flattened and subdiscoid
▥ Equivocal

B

Darker central band of tepals
☐ Absent
█ Only visible on the abaxial side
▨ Visible on both sides
▥ Uncertain
▥ Equivocal

Ornithogalum baeticum
Ornithogalum montanurn
Ornithogalum orthophyllum
Ornithogalum lanceolaturn
Ornithogalum bourgaeanum
Ornithogalurn armeniacum
Ornithogalum kochii
Ornithogalum monticolum
Ornithogalum refractum
Ornithogalum oligophyllum
Ornithogalurn pedicellare
Ornithogalum sintenisi
Ornithogalum chionophilum
Ornithogalurn nutans
Ornithogalum pyrenaicurn
Ornithogalum narbonense
Ornithogalum arabicum
Ornithogalum broteroi
Ornithogalurn reverchonii
Ornithogalum concinnum
Ornithogalum graminifoliurn
Ornithogalum juncifollum
Ornithogalum paludosurn
Ornithogalum gracillimum
Ornithogalum sephtonii
Ornithogalum esterhuyseniae
Ornithogalum rotatum
Neopatersonia uitenhagensis
Neopatersonia namaquensis
Ornithogalurn convallarioides
Ornithogalum conicurn
Ornithogalum thyrsoides
Ornithogalum ceresianum
Ornithogalum stricturn
Ornithogalum corticatum
Ornithogalum pruinosum
Ornithogalum hispidum
Ornithogalum constnictum
Ornithogalum bicornutum
Ornithogalum dubium
Ornithogalum firnbrimarginatum
Ornithogalum rupestre
Ornithogalum maculatum
Ornithogalum haalenbergense
Ornithogalum xanthochlorum
Ornithogalum saundersiae
Galtonia viridiflora
Galtonia candicans
Ornithogalum longebracteatum
Ornithogalum sordidum
Ornithogalum tenuifolium
Ornithogalum polyphyllum
Ornithogalum suaveolens
Ornithogalum concordianum
Ornithogalum secundum
Albuca abyssinica
Albuca chaetopoda
Albuca wakefieldii
Albuca amboensis
Albuca pendula
Albuca cooperi
Albuca tortuosa
Albuca setosa
Albuca rupestris
Albuca fragrans
Albuca shawii
Albuca glandulosa
Ornithogalum unifolium
Ornithogalum etesiogaripense
Ornithogalum seineri
Ornithogalum pulchrum
Ornithogalum stapffii
Ornithogalum amoenum
Dipcadi filifolium
Dipcadi viride
Dipcadi gracillirnum
Dipcadi longifolium
Dipcadi glaucum
Dipcadi serotinum
Pseudogaltonia clavata
Bowlea volubilis

F<small>IG</small>. 3. Recontruction of character distribution in a post-burn-in tree obtained by a Bayesian inference, after combination of all the DNA regions studied: (A) main colour of tepals; (B) darker central band on tepals; (C) fusion of tepals and adnation of filaments to tepals; (D) seed morphology. All characters are unordered.

granulate to echinulate testa in which the basal puzzle-like pattern can sometimes also be observed.

Seed disposition (character 32) Most species of Ornithogaloideae have biseriate or multiseriate seeds per locule of the capsule, this being the plesiomorphic state. Uniseriate seeds are present in *Pseudogaltonia*, *Dipcadi* and *Battandiera*, the seeds being flattened and horizontally stacked in each locule.

DISCUSSION

Recent studies by Manning *et al.* (2004, 2009*a*) and Wetschnig *et al.* (2007) have greatly clarified phylogenetic relationships in Ornithogaloideae. In their most recent paper, Manning *et al.* (2009*a*) found three major clades within Ornithogaloideae that they treated as three tribes and four genera: Dipcadieae (*Pseudogaltonia* and *Dipcadi*), Albuceae (*Albuca*) and Ornithogaleae (*Ornithogalum*). Furthermore, they recognized many subgenera, sections and series, mainly in *Albuca* and *Ornithogalum*. Both these genera *sensu* Manning *et al.* (2009*a*) are extremely variable from a morphological point of view, and are difficult to define within Hyacinthaceae.

In the present study, the combination of plastid and nuclear DNA sequences resulted in well-supported phylogenetic trees (Fig. 2) in which most of the clades are congruent with monophyletic genera previously described on the basis of morphological syndromes (Table 2). The addition of ITS sequences generated trees with greater resolution and support than those based only on plastid regions. The topology of our combined trees is similar in some aspects to the one obtained by Manning *et al.* (2009*a*). The three tribes they accepted, clade A (Albuceae), clade B (Dipcadieae) and clade C (Ornithogaleae), are also present in our combined trees (Fig. 2). However, notable differences can be identified.

Dipcadieae are sister to Albuceae, not to Ornithogaleae, though with only moderate support. This relationship is founded on some morphological synapomorphies which are exclusive in the subfamily and common to most of Dipcadieae plus Albuceae, such as the coloured band usually visible on both sides of the tepals and associated with several aggregated medial nerves, or on other features shared by *Dipcadi* and *Battandiera* (tribe Albuceae) such as the wide, quadrate and apically truncate capsule and flat, discoid, horizontally stacked and uniseriate seeds. These new relationships found in the combined trees make these groups more homogeneous, reducing the number of homoplasious characters. Moreover, another important difference is found in the Albuceae. Manning *et al.* (2009*a*) accepted *Coilonox* as a monophyletic subgenus of *Albuca* (as *A.* subgenus *Osmyne*), resulting in their *A.* subgenus *Albuca* not being monophyletic. In contrast, the present results demonstrate monophyly of both groups, with complete separation fully supported in the Bayesian analysis (1·00 PP).

Another important divergence is found in the Ornithogaleae clade, which Manning *et al.* (2009*a*) regarded as the single, extremely variable genus *Ornithogalum*. They divided *Ornithogalum* into four subgenera: *Avonsera*, *Galtonia*, *Aspasia* and *Ornithogalum*. Although the first three are rather homogeneous in morphology, *Ornithogalum* remained extremely heterogeneous, with seven sections most of which have sometimes been treated as separate genera. First, they placed the monophyletic *O.* section *Linaspasia* (southern and eastern Africa) embedded with a low support among sections *Cathissa*, *Melomphis*, *Ornithogalum* and *Honorius* (all of them native to Eurasia and North Africa). Our tree shows the *Nicipe* clade as sister to the rest of Eurasian sections, a position that makes phylogenetic relationships in the group much more understandable as discussed later. Moreover, in order to make *O.* section *Ornithogalum* monophyletic, Manning *et al.* (2009*a*) expanded it to include *Loncomelos* (*O.* subgenus *Beryllis*), therefore constructing a morphologically heterogeneous aggregate which is difficult to define with regard to other sections. In our trees, the *Loncomelos* clade is sister to the monophyletic *Ornithogalum*, allowing easy morphological circumscription of both groups. Relationships of the remaining groups are similar to those obtained by Wetschnig *et al.* (2007) and Manning *et al.* (2009*a*), and will be discussed later.

Finally, Wetschnig *et al.* (2007) found *Igidia volubilis* (H.Perrier) Speta, a monotypic genus native to Madagascar, to be sister to the clade comprising taxa of *Albuca*, *Coilonox* and *Stellarioides*, though based exclusively on sequences of the *trnL-F* region. Manning *et al.* (2009*a*) included only that same sequence in their analysis (they did not obtain *rbcL* or *matK*) and *Igidia* was sister to the *Stellarioides* (*sensu stricto*) clade (as *Albuca* subgenus *Urophyllon*). In our analyses, no sequences of that genus were included, and hence its phylogenetic relationships to the rest of Ornithogaloideae will not be elucidated until new molecular evidence is available. Nonetheless, if one accepts that *Igidia* is related to the *Stellarioides sensu stricto* clade, it should constitute an independent genus on the basis of its remarkable morphological apomorphies (cf. Speta, 1998*a*, *b*; Wetschnig *et al.*, 2007). Further research is currently being carried out to clarify this point (W. Wetschnig, pers. comm.).

Why the need for another new arrangement?

Following studies by Speta (1998*a*) and Pfosser and Speta (1999), 13–15 genera were accepted within Ornithogaloideae (Table 2). This arrangement was based exclusively on morphology and/or sequencing of a single plastid region (*trnL-F*). Some genera as circumscribed by these authors (e.g. *Stellarioides*, *Eliokarmos* and *Neopatersonia*) have, however, been demostrated to be para- or polyphyletic in recent studies (including the present one, as discussed below).

The phylogenetic studies of Hyacinthaceae by Manning *et al.* (2004) added the *rbcL* region to the previous studies with *trnL-F*, and improved knowledge of the phylogenetic relationships of some groups. They reported a strict consensus tree with many polytomies, notably in Ornithogaloideae, perhaps due to the low nucleotide variation in these regions (Lihová *et al.*, 2004; Shaw *et al.*, 2005; Pirie *et al.*, 2007). Nonetheless, Manning *et al.* (2004) adopted a 'maximally stable arrangement', with a single genus *Ornithogalum* for the whole subfamily. According to Lebatha *et al.* (2006), the polytomies in the strict consensus trees for Hyacinthaceae show a conflict or lack of hierarchy among groups, though it

TABLE 2. *Summary of the main taxonomic treatments of Ornithogaloideae*

Linneus (1753, 1762) Genus	Medikus (1790) Genus	Gray (1821) Genus	Link (1829) Genus	Reichenbach (1830) Genus	Rafinesque (1837) Genus	Parlatore (1854) Genus	Salisbury (1866) Genus	Baker (1872) Subgenus	Engler (1888) Section or genus*	Zahariadi (1965, 1980) Subgenus	Obermeyer (1978) Subgenus	Speta (1998a) Genus	Müller-Doblies & Müller-Doblies (1996) Section	Manning et al. (2004) Genus	Manning et al. (2009a) Genus	Present study Genus
Ornithogalum					*Ornithogalon*		*Ornithogalum*	*Heliocharmos*	*Heliocharmos*	*Ornithogalum* *Leptotesta* *Ophiogalum* *Oreogalum* *Hypogaeum* *Amphibolum* *Anosmium* *Amphigalum*		*Ornithogalum*				**Ornithogalum**
		Honorius	*Myogalum*	*Albucea*	*Syncodium*		*Brizophile*	*Myogalum*	*Myogalum*	*Myogalum*		*Honorius*				**Honorius**
					Loncomelos *Loncoxis*		*Beryllis* *Eustachys*	*Beryllis p.p.* *Cathissa p.p.*	*Beryllis p.p.* *Cathissa p.p.*	*Beryllis* *Eustachys*		*Loncomelos*			*Ornithogalum*	**Loncomelos**
					Melomphis	*Caruelia*	*Myanthe*	*Caruelia p.p.*	*Caruelia p.p.*	*Caruelia*		*Melomphis*				**Melomphis**
							Cathissa	*Cathissa p.p.*	*Cathissa p.p.*	*Cathissa*		*Cathissa*				**Cathissa**
					Eliokarmos *Tomoxis* *Lomaresis*		*Aspasia* *Phaeocles*	*Caruelia p.p.*	*Caruelia p.p.*		*Aspasia*	*Eliokarmos*	*Aspasia* *Hispidaspasia*			**Eliokarmos**
					Nicipe			*Cathissa p.p.* *Beryllis p.p.* *Osmyne p.p.*					*Linaspasia* *Vaginaspasia* *Nanaspasia*			**Nicipe**
													Helogalum			**Elsiea**
					Ethesia			*Osmyne p.p.*								**Ethesia**
												Zahariadia	*Urophyllon*			**Galtonia p.p.**
	Stellarioides						*Urophyllon*	*Beryllis p.p.*			*Urophyllon*	*Stellarioides*		*Ornithogalum*	**Stellarioides**
													Namibiogalum			**Battandiera**
					Trimelopter		*Ardernia*	*Beryllis p.p.*	*Beryllis p.p.*				*Monarchos*			**Trimelopter**
					Coilonox		*Taeniola*	*Osmyne p.p.*			*Osmyne*	*Coilonox*	*Monosmyne* *Osmyne*		*Albuca*	**Coilonox**
							Montassa		*Osmyne*							
							Osmyne									
Albuca							*Albuca* *Branciona* *Falconera* *Pallastema*	*Osmyne p.p.* *Eualbuca* *Falconera* *Pallastema*	*Eualbuca* *Falconera* *Pallastema*			*Albuca*				**Albuca**
												Avonsera				**Avonsera**
												Neopatersonia			*Ornithogalum*	**Neopatersonia**
									*Galtonia**			*Galtonia*				**Galtonia p.p.**
	Dipcadi								*Dipcadi**			*Dipcadi*			*Dipcadi*	**Dipcadi**
									*Pseudogaltonia**			*Pseudogaltonia*			*Pseudogaltonia*	**Pseudogaltonia**

Horizontal lines indicate approximate equivalences among taxa.

would not justify their fusion. These latter authors also pointed out that morphology can be useful in elucidating phylogenetic relationships in the family.

The addition of another plastid region (*matK*) resulted in a better-resolved topology and in a new taxonomic arrangement (Manning *et al.*, 2009a). Their new proposal was produced in a scenario in which three more or less contradictory taxonomies were discussed. The first (Option 1) retains as far as possible genera accepted by Speta (1998a), with the recircumscription or addition of as many genera as necessary to preserve monophyly. The second (Option 2) assumes only one genus, *Ornithogalum*, following Manning *et al.* (2004). The third (Option 3) is an intermediate, medium-conservative solution in which only four genera are accepted, corresponding to the four main lineages found in the plastid tree. All three options were extensively discussed, and finally the solution with four genera was favoured (Table 2). However, different criteria appear to be used to assign generic rank to particular clades. For instance, the sister groups *Pseudogaltonia* and *Dipcadi* are segregated as proper genera on the basis of morphological characters that are of a similar degree (or even weaker) than those separating other related clades, such as *Neopatersonia*–*Ornithogalum*, *Galtonia*–*Ornithogalum*, *Battandiera*–*Albuca* or *Coilonox*–*Albuca*, which are treated as subgenera or sections.

As pointed out by Manning *et al.* (2009a), recognition of many monophyletic genera (as favoured here), or acceptance of only four genera with many subgenera and sections (as they proposed), are both equally valid on theoretical grounds. However, Manning *et al.* (2009a) rejected the solution with many genera (Option 1) since it would require radical taxonomic changes including 'the creation of six or seven new genera, and the unprecedented dismemberment of *Ornithogalum*' and the need for a large number of combinations in 'genera that are either new or have not been used in modern times'. In their opinion, all these 'obligate' new nomenclatural proposals would be a handicap to acceptance of such an arrangement, and hence it would not be supported by botanists (mainly South African), since it is more disruptive and appears to lack nomenclatural stability.

In their arrangement, the genera *Albuca* and *Ornithogalum* are hard to recognize, since they are broadly defined from a morphological point of view. However, they are divided in nine subgenera, 13 sections and 12 series, mostly on the basis of morphological affinities, although one (*A.* subgenus *Albuca*) is not supported as monophyletic in their trees (cf. Manning *et al.*, 2009a).

Contrary to Stedje (2001b), the arrangement with many genera favoured here is much more consistent with morphology, and matches the molecular phylogenetic data. The new arrangement is not handicapped by any previous treatment and represents a logical circumscription of clades only when sufficient morphological evidence is combined with molecular data and monophyletic groups, as claimed by Manning *et al.* (2009a). Any *a priori* constraint (e.g. criticism by local taxonomists or apparent nomenclatural unstability) is unwarranted and counterproductive in taxonomy and systematics. Nomenclatural stability is warranted only by solid establishment of consistent taxonomic groups and a sensible application of rules in the International Code of Botanical Nomenclature (ICBN), and

does not depend necessarily on taxonomic arrangements themselves. A proposed new arrangement will become stable only when it is based on a successful combination of phylogenetic, morphological and biogeographical information, and when it is comprehensive and overlooks taxonomic prejudices and/or regional botanical practices.

On the basis of these considerations, we accept 19 phylogenetically monophyletic groups, which are here treated as separate genera and which are supported by syndromes of morphological characteristics as shown below. The most informative phylogenetically characters correspond namely to the colour of, and presence of, a band on tepals, capsule shape, seed morphology and seed disposition in the capsule locules. Other characters such as perigone features, tepal fusion, disposition of leaves and bulb shape and size, are homoplasious in the subfamily. However, contrary to the arguments of Stedje (2001b) and Manning *et al.* (2009a), they are useful for taxonomy and do not generate inappropriate or unstable associations when they are properly combined with the other relevant features.

Homoplasy is common in most large families of monocots (e.g. Orchidaceae and Amaryllidaceae, among others), and Hyacinthaceae are no exception. Contrary to arguments of Stedje (2001b) and Manning *et al.* (2009a), broader generic circumscriptions make it more difficult to understand relationships among species groups, from morphological and phylogenetic points of view, since they underestimate the value of particular apomorphies. Recognition of groups which are too wide (such as *Albuca* and/or *Ornithogalum*, in Options 2 and 3 *sensu* Manning *et al.*, 2009a), although monophyletic, only increases heterogeneity in each and causes difficulties in morphological definition. The existence of small genera (monotypic or with two or three species) is not necessarily an inconvenience; in contrast, when small clades are well defined morphologically, molecularly and phylogenetically, they can merit generic rank, depending on the general criteria used. Other subfamilies of Hyacinthaceae (e.g. Hyacinthoideae) are treated by Manning *et al.* (2004) in a narrower way, with ≤11 genera being recognized. Morphological syndromes characterizing genera in Hyacinthoideae are similar to those allowing recognition of 19 genera in Ornithogaloideae. The use of two different criteria in these close subfamilies appears to be inappropriate, since homoplasy is equally common in both groups. Therefore, the arrangement favoured here (with many genera, based on clades obtained in the combined trees) is more natural and easier to understand from a global view of the family. Furthermore, as asserted by Müller-Doblies (2006) 'a splitting of *Ornithogalum* seems to be by far the better taxonomic solution of the molecular data than the sinking of *Albuca* and other genera into *Ornithogalum*, which results in a huge taxonomic dustbin'.

A discussion of clades accepted at the genus rank in the taxonomic arrangement follows below. Disagreements and/or incongruence with previous, recent comprehensive treatments (Speta, 1998a; Manning *et al.*, 2004, 2009a) are also discussed.

The *Pseudogaltonia* clade

For a long time, *Pseudogaltonia* has been accepted as including a single species, *P. clavata* (Mast.) Phillips, distributed

throughout arid regions of north-west South Africa (Richtersveld), Namibia and Botswana. It was first described within the genus *Galtonia*, which grows exclusively in precipitation-rich, summer-rainfall, high-elevation regions of the Drakensberg, Low Drakensberg, Southern Berg and Natal Midlands in the eastern provinces of South Africa (KwaZulu-Natal, Free State, Mpumalanga and Eastern Cape). However, most later experts on Hyacinthaceae recognized *Pseudogaltonia* as a separate genus (Kuntze, 1886; Durand, 1890; Phillips, 1935; Hilliard and Burt, 1988; Speta, 1998*a*, *b*; Manning *et al.*, 2009*a*, *b*), based on biogeography and morphological features, including the large bulb with cartilaginous and fibrous outer tunics, the racemose pyramidal inflorescence, tepals fused to form a long tube (for about three-quarters of their length) and somewhat curved and swollen at the base (autapomorphy), stamens exserted and inserted at the mouth of the perianth tube (autapomorphy), style thin and >2 cm long (autapomorphy), capsule quadrate, truncate and deeply trilobate and uniseriate seeds with five to seven angled polygonal testa cells (see Phillips, 1935; Jessop, 1975; Speta, 1998*a*; Manning *et al.*, 2009*a*, *b*). Recently, an additional species, *P. liliiflora* J.C.Manning & Goldblatt has been described (cf. Manning *et al.*, 2009*b*) from Richtersveld, which is morphologically close to the former. Our phylogenetic studies provide further evidence for *P. clavata* being placed far from *Galtonia* as sister to the *Dipcadi* clade, as previously pointed out (Pfosser and Speta, 1999; Manning *et al.*, 2004, 2009*a*; Wetschnig *et al.*, 2007). Accordingly, *Pseudogaltonia* is here accepted at the generic rank.

The Dipcadi clade

Dipcadi has been widely accepted by most researchers on Ornithogaloideae (Heywood, 1980; Valdés, 1987; Speta, 1998*a*, *b*; Manning *et al.*, 2002, 2009*a*). It is characterized by two autapomorphies (the usually unilateral raceme and tepals curved outwards in the apical part) and by other features such as the tepals fused into a tube approx. one-quarter to one-third (to two-thirds) of their length, stamens adnate to the tube and included, capsule quadrate in outline, as broad as or broader than long, truncate at the apex, and seeds discoid, flattened, horizontally stacked and uniseriate in each locule with five to seven angled polygonal testa cells (cf. Obermeyer, 1964; Jessop, 1975; Heywood, 1980; Valdés, 1987; Speta, 1998*a*; Manning *et al.*, 2002, 2009*a*). It is important to note that some species of *Albuca* produce almost unilateral racemes due to the decumbent growth of scapes, a pattern which is quite different from that found in *Dipcadi*.

All the species of *Dipcadi* studied in these phylogenetic analyses form a fully supported clade, sister to *Pseudogaltonia*. These results are identical to those obtained by Pfosser and Speta (1999) and Manning *et al.* (2004). The former authors recognized both genera, whereas the latter authors combined them under *Ornithogalum*. Recently Manning *et al.* (2009*a*) reversed their previous opinion (cf. Manning *et al.*, 2004) and recognized the generic identity of both *Pseudogaltonia* and *Dipcadi*. Based on the data presented here and on unequivocal morphological and phylogenetic evidence, the traditional concept of *Dipcadi*, following Pfosser and Speta (1999), is maintained. Manning *et al.* (2009*a*)

suggested two series within *Dipcadi*, one including species with caudate apical appendages (*D.* series *Uropetalon*), and the other including those lacking these appendages (*D.* series *Dipcadi*). However, their phylogenetic tree does not provide support for that classification, since neither series was monophyletic. Our phylogenetic results also recovered the polyphyly of these series.

The Battandiera clade

Manning *et al.* (2004, 2009*a*) showed that three species of *Ornithogalum* occurring in the desert regions of Namibia and South Africa (*O. seineri*, *O. pulchrum* and *O. stapffii*) form a well supported clade, sister to the rest of Albuceae. This result is also found in our combined analysis. However, our ITS data (Fig. 1) placed this clade as sister to *Dipcadi*, with moderate support. This can be explained because all these latter taxa share the same type of discoid, flat seeds, horizontally stacked and uniseriate in each locule, with angled polygonal or slightly undulate testa cells (Fig. 4I and J), a rare character in the subfamily which supports their close phylogenetic relationship. The uncertain position of this group raises questions about the circumscription of Dipcadieae (*sensu* Manning *et al.*, 2009*a*), and even the necessity for its segregation from Albuceae. In Fig. 2, these tribes are thus grouped as 'Clade A + B'.

All three species in this clade are characterized by tepals with an evident longitudinal band visible on both sides, the wide capsule, quadrate and truncate at the apex, with darker transverse nerves, and the peculiar seed testa, shape and disposition (cf. Leighton, 1945; Obermeyer, 1978; Manning *et al.*, 2009*a*), similar to those of *Dipcadi*. In our combined phylogenetic trees, and after the expansion of sampling to include more Eurasian and north African species, *O. amoenum* (Fig. 4I and J) was found to be deeply embedded in this clade. It is a rare and rarely collected plant which comes from the desert regions of North Africa (Morocco and Algeria), and shares the habitat, capsule and seed morphology with *O. seineri*, *O. pulchrum* and *O. stapffii*. These peculiar features, different from all Eurasian species of *Ornithogalum*, led Maire (1926) to describe the monospecific genus *Battandiera* to include *O. amoenum*. Similarly, the Namibian and South African species of this clade were segregated in the past in different taxa (Table 2). In our phylogenetic studies, the clade *O. seineri*−*O. amoenum* receives strong support. This fact, together with a clear morphological and phylogenetic difference (cf. Obermeyer, 1978; Müller-Doblies and Müller-Doblies, 1996; Manning *et al.*, 2009*a*) with regard to related taxa, leads us to recognize *Battandiera* as a separate genus, though with some necessary recircumscription. Some species of this group, including *O. amoenum*, *O. stapffii*, *O. candidum* Oberm., *O. tubiforme* (Oberm.) Oberm. and *O. rautanenii* Schinz, occurring mainly in the western arid regions of Africa (Namibia and Morocco−Algeria), have tepals fused in a short tube ≤5 mm long, whereas others such as *O. seineri*, *O. donaldsonii* (Rendle) Greenway and *O. pulchrum* have free tepals and grow mostly in the eastern regions of Africa (from western Namibia to Kenya). The existence of fused or free tepals in this genus can be explained by the former state being

plesiomorphic in the subfamily and having evolved independently in several clades (Fig. 3C). The cited morphological and biogeographical differences are also supported by our phylogenetic analysis, since *O. amoenum* plus *O. stapffii* form a clade sister to the *O. seineri* plus *O. pulchrum* clade, both of which are strongly supported. Further studies, including wider sampling, are being carried out to clarify internal relationships among members of this genus.

Inclusion of *Battandiera* in *Albuca* (as *A.* subgenus *Namibiogalum*) as Manning *et al.* (2009a) suggested, results in a highly heterogeneous *Albuca*, which does not reflect the clear morphological divergence with highly informative phylogenetic characters (e.g. capsule shape, seed morphology and arrangement in the capsule). Moreover, that inclusion would not be possible on the basis of the ITS tree obtained, as

stated above. Segregation of *Battandiera* reduces heterogeneity in genera of the subfamily (cf. Manning *et al.*, 2009a), making *Albuca* more coherent. Moreover, circumscription of *O.* subgenus *Namibiogalum sensu* Manning *et al.* (2009a), with the inclusion of *O. prasinum* and *O. toxicarium* C.Archer & R.H.Archer, is not consistent with morphology (cf. Lindley, 1816; Archer and Archer, 1999) or our combined trees. *Ornithogalum prasinum* and *O. toxicarium* are not related to one another, and are allied to other groups as shown below.

The Trimelopter clade

The *Trimelopter* clade includes *O. unifolium* and *O. etesiogaripense*, two species occurring in arid regions of western South Africa and southern Namibia (Sperrgebiet). These taxa are differentiated from the rest of the subfamily by the presence of a single, elliptic to narrowly oblong leaf (exceptionally two or three leaves), usually flattened against the ground, an apomorphy of the group (cf. Manning *et al.*, 2009a); the ovaries and capsules have three prominent carpels, each with two longitudinal keels down the back and a groove between (Fig. 4G and H); and the seeds are unequally compressed or semi-discoid (cf. Dyer, 1931; Leighton, 1944; Obermeyer, 1978; Manning *et al.*, 2009a). Due to their morphological peculiarities, these plants have been treated at various taxonomic ranks (Table 2). Rafinesque (1837) described the genus *Trimelopter*, including only *O. fuscatum* Jacq. (=*O. unifolium* Retz.) (Fig. 4F), which Obermeyer (1978) included (as *O. unifolium*) in *O.* subgenus *Urophyllon*. Müller-Doblies and Müller-Doblies (1996) described *O.* subgenus *Urophyllon* section *Monarchos* to accommodate 11 related species. Finally, Manning *et al.* (2009a) recognized section *Monarchos* as *Albuca* subgenus *Monarchos*. The phylogenetic study by Manning *et al.* (2004, 2009a) found strong support for the clade of *O. unifolium* and *O. etesiogaripense* (97–100 % BS) and revealed its sister relationship with clades including *Albuca*, *Coilonox* and *Stellarioides sensu stricto*. Our phylogenetic study reveals the same relationship, also with a strong support (Fig. 2). Due to the clear morphological and phylogenetic identity of this clade, the genus *Trimelopter* is accepted here, following Rafinesque (1837), though it is expanded to include the species of *O.* section *Monarchos* (*sensu* Müller-Doblies and Müller-Doblies, 1996), with the exclusion of *O. rotatum* because of its disruptive morphology and phylogenetic position. This latter species is evidently connected to taxa in the *Neopatersonia* clade, as discussed later.
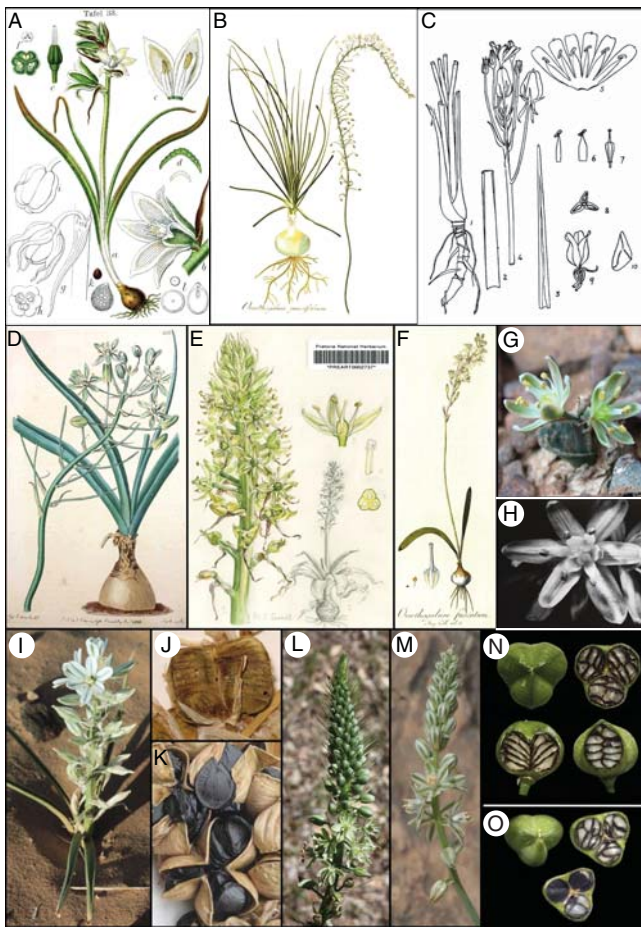
FIG. 4. Morphological variation in several genera of Ornithogaloideae: (A) *Honorius boucheanum* (from Sturm, Deutschlands Flora in Abbildungen: tab. 33. 1796, as *Ornithogalum boucheanum*); (B) *Nicipe juncifolia* (from Jacquin, Plantarum Rariorum Horti Caesarei Schoenbrunnensis Descriptiones et Icones, 1: tab. 90. 1797, as *O. juncifolium*); (C) *Elsiea corymbosa* (from Leighton in J. S. African Bot. 10: 56. 1944); (D) *Ethesia prasina* (from Lindl., Bot. Reg. 2: tab. 158. 1816, as *O. prasinum*); (E) *E. xanthochlora* (from Pretoria National Herbarium PREART 0002737, as *O. xanthochlorum*); (F) *Trimelopter unifolium* (from Jacquin, Icones Plantarum Rariorum, 2(16): tab. 429. 1795, as *O. fuscatum*); (G and H) *T. dyeri* (pictures by A. P. Dold); (I) *Battandiera amoena* (picture by Stephen L. Jury); (J) capsule of *B. amoena*; (K) capsules and seeds of *B. pulchra*; (L) *Stellarioides longebracteata*; (M) *S. sessiliflora*; (N) Capsules and seeds of *S. longebracteata*; (O) capsules and seeds of *S. sessiliflora*.

The Albuca clade

The well-established genus *Albuca* comprises at least 60 species, as traditionally circumscribed (Speta, 1998a), though this number will probably reach approx. 100. They are readily characterized by their floral structures, which clearly differentiate them from the rest of the subfamily. Flowers are nodding, patent or erect, and the tepals are usually dimorphic: the inner ones are erect and connivent, overtopping the stamen and gynoecium, whereas the outers are erect–patent. The filaments have basal constrictions (apomorphy), the ovary has paraseptal crests, the styles are thick and prismatic (autapomorphy) or

narrower and tapering, the capsule is ovoid or oblong, acute or obtuse, and the seeds are flattened, semi-lunate or discoid with smooth or rarely granulate puzzle-like testa (cf. Baker, 1897a, 1898, 1904; Jessop, 1975; Müller-Doblies, 1994, 1995; Speta, 1998a; Manning *et al.*, 1999, 2002, 2009a). Based on a combined *trnL-F* plus *rbcL* phylogeny, Manning *et al.* (2004) combined all these species into *Ornithogalum*. When they extended the sampling of taxa and sequenced other plastid regions, they considered the traditionally accepted species of *Albuca* as *A.* subgenus *Albuca*, though in their tree it was not clearly monophyletic, without the inclusion of the taxa of *Coilonox*.

In the Bayesian analysis, the present data provide a much better resolved tree, in which the species of *Albuca* form a clade sister to *Coilonox*. This fact, together with the remarkable morphological differences between the groups, supports recognition of *Albuca* at the generic rank, as suggested by Müller-Doblies (2006) and adopted here. Manning *et al.* (2009a) suggested four sections within *Albuca* subgenus *Albuca*, which we choose not to accept here because they have not been shown to be monophyletic. In the combined trees, species of *Albuca* form two strongly supported groups. One of these fits the concept of the former genus *Pallastema* Salisb., which is well characterized by the slender, almost cylindrical style, and the slightly zygomorphic flowers with all stamen similar and fertile. The other group includes a mixture of taxa formerly referred either to subgenera *Albuca*, *Falconera* and *Leptostyla* (cf. Baker, 1897a; Müller-Doblies, 2006), or to sections *Albuca*, *Falconera* or *Branciona* (cf. Manning *et al.*, 2009a). However, none of these receives support in our phylogenetic trees, perhaps due to the still poor sampling of all these groups. Further research is currently being carried out to clarify this point.

The *Coilonox* clade

Some species of *Ornithogalum* (e.g. *O. albucoides* (Ait.) Thunb., *O. secundum* Jacq., *O. suaveolens*, etc.) were segregated in the past at different ranks (Table 2). At the generic rank, *Coilonox* (Rafinesque, 1837) has priority. Species of *Coilonox* possess some similarities with *Albuca* that led several authors to describe species of the former in the latter (cf. Manning *et al.*, 2009a). Although in general terms *Coilonox* and *Albuca* share the longer than wide capsules, the style longer than the ovary and stamens, and the phenology of the flowers, closing at night (cf. Manning *et al.*, 2009a), *Coilonox* does not show the floral structures typical of *Albuca* and hence is quite simple to differentiate (cf. Manning *et al.*, 2009a). In fact, as Müller-Doblies (2006) pointed out 'there are no real transitions between both genera'. Our phylogenetic results demonstrate the monophyly of both groups and, together with the clear morphological differences, support recognition of both genera, which can be easily differentiated by their floral structure.

The *Stellarioides* clade

Ornithogalum longebracteatum, *O. sordidum* and *O. tenuifolium* are characterized by large bulbs, sometimes epigeous, with papery and greyish or fleshy and green outer tunics. They usually produce aerial or hypogeous bulbils and have long, narrow and dense cylindrical inflorescences (Fig. 4L and M), flowers small and numerous, capsule subglobose or widely ovoid to obovoid, trilobate, and seeds flattened or irregularly compressed, with sharpened edges, obliquely stalked in each locule (Fig. 4N) and a puzzle-like testa (cf. Leighton, 1945; Obermeyer, 1978; Speta, 1998a; Manning *et al.*, 2009a). In Africa, the species of this group are mostly distributed in areas characterized by abundant, mainly summer rainfall. They also occur in regions with a bimodal autumn–summer rainfall regime (*O. tenuifolium*) or in semi-arid Mediterranean-climate areas, ranging from high-altitude warm-temperate regions of highveld in South Africa, through the mountains of southern and East Africa as far north as Ethiopia and Morocco–Algeria (*O. sessiliflorum* Desf., Fig. 4M and O). In South Africa, *O. longebracteatum* is usually found in dense thickets and edges of both subtropical and afromontane forests (Manning *et al.*, 2009a). All these species have been recognized at various ranks (Table 2), and *Stellarioides* (Medikus, 1790) has priority at the generic level. They share a unique syndrome of morphological characters, including the dense and many-flowered inflorescences, with small flowers (tepals ≤12 mm long), almost sessile to shortly/pedicellate and small capsules ≤1·4 cm long. The present results show that *O. longebracteatum*, *O. sordidum* and *O. tenuifolium* form a fully supported clade, sister to the *Albuca–Coilonox* alliance. With the cited morphological syndrome, this justifies acceptance of *Stellarioides* at the generic rank. In contrast, recircumscription of *Albuca* to include *Stellarioides* as suggested by Manning *et al.* (2009a) greatly increases the heterogeneity of *Albuca*.

Speta's (1998a, 2001) concept of *Stellarioides* is almost coincident with that accepted here, and not with that in the tree of Manning *et al.* (2009a), in which several taxa (e.g. *O. etesiogaripense*, *O. haalenbergense*, *O. pulchrum*, *O. rotatum*, *O. seineri*, *O. stapffii* and *O. unifolium*) are treated as members of *Stellarioides*, supposedly following Speta (1998a). Nonetheless, the treatment of Speta (2001) is in need of a few changes: first, the exclusion of *S. donaldsonii* (≡*Albuca donaldsonii*), which is included here in *Battandiera*, and, second, the exclusion of *Trimelopter* and *Ardernia* Salisb. from synonymy, which are synonyms and accepted here as a different genus. It is worth mentioning here that Stedje (2001b) used some taxa of the present clade to exemplify her criticism of Speta's treatment. In her opinion *O. tenuifolium* Redouté, *O. sessiliflorum* and *O. narbonense* where supposedly undistinguishable from a morphological point of view (only by minor quantitative characters), but apparently they should be included in three different genera (*Stellarioides*, *Cathissa* and *Loncomelos*, respectively) following Speta. However, evidence is here shown that the first two species indeed belong to *Stellarioides*, whereas *O. narbonense* is a member of *Loncomelos* (see below), all showing clear morphological differences and being placed in clades far apart from each other.

The *Galtonia* clade

Four species are traditionally included in the genus *Galtonia* (cf. Hilliard and Burt, 1988): *G. candicans*

Decne., *G. princeps* Decne., *G. regalis* Hilliard & B.L.Burtt and *G. viridiflora* Verdoorn. They are found in summer-rainfall, high-altitude regions of the Drakensberg, Low Drakensberg, Southern Berg and Natal Midlands (South Africa and Lesotho; Hilliard and Burt, 1988; PRECIS database). *Galtonia* is characterized by large leaves sheathing the stem, racemose inflorescence, with flowers nodding, tepals fused into a campanulate tube for approx. half of their length, filaments cylindrical and adnate, capsule lanceolate cylindric and acute, and seeds irregularly compressed or flattened with smooth puzzle-like testa (cf. Verdoorn, 1955; Jessop, 1975, Hilliard and Burt, 1988; Riddles and Condy, 2001; Manning *et al.*, 2009a). Because of the unique combination of morphological features, many authors (e.g. Decaisne, 1880; Verdoorn, 1955; Hilliard and Burt, 1986, 1988; Speta, 1998a, b; Riddles and Condy, 2001) recognized *Galtonia* as a genus distinct from *Ornithogalum*. Taxa belonging to *Galtonia* had been also classified as *Hyacinthus* (Baker, 1870) or *Ornithogalum* subgenus *Galtonia* section *Galtonia* (Manning *et al.*, 2009a). In the early molecular phylogenetic work of Pfosser and Speta (1999), *Galtonia* appeared to be polyphyletic, since *G. candicans* was related to *Stellarioides* and *Albuca* and *G. princeps* and *G. viridiflora* fell as sister to *Ornithogalum saundersiae*, a species which has been included in *O.* subgenus *Urophyllon* (Obermeyer, 1978; Müller-Doblies and Müller-Doblies, 1996) or in the monospecific genus *Zahariadia* Speta (nom. nud.). Manning *et al.* (2004, 2009a) presented evidence for the monophyly of *Galtonia*, with the necessary inclusion of *O. saundersiae*. In their studies *G. candicans*, *G. viridiflora* and *O. saundersiae* formed a strongly supported clade, sister to *O. xanthochlorum* and *O. haalenbergense*. First, they (Manning *et al.*, 2004) synonymized both genera, though later they (Manning *et al.*, 2009a) segregated *Galtonia* as a subgenus of *Ornithogalum*. Our molecular data corroborate their later results and show *Galtonia* plus *O. saundersiae* to constitute a strongly supported clade, which is sister to that comprising *O. xanthochlorum* and *O. haalenbergense*. Connections between *O. saundersiae* and *Galtonia* are surprising, since *O. saundersiae* has a pseudocorymbose inflorescence, erect flowers and free tepals and filaments (cf. Leighton, 1945; Obermeyer, 1978), traits all different from typical *Galtonia*. Moreover, chromosome numbers support separation of these groups, being $2n = 16$ in *Galtonia* (Speta, 1998a; Forrest and Jong, 2004; Wetschnig *et al.*, 2007) and $2n = 12, 14$ in *O. saundersiae* (Obermeyer, 1978; Speta, 1998a). However, some morphological features, including the large and sheathing leaves, fleshy tepals, acute capsules and irregularly compressed seeds and biogeography are shared. Although some plastid molecular trees (Pfosser and Speta, 1999; Wetschnig *et al.*, 2007) showed both genera to be monophyletic, our combined results place *O. saundersiae* inside *Galtonia*. Therefore, until new molecular evidence is available, we suggest treating it as a member of *Galtonia*. Related to this matter, Hammet and Murray (1993) found that some tetraploid ($2n = 32$) cultivars of *Galtonia candicans* produced inflorescences up to 2 m, with erect flowers, somewhat similar to those of *O. saundersiae*, which support the discussion above.

The Ethesia *clade*

The genus *Ethesia* was described by Rafinesque (1837) to include *O. prasinum* as the sole species (Fig. 4D). Later, Obermeyer (1978) and Müller-Doblies and Müller-Doblies (1996) classified *O. prasinum*, *O. xanthochlorum* (Fig. 4E) and other related species within *O.* subgenus *Urophyllon*. Manning *et al.* (2009a) presented molecular phylogenetic evidence for a close relationship between *O. haalenbergense*, similar to *O. prasinum* (cf. Müller-Doblies and Müller-Doblies, 1996), and *O. xanthochlorum*, both forming a clade sister to *Galtonia*, and taxonomically interpreted as *O.* subgenus *Galtonia* section *Xanthochlora*. The present molecular phylogenetic study corroborates the results of Manning *et al.* (2009a). Both species are well differentiated from *Galtonia* by their smaller size; leaves lacking sheaths, sometimes not coinciding with the flowers; tepals greenish; filaments petaloid, white, showy and spreading; capsule obcordate or widely globose and truncate to retuse at the apex; and seeds compresso-angulose, ovate or discoid with one or two ribs and biseriate per locule (cf. Lindley, 1816; Leighton, 1945; Obermeyer, 1978; Manning *et al.*, 2009a). Moreover, *Galtonia* and *Ethesia* have contrasting distribution areas, being found in summer-rainfall and winter-rainfall regions, respectively. Because of the differences in crucial morphological characters we recognize the genus *Ethesia* (Rafinesque, 1837), although with a minimal recircumscription. Inclusion of *O. prasinum* in *Battandiera* (=*A.* subgenus *Namibiogalum*) as proposed by Manning *et al.* (2009a) is not justified on the basis of the morphology discussed above (cf. Lindley, 1816). On the contrary, this species appears to be closely connected to *O. haalenbergense* (cf. Müller-Doblies and Müller-Doblies, 1996).

The Eliokarmos *clade*

Ornithogalum conicum Jacq., *O. thyrsoides* Jacq., *O. dubium* Houtt., *O. maculatum* and other related taxa (cf. Manning *et al.*, 2007) form a well-characterized group, defined by their ciliate or fimbriate (rarely glabrous) leaves; membranous, ovoid, wide and petaloid bracts; large colourful flowers; concolourous, white, yellow, orange or reddish tepals, sometimes with basal or apical maculae; filaments usually expanded or winged; capsules lanceolate or fusiform, usually hidden among the dry perianth segments; and small abundant and irregularly compressed seeds (0·5–2·0 mm), with papillate to echinulate or puzzle-like testa (cf. Baker, 1897b; Leighton, 1944, 1945; Obermeyer, 1978; Manning *et al.*, 2007). Some have great ornamental value and are widely cultivated (Obermeyer, 1978). These species have been recognized at different ranks (Table 2), with *Eliokarmos*, *Tomoxis* Raf. and *Lomaresis* Raf. being published first and simultaneously at the generic level (Rafinesque, 1837). *Eliokarmos* has been recently used by Speta (1998a) at that rank.

Species such as *O. constrictum* F.M.Leight., *O. bicornutum* F.M.Leight., *O. hispidum* Hornem. and other relatives produce capsules and seeds similar to those of section *Aspasia*, but they differ in the long sheathing and ascending leaves, with patent blades arranged at different levels and a tubular cataphyll along the stem, usually not coinciding with the flowers,

bracts narrower and apiculate or aristate, flowers smaller, and tepals usually having a darker longitudinal band only apparent on the abaxial side (cf. Obermeyer, 1978). These species were included in *O.* subgenus *Aspasia* group Hispidae (cf. Obemeyer, 1978) or in *O.* section *Hispidaspasia* (cf. Müller-Doblies and Müller-Doblies, 1996).

The phylogenetic studies of Manning *et al.* (2004, 2009*a*) revealed that all these species form a strongly supported clade. In this clade, two well-supported subclades can be identified: one comprising *O. maculatum* and *O. rupestre*, and the other grouping the rest of species of sections *Aspasia* and *Hispidaspasia*. Our phylogenetic data confirm the findings of Manning *et al.* (2009*a*), which would support the independent status of *Phaeocles* Salisb. (Salisbury, 1866), including *O. maculatum* and *O. rupestre*, apart from the rest of section. These taxa are peculiar in their glabrous leaves, a rare character in the group. However, no other relevant differences to the rest of the related taxa seem to exist, and therefore we prefer to accept a single genus *Eliokarmos* (including *Phaeocles*) to group all taxa discussed in these paragraphs. This concept is similar to that proposed by Speta (1998*a*), with the exclusion of taxa belonging to *O.* group Angustifoliati (*sensu* Obermeyer, 1978) that is phylogenetically distant from this group and which we recognize as the genus *Nicipe*. Further studies and a more extensive sampling in this group are needed to shed more light on phylogenetic relationships within this clade and on eventual recognition of subgeneric ranks.

The *Avonsera* clade

Ornithogalum convallarioides is endemic to Madagascar and is characterized by its wide, pseudopetiolate leaves, loosely racemose inflorescence (usually with two flowers per bract in the lower part), small bracts; tepals completely white and connate at the basal part, filaments tapering, connate and adnate to the perianth, capsules retuse and trilobate and seeds large and ovoid (cf. Speta, 1998*a*; Wetschnig *et al.*, 2007). The occurrence of two flowers per bract is an autapomorphy within Ornithogaloideae, though it is shared with the genus *Oziroë* Raf. (Guaglianone and Arroyo-Leuenberger, 2002), the only representative of Oziroëoideae (Speta, 1998*a*, *b*). The trilobate capsules have a peculiar structure with each lobe having a longitudinal central furrow (cf. Wetschnig *et al.*, 2007; fig. 3·5), much resembling the six-lobed capsules of *Ornithogalum sensu stricto*. The genus *Avonsera* was described by Speta (1998*b*) to group *O. convallarioides* (the type species) and *Resnova lachenalioides* (Baker) Van der Merwe, arguing that it was the only genus having a multinerved perigone in Hyacinthoideae (the subfamily into which it was erroneously misplaced). Molecular phylogenetic studies by Wetschnig *et al.* (2007) and Manning *et al.* (2009*a*) demonstrated *Avonsera* (*sensu* Speta, l.c.) to be polyphyletic. *Resnova* species were true Hyacinthoideae, sister to species of *Ledebouria*, whereas *A. convallarioides* nested unequivocally within Ornithogaloideae. Therefore, Manning *et al.* (2009*a*) proposed creation of subgenus *Avonsera* within *Ornithogalum*. Our phylogenetic analyses show *O. convallarioides* to be an isolated clade, probably sister to the Mediterranean species of *Ornithogalum* plus those of *Elsiea* and *O.* subgenus *Aspasia*

group Angustifoliati (Obermeyer, 1978), though its relationships are not fully resolved or supported. These morphological, phylogenetic and biogeographical (Malagasy endemism) characters warrant recognition of the so-far monotypic *Avonsera* as an independent genus.

The *Neopatersonia* clade

Schönland (1912) described the genus *Neopatersonia* to include *N. uitenhagensis* Schönland. Later, Lewis (1952) added *N. namaquensis* G.J.Lewis and *N. falcata* G.J.Lewis, to complete the three traditionally accepted species in the genus. As usually defined, *Neopatersonia* is characterized by the tepals fused in a short basal tube, filaments adnate and somewhat connate at the base (autapomorphy), stigma long trilobate and somewhat reflexed, capsule lanceolate, acute, and seeds subglobose or urceolate with pitted puzzle-like or granulate testa (cf. Schönland, 1912; Lewis, 1952; Jessop, 1975). Different classifications have treated them (Table 2) as *Neopatersonia* (Schönland, 1912; Lewis, 1952; Speta, 1998*a*, *b*), *Ornithogalum* subgenus *Neopatersonia* (Hutchinson, 1934), *O.* subgenus *Ornithogalum* section *Neopatersonia* (Manning *et al.*, 2009*a*), or as members of a widely defined *Ornithogalum* (Manning *et al.*, 2004). Speta (1998*a*, *b*) accepted *Neopatersonia* as a member of Hyacinthaceae, though with doubts about its possible inclusion in Ornithogaloideae. Molecular studies (Manning *et al.*, 2004, 2009*a*) revealed a close relationship between *Neopatersonia* and *O. rotatum*, a species first included in *O.* section *Monarchos* (Müller-Doblies and Müller-Doblies, 1996), and recently placed in *O.* section *Neopatersonia*, according to molecular data (Manning *et al.*, 2009*a*). In this analysis *Neopatersonia* plus *O. rotatum* appear as the sister group of the clade formed by the European species of *Ornithogalum* plus the African *Nicipe*. After combining the nuclear and plastid data, our phylogenetic analyses also show clear support for *Neopatersonia* in the traditional sense, to which *O. rotatum* is sister, being both sister to other European and African clades of ornithogaloids. Relationships of *O. rotatum* to *Neopatersonia* are supported by shared floral characters (e.g. tepals connate at the base, filaments connate and adnate), and inclusion of that species into *Neopatersonia* is therefore justified.

The *Elsiea* clade

Leighton and Salter (1944) described the genus *Elsiea* for peculiar plants growing in permanently wet habitats, with poorly developed and subrhizomatous bulbs, connate tepals and adnate filaments (Fig. 4C). Two species were first included in the new genus: *E. corymbosa* F.M.Leight. (currently *O. esterhuyseniae*) and *E. flanaganii* (Baker) F.M.Leight. (currently *O. paludosum* Baker). However, Obermeyer (1978) found this segregation unjustified, since she was not able to corroborate the fusion of perianth segments. Müller-Doblies and Müller-Doblies (1996) placed both taxa, together with *O. flexuosum* (Thunb.) U.Mull.-Doblies & D.Müll.-Doblies and *O. dregeanum* Kunth, in series *Flexuosa* of *O.* subgenus *Urophyllon* section *Helogalum* U.Müll.-Doblies & D.Müll.-Doblies, on the basis of the poorly developed bulbs.

However, *O. synanthifolium* F.M.Leight., which belongs to *O.* subgenus *Aspasia* group Aspasiae, also shows this type of bulb and also occurs in permanently wet habitats (cf. Manning *et al.*, 2007). Consequently, this bulb character appears to be a morphological convergence to that peculiar environment (cf. Manning *et al.*, 2009a), and thus it is not suitable for systematics. Our phylogenetic studies confirm this idea, since *O. esterhuyseniae* falls in an isolated position in its own clade, far away from *O. paludosum*, which is placed together with taxa of *O.* section *Linaspasia* (the *Nicipe* clade). These results agree with those presented by Manning *et al.* (2009a), who proposed *O.* subgenus *Ornithogalum* section *Elsiea* to include only *O. esterhuyseniae*, and also demonstrate that proposals by Leighton and Salter (1944) and Müller-Doblies and Müller-Doblies (1996) are not supported from a phylogenetic point of view. However, phylogenetic divergence of these groups is reasonable on the basis of morphological and biogeographical evidence. First, *O. esterhuyseniae* (=*Elsiea corymbosa*) has a corymbose inflorescence, tepals white and connate, filaments adnate, ovary obovoid and stipitate, and capsule black (cf. Obermeyer, 1978; Manning *et al.*, 2009a), and it is restricted to a small mountainous area in south-west South Africa. Secondly, *O. paludosum*, *O. flexuosum* and *O. dregeanum* have long and narrow racemose to spicate inflorescences, tepals and filaments free, ovary sessile, and capsule not black coloured (cf. Obermeyer, 1978), and occur in the eastern part of south Africa, as far north as Zambia and Malawi (cf. Obermeyer, 1978; Müller-Doblies and Müller-Doblies, 1996). The isolated phylogenetic position of *O. esterhuyseniae*, together with its characteristic syndrome of morphological features, warrants recognition of *Elsiea* as a monotypic genus.

The Nicipe clade

This clade includes *O. juncifolium* Jacq. (Fig. 4B), *O. graminifolium* Thunb., *O. gracillimum* R.E.Fr., *O. sephtonii* Hilliard & B.L.Burtt. and *O. paludosum*, a group of taxa growing in eastern and southern Africa and forming a strongly supported clade. They have been recognized in the past at different ranks (Table 2), including *Nicipe* (Rafinesque, 1837), *O.* group Angustifoliati (Obermeyer, 1978) and *O.* section *Linaspasia, Vaginaspasia, Nanaspasia* and *Helogalum* (Müller-Doblies and Müller-Doblies, 1996). Some morphological features characterize this clade, such as bulbs mostly with membranous tunics, usually ending abruptly in an epigeous neck, occasionally surrounded by tubular, transversally banded and epigeous cataphylls; leaves usually occurring with flowers, numerous, all emerging almost at the same level from the bulb neck, often filiform with enrolled margins, rarely flat and broader or even coriaceous and boat-shaped; inflorescence racemose, cylindrical to subcorymbose; bracts small and aristate, auriculate and sometimes denticulate at the base; tepals white to yellowish on the adaxial side, and usually with a dark longitudinal band on the abaxial one, almost free to fused ≤ one-third; capsule trigonous-elliptical to trilobate-turbinate, usually hidden among the dry perianth segments; and seeds variable in size and irregularly compressed (cf. Leighton, 1944, 1945; Obermeyer, 1978; Müller-Doblies and Müller-Doblies, 1996; Manning *et al.*, 2009a).

According to this evidence, we accept this group at the generic rank, with the name *Nicipe*. As here circumscribed, this genus includes several groups that are quite well characterized morphologically and have peculiar distribution patterns. Species from eastern South Africa to Kenya (*O. sephtonii* and *O. gracillimum*) produce turbinate capsules, trilobate in section, and form a clade in our combined tree. *Ornithogalum baurii* Baker and *O. diphyllum* Baker share a similar fruit structure, as pointed out by Manning *et al.* (2007). Species from the western to eastern Cape (*O. graminifolium*, *O. juncifolium* and *O. paludosum*) also form a monophyletic group, and they have elliptical capsules, trigonous in section with blunt angles. Related to this group, species of *O.* series *Zebrinella*, such as *O. monophyllum* Baker, *O. anguinum* F.M.Leight. ex Oberm. and *O. zebrinellum* U.Müll.-Doblies & D.Müll.-Doblies show characteristic tubular, transversally banded cataphylls.

Nicipe as recognized here is mostly congruent with *O.* group Angustifoliati (Obermeyer, 1978), though it also includes *O. pilosum* L.f., a species Obermeyer placed in *O.* group Hispidae. That concept is supported by both molecular data (M. Martínez-Azorín *et al.*, unpubl. res.) and morphology, as this species lacks the typical vaginate, superposed and clearly distant leaves characterizing the latter group, as pointed out by Müller-Doblies and Müller-Doblies (1996). Although the traditional concept of *O.* group Angustifoliati included plants with narrow to filiform leaves, *Nicipe* as treated here includes a wide range of leaf morphology, usually associated with particular habitats. Taxa such as *O. baurii*, *O. pilosum*, *O. natalense* Baker and *O. aloiforme* Oberm. have wide, oblong-lanceolate and flat leaves, whereas others including *O. paludosum* and *O. flexuosum* have flattened to terete, somewhat succulent leaves. These species grow mostly on moist soils or high mountain environments. *Ornithogalum britteniae* F.M.Leight. ex Oberm. is an extremely rare plant with evergreen, distichous, coriaceous, boat-shaped leaves with fimbriate margins resembling those of some *Gasteria* Duval, which grows in grassy karroid dwarf shrubland (Dold, 2003). Another group of species (*O. annae-ameliae* U.Müll.-Doblies & D.Müll.-Doblies, *O. campanulatum* U.Müll.-Doblies & D.Müll.-Doblies, *O. synadelphicum* U.Müll.-Doblies & D.Müll.-Doblies and *O. verae* U.Müll.-Doblies & D.Müll.-Doblies) have peculiar floral features, such as tepals fused, and filaments adnate to perigone and/or connate into a short tube. Connation of perigone segments is a plesiomorphy which has evolved several times in different genera of the subfamily (Fig. 3C), including *Pseudogaltonia, Dipcadi, Battandiera, Galtonia, Avonsera, Neopatersonia* and *Elsiea*. Furthermore, *Battandiera* and *Galtonia* include species with either connate or almost free tepals, as in *Nicipe*.

From a phylogenetic point of view, *Nicipe* is sister to the rest of Eurasian genera of Ornithogaloideae, and it could constitute the link with the lineages from southern Africa (cf. Manning *et al.*, 2009a), where the origin of this genus would be placed (Feinbrun, 1941). Furthermore, the Kenyan species *O. gracillimum* provides evidence for this (Fig. 2). Migrations across East Africa would have connected floristic regions of both hemispheres in two different ways. On the one hand, the 'arid corridor' or 'arid track' migration

hypothesis (cf. Verdcourt, 1969; Thulin, 1994; Jürgens, 1997; Linder *et al.*, 2005; Hoyo and Pedrola-Monfort, 2006) and, on the other, the high-altitude corridor (cf. Linder *et al.*, 2005; Devos *et al.*, 2009), which jointly would have favoured disjunctions in genera such as *Colchicum* L. (including *Androcymbium* Willd.), *Euryops* (Cass.) Cass., *Delosperma* N.E.Br., *Matthiola* W.T.Aiton, *Albuca*, *Battandiera*, *Dipcadi*, *Stellarioides* and *Nicipe* itself.

The Cathissa *clade*

The Mediterranean species traditionally placed in *O.* subgenus *Cathissa* (*O. concinnum* Salisb., *O. broteroi* M.Laínz and *O. reverchonii* Lange ex Willk.) are characterized by their leaves glabrous, lanceolate to tapering; tepals white and ovoid or obovoid; filaments lanceolate to tapering; capsule ovoid to elliptical; and seeds irregularly flattened with papillate or puzzle-like testa (Figs 5A–C and 6A–C) (cf. Zahariadi, 1980; Pastor, 1987; Moret *et al.*, 1990; Martínez-Azorín *et al.*, 2006, 2007). These species were placed in *Cathissa* (Salisbury, 1866; Speta, 1998*a*, *b*, 2001), a group treated as a genus, subgenus or section (Table 2). Our phylogenetic results confirm the monophyly of this group of three currently accepted taxa (Martínez-Azorín *et al.*, 2007), which are well characterized morphologically and are restricted to the western part of the Iberian Peninsula and western Morocco. Acceptance of *Cathissa* at the generic rank is thus justified.
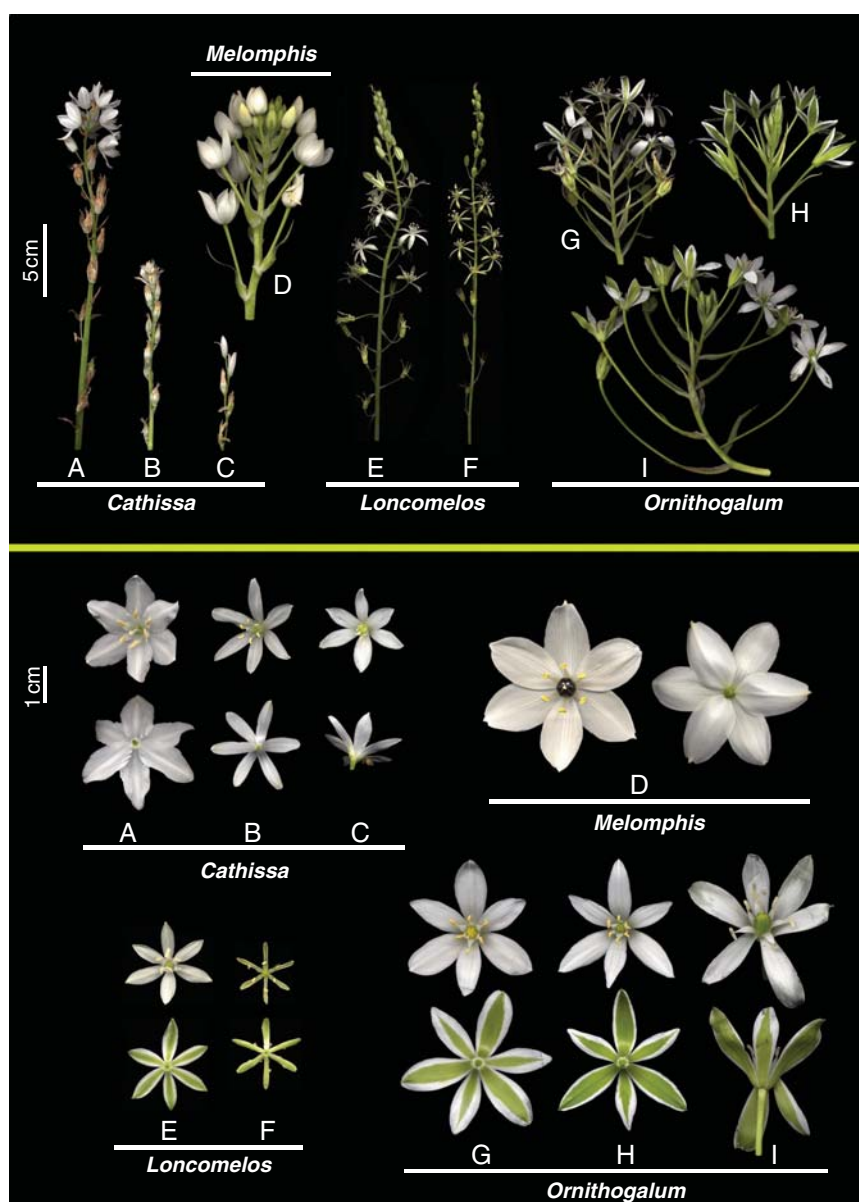
FIG. 5. Inflorescence and flower features of most of the Eurasian genera of Ornithogaloideae: (A) *Cathissa reverchonii*; (B) *C. concinna*; (C) *C. unifolia*; (D) *Melomphis arabica*; (E) *Loncomelos narbonense*; (F) *L. pyrenaicus*; (G) *Ornithogalum baeticum*; (H) *O. bourgaeanum*; (I) *O. divergens*.
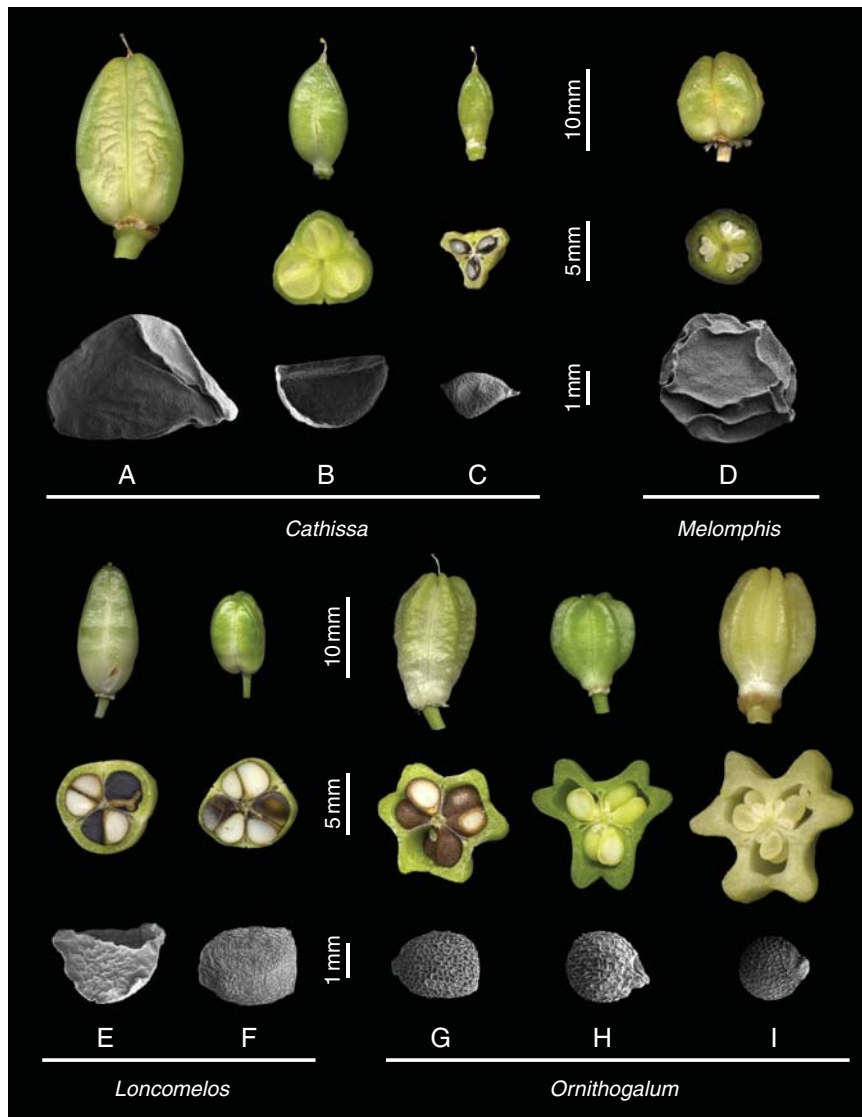
Fɪɢ. 6. Capsule (lateral and section views) and seed features of most of the Eurasian genera of Ornithogaloideae: (A) *Cathissa reverchonii*; (B) *C. concinna*; (C) *C. unifolia*; (D) *Melomphis arabica*; (E) *Loncomelos narbonense*; (F) *L. pyrenaicus*; (G) *Ornithogalum baeticum*; (H) *O. bourgaeanum*; (I) *O. divergens*.

The Melomphis *clade*

In our phylogenetic analyses, *O. arabicum*, traditionally included in *Melomphis* (Rafinesque, 1837; Garbari *et al.*, 2008), *Caruelia* Parl. (Parlatore, 1854), *O.* subgenus *Caruelia* (Parl.) Baker (Baker, 1872) or *Myanthe* Salisb. (Salisbury, 1866), appears as an independent clade, the position of which is not fully resolved as previously demonstrated by Manning *et al.* (2009a). *Melomphis* species are distributed in the Mediterranean basin eastwards, and are characterized by the corymbose to pseudocorymbose inflorescence, globose and shining black ovary, plain white tepals, globose and truncate to retuse capsule and irregularly compressed seeds with granulate testa (Figs 5D and 6D). Some authors have recently accepted the independence of this genus (Garbari *et al.*, 2008). Although a wider sampling is needed to clarify relationships to other ornithogaloid clades, notable morphological differences exist to justify segregation of *Melomphis* at the generic rank. The globose and

shining ovary of these species is similar to that occurring in the South African *O. saundersiae* (cf. Baker, 1891), here treated as *Galtonia*. Therefore, it can be interpreted as a morphological convergence between these groups, which are distant from each other in the phylogenetic analyses. Morphological features exist which allow easy differentiation of these groups, including tepals fleshy, reflexed and persistent for a long time in fruit, and capsule acute and ovate in *O. saundersiae*.

The Loncomelos *clade*

The species traditionally included in *O.* subgenus *Beryllis* are characterized by their concolourous leaves long and tapering; inflorescence racemose, much longer than wide; tepals white or rarely yellowish with a green longitudinal band on the abaxial side; filament expanded in the lower half; capsule trigonous with obtuse angles, ovate-lanceolate; and

seeds biseriate, horizontally disposed and irregularly compressed, with papillate, rugose testa (Figs 5E and F and 6E and F) (cf. Baker, 1872; Zahariadi, 1980; Cullen, 1984; Wittmann, 1985; Feinbrun, 1986; Pastor, 1987; Moret *et al.*, 1990; Rechinger, 1990; Speta, 1998*a*; Martínez-Azorín *et al.*, 2010*a*). These plants have been placed in different taxa (Table 2), including the genus *Loncomelos* (Rafinesque, 1837). Our phylogenetic results support the monophyly of this group of plants. *Ornithogalum narbonense* L. and *O. pyrenaicum* L. form a strongly supported clade sister to *Ornithogalum sensu stricto* plus *Honorius*, which is clearly differentiated by the morphology of inflorescences, capsules and seeds. The inclusion of *Loncomelos* in the synonymy of *Ornithogalum* section *Ornithogalum*, as proposed by Manning *et al.* (2009*a*), generates a highly heterogeneous group mixing different capsule and seed morphology, characters that have been treated as highly informative phylogenetically. Therefore, we adopt the generic rank for *Loncomelos*, following the concept of Wittmann (1985) and Speta (1998*a*), on the basis of clear morphological and phylogenetic evidence. Similarly, segregation of *Loncomelos* has been accepted increasingly in recent times (cf. Speta, 1998*a*, *b*, 2000, 2006; Spies, 2004; Peruzzi *et al.*, 2007; Ravenna, 2007; Garbari *et al.*, 2008).

Maire (1958) included the north African *O. sessiliflorum* in *O.* subgenus *Beryllis*, mainly on the basis of its long and narrow inflorescence, whereas Stedje (2001*b*) connected it to *Cathissa*. However, this species shows other evident differences with regard to the rest of the Eurasian and north African taxa of both cited groups, such as the flowers with a green band visible on both sides of tepals, the subglobose capsule, and the compressed seeds obliquely stalked in each locule and with puzzle-like testa (Fig. 4M and O). All those features strongly connect it to *Stellarioides*, which led Speta (2001) to establish the combination *S. sessiliflora* (Desf.) Speta. The exclusion of *O. sessiliflorum* from *O.* subgenus *Beryllis* (=*Loncomelos*) gives homogeneity to the latter as regards to testa morphology (only granulate or rugose, never puzzle-like as reported by Moret *et al.*, 1990).

The *Honorius* clade

Ornithogalum nutans L. is characterized by the racemose inflorescence; filaments tapering, with two apical lobes overtopping the anther; the capsule nodding at maturity (autapomorphy) and with six weak ribs in section and globose seeds with prominently reticulate testa (Fig. 4A) (cf. Baker, 1872; Zahariadi, 1980; Uysal *et al.*, 2005). Due to these features, it was segregated at different ranks (Table 2), of which *Honorius* (Gray, 1821) has priority at the generic rank. Our phylogenetic results place *O. nutans* as sister to the *Ornithogalum sensu stricto* clade. Phylogenetic and morphological evidence justifies its segregation at the generic rank, as accepted by some recent authors (cf. Holub, 1976; Speta, 2000; Garbari *et al.*, 2008). The recently described *O. chetikianum* Uysal, Ertuğrul & Dural, a Turkish taxon close to *O. nutans*, is said to have leaves with a longitudinal greyish band, which connects it to many representatives of *Ornithogalum sensu stricto*. A wider sampling of related taxa

from Anatolia and the Middle East is still needed to improve our knowledge of phylogenetic relationships within *Honorius*.

The *Ornithogalum* clade

The final clade corresponds to *Ornithogalum sensu stricto*, which includes Eurasian and North African species well characterized by their long linear to oblong-lanceolate leaves, sometimes with a white longitudinal band on the adaxial side; inflorescence corymbose or pseudocorymbose; tepals white with a longitudinal green band only visible on the abaxial side; capsule obovate or oblong, truncate with six evident ribs in section; and seeds globose with prominently reticulate testa (Figs 5G–I and 6G–I) (cf. Baker, 1872; Cullen, 1984; Feinbrun, 1986; Moret *et al.*, 1990; Rechinger, 1990; Speta, 1998*a*; Martínez-Azorín *et al.*, 2009, 2010*b*). The white longitudinal band is due to an interruption of palisade tissue in the central portion of the leaf (cf. Peruzzi *et al.*, 2007), being an apomorphy absent in the early diverging lineages of the present clade. This character is also present in a few species of *Albuca*.

Species in this clade represent the typical, strict concept of *Ornithogalum*, which includes its type, *O. umbellatum* L. (cf. Stearn, 1983). Baker (1872) grouped them into *O.* subgenus *Heliocharmos*, which was reduced later to *O.* section *Heliocharmos* by Engler (1888), and which Zahariadi (1965, 1980) divided in eight subgenera (cf. Cullen and Ratter, 1967) on the basis of features such as the type of seed germination (hypogeal vs. epigeal), concrescence and consistence of bulb scales, presence or absence of central band on the leaves, inflorescence structure, position of fruting pedicels, capsule shape, etc. However, our sampling is insufficient and does not cover some of those subgenera; thus further studies are necessary to evaluate their monophyly and significance. In our phylogenetic studies, all sampled taxa of this group form a clade, strongly supported in the Bayesian analysis. Furthermore, this clade is relatively derived in the subfamily, a fact that could explain the large number of species and the scant morphological differentiation among these, probably due to recent speciation.

TAXONOMIC PROPOSAL

On the basis of the evidence presented above, 19 phylogenetically monophyletic groups are accepted (Table 3) and are treated here as independent genera since they are supported by syndromes of morphological characters. No new taxa need to be described to accommodate these monophyletic groups at generic rank (cf. Manning *et al.*, 2009*a*). All genera accepted here are already described and most have been used increasingly in recent times (cf. Holub, 1976; Speta, 1998*a*, *b*, 2000, 2001, 2006; Spies, 2004; Peruzzi *et al.*, 2007; Ravenna, 2007; Garbari *et al.*, 2008). They are well characterized morphologically, and are here circumscribed in such a way that allows easy definition and makes easier subsequent attribution of a taxon to a given genus. Similarly, most of combinations required are available, with the exception of those affecting the newly accepted or resurrected genera, given below.

TABLE 3. *Key for identification of taxa in Ornithogaloideae*

1a.	Floral bract with small bracteoles. Tepals all fused over two-thirds of their length, into a cylindrical tube, slightly swollen at the base and somewhat curved; filaments inserted at the mouth of the tube	**1. Pseudogaltonia**
1b.	Floral bract without bracteoles (if present, then leaves narrowed in a pseudopetiole). Tepals free or fused into a shorter, campanulate to cylindrical, straight tube; filaments free, connate or adnate to the tube	2
2a.	Tepals with a broad and dark longitudinal band – green to brownish, evident on both sides and usually associated with three to many aggregated medial nerves	3
2b.	Tepals concolour, exceptionally with dark maculae at the base or apex, or sometimes with a broad longitudinal coloured band, only visible on the abaxial side, not well defined along the medial nerve	8
3a.	Ovary with two prominent dorsal keels on each carpel. Plants with only one leaf (exceptionally up to three), usually flat on the ground	**4. Trimelopter**
3b.	Ovary without such prominent dorsal keel. Plants usually with numerous leaves, erect or spreading (exceptionally solitary, varying in morphology)	4
4a.	Seed obliquely stalked in each locule. Inflorescence usually subspiciform, dense, and many flowered	**7. Stellarioides**
4b.	Seed horizontally stalked in each locule. Inflorescence usually racemose to subcorymbose, lax, with long pedicellate flowers	5
5a.	Capsule widely quadrate in outline, deeply three lobed; seeds uniseriate in each locule	6
5b.	Capsule ovate, oblong or obovate in outline, trigonous to trilobate; seeds biseriate in each locule (exceptionally uniseriate)	7
6a.	Inflorescence subspicate, mostly secund, with shortly pedicellate flowers. Outer tepals curved outwards, inners long connivent to form a cylindrical tube with reflexed tips	**2. Dipcadi**
6b.	Inflorescence racemose, cylindrical, conical or subpyramidal, with long pedicellate flowers. Tepals all similar and spreading	**3. Battandiera**
7a.	Tepals usually dimorphic: the outers mucronate and the inners cucullate or with an inflexed flap at the apex; filaments usually with basal constrictions; ovary with paraseptal keels; style trigonous in section, prismatic to obtriangular or sometimes thin or tapering; stigma not capitate, usually trilobed	**5. Albuca**
7b.	Tepals monomorphic, all similar; filaments without basal constrictions; ovary without paraseptal keels; style circular in section, subcylindric, usually deflexed; stigma capitate	**6. Coilonox**
8a.	Tepals fused at the base	9
8b.	Tepals completely free at the base	12
9a.	Flowers nodding. Tepals fused into a long campanulate tube of approx. half of their length. Stamens hidden among the perianth lobes	**8. Galtonia**
9b.	Flowers patent to erect-patent. Tepals fused into a tube ≤ one-third of their length. Stamens clearly visible	10
10a.	Leaves tapering at the base and pseudopetiolate; inflorescence usually with two flowers per bract in the lower part; bracteoles present in the upper flowers; capsule retuse or truncate at the apex	**11. Avonsera**
10b	Leaves sheathing at the base, never pseudopetiolate; inflorescence always with one flower per bract; bracteoles absent; capsule acute to subacute at the apex	11
11a.	Tepals ≤ half the length of capsule; seeds piriform or subglobose; filaments of stamen connate	**12. Neopatersonia**
11b.	Tepals longer than capsule or rarely slightly shorter; seeds angular, irregularly compressed; filaments of stamen free to adnate, exceptionally connate	**14. Nicipe**
12a.	Ovary globose, shining black. Inflorescence subcorymbose	13
12b.	Ovary fusiform to oblong, green or yellow. Inflorescence racemose to corymbose	14
13a.	Capsule ovate, with acute apex. Tepals fleshy, long persistent and reflexed in young fruits	**8. Galtonia**
13b.	Capsule subglobose, with truncate apex. Tepals not fleshy, withering soon and never reflexed in fruit	**16. Melomphis**
14a.	Tepals bearing a wide longitudinal band, green, pinkish or brownish, along the medial nerve, only visible on the abaxial side	15
14b.	Tepals concolour, without a longitudinal coloured band on the abaxial side, sometimes with maculae at the base or apex	19
15a.	Capsule with six evident ribs in section. Seeds globose, with reticulate testa	16
15b.	Capsule trigonous or trilobate in section. Seeds irregularly compressed, with papillate to echinulate or puzzle-like testa	17
16a.	Infloresece corymbose to racemose, with basal pedicels >1 cm. Flowers stellate at the anthesis, erect to erect-patent; filaments lanceolate to tapering, attenuate at the apex	**19. Ornithogalum**
16b.	Inflorescence racemose, with basal pedicels ≤1 cm long. Flowers campanulate at the anthesis, erect to slightly nodding; filaments tapering, at least the inner ones with two evident lobes or teeth accompanying the anther	**18. Honorius**
17a.	Plants tall, ≤140 cm. Leaves glabrous, not sheathing the stem by a tubular cataphyll; inflorescence (excluding the stem) ≤50 cm long; capsule not hidden by the withered perianth	**17. Loncomelos**
17b.	Plants small to middle size, ≤50 cm. Leaves usually ciliate or hirsute, sheathing the stem by a tubular cataphyll; inflorescences shorter; capsule usually hidden by the withered perianth	18
18a.	Leaves commonly not occurring with the flowers, sheathing and ascending upon the stem, being the limbs patent and usually arranged at different heights. Seeds mostly apiculate (comma-shaped), usually tuberculate or long papilose	**10. Eliokarmos**
18b.	Leaves usually occurring with the flowers, all emerging almost at the same level and disposed mostly on an epigeous neck. Seeds many angled, smooth	**14. Nicipe**

Continued

TABLE 3. *Continued*

19a.	Flowers greenish. Filaments petaloid, showy, pure white, and spreading. Capsule obcordate or widely globose and truncate to retuse at the apex, equal or wider than long	**9. Ethesia**
19b.	Flowers white, yellow or orange. Filaments neither clearly spreading nor showy. Capsule elliptical, longer than wide	20
20a.	Tepals white, yellow, orange or reddish, usually with evident dark maculae at their base or apex; leaves usually ciliate or fimbriate on the edge, or pilose on the blade, rarely glabrous; filaments subulate or lanceolate and flat, usually with quadrate basal expansions or with two erect lobes concealing the ovary	**10. Eliokarmos**
20b.	Tepals always white, not maculate; leaves glabrous; filaments flat, lanceolate to tapering, without abrupt basal expansions	21
21a.	Plants with scarcely developed bulbs, subrhizomatous. Inflorescence corymbose. Ovary stipitate. Capsule black	**13. Elsiea**
21b.	Plants with swollen, well-developed bulb. Inflorescence racemose to spiciform. Ovary not stipitate. Capsule pale brown	**15. Cathissa**

1. Pseudogaltonia Kuntze in Jahrb. Königl. Bot. Gart. Berlin 4: 274. 1886 [nom. alternat.] ≡ *Hyacinthus* section *Pseudogaltonia* Kuntze in Jahrb. Königl. Bot. Gart. Berlin 4: 274. 1886 [nom. alternat.] – Holotype: *P. pechuelii* Kuntze ≡ *Hyacinthus pechuelii* Kuntze = *P. clavata* (Mast.) E. Phillips ≡ *Galtonia clavata* Mast.

= *Lindneria* T. Durand & Lubbers in Bull. Soc. Bot. France 36: CCXVII. 1890 – Holotype: *L. fibrillosa* T. Durand & Lubbers = *P. clavata* (Mast.) E. Phillips

Plants large. Bulb large, with outer tunics cartilaginous and fibrous. Leaves widely lanceolate, flat, long, acute, glabrous. Inflorescence in a loose pyramidal raceme; bracts linear-acuminate; bracteoles (prophylls) present. Tepals white with greenish or greyish longitudinal band, fused over two-thirds of their length, into a tube approx. 3 cm long, slightly swollen at the base and somewhat curved; filaments exerted, flat, insert at the mouth of the tube; style filiform and long (>2 cm). Capsule quadrate, truncate, and deeply trilobate. Seeds flat, disciform and uniseriate in each locule, with five to seven angled polygonal subisodiametric testa cells with shallow depressions and pitted surface.

Chromosome number: $2n = 18$ (cf. Speta, 1998a; Forrest and Jong, 2004).

Number of species: 2 (cf. Manning *et al.*, 2009b).

Distribution: north-western South Africa, Namibia and Botswana.

2. Dipcadi Medik. in Hist. & Commentat. Acad. Elect. Sci. Theod.-Palat. 6: 431. 1790 – Holotype: *D. serotinum* (L.) Medik. ≡ *Hyacinthus serotinus* L.

= *Zuccagnia* Thunb., Nov. Gen. Pl. 9: 127. 1798. – Type: *Z. viridis* (L.) Thunb. ≡ *D. viride* (L.) Moench.

= *Uropetalon* Burch. ex Ker Gawl. in Bot. Reg. 2: t. 156. 1816 ≡ *D.* ser. *Uropetalon* (Burch. ex Ker Gawl.) J.C. Manning & Goldblatt in Taxon 58(1): 99. 2009 – Type: *U. glaucum* Burch. ex Ker Gawl. in Bot. Reg. 2: t. 156. 1816 ≡ *D. glaucum* (Burch. ex Kew Gawl.) Baker

= *Polemannia* K. Bergius ex Schltdl. in Linnaea 1: 250. 1826, nom. rej. [non *Polemannia* Eckl. & Zeyh. in Enum. Pl. Afric. Austral. 3: 347. 1837, nom. cons. (*Umbelliferae*)] – Type: *P. hyacinthiflora* Berg. ex Schltdl. = *D. brevifolium* (Thunb.) Fourc.

= *Tricharis* Salisb., Gen. Pl. [Salisbury]: 24. 1866 – Type: *T. serotina* (L.) Salisb. ≡ *D. serotinum* (L.) Medik.

Plants small to middle size. Leaves variable, usually linear, flattened or caniculate, or more or less twisted, glabrous to hirsute. Inflorescence racemose or subspiciform, usually secund, with patent or nodding flowers; bracts ovate or attenuate, membranous; bracteoles absent. Tepals lanceolate-tapering, fused at the base into a tube approx. one-quarter to one-third (to two-thirds) of their length; inner ones suberect or connivent and reflexed at the apical third; outer ones reflexed, sometimes with filiform caudate apendixes; filaments short, linear to flatish, adnate to the tube and included. Capsule deeply 3-lobed, quadrate in outline, truncate at the apex, rarely umbonate, sometimes stipitate. Seeds black, discoid, flat, horizontally stacked and uniseriate per locule, with 5–6 angled polygonal subisodiametric or up to twice as long as broad testa cells with shallow depressions and smooth or pitted surface.

Chromosome number: $2n = 8, 12, 18, 20, 24, 36, 64$ (cf. Speta, 1998a, Jones and Smith, 1967).

Number of species: approx. 30 (cf. Obermeyer, 1964; Speta, 1998a; Manning *et al.*, 2002, 2009a).

Distribution: south, east and north Africa, Socotra, Madagascar, Europe, Middle East and India.

3. Battandiera Maire in Bull. Soc. Hist. Nat. Afr. Nord 17(3): 125. 1926 ≡ *Ornithogalum* section *Trineuron* Batt. in Bull. Soc. Bot. France 63: 195. 1919 – Holotype: *B. amoena* (Batt.) Maire ≡ *O. amoenum* Batt.

= *Ornithogalum* section *Namibiogalum* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert. 107(5–6): 487. 1996 [basion.] ≡ *Albuca* subgenus *Namibiogalum* (U.Müll.-Doblies & D.Müll.-Doblies) J.C.Manning & Goldblatt in Taxon 58(1): 92. 2009 – Holotype: *B. rautanenii* (Schinz) Mart.-Azorín, M.B.Crespo & Juan ≡ *O. rautanenii* Schinz.

Plants usually middle size. Bulb ovoid, often with an evident neck at the apex with transverse thin darker nerves; outer tunics numerous, coriaceous, coarse and greyish, protecting the bulb. Leaves usually narrowly lanceolate to filiform, flat to folded, glabrous and somewhat glaucous and sometimes with darker spots at the base beneath; bracteoles absent. Inflorescence conical to subpyramidal, elongating with age, sometimes with a plumose or pendulous apex; bracts membranous, deltoid to filiform, usually longer than flowers. Tepals white or greenish, oblong, linear, obtuse, spreading or rarely reflexed, with a green or brownish longitudinal band visible on both sides (rarely the band indistinct but with darker medial aggregated nerves evident when dried), free or shortly fused into a tube ≤5 mm long; filaments linear-acuminate or ovate-acuminate, sometimes with quadrate basal expansions or shortly adnate to the perianth; ovary ovoid or oblong-globose, trigonous or trilobate, sometimes

stipitate or expanded at the base into a 6-lobed disc . Capsule deeply trilobate with narrow lobes, often widely quadrate in outline, wider than long, truncate at the apex or emarginate, with darker transversal nerves. Seeds large, discoid, flat, horizontally stacked and uniseriate in each locule, with angled and polygonal or slightly undulate testa cells.

Chromosome number: 2n = 20, 24 (cf. Speta, 2001; Vosa, 1980).

Number of species: 8 (according to the present study).

Distribution: arid regions of southern and East Africa (excepting the southern half of South Africa), with a disjoint species in North Africa (*B. amoena*).

Necessary combinations:

Battandiera candida (Oberm.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum candidum* Oberm. in Bothalia 10: 355. 1971 [basion.]

Battandiera donaldsonii (Rendle) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Albuca donaldsonii* Rendle in J. Bot. 34: 131. 1896 [basion.] ≡ *O. donaldsonii* (Rendle) Greenway in Journ. E. Afr. Nat. Hist. Soc. 27: 203. 1969

Battandiera pulchra (Schinz) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum pulchrum* Schinz in Verh. Bot. Ver. Brandenb. 31: 221. 1890 [basion.]

Battandiera rautanenii (Schinz) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum rautanenii* Schinz in Verh. Bot. Ver. Brandenb. 31: 221. 1890 [basion.]

Battandiera seineri (Engl. & K.Krause) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Bulbine seineri* Engl. & K.Krause in Bot. Jahrb. 45: 124. 1910 [basion.]

Battandiera stapffii (Schinz) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum stapffii* Schinz in Bull. Herb. Boiss. 4, App. 3: 42. 1896 [basion.]

Battandiera tubiformis (Oberm.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum candidum* var. *tubiforme* Oberm. in Bothalia 10: 357. 1971 [basion.]

4. Trimelopter Raf., Fl. Tellur. 2: 24. 1837 ≡ *Ardernia* Salisb., Gen. Pl.: 35. 1866 ≡ *Ornithogalum* section *Monarchos* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert. 107(5–6): 470. 1996 ≡ *Albuca* subgenus *Monarchos* (U.Müll.-Doblies & D.Müll.-Doblies) J.C.Manning & Goldblatt in Taxon 58(1): 92. 2009 – Holotype: *T. fuscatum* (Jacq.) Raf. ≡ *O. fuscatum* Jacq. = *T. unifolium* (Retz.) Mart.-Azorín, M.B.Crespo & Juan ≡ *O. unifolium* Retz.

Plants small to middle size. Bulb ovate, outer tunics membranous or coriaceous, greyish, usually with a long neck. Leaf one (rarely ≤3 in cultivation), ovate to elliptical or narrowly oblong, with obtuse to acute apex, glabrous or diversely pubescent, occurring with flowers or withering at flowering time, sheathing into a contracted tubular base, and firm blade, usually appressed to the ground or spreading; bracteoles absent. Inflorescence racemose or pyramidal; bracts deltoid, aristate, auriculate, sometimes with papillate adaxial side and edges. Tepals pale yellow, brownish or whitish, with a central greenish or brownish band visible on both sides (sometimes indistinct on the adaxial side, though associated to evident medial nerves); filaments narrowly ovate, expanded below; ovary ovoid or obovoid, trilobate with three prominent carpels, each one with two longitudinal keels down the back and a groove between. Capsule globose, small (≤4 mm),

trilobate, with two prominent keels on each carpel. Seeds flat, semidiscoid, or irregularly compressed, with a straight side and the other curved, with double ridge, and subpolygonal, granulate testa.

Chromosome number: no data available.

Number of species: approx. 10 (according to the present study).

Distribution: mainly in southern Namibia and western South Africa, spreading to central and north-eastern South Africa.

Necessary combinations:

Trimelopter costatulum (U.Müll.-Doblies & D.Müll.-Doblies) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum costatulum* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert. 107(5–6): 482. 1996 [basion.]

Trimelopter etesiogaripense (U.Müll.-Doblies & D.Müll.-Doblies) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum etesiogaripense* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert. 107(5–6): 476. 1996 [basion.]

Trimelopter etesiogaripense subsp. **longipilosum** (U.Müll.-Doblies & D.Müll.-Doblies) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum etesiogaripense* subsp. *longipilosum* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert. 107(5–6): 478. 1996 [basion.]

Trimelopter dyeri (Poelln.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum dyeri* Poelln. in Ber. Deutsch. Bot. Ges. 61: 209. 1944 [basion.]

Trimelopter monarchos (U.Müll.-Doblies & D.Müll.-Doblies) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum monarchos* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert. 107(5–6): 476. 1996 [basion.]

Trimelopter ovatum (Thunb.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum ovatum* Thunb., Prodr. 62. 1794 [basion.]

Trimelopter ovatum subsp. **oliverorum** (U.Müll.-Doblies & D.Müll.-Doblies) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum ovatum* subsp. *oliverorum* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert. 107(5–6): 474. 1996 [basion.]

Trimelopter pendulinum (U.Müll.-Doblies & D.Müll.-Doblies) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum pendulinum* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert. 107(5–6): 480. 1996 [basion.]

Trimelopter psammophorum (U.Müll.-Doblies & D.Müll.-Doblies) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum psammophorum* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert. 107(5–6): 482. 1996 [basion.]

Trimelopter strigulosum (U.Müll.-Doblies & D.Müll.-Doblies) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum strigulosum* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert. 107(5–6): 480. 1996 [basion.]

Trimelopter unifolium (Retz.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum unifolium* Retz., Obs. 2: 17. 1781 [basion.] = *T. fuscatum* (Jacq.) Raf. ≡ *O. fuscatum* Jacq.

Trimelopter watermeyeri (L.Bolus) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum watermeyeri* L.Bolus in S. African Gard. 21: 13. 1931 [basion.]

5. Albuca L., Sp. Pl., ed. 2. 1: 438. 1762 – Lectotype: *Albuca canadensis* (L.) F.M. Leight. [≡ *Ornithogalum canadense* L. ≡ *A. major* L., *nom. illeg.*]

Plants mostly middle to large size. Bulb hypogeous or epigeous, diverse in size; outer tunics membranous, coriaceous, fibrous or fleshy and green. Leaves variable, usually narrowly lanceolate to filiform, flattened to folded or inrolled, glabrous, hirsute or glandular, sometimes spirally twisted or coiled, and exceptionally with a longitudinal white band. Inflorescence racemose or subcorymbose, glabrous, papillose or glandular; bracteoles absent. Flowers nodding, patent or erect; tepals white to yellow with a broad central greenish to brownish band visible on both sides, whorls dimorphic: the outer ones mucronate, suberect or spreading, and the inner ones cucullate, hooked or with an inflexed flap at the apex, erect and more or less connivent and hiding the stamens and the style; filaments narrowly oblong or linear-lanceolate, more or less expanded at the base, with a constriction or folded basally, sometimes at least the outers with anthers smaller or absent; ovary ovoid to elliptical, with conspicuous paraseptal crests, with many ovules per locule; style as long as the perianth, trigonous in section, prismatic to obtriangular or thin and tapering, sometimes strongly papillate; stigma trilobate, truncate, depressed or conical, sometimes with horns, papillate or fimbriate with long papillae. Capsule ovoid or oblong, acute or obtuse, more or less triangular in section with blunt edges. Seeds black, numerous, flattened, horizontally stacked, semicircular with one straight side forming a thicked ridge and biseriate in each locule (or rarely discoid and uniseriate), with puzzle-like (or rarely granulate) testa.

Chromosome number: $2n = 16, 18, 20, 36, 40$ (cf. Jones and Smith, 1967; Speta, 1998*a*).

Number of species: ranging from 60 to approx. 130 (cf. Speta, 1998*a*; Manning *et al.*, 2002; Phillips, 1926).

Distribution: mainly in southern and east Africa, extending to Ethiopia and Saudi Arabia, and north of Chad and Nigeria.

6. Coilonox Raf., Fl. Tellur. 2: 28. 1837 – Holotype: *C. albucoides* (Aiton) Raf. ≡ *Anthericum albucoides* Aiton

= *Osmyne* Salisb., Gen. Pl. [Salisbury]: 35. 1866 ≡ *Ornithogalum* subgenus *Osmyne* (Salisb.) Baker in J. Linn. Soc., Bot. 13(68): 278. 1872 ≡ *Ornithogalum.* section *Osmyne* (Salisb.) Engl., Nat. Planzenfam. [Engler & Prantl] 2, Abt. 5: 67. 1888 ≡ *Albuca* subgenus *Osmyne* (Salisb.) J.C.Manning & Goldblatt in Taxon 58(1): 93. 2009 ≡ *Monotassa* Salisb., Gen Pl. [Salisbury]: 36. 1866 – Holotype: *Osmyne odorata* (Jacq.) Salisb. [≡ *Ornithogalum odoratum* Jacq.] = *C. secundum* (Jacq.) Speta ≡ *Ornithogalum secundum* Jacq. ≡ *Monotassa secunda* (Jacq.) Salisb.
= *Taeniola* Salisb., Gen Pl. [Salisbury]: 35. 1866 [non *Taeniola* Bonorden, Handb. Allg. Mykol.: 36. 1851 (*Fungi*)] – Holotype: *T. vittata* (Ker Gawl.) Salisb. ≡ *Albuca vittata* Ker Gawl. ≡ *C. vittatum* (Ker. Gawl.) Speta
= *Ornithogalum* section *Monosmyne* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert. 107(5–6): 515. 1996 – Holotype: *Ornithogalum zebrinum* (Baker) Oberm. ≡ *Albuca zebrina* Baker ≡ *C. zebrinum* (Baker) Speta
= *Ornithogalum* ser. *Clavifolia* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert. 107(5–6): 516. 1996 – Holotype: *Albuca unifoliata* Rowley ≡ *C. unifoliatum* (Rowley) Speta

Plants usually medium size. Bulb usually large, hypogeous or epigeous; outer tunics membranous, coriaceous or fleshy and green. Leaves variable, usually narrowly lanceolate to succulent and claviform, glabrous, hirsute or glandular, sometimes spirally twisted or coiled. Inflorescence racemose or subcorymbose, glabrous, hirsute or glandular; bracteoles absent. Flowers spreading, patent; tepals whitish or yellowish with a broad central green band visible on both sides; whorls equal; filaments subulate and narrowly oblong or linear-lanceolate, not constricted and all anthers well developed; ovary ovoid to elliptical, without paraseptal crests, with many ovules per locule; style as long as the perianth, subcylindrical, usually deflexed at anthesis; stigma capitate, long papillate or fimbriate. Capsule ovoid or oblong, acute or obtuse, more or less triangular in section with blunt edges. Seeds black, numerous, flattened, semicircular with one straight side forming a thicked ridge, or discoid, horizontally stacked and biseriate in each locule, with puzzle-like testa.

Chromosome number: $2n = 18$ (cf. Speta, 1998*a*).

Number of species: approx. 30 (cf. Speta, 2001; Manning *et al.*, 2009*a*).

Distribution: mainly in western South Africa, extending to southern Namibia, in winter-rainfall areas.

Necessary combination:

Coilonox paucifolium subsp. **karooparkense** (U.Müll.-Doblies & D.Müll.-Doblies) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum paucifolium* subsp. *karooparkense* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert. 107(5–6): 515. 1996 [basion.]

7. Stellarioides Medik., Hist. & Commentat. Acad. Elect. Sci. Theod.-Palat. 6: 369. 1790 – Holotype: *S. canaliculata* Medik. = *Ornithogalum longebracteatum* Jacq. ≡ *S. longebracteata* (Jacq.) Speta

= *Urophyllon* Salisb., Gen. Pl. [Salisbury]: 34. 1866 ≡ *O.* subgenus *Urophyllon* (Salisb.) Baker ≡ *O.* section *Urophyllon* series *Urophyllon* (Salisb.) U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert. 107(5–6): 488. 1996 ≡ *Albuca* subgenus *Urophyllon* (Salisb.) J.C.Manning & Goldblatt in Taxon 58(1): 93. 2009 – Lectotype: *U. caudatum* (Jacq.) Salisb. = *O. longebracteatum* Jacq. [cf. Speta (2001); lectotypifications by Obermeyer (1978) and Müller-Doblies & Müller-Doblies (1996) are incorrect or superfluous].

Plants variable in habit, usually medium to large size. Bulb globose to ovoid, hypogeous or sometimes epigeous, green and bulbilliferous (rarely with a long neck in plants from arid regions); outer tunics membranous and greyish or fleshy and green. Leaves lanceolate or linear, long tapering, flat to canaliculate, glabrous. Inflorescence 1–3 per bulb, usually long racemose and many flowered, subspiciform, dense; bracts narrowly ovate-acuminate or filiform, aristate, membranous, usually long and exceeding the buds, or rarely shorter and simply ovate; bracteoles absent. Flowers small; tepals whitish to greenish, with a dark longitudinal green band visible on both sides, oblong or narrowly elliptical, ≤12 mm long; filaments ovate-acuminate or linear, flattened, sometimes with basal lobed expansions; ovary ovoid or globose, obtuse,

trigonous, and with biseriate ovules; style thickened, sometimes widened at the base; stigma tapering, not capitate. Capsule usually small, ≤ 14 mm long, ovoid to obovate, obtuse or acute, and trilobate in section. Seeds variable in size, numerous, irregularly compressed, flattened, roundish, angular or semicircular, biseriate and obliquely stalked in each locule, with puzzle-like testa.

Chromosome number: $2n = 4, 6, 8, 10, 12, 16, 18, 20, 24, 26, 36, 54$ (cf. Stedje, 1989; Nordal and Stedje, 1993; Speta, 1998*a*, 2001).

Number of species: approx. 25 (cf. Speta, 2001; and according to the present study) to 2 (with three additional subspecies; cf. Manning *et al.*, 2009*a*, but excluding *Igidia volubilis*). A comprehensive revision is still needed for this genus.

Distribution: temperate and subtropical regions of southern Africa, spreading north $\leq$ Ethiopia, and with a species reaching disjointly Algeria and Morocco (*S. sessiliflorum*).

Necessary combinations:

Stellarioides bakeri Mart.-Azorín, M.B.Crespo & Juan, **nom. nov.** $\equiv$ *Ornithogalum chloranthum* Baker in Gard. Chron. n.s. 2: 323. 1875, nom. illeg. (syn. subst.) [non M.Bieb., Fl. Taur.-Caucas. 2: 264. 1808 $\equiv$ *Gagea chlorantha* (M.Bieb.) Schult.f.]

Stellarioides cernua (Baker) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** $\equiv$ *Ornithogalum cernuum* Baker, Fl. Trop. Afr. [Oliver *et al.*] 7(3): 547. 1898 [basion.]

Stellarioides gambosana (Baker) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** $\equiv$ *Ornithogalum gambosanum* Baker, Fl. Trop. Afr. [Oliver *et al.*] 7(3): 547. 1898 [basion.]

8. *Galtonia* Decne. in Fl. Serres Jard. Eur. 23: 32. 1880 – Lectotype: *G. princeps* (Baker) Decne. $\equiv$ *Hyacinthus princeps* Baker (cf. Manning *et al.*, 2004).

Plants large and vigorous. Bulb globose; outer tunics soft and membranous. Leaves numerous, lanceolate tapering, wide (>5 cm), glabrous and somewhat sheathing and ascending upon the stem. Inflorescence widely racemose, conical or cylindrical, sometimes corymbose; pedicels patent, with nodding apices in flower (rarely erect) and always erect in fruit; bracts membranous, linear-acuminate; bracteoles absent. Flowers never fragrant, nodding, exceptionally erect; tepals fleshy, whitish or greenish-yellowish, fused into a campanulate tube $\leq$ half of their length or rarely free; filaments ovate-acuminate, insert at the base of the perianth and adnate to the perianth tube, merging at its end, sometimes completely free; ovary green, yellowish or black, cylindrical or ovoid; style white, filiform; stigma slightly trilobate and glandular. Capsule lanceolate, lanceolate-cylindrical or ovate, acute, widened in the basal third, triangular in section with blunt edges. Seeds large, polygonal or irregularly compressed or semicircular and flattened, biseriate and obliquely stalked in each locule, with smooth puzzle-like testa.

Chromosome number: $2n = 12, 14, 16$ (cf. Obermeyer, 1978; Speta, 1998*a*; Forrest and Jong, 2004). Exceptionally, some counts for *G. candicans* yielded $2n = 22, 32$ (cf. Hammett and Murray, 1993).

Number of species: 5 (according to the present study).

Distribution: temperate and subtropical regions of eastern South Africa and Swaziland.

Necessary combination:

Galtonia saundersiae (Baker) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** $\equiv$ *Ornithogalum saundersiae* Baker in Gard. Chron., ser. 3, 10: 452. 1891 [basion.]

9. *Ethesia* Raf., Fl. Tellur. 3: 60. 1837 $\equiv$ *Ornithogalum* series *Xanthochlora* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert 107: 492. 1996 $\equiv$ *O.* section *Xanthochlora* (U.Müll.-Doblies & D.Müll.-Doblies) J.C.Manning & Goldblatt in Taxon 58(1): 100. 2009 – Holotype: *E. prasina* (Ker Gawl.) Raf. $\equiv$ *O. prasinum* Ker Gawl.

Plants middle size. Bulb ovoid; outer tunics membranous or coriaceous, rough, greyish. Leaves numerous, linear to lanceolate or oblong, caniculate or lorate and flat, somewhat succulent, glaucous or green, glabrous, rarely not occurring with the flowers. Inflorescence a raceme cylindrical or pyramidal at the begining; pedicels erect, firm, sometimes arcuate and lengthening and hardening in fruit, with an obtuse callus above; bracts linear to lanceolate, acuminate, membranous, equalling, shorter or longer than the pedicels; bracteoles absent. Flowers usually fragrant; tepals greenish, or green with a white marginal region, narrowly oblong or ovate, obtuse to subacute; filaments petaloid, showy, pure white, spreading, ovate-acuminate and almost overlapping at the base; ovary green, oblong-ovoid or oblong-globose, triangular; style erect, filiform; stigma slightly trilobate and papillate. Capsule oblong to obcordate or widely globose and truncate to retuse at the apex, as wide as long, trilobate in section. Seeds numerous, large, irregularly compressed (with one or two edges) to ovate-discoid, biseriate in each locule, with blackish testa.

Chromosome number: $2n = 16$ (cf. Obermeyer, 1978).

Number of species: 4 (according to the present study).

Distribution: southern Namibia and arid regions of western and center South Africa.

Necessary combinations:

Ethesia haalenbergensis (U.Müll.-Doblies & D.Müll.-Doblies) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** $\equiv$ *Ornithogalum haalenbergense* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert. 107(5–6): 492. 1996 [basion.]

Ethesia polyphlebia (Baker) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** $\equiv$ *Ornithogalum polyphlebium* Baker, Fl. Cap. 6(3): 507. 1897 [basion.]

Ethesia xanthochlora (Baker) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** $\equiv$ *Ornithogalum xanthochlorum* Baker, Fl. Cap. 6(3): 508. 1897 [basion.]

10. *Eliokarmos* Raf., Fl. Tellur. 2: 24. 1837 – Lectotype: *E. thyrsoides* (Jacq.) Raf. $\equiv$ *Ornithogalum thyrsoides* Jacq. (cf. Rafinesque, Fl. Tellur. 3: 58. 1837).

$=$ *Tomoxis* Raf., Fl. Tellur. 3: 54. 1837 – Lectotype (designated by Speta, 2001): *T. coarctata* (Jacq.) Raf. $\equiv$ *O. coarctatum* Jacq. [$=$ *O. thyrsoides* Jacq.]
$=$ *Lomaresis* Raf., Fl. Tellur. 3: 59. 1837 – Holotype: *L. alba* Raf., nom. illeg. (syn. subst.) $\equiv$ *O. revolutum* Jacq. [$=$ *O. thyrsoides* Jacq.]

= *Aspasia* Salisb., Gen. Pl. [Salisbury]: 34 & 40. 1866 ≡ *O.* subgenus *Aspasia* (Salisb.) Oberm. ≡ *O.* subgenus *Aspasia* section *Aspasia* (Salisb.) U.Müll.-Doblies & D.Müll.-Doblies – Lectotype (designated by Obermeyer, 1978): *O. conicum* Jacq.
= *Phaeocles* Salisb., Gen. Pl. [Salisbury]: 35. 1866 – Holotype: *P. maculata* (Jacq.) Salisb. ≡ *O. maculatum* Jacq.
= *O.* subgenus *Aspasia* section *Hispidaspasia* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert 107: 404. 1996 – Holotype: *O. hispidum* Hornem.

Plants small to middle size. Bulb globose; outer tunics thin and membranous to firm, thickened and rough, pale or dark coloured. Leaves numerous, lanceolate or ovate, usually ciliate or fimbriate on margins, the blade glabrous or rarely hirsute, sometimes not occurring with the flowers, or sheathing and ascending along the stem, with patent and subdistichous blades, arranged at different levels. Inflorescence racemose, cylindrical or corymbose; pedicels erect to patent in flower and erect in fruit; bracts membranous, lanceolate, wider at the base, auriculate and petaloid, or aristate; bracteoles absent. Flowers erect or spreading, diurnal (rarely nocturnal); tepals thin textured, free, diversely coloured, from pure white to yellow, orange or reddish, sometimes with dark maculae at the base or the apex, concolour or sometimes with a narrow greenish, brownish or pinkish band only visible on the abaxial side, persistent and papery in fruit, not rolled or reflexed when withering; filaments variously expanded, from linear-subulate to lanceolate or widened at the base, sometimes generating erect lobes, the inners usually wider than the outers; ovary green, yellow or dark grey, ovoid; style filiform, erect or rarely deflexed; stigma slightly trigonous and papillate. Capsule ovate, lanceolate, elliptical or fusiform, with thin walls, hidden among the persistent dry perianth, with triangular section and blunt edges. Seeds small (0·5–2 mm), numerous, irregularly angular to piriform, variously compressed, biseriate or multiseriate per locule, with papillate, echinulate, or/and puzzle-like testa.

Chromosome number: $2n = 12$ (cf. Neves, 1962; Obermeyer, 1978; Speta, 1998*a*).

Number of species: approx. 28 (according to the present study).

Distribution: from southern Namibia to western and southwest South Africa, mainly in winter rainfall regions.

Necessary combinations:

Eliokarmos bicornutus (F.M.Leight.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum bicornutum* F.M.Leight. in J. S. African Bot. 11: 143. 1945 [basion.]

Eliokarmos bolusianus (Baker) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum bolusianum* Baker in J. Linn. Soc., Bot. 13: 279. 1872 [basion.]

Eliokarmos ceresianus (F.M.Leight.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum ceresianum* F.M.Leight. in J. Bot., Lond. 71: 72. 1933 [basion.]

Eliokarmos ciliiferus (U.Müll.-Doblies & D.Müll.-Doblies) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum ciliiferum* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert. 107(5–6): 414. 1996 [basion.]

Eliokarmos conicus (Jacq.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum conicum* Jacq., Collectanea [Jacquin] 3: 232. 1791 [basion.]

Eliokarmos constrictus (F.M.Leight.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum constrictum* F.M.Leight. in J. S. African Bot. 11: 136. 1945 [basion.]

Eliokarmos corticatus (Mart.-Azorín) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum corticatum* Mart.-Azorín in Bothalia 37(2): 140. 2007 [basion.]

Eliokarmos decus-montium (G.Will.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum decus-montium* G.Will. in Bothalia 28(1): 63. 1998 [basion.]

Eliokarmos deltoideus (Baker) Mart.-Azorín, M.B. Crespo & Juan, **comb. nov.** ≡ *Ornithogalum deltoideum* Baker in J. Linn. Soc. (Bot.) 13: 281. 1872 [basion.]

Eliokarmos dubius (Houtt.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum dubium* Houtt., Handl. Pl.-Kruidk. 2(12): 309, t. 82, fig. 3. 1780 [basion.] =*E. aureus* (Curtis) Raf. ≡ *O. aureum* Curtis

Eliokarmos geniculatus (Oberm.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum geniculatum* Oberm. in Bothalia 12(3): 344. 1978 [basion.]

Eliokarmos gifbergensis (U.Müll.-Doblies & D.Müll.-Doblies) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum gifbergense* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert. 107(5–6): 418. 1996 [basion.]

Eliokarmos hallii (Oberm.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum hallii* Oberm. in Bothalia 12(3): 347. 1978 [basion.]

Eliokarmos hispidulus (U.Müll.-Doblies & D.Müll.-Doblies) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *O. hispidulum* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert. 107(5–6): 411. 1996 [basion.]

Eliokarmos inandensis (Baker) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum inandense* Baker, Fl. Cap. (Harvey) 6(3): 503. 1897 [basion.]

Eliokarmos inclusus (F.M.Leight.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum inclusum* F.M.Leight. in S. African Gard. 24: 50. 1934 [basion.]

Eliokarmos leeupoortensis (U.Müll.-Doblies & D.Müll.-Doblies) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum leeupoortense* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert. 107(5–6): 396. 1996 [basion.]

Eliokarmos namaquanulus (U.Müll.-Doblies & D.Müll.-Doblies) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum namaquanulum* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert. 107(5–6): 410. 1996 [basion.]

Eliokarmos naviculus (F.W.Barker ex Oberm.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum naviculum* F.W.Barker ex Oberm. in Bothalia 12(3): 348. 1978 [basion.]

Eliokarmos neomaculatus Mart.-Azorín, M.B.Crespo & Juan, **nom. nov.** ≡ *Ornithogalum maculatum* Jacq., Collectanea [Jacquin] 3: 368. 1791 (syn. subst.) [non *E. maculatus* Raf., Fl. Tellur. 3: 59. 1837 =*E. thyrsoides* (Jacq.) Raf.]

Eliokarmos pilosus (Jacq.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Anthericum pilosum* Jacq., Ic. Pl. Rar. 2(15): t. 416. 1794 [basion.] = *Ornithogalum hispidum* Hornem.

Eliokarmos pilosus subsp. *bergii* (Schltdl.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum bergii* Schltdl. in Linnaea 1: 254. 1826 [basion.]

Eliokarmos pruinosus (F.M.Leight.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum pruinosum* F.M.Leight. in J. S. African Bot. 10: 104. 1944 [basion.]

Eliokarmos puberulus (Oberm.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum puberulum* Oberm. in Bothalia 12(3): 337. 1978 [basion.]

Eliokarmos rubescens (F.M.Leight.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum rubescens* F.M.Leight. in J. S. African Bot. 11: 142. 1945

Eliokarmos rupestris (L.f.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum rupestre* L.f., Suppl. Pl.: 199. 1782 [basion.]

Eliokarmos strictus (L.Bolus) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum strictum* L.Bolus in J. Bot. 71: 72. 1933 [basion.]

Eliokarmos synanthifolius (F.M.Leight.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum synanthifolium* F.M.Leight. in J. S. African Bot. 11: 176. 1945 [basion.]

Eliokarmos thermophilus (F.M.Leight.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum thermophilum* F.M.Leight. in J. S. African Bot. 11: 145. 1945 [basion.]

11. Avonsera Speta in Phyton 38: 95. 1998 ≡ *Ornithogalum* subgenus *Avonsera* (Speta) J.C.Manning & Goldblatt in Taxon 58(1): 100. 2009 – Holotype: *A. convallarioides* (H.Perrier) Speta ≡ *O. convallarioides* H.Perrier

Plants middle size. Bulbs with membranous outer tunics. Leaves various, wide, elliptical to oblong or obovate, abruptly contracted at the base in a pseudopetiole, glabrous, occurring with flowers. Inflorescence loosely racemose, usually with two flowers per bract in its lower part; pedicel long and thin, erect to patent in flower and patent in fruit; bracts lanceolate, membranous, small; bracteoles present. Flowers diurnal, spreading; tepals thin, white, connate at the base; filaments deltoid or tapering and acute at the apex, connate at the base forming a short tube; ovary green, obovoid, truncate at the apex; style white, filiform; stigma punctiform. Capsule obovate, truncate at the apex, trilobate in section. Seeds ovoid.

Chromosome number: $2n = 14$ (cf. Wetschnig *et al.*, 2007).
Number of species: 1 (cf. Speta, 1998*a*).
Distribution: Madagascar.

12. Neopatersonia Schönland in Rec. Albany Mus. 2: 251. 1912 ≡ *Ornithogalum* section *Neopatersonia* (Schönland) J.C.Manning & Goldblatt in Taxon 58(1): 101. 2009 – Holotype: *N. uitenhagensis* Schönland

Plants small. Bulb globose; outer tunics membranous or coriaceous, greyish, sometimes with a long neck. Leaf solitary to various, lanceolate, tapering or oblong, somewhat sheathing at the base. Inflorescence in subcorymbose raceme; pedicels erect-patent in flower and erect in fruit; bracts membranous, linear-acuminate, shorter than the pedicels; bracteoles absent. Flowers erect, remaining open; tepals somewhat fleshy, whitish or greenish, sometimes with longitudinal dark green nerves, oblong, and fused at the base in a very short tube;

filaments subulate, with a expanded triangular or lobate base, connate and adnate to perianth; ovary green and ovoid; style whitish, filiform; stigma with three patent long and deflexed lobes, sometimes only trigonous. Capsule lanceolate or ovoid-triangular, acute or apiculate, triangular in section with blunt edges. Seeds black, small, angular, piriform or subglobose, biseriate in each locule, somewhat verruculose, with pitted puzzle-like testa cells.

Chromosome number: no data available.
Number of species: 4 (according to the present study).
Distribution: south-west and southern parts of South Africa.
Necessary combination:

Neopatersonia rotata (U.Müll.-Doblies & D.Müll.-Doblies) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum rotatum* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert. 107(5–6): 482. 1996 [basion.]

13. Elsiea F.M.Leight. in J. S. African Bot. 10: 55. 1944 ≡ *Ornithogalum* section *Elsiea* (F.M.Leight.) J.C.Manning & Goldblatt in Taxon 58(1): 102. 2009 – Type: *E. corymbosa* F.M.Leight. ≡ *O. esterhuyseniae* Oberm. [non *O. corymbosum* Ruiz & Pavón (1802)]

Plant middle size, ≤70 cm. Bulb few developed, composed by tubular foliar sheaths growing up from a thick subterranean and subrhizomatous stem. Leaves numerous, occurring with the flowers, glabrous, smooth, linear-convolute, with margins rolled in a terete appendix at the apex. Inflorescence racemose-corymbose, erect, 60 cm long; with erect pedicels, 1–6 cm long; bracts shorter than the pedicels, linear-lanceolate, acuminate, auriculate and membranous; bracteoles absent. Flowers small, erect, white, thin; tepals white, linear, connate into a short tube 3–4 mm, and somewhat reflexed and persistent after withering; filaments linear-lanceolate, acute and shortly adnate to perianth, the inner ones somewhat wider than the outer ones; ovary obovoid, triangular, substipitate; style filiform; stigma slightly trigonous and papillate. Capsule black, ovoid-triangular sharply angled, stipitate, obtuse and depressed at the apex. Seeds small or medium size, angular, irregularly compressed, almost winged.

Chromosome number: no data available.
Number of species: 1 (according to the present study).
Distribution: mountainous areas of south-west of South Africa.

14. Nicipe Raf., Fl. Tellur. 3: 54. 1837 – Holotype: *N. nivea* (Aiton) Raf. ≡ *Ornithogalum niveum* Aiton

= *O.* group Angustifoliati Oberm. in Bothalia 12: 349. 1978 ≡ *O.* subgenus *Aspasia* section *Linaspasia* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert 107: 436. 1996 – Holotype: *O. juncifolium* Jacq.
= *O.* subgenus *Aspasia* section *Vaginaspasia* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert 107: 428. 1996 ≡ *O.* series *Vaginaspasia* (U.Müll.-Doblies & D.Müll.-Doblies) J.C.Manning & Goldblatt in Taxon 58(1): 102. 2009 – Holotype: *O. zebrinellum* U.Müll.-Doblies & D.Müll.-Doblies
= *O.* subgenus *Aspasia* section *Nanaspasia* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert 107: 459. 1996 ≡ *O.* series *Nanaspasia* (U.Müll.-Doblies & D.Müll.-Doblies) J.C.Manning & Goldblatt in Taxon 58(1): 103. 2009 – Holotype: *O. nanodes* F.M.Leight.

= *O.* subgenus *Urophyllon* section *Helogalum* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert 107: 483. 1996 – Holotype: *O. flexusoum* (Thunb.) U.Müll.-Doblies & D.Müll.-Doblies

Plants small to middle size. Bulb globose, rarely few developed in wet habitats, ending abruptly in an epigeous neck, occasionally surrounded by tubular, transversally banded and epigeous cataphylls; outer tunics membranous or coriaceous; roots usually branched. Leaves numerous, all emerging almost at the same level from the bulb neck, narrow and long, 0·5–6 mm wide (rarely ≤20 mm), linear to cylindrical or lanceolate, often with margins enrolled, rarely flat and broader or even coriaceous and boat-shapped, glabrous or hirsute, spreading or rarely twisted, with entire blunt, ciliate or crispate, sometimes not occurring with the flowers. Inflorescence in raceme cylindrical to subcorymbose, one to three per bulb, dense and many-flowered, elongating with age; pedicels erect or erect-patent; bracts small, membranous, deltoid-aristate or acuminate, auriculate and sometimes denticulate at the base. Flowers erect or spreading, diurnal; tepals almost free to fused at the base up to one-third, thin textured, white to yellowish on the adaxial side and usually with a dark pinkish, reddish, greenish or brownish not defined band on the abaxial side, lanceolate to ovate, acute or obtuse, spreading or reflexed when withering; filaments subulate to linear or ovate-acuminate, expanded at the base, the inners usually wider than the outers, free and adnate (exceptionally connate in *O. synadelphicum*); ovary elliptical, ovoid or obovoid, contracted in the lower part, ovules biseriate or multiseriate per locule; style filiform; stigma capitate, slightly trigonous or trilobate. Capsule trigonous-elliptical to trilobate-turbinate, with thin walls; usually hidden among the dry and persistent perianth or exposed. Seeds small or large (0·5–5 mm), cuneate, subovoid, angular and irregularly compressed, multiseriate in each locule, with smooth testa.

Chromosome number: 2*n* = 10, 12 (cf. Obermeyer, 1978).
Number of species: approx. 44 (according to the present study).
Distribution: mainly in the south and east of Africa, not crossing the Sahara desert northwards.
Necessary combinations:

Nicipe adseptentrionesvergentula (U.Müll.-Doblies & D.Müll.-Doblies) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum adseptentrionesvergentulum* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert. 107(5–6): 446. 1996 [basion.]

Nicipe aetfatensis (U.Müll.-Doblies & D.Müll.-Doblies) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum aetfatense* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert. 107(5–6): 459. 1996 [basion.]

Nicipe aloiformis (Oberm.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum aloiforme* Oberm. in Bothalia 12(1): 61. 1976 [basion.]

Nicipe anguina (F.M.Leight. ex Oberm.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum anguinum* F.M.Leight. ex Oberm. in Bothalia 12(3): 356. 1978 [basion.]

Nicipe annae-ameliae (U.Müll.-Doblies & D.Müll.-Doblies) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum annae-ameliae* U.Müll.-Doblies & D.Müll.-Doblies in Willdenowia 11(1): 64. 1981 [basion.]

Nicipe baurii (Baker) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum baurii* Baker, Fl. Cap. (Harvey) 6(3): 504. 1897 [basion.]

Nicipe britteniae (F.M.Leight. ex Oberm.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum britteniae* F.M.Leight. ex Oberm. in Bothalia 12(3): 352. 1978 [basion.]

Nicipe campanulata (U.Müll.-Doblies & D.Müll.-Doblies) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum campanulatum* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert. 107(5–6): 450. 1996 [basion.]

Nicipe capillaris (J.M.Wood & M.S.Evans) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum capillare* J.M.Wood & M.S.Evans in J. Bot. 35: 490. 1897, '*capillaris*' [basion.]

Nicipe capillifolia (Fourc.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum capillifolium* Fourc. in Trans. Roy. Soc. South Africa 21: 80. 1932 [basion.]

Nicipe comptonii (F.M.Leight.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum comptonii* F.M.Leight. in J. S. African Bot. 10: 119. 1944 [basion.]

Nicipe comptum (Baker) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum comptum* Baker in J. Linn. Soc., Bot. 13: 274. 1872 [basion.]

Nicipe diphylla (Baker) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum diphyllum* Baker in Bull. Misc. Inform. Kew 1895: 153. 1895 [basion.]

Nicipe dolichopharynx (U.Müll.-Doblies & D.Müll.-Doblies) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum dolichopharynx* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert. 107(5–6): 466. 1996 [basion.]

Nicipe dregeana (Kunth) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum dregeanum* Kunth in Enum. Pl. [Kunth] 4: 351. 1843 [basion.]

Nicipe filifolia (Thunb.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Anthericum filifolium* Thunb., Prod. Pl. Cap. 1: 62. 1794 [basion.] ≡ *O. thunbergianulum* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert. 107(5–6): 440. 1996

Nicipe fissurisedula (U.Müll.-Doblies & D.Müll.-Doblies) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum fissurisedulum* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert. 107(5–6): 466. 1996 [basion.]

Nicipe flexuosa (Thunb.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Hyacinthus flexuosus* Thunb. Prodr. Pl. Cap. 63. 1794 [basion.] = *O. ornithogaloides* (Kunth) Oberm.

Nicipe gracillima (R.E.Fr.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum gracillimum* R.E.Fr. in Acta Horti Berg. 9: 77. 1927 [basion.]

Nicipe graminifolia (Thunb.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum graminifolium* Thunb. in Prodr. Pl. Cap. 1: 61. 1794 [basion.]

Nicipe gregoriana (U.Müll.-Doblies & D.Müll.-Doblies) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum gregorianum* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert. 107(5–6): 462. 1996 [basion.]

Nicipe hesperantha (U.Müll.-Doblies & D.Müll.-Doblies) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡

Ornithogalum hesperanthum U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert. 107(5–6): 443. 1996 [basion.]

Nicipe juncifolia (Jacq.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum juncifolium* Jacq., Pl. Rar. Hort. Schoenbr. 1: 46, t. 90. 1797 [basion.]

Nicipe longicollum (U.Müll.-Doblies & D.Müll.-Doblies) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum longicollum* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert. 107(5–6): 462. 1996 [basion.]

Nicipe mater-familias (U.Müll.-Doblies & D.Müll.-Doblies) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum mater-familias* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert. 107(5–6): 444. 1996 [basion.]

Nicipe monophylla (Baker) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum monophyllum* Baker, Fl. Cap. (Harvey) 6(3): 502. 1897 [basion.]

Nicipe monophylla subsp. *eckardtiana* (U.Müll.-Doblies & D.Müll.-Doblies) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum monophyllum* subsp. *eckardtianum* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert. 107(5–6): 434. 1996 [basion.]

Nicipe nanodes (F.M.Leight.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum nanodes* F.M.Leight. in J. S. African Bot. 9: 113. 1943 [basion.]

Nicipe natalensis (Baker) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum natalense* Baker in Bull. Misc. Inform. Kew. 1893: 210. 1893 [basion.]

Nicipe oreogenes (Schltr. ex Poelln.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum oreogenes* Schltr. ex Poelln. in Feddes Repert. Spec. Nov. Regni Veg. 54: 24. 1944 [basion.]

Nicipe paludosa (Baker) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum paludosum* Baker in J. Bot. 12: 366. 1874 [basion.]

Nicipe perdurans (A.P.Dold & S.A.Hammer) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum perdurans* A.P.Dold & S.A.Hammer in Bothalia 33(1): 112. 2003 [basion.]

Nicipe perparva (V.Poelln.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum perparvum* V.Poelln. in Portugaliae Acta Biol., Sér. B, Sist., 1: 214. 1945 [basion.]

Nicipe petraea (Fourc.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum petraeum* Fourc. in Trans. Roy. Soc. South Africa 21: 81. 1932 [basion.]

Nicipe pilosa (L.f.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum pilosum* L.f., Suppl. Pl.: 199. 1782 [basion.]

Nicipe pullata (F.M.Leight.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum pullatum* F.M.Leight. in J. S. African Bot. 11: 153. 1945 [basion.]

Nicipe rogersii (Baker) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum rogersii* Baker, Fl. Cap. (Harvey) 6(3): 501. 1897 [basion.]

Nicipe sardienii (van Jaarsv.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum sardienii* van Jaarsv. in Bradleya 12: 33. 1994 [basion.]

Nicipe schlecteriana (Schinz.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum schlecterianum* Schinz. in Bull. Herb. Boissier 2: 223. 1894 [basion.]

Nicipe sephtonii (Hilliard & B.L.Burtt) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum sephtonii* Hilliard & B.L.Burtt in Notes Roy. Bot. Gard. Edinburgh 41(2): 308. 1983 [basion.]

Nicipe synadelphica (U.Müll.-Doblies & D.Müll.-Doblies) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum synadelphicum* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert. 107(5–6): 452. 1996 [basion.]

Nicipe tortuosa (Baker) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum tortuosum* Baker, Fl. Cap. (Harvey) 6(3): 510. 1897 [basion.]

Nicipe vallis-gratiae (Schltr.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum vallis-gratiae* Schltr. in Feddes Repert. Spec. Nov. Regni Veg. 54: 26. 1944 [basion.]

Nicipe verae (U.Müll.-Doblies & D.Müll.-Doblies) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum verae* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert. 107(5–6): 432. 1996 [basion.]

Nicipe zebrinella (U.Müll.-Doblies & D.Müll.-Doblies) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum zebrinellum* U.Müll.-Doblies & D.Müll.-Doblies in Willdenowia 11(1): 47. 1981 [basion.]

15. Cathissa Salisb., Gen. Pl. [Salisbury]: 34. 1866 ≡ *Ornithogalum* subgenus *Cathissa* (Salisb.) Baker in J. Linn. Soc., Bot. 13: 261. 1872 ≡ *O.* section *Cathissa* (Salisb.) Engl., Nat. Planzenfam. [Engler & Prantl] 2, Abt. 5: 67. 1888 – Holotype: *C. cocinna* (Salisb.) Speta ≡ *O. concinnum* Salisb.

Plants small, middle size or large. Bulb ovate; with greyish to brownish, membranous outer tunics. Leaves sole to numerous, green, narrowly lanceolate to long tapering, glabrous and occurring with the flowers, sometimes with a long terminal terete appendix. Inflorescence racemose or subspicate, longer than wide; pedicels erect-patent in flower and adpressed to stem in fruit; bracts large, triangular to lanceolate, membranous or papery, petaloid and auriculate; bracteoles absent. Flowers white, suberect, patent or slightly nodding; tepals free, completely white, widely ovate or obovate, rarely with small greenish dots at the apex of the abaxial side; filament subulate to tapering; ovary green or yellowish, ovoid-fusiform; style white and filiform, or greenish in the lower part and white at the apex; stigma slightly capitate, trigonous and glandular-papillate. Capsule ovate-lanceolate, oblong and triangular with blunt edges section. Seeds semicircular, irregular or angular, polygonal or apiculate, biseriate or multiseriate per locule, with granulate or puzzle-like testa.

Chromosome number: $2n = 32, 34, 36$ (cf. Speta, 1998*a*).
Number of species: 3 (cf. Martínez-Azorín *et al.*, 2007).
Distribution: Spain, Portugal and Morocco.
Necessary combinations:

Cathissa unifolia (L.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Scilla unifolia* L., Sp. Pl.: 309 (1753) [basion.] ≡ *C. unifolia* (L.) Salisb., Gen. Pl. [Salisbury]: 34 (1866), comb. inval. (according to art. 33·1, ICBN) ≡ *C. broteroi* (M.Laínz) Speta in Stapfia 75: 171 (2001)

16. Melomphis Raf., Fl. Tell. 2: 21. 1837 ≡ *Caruelia* Parl., Nouv. Gen. Sp. Monocot.: 21. 1854 ≡ *Ornithogalum* subgenus *Caruelia* (Parl.) Baker in J. Linn. Soc. (Bot.) 13: 259. 1872 ≡

O. section *Caruelia* (Parl.) Engl., Nat. Planzenfam. [Engler & Prantl] 2, Abt. 5: 67. 1888 ≡ *Myanthe* Salisb., Gen. Pl. [Salisbury]: 34. 1866 ≡ *O.* section *Melomphis* (Raf.) J.C.Manning & Goldblatt in Taxon 58(1): 103. 2009 – Lectotype: *M. arabica* (L.) Raf. (cf. Speta, 2001) ≡ *C. arabica* (L.) Parl. ≡ *M. arabica* (L.) Salisb. ≡ *O. arabicum* L.

Plants large. Bulb ovoid, with membranous outer tunics. Leaves green, lanceolate-oblong, wide, long tapering. Inflorescence corymbose or subcorymbose-pyramidal, bracts membranous, ovate-triangular, wide and petaloid (white with greenish apex); bracteoles absent. Flowers white, showy; tepals white all over, wide, ovate or obovate, withering soon after anthesis; filaments white, narrowly triangular; ovary globose and shining black; style filiform and white or blackish below; stigma trigonous, glandular. Capsule subglobose, trigonous, with truncate apex. Seeds blackish, polygonal or irregularly compressed, with tuberculate or papillate testa.

Chromosome number: $2n = 28, 51$ (cf. Speta, 1998a)
Number of species: 3 (according to the present study).
Distribution: Mediterranean basin, extending to the Middle East.
Necessary combinations:
Melomphis melanogyna (Cullen) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum melanogynum* Cullen in Notes Roy. Bot. Gard. Edinburgh 27: 309. 1967 [basion.]
Melomphis persica (Hausskn. ex Bornm.) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum persicum* Hausskn. ex Bornm. in Beih. Bot. Centralbl. 24(2): 102. 1908 [basion.]

17. Loncomelos Raf., Fl. Tell. 2: 24. 1837 – Lectotype: *L. pyrenaicus* (L.) L.D.Hrouda ex Holub (cf. Speta, 2001) ≡ *Ornithogalum pyrenaicum* L.

= *Celsia* Heist. ex Fabr., Enum. (ed. 2) [Fabr.]: 22. 1763, pro parte [*O. latifolium* L.], nom. illeg. [non *Celsia* L., Sp. Pl.: 621. 1753; Scrophulariaceae]
= *Beryllis* Salisb., Gen. Pl. [Salisbury]: 33. 1866 ≡ *O.* subgenus *Beryllis* (Salisb.) Baker in J. Linn. Soc. (Bot.) 13: 260. 1872 ≡ *O.* section *Beryllis* (Salisb.) Engl., Nat. Planzenfam. [Engler & Prantl] 2, Abt. 5: 67. 1888 ≡ *O.* subgenus *Spetagalum* U.Müll.-Doblies & D.Müll.-Doblies in Feddes Repert. 107(5–6): 520. 1996 [nom. superfl.] – Lectotype: *O. pyrenaicum* L. (cf. Stearn, 1983)
≡ *Eustachys* Salisb., Gen. Pl. [Salisbury]: 33. 1866

Bulb with outer tunics membranous, sometimes with long neck. Leaves tapering, wide, long, glabrous, sometimes not occurring with the flowers. Inflorescence racemose, narrow, much longer than wide; pedicels erect-patent in flower and erect and appressed to the stem in fruit; bracts membranous, deltoid-aristate, usually shorter than the pedicels; bracteoles absent. Flowers white or yellowish; tepals with a greenish longitudinal band only evident on the abaxial side; filaments flattish and expanded at the base; ovary green, ovate to spherical; style white and filiform; stigma puntiform and slightly trigonous. Capsule ovate-lanceolate, triangular with blunt edges in section. Seeds polygonal or irregularly compressed, biseriate per locule, with tuberculate, papillate or rugose testa.

Chromosome number: $2n = 16, 18, 22, 24, 26, 28, 32, 36, 54$ (cf. Speta, 1998a).
Number of species: approx. 20 (cf. Speta, 1998a, 2001).
Distribution: Mediterranean basin.
Observations: when the name *O.* subgenus *Beryllis* (Salisb.) Baker was published it was nomenclaturally superfluous, since the type of *Urophyllon* was included in it (Art. 52·1, 52·2e; McNeill *et al.*, 2006). Consequently it was a synonym of *O.* subgenus *Urophyllon* (Salisb.) Baker; though it was not illegitimate (Art. 52·3). When both subgenera are recognized, both names recover their validity and they can be used, each one with its corresponding circumscription. In this way, the new name *O.* subgenus *Spetagalum*, proposed by Müller-Doblies and Müller-Doblies (1996) to replace the supposedly illegitimate *O.* subgenus *Beryllis*, is superfluous, since these authors noted explicitly that this new name should be used exclusively for the Mediterranean plants, keeping the South African ones in *O.* subgenus *Urophyllon* (*Urophyllon sensu stricto*).

18. Honorius Gray in Nat. Arr. Brit. Pl. 2: 177. 1821 ≡ *Albucea* Rchb., Fl. Germ. Excurs.: 109. 1830 ≡ *Myogalum* Link in Handb. 1: 163. 1829 ≡ *Ornithogalum* subgenus *Myogalum* (Link) Baker in J. Linn. Soc. (Bot.) 13: 260. 1872 ≡ *O.* section *Myogalum* (Link) Engl., Nat. Planzenfam. [Engler & Prantl] 2, Abt. 5: 67. 1888 ≡ *Syncodium* Raf., Fl. Tell. 2: 22. 1837 ≡ *Brizophile* Salisb., Gen. Pl. [Salisbury]: 34. 1866 – Holotype: *H. nutans* (L.) Gray ≡ *O. nutans* L.

Plants middle size. Bulb with brown or whitish membranous outer tunics. Leaves linear and tapering to lanceolate or oblong, occurring with the flowers, glabrous, sometimes with a longitudinal greyish band. Inflorescence racemose; pedicels erect-patent in flower, erect to reflexed in fruit; bracts lanceolate or ovate-lanceolate, membranous or papery; bracteoles absent. Flowers suberect or patent, campanulate at the anthesis; tepals free, ovate-lanceolate, erect, white with a wide longitudinal green band only visible on the abaxial side; filaments lanceolate to tapering, at least outers wider at the apex and forming two erect lobes accompanying the anther; ovary green, ovate, trigonous, with six blunt edges; style white and filiform; stigma puntiform slightly trigonous and glandular. Capsule ovate or oblong, sometimes truncate at the apex, with six weak ribs in section, mostly nodding. Seeds globose, with prominent sinuose-reticulate testa.

Chromosome number: $2n = 14, 28, 30, 35, 42$ (cf. Speta, 1998a).
Number of species: 8 (cf. Speta, 1998a; Holub, 1976).
Distribution: south-eastern Europe, western Turkey and Middle East (cf. Speta, 1998a).
Observations: *O. pamphylicum* was described by Düşen and Sümbül (2002) as a member of *O.* subg. *Myogalum*, close to *O. nutans*. However, the former species lacks some of the morphological traits defining *Honorius*, such as the filaments lobed, winged or toothed in the upper part, or the subacute to truncate capsule. Therefore it is here excluded from *Honorius*. New data are needed for a more accurate placement of *O. pamphylicum* in Ornithogaleae.
Necessary combinations:
Honorius demirizianus (H.Malyer & Koyuncu) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡

Ornithogalum demirizianum H.Malyer & Koyuncu in Turkish J. Bot. 13(2): 301. 1989 [basion.]

Honorius chetikianus (Uysal, Ertugrul & Dural) Mart.-Azorín, M.B.Crespo & Juan, **comb. nov.** ≡ *Ornithogalum chetikianum* Uysal, Ertugrul & Dural in Bot. J. Lin. Soc. 148: 501. 2005 [basion.]

19. **Ornithogalum** L., Sp. Pl.: 306. 1753 ≡ *O.* subgenus *Heliocharmos* Baker in J. Linn. Soc. (Bot.) 13: 258. 1872 ≡ *O.* section *Heliocharmos* (Baker) Engl., Nat. Planzenfam. [Engler & Prantl] 2, Abt. 5: 67. 1888 – Lectotype: *O. umbellatum* L. (cf. Stearn, 1983).

= *Celsia* Heist. ex Fabr., Enum. (ed. 2). [Fabr.].: 22. 1763, pro parte, nom. illeg. [non *Celsia* L., Sp. Pl.: 621. 1753; *Scrophulariaceae*] – Lectotype: *O. umbellatum* L.

Plants small to middle size. Bulb with brown or whitish membranous outer tunics, sometimes with sessile or pediculate bulbils. Leaves numerous, linear and tapering to lanceolate or oblong, sometimes not occurring with the flowers, glabrous or rarely ciliate, sometimes with a longitudinal white band. Inflorescence corymbose or racemose corymbose, a little longer than wide; pedicels erect-patent in flower and patent or sometimes deflexed in fruit; bracts large, lanceolate or ovate-lanceolate, membranous or papery; bracteoles absent. Flowers suberect, erect or patent, diurnal; tepals free, ovate-lanceolate, white with a wide longitudinal green band only visible by the abaxial side; filaments free and flat, lanceolate to tapering; ovary green, ovate or obovate and truncate at the apex, deeply trilobate, with six evident ribs; style white and filiform; stigma punctiform slightly trigonous and glandular. Capsule obovate or oblong, usually truncate at the apex, deeply trilobate with six evident ribs in section. Seeds globose, biseriate per locule, with sinuose and prominent reticulate testa.

Chromosome number: 2n = 12, 14, 16, 18, 20, 22, 24, 26, 28, 32, 36, 45, 52, 54, 72, 90, 108 (cf. Speta, 1998*a*).

Number of species: about 50 (cf. Speta, 1998*a*).

Distribution: Europe, south-west Asia (Middle East to Afghanistan), and northern Africa.

Incertae sedis

Ornithogalum toxicarium C.Archer & R.H.Archer in S. Afr. J. Bot. 65: 431. 1999.

This peculiar plant was described from karoo shrublands and dry grassland in South Africa and Namibia. Its peculiar floral, fruit and seed features do not match any of the accepted genera of Ornithogaloideae. Further studies, including molecular data, are needed to resolve the taxonomic position of this remarkable taxon. In the meantime, we prefer not to place it in the proposed arrangement.

SUPPLEMENTARY DATA

Supplementary data are available online at www.aob.oxford-journals.org and consist of the following tables. Table S1: Characters and character states for the morphological study. Table S2: Morphological data matrix. Table S3: GenBank accession numbers for samples included in the phylogenetic analyses of the Hyacinthaceae, mainly the subfamily Ornithogaloideae.

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