Phylogeny and taxonomy of the bluebell genus *Hyacinthoides*, Asparagaceae [Hyacinthaceae]

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Abstract　A robust phylogeny for the genus *Hyacinthoides* (bluebells) was established using cpDNA sequences and evaluated in light of a re-assessment of morphological diversity, cytology, distribution patterns and field observations. The genus is distributed in the western Mediterranean–Atlantic region and the northern African mountains. Within this area, there is a major divide between an eastern and western clade, each of them with their own radiations, mainly in autumn-winter flowering taxa in northern Africa and spring flowering taxa in the Iberian Peninsula. We now recognise eleven taxa and one hybrid taxon, which are separated into five clades. Polyploidy is confined to the *H. non-scripta–hispanica* clade with diploid and triploid taxa as well as a newly recognized tetraploid taxon. For the eleven taxa, distribution ranges, taxonomy, morphology, descriptions and a new key are presented. The nomenclatural history of the genus has been reviewed. Generitypes have been designated for *Hyacinthoides* Heist. ex Fabr. and *Endymion* Dumort. and lectotypes selected for four species, three of which are combined for the first time in *Hyacinthoides*: *H. cedretorum, H. ciliolata* and *H. flahaultiana*. Several important questions worthy of further investigation, such as evolutionary processes and their major drivers, e.g. environmental change in the Mediterranean basin, flower morphology and associated pollinators, or sympatric versus allopatric speciation have come into sharper focus through this phylogenetic investigation.

Keywords　cpDNA; Iberian Peninsula; monocots; phylogeography; Western Mediterranean

■ INTRODUCTION

Hyacinthoides Heist. ex Fabr. is a small enigmatic genus of about ten species within the subfamily Hyacinthoideae of Hyacinthaceae (Pfosser & Speta, 1999), a family treated currently as part of the Asparagaceae (Angiosperm Phylogeny Group, 2003). Phylogenetic studies found strong support for the monophyly of the genus and clearly separated it from *Scilla* L. (Pfosser & Speta, 1999; Pfosser & al., 2003). The distinction of *Hyacinthoides* and other genera belonging to the Hyacinthoideae were originally established using morphological features. Characters used to separate *Hyacinthoides* from other genera of the subfamily include bulb morphology and floral bract (bracteole) number (Chouard, 1930, 1934; Speta, 1987). Members of the genus are commonly known as 'bluebells', reflecting the flower colour and shape of the British Bluebell, *H. non-scripta* (L.) Chouard ex Rothm. (Fig. 1). *Hyacinthoides* occurs mainly in the western Mediterranean region, including North Africa (Morocco to Tunisia), the Iberian Peninsula, and the Maritime Alps of France and Italy. Only *H. non-scripta* has a native distribution range extending towards North-Central Europe (northwestern France, Belgium, Netherlands) and the British Isles.

The need for a comprehensive phylogenetic hypothesis and taxonomic revision is required due to both a conflicting number of recognised species and uncertainty when

interpreting their relationships (e.g., Rothmaler, 1944; Tutin & al., 1980; Speta, 1987; Ortiz & Rodriguez-Oubiña, 1996; Pfosser & Speta, 1999; Ortiz & al., 1999). A better understanding of the natural classification of the genus has been hampered by a Euro-centric approach, neglecting much of the diversity occuring in North Africa. Only Jordan & Fourreau (1903) and Maire (1958) studied the diversity within the autumn/winter-flowering species, which are exclusively North African. Both studies pointed towards the considerable variability within northern African taxa, and although these authors recognised numerous taxa, the status of the latter has never been adequately investigated.

This study was designed to reconstruct a complete and robust phylogeny and preliminary phylogeography of the whole genus for which we included more than one specimen of each putative taxon. Sequences were generated for five chloroplast genome regions and a thorough revision of caryological evidence was conducted. The latter was augmented by new chromosome counts for vouchered specimens and of taxa that had not previously been counted, or where the taxonomic identity of existing counts was deemed ambiguous. This research is part of a larger study to investigate the relationships and interactions between *H. non-scripta* and *H. hispanica* (Mill.) Rothm. in northern and western Europe, where the latter taxon is deemed an invasive. Thus, we placed special emphasis on these two taxa throughout their native distribution ranges in

the Iberian Peninsula and oceanic, western Europe. Finally, we have attempted to infer biogeographical patterns and establish a robust hypothesis describing the diversification of these beautiful plants in the western Mediterranean region.

Such work on bluebells will contribute to the understanding of the evolution of the western Mediterranean vegetation, in particular the evolution of vegetation in the western Iberian Peninsula.
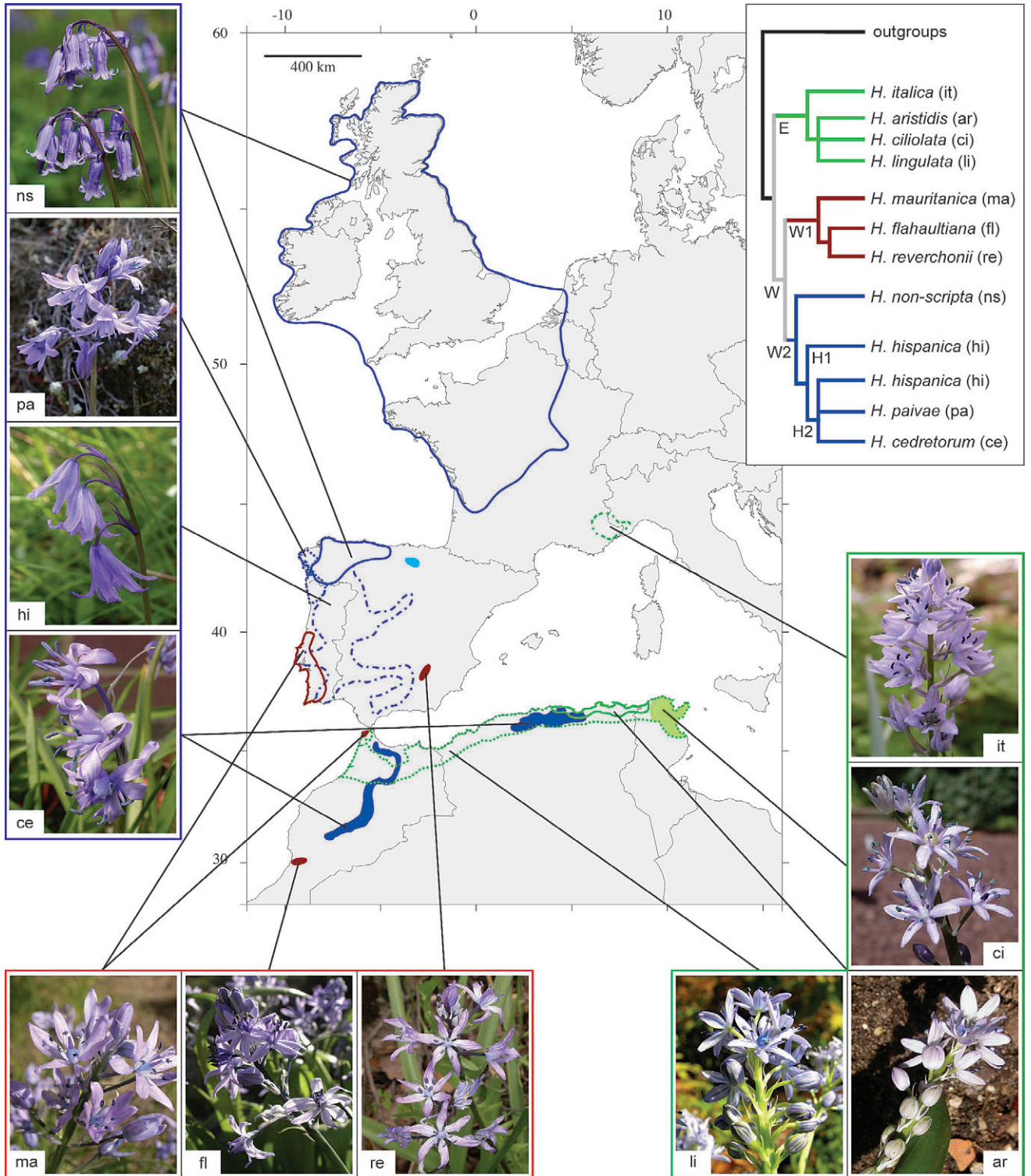

Fig. 1. Geographical distribution, flower variation and simplified phylogeny of *Hyacinthoides* species. The light blue area in northern Spain indicates the distribution area of the unidentified specimen. Figures ci and li kindly provided by John T. Lonsdale, www.edgewoodgardens.net.

■ MATERIALS AND METHODS

Plant materials. — A total of 72 accessions representing all currently accepted species of the genus *Hyacinthoides* and eight outgroup taxa selected from the Hyacinthoideae (Pfosser & Speta, 1999; Pfosser & al., 2003) were used. Material was collected during fieldwork across Western Europe and Morocco, taken from cultivated material in Botanical Gardens or from specialist nurseries, or taken from herbarium specimens (Appendix). Special care was taken to encompass the whole geographical range, taxonomic and morphological diversity of the genus.

Caryological studies. — Published chromosome counts were compiled and critically evaluated to identify incorrect, ambiguous identifications or erroneous taxonomic treatments (Speta, 1987). Seven new chromosome counts are recorded here. Actively growing root tips were pre-treated in 0.002 M 8-hydroxyquinoline for 24 h at 4°C. Pre-treatment solutions were subsequently removed and replaced by fixative (3 parts absolute ethanol : 1 part glacial acetic acid). Root tips were hydrolysed in 5 M hydrochloric acid for 10 min at room temperature and then stored in 70% ethanol. Roots were dissected in 40% acetic acid and the root tip transferred to a drop of 2% certified aceto-orcein prior to maceration and squashing. Chromosome numbers were determined from metaphase preparations examined using an Axioskop (Zeiss) light microscope.

DNA extraction, PCR amplification and sequencing. — Total genomic DNA was extracted using a Retsch Tissue-Lyser and the DNA Plant Kit on a Qiagen Biosprint 96 Bio-Robot workstation according to manufacturer's protocols. Five non-coding regions of the chloroplast genome (cpDNA) were sequenced, *(1)* the *atpB-rbcL* intergenic spacer (IGS) using the primers atpB-1 and rbcL-1 (Chiang & al., 1998), *(2)* the *trnH*$_{GUG}$-*psbA* IGS using the primers psbAF and trnHR (Sang & al. 1997), *(3)* the *trnC*$_{GCA}$-*ycf6* IGS using the primers trnC (Demesure & al., 1995) and ycf6R (Shaw & al., 2005), *(4)* the *trnG*$_{UUC}$-*trnR*$_{UCU}$ region including *trnG* intron and *trnG-trnR* IGS using the primers trnGF and trnGR (Pacak & Szweykowska-Kulinska, 2000), and *(5)* the *trnL*$_{UAA}$-*trnF*$_{GAA}$ region including the *trnL* intron and the *trnL-trnF* IGS using the primers C and F (Taberlet & al., 1991). PCRs were performed as 25 µl reactions containing 1× NH$_4$ reaction buffer, 3 mM MgCl$_2$, 0.4 mM of each primer, 0.5 mM dNTPs in equimolar ratio, two units of BIOTAQ™ DNA polymerase (Bioline), and 1 µl of template DNA. The thermal cycling protocol used for the *atpB-rbcL*-spacer comprised an initial melting step of 5 min at 94°C, followed by 30 cycles of 45 s at 94°C, 75 s at 57°C, and 75 s at 72°C; and a final extension of 10 min at 72°C. The cycling protocol used for all other DNA regions comprised an initial melting step of 2 min at 94°C, followed by 30 cycles of 30 s at 94°C, 30 s at 50°C, and 2 min at 72°C; and a final extension of 5 min at 72°C. Purified PCR products were directly sequenced on an ABI 3730 capillary DNA Analyser (Applied Biosystems Inc.) using Big Dye version 3.1 sequencing mix (Applied Biosystems Inc.) and the PCR primers. A total of 354 new DNA sequences were deposited in GenBank as part of this study (314 for ingroup taxa; 40 for outgroup taxa). Specimen information and GenBank accession numbers are given in the Appendix.

Sequence editing and alignment. — Complementary DNA sequence strands were assembled and edited in SeqMan II (LaserGene Systems Software, DNAStar Inc.). Consensus sequences were aligned manually using MegAlign (LaserGene Systems Software, DNAStar Inc.) and MacClade 4.0 (Maddison & Maddison, 2000). Ambiguously aligned regions, in the majority of cases homopolymers, which are very likely to be homoplasious, were excluded from the analyses. We also excluded a 6-bp repeat which occurred up to 21 times in the *trnH-psbA* IGS, and a region of 16 bp from the *trnH-psbA* IGS which occurs either as GCTTGTTTTCGTAAAA or in the inverse form in the region. The phylogenetic distribution of this microinversion suggested multiple inversion events. The remaining indels were scored using a simple indel coding procedure (Simmons & Ochoterena, 2000).

Phylogenetic analyses. — Three methods of phylogenetic analysis were performed on the combined five cpDNA regions: *(1)* maximum parsimony (MP), with and without indels scored; *(2)* maximum likelihood (ML; indels not scored), and *(3)* Bayesian inferences of phylogeny (BI; indels not scored). Maximum parsimony analyses were obtained by using PAUP* version 4.0 beta 10 (Swofford, 2002) as heuristic analyses with 1000 random-starting trees, and TBR branch swapping to completion. Bootstrap analyses for the maximum parsimony (BP$_{MP}$) were also carried out using PAUP* with 1000 bootstrap replicates, heuristic mode, 10 random-starting trees, and TBR to completion. Maximum likelihood analyses were carried out using GARLI (Zwickl, 2006) with the GTR model plus invariable sites (I) and GAMMA distribution (G). Maximum likelihood bootstrap trees (BP$_{ML}$) were calculated using GARLI with 1000 bootstrap replicates and the same conditions as given for the maximum likelihood analysis. The model parameters were estimated during the searches. Searches were performed using the default options of GARLI. Modeltest 3.7 (Posada & Crandall, 1998) was employed to determine the preferred model for this dataset. Bayesian inference of phylogeny (PP$_{Bay}$) was carried out with MrBayes 3.1 (Huelsenbeck & Ronquist, 2001) with a single GTR+I+G model for all five regions. Bayesian analyses were run for 1,000,000 generations for eight chains. The software tool Tracer v.1.4 (Rambaut & Drummond, 2007 at http://tree.bio.ed.ac.uk/software/tracer/ was used to determine the burn-in phase and the convergence of all parameters. PAUP* was used to calculate the majority role consensus tree for all trees sampled within the stable-phase. Combinability was tested for the five cpDNA regions and inferred by visual comparison of the bootstrap consensus trees obtained in independent maximum parsimony bootstrap analyses of each region. Fitch parsimony analyses were carried out for a dataset combining the DNA sequence data with the indel matrix using PAUP* under the same conditions as described above. The results for maximum parsimony were obtained using tree statistics, e.g., tree length, number of most parsimonious trees, consistency index (CI), retention index (RI), and rescaled consistency index (RC).

Biogeographic and taxonomic information. — Biogeographic distribution and taxonomy were inferred after a comprehensive literature search, the study of numerous herbarium collections and field observations, mainly by FJR and MG.

■ RESULTS

Cytology. —Table S1 (in the Electronic Supplement) gives a summary of all chromosome counts in *Hyacinthoides*. Given the previous confusion about taxon identification and distribution we divide the large number of cytological studies (69) and numerous counts into two categories: *(1)* counts with a high degree of certainty including our own counts on material that has also been examined genetically and morphologically; *(2)* counts with various degrees of uncertainty, because of uncertain origin, e.g., counts on cultivated material, and/or erroneous identification. We have found three ploidy levels in *Hyacinthoides*, diploidy with $2n = 16$ is most common across the genus, while triploidy, $2n = 24$, and tetraploidy, $2n = 32$ (Fig. 2), are confined to the *H. non-scripta–H. hispanica* clade.

Phylogenetic relationships. —Our results showed mostly well-supported relationships to the species level and we recognise six well-supported clades within *Hyacinthoides* (Figs. 3, 4). No evidence for topological heterogeneity was found among the five cpDNA regions. The four phylogenetic analyses of the combined DNA datasets (Figs. 3, 4), MP, MP plus indels, ML and BY, resulted in only a few conflicts and these will be explained in more detail below. All bifurcations mentioned below are well supported (BP_{MP} and $BP_{ML} \geq 90\%$, $PP_{Bay} \geq 95$) unless otherwise stated. Support values are given in Figs. 3 and 4 and informative indels were plotted on the tree. Table 1 provides information about the number of variable sites, parsimonious sites per locus and the tree statistics of MP analyses. The phylogenetic hypothesis found in the ML analysis had a log likelihood of $-\ln = -9002.4134$ with the estimated nucleotide frequencies f(A) = 0.3333, f(C) = 0.1638, f(G) = 0.1666, f(T) = 0.3363, gamma shape parameter = 0.235, proportion of invariant = 0.0000, and GTR relative rate parameters A-C = 0.9817, A-G = 1.2963, A-T = 0.2556, C-G = 0.2124, C-T = 1.8082, G-T = 1.0 (fixed).

There is a basal dichotomy within the genus *Hyacinthoides* separating an eastern [E] and western [W] clade (Fig. 3). The eastern clade includes three North African species, *H. aristidis* (Coss.) Rothm., *H. ciliolata* (Pomel) Rumsey, and *H. lingulata* (Poir.) Rothm. occuring from Morocco to Tunisia, along with *H. italica* (L.) Rothm., endemic to the Maritime Alps of France and Italy. The western clade comprises seven species, *H. cedretorum* (Pomel) Rumsey, *H. flahaultiana* (Emb.) Rumsey, *H. hispanica*, *H. mauritanica* (Schousb.) Speta, *H. non-scripta*, *H. paivae* S. Ortiz & Rodr.- Oubiña and *H. reverchonii* (Degen & Hervier) Speta. All of these taxa either occur in northwest Africa or western Europe (Fig. 1).

In the eastern clade, *H. italica* is sister to the clade comprising the three African species. The African lineage possesses four apomorphic indels, whereas *H. italica* possesses

Fig. 2. Tetraploid *Hyacinthoides cedretorum* from Rif Mts., Morocco (BB 072) with $2n = 32$ chromosomes viewed at 400× magnification.

two. The monophyly of three taxa within the African lineage, *H. aristidis*, *H. ciliolata* and *H. lingulata*, is well supported in all analyses (Figs. 3, 4). However, the relationships within this clade are poorly resolved.

In the western clade [W], the species with star-shaped flowers, *H. mauritanica* (northern Morocco, Portugal), *H. flahaultiana* (Anti-Atlas, Morocco) and *H. reverchonii* (endemic to Sierra de Cazorla, Jaén, Spain) form the sub-clade [W1], sister to *H. non-scripta*, *H. hispanica*, *H. cedretorum* and *H. paivae* [W2], which demonstrate a variety of flower forms, from star-shaped to narrowly tubular. Within the first sub-clade [W1], *H. mauritanica* is sister to a group comprising two narrow endemics, *H. flahaultiana* and *H. reverchonii*. *Hyacinthoides mauritanica* is characterised by four apomorphic indels. Material from the type locality on the Atlantic coast of northern Morocco (BB 336) is sister to a clade comprising all specimens from Portugal [BB 179, 184, 264] (Figs. 3, 4).

The second sub-clade [W2] comprises the widespread species *H. non-scripta* and *H. hispanica* plus two species with more restricted ranges, *H. cedretorum* and *H. paivae*. *Hyacinthoides non-scripta* was found to be sister to the *H. hispanica* clade, which comprises three species. The *H. hispanica* clade comprises two well-supported lineages, with one representing populations collected between central Portugal and the Sistema Central, and along the northern boundary of the southern Iberian range. The other lineage comprises all other populations of *H. hispanica* plus two other taxa. These are the North African tetraploid *H. cedretorum*, which is monophyletic and exhibits just one change across all cpDNA regions in four accessions collected over a wide geographic range (Rif Mts, High Atlas, Anti-Atlas), and *H. paivae* which is endemic to Galicia and adjacent regions of north-western Iberia.
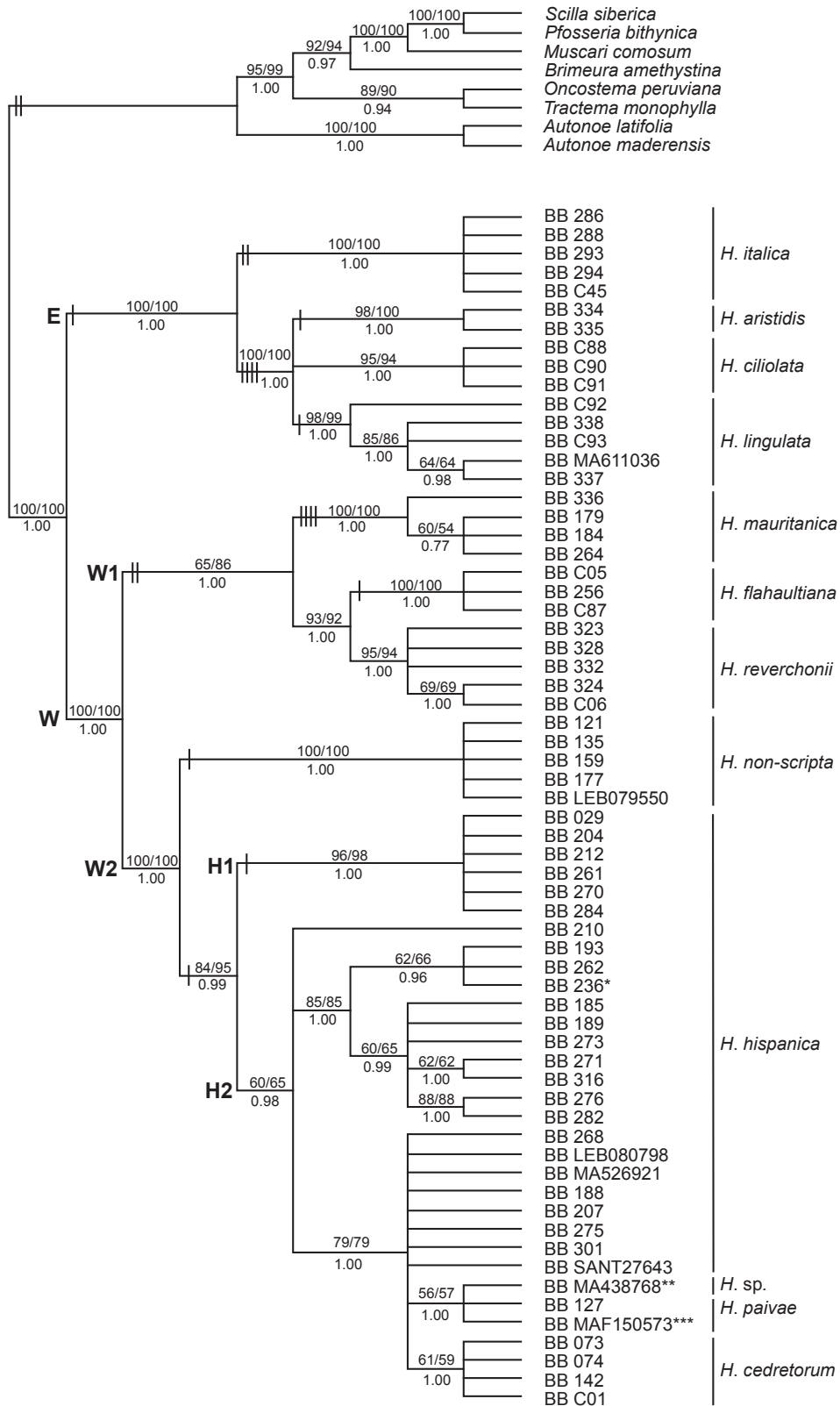
Fig. 3. Strict consensus tree of 96 most parsimonious trees obtained in the MP analyses of a dataset including five cpDNA regions plus the indel matrix. Bootstrap percentage numbers are given above branches correspond to the BP$_{MP}$ without the indel matrix/percentage BP$_{MP}$ including the indel matrix. Bayesian posterior confidence values (PP$_{Bay}$) are given below branches. Vertical bars indicate the number of indels unique to each branch. The proposed taxonomy is plotted to the right site of the tree. * = *H. hispanica* cultivar ("Spanish Bluebell") from Sydenham Hill, London; ** = specimen from LaRioja, Spain, morphologically similar to *H. non-scripta*; *** = isotype of *H. paivae*.
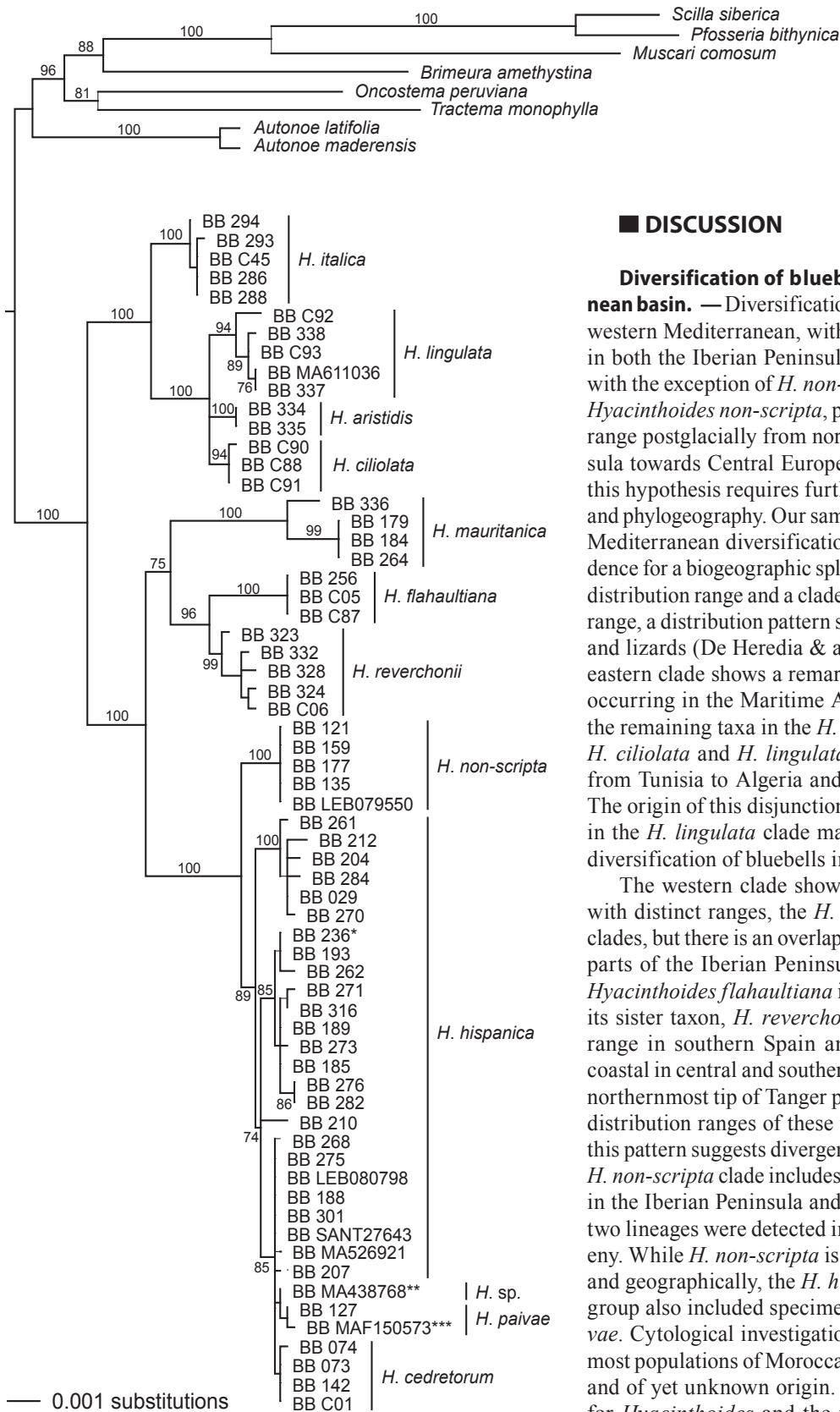
Fig. 4. Phylogram of the maximum likelihood tree calculated using the combined dataset. Bootstrap percentage numbers (BP$_{ML}$) >75% are given above branches. For asterisks see Fig. 2.

■ **DISCUSSION**

Diversification of bluebells in the western Mediterranean basin. —Diversification of bluebells has occurred in the western Mediterranean, with distinct lineages and radiations in both the Iberian Peninsula and northern Africa. All taxa, with the exception of *H. non-scripta* are confined to this area. *Hyacinthoides non-scripta*, probably expanded its distribution range postglacially from northern parts of the Iberian Peninsula towards Central Europe and the British Isles. However, this hypothesis requires further study of population structure and phylogeography. Our sampling was designed to explore the Mediterranean diversification of these plants. We found evidence for a biogeographic split into a clade with a more eastern distribution range and a clade with a more western distribution range, a distribution pattern seen also in, amongst others, oaks and lizards (De Heredia & al., 2007; Paulo & al., 2008). The eastern clade shows a remarkable disjunction with *H. italica* occurring in the Maritime Alps of France and Italy whereas the remaining taxa in the *H. lingulata* clade, i.e., *H. aristidis*, *H. ciliolata* and *H. lingulata*, are confined to North Africa, from Tunisia to Algeria and then towards Morocco (Fig. 1). The origin of this disjunction is currently unknown. The taxa in the *H. lingulata* clade may be the result of a more recent diversification of bluebells in this region.

The western clade shows a similar split into two clades with distinct ranges, the *H. non-scripta* and *H. mauritanica* clades, but there is an overlap in the latter clade in the southern parts of the Iberian Peninsula and north-western Morocco. *Hyacinthoides flahaultiana* is confined to southern Morocco, its sister taxon, *H. reverchonii* is confined to one mountain range in southern Spain and *H. mauritanica* is primarily coastal in central and southern Portugal, also occurring on the northernmost tip of Tanger province in Morocco (Fig. 1). The distribution ranges of these three species do not overlap and this pattern suggests divergence in geographical isolation. The *H. non-scripta* clade includes four species of which three occur in the Iberian Peninsula and one in Morocco. However, only two lineages were detected in the chloroplast genome phylogeny. While *H. non-scripta* is clearly defined, both genetically and geographically, the *H. hispanica* chloroplast DNA clade/group also included specimens of *H. cedretorum* and *H. paivae*. Cytological investigations confirmed that the northernmost populations of Moroccan *H. cedretorum* were tetraploid, and of yet unknown origin. This is the first tetraploid count for *Hyacinthoides* and the plant is either an autopolyploid offspring of *H. hispanica*, or an allotetraploid formed by a cross between *H. hispanica* and an unknown second parent. The status of *H. paivae* requires further attention because this

Table 1. Information to the MP analyses conducted.

Region	IC	VA	PI	TL	MPs	CI	RI	RC
atpB-rbcL IGS	934	40	45	104	>1000	0.7619	0.9257	0.7922
trnC-ycf6	968	71	75	179	36	0.7736	0.9413	0.8954
trnH-psbA IGS	642	14	19	38	120	0.8696	0.9739	0.8979
trnL-trnF region	1009	36	65	125	>1000	0.7955	0.9653	0.8263
trnG-trnR region	734	31	48	99	5	0.8060	0.9632	0.8367
Combined	4288	192	252	551	192	0.7762	0.9506	0.8143
Combined plus Indels	4363	225	294	635	96	0.7822	0.9513	0.8194

IC = number of included characters; VA = number of variable parsimonious not informative positions; PI = number of parsimonious informative positions; TL = length of the most parsimonious tree(s); MPs = number of most parsimonious trees; CI = consistency index; RI = retention index; RC = rescaled consistency index.

taxon is distinct from the other members of this clade in its flower shape (Ortiz & al., 1999). Further investigations using nuclear markers, field observations, including pollinators and their behaviour, may help to elucidate this situation.

The two most widespread species, *H. hispanica* and *H. non-scripta*, also show a range differentiation, with *H. hispanica* occurring in the southern and middle parts of the western Iberian Peninsula and *H. non-scripta* in the northern parts of the western Iberian Peninsula. The separation line appears to follow the northern border between Portugal and Spain and extends along the Duero towards the heart of Castilla y León. Reports of *H. non-scripta* from central Spain, e.g., Madrid, Segovia and Avila provinces, require substantiation. No material seen by the authors in herbaria or during our fieldwork in this area are unequivocally identifiable with this taxon. The two species phylogenetically nested within *H. hispanica* have distribution ranges currently beyond the distribution of *H. hispanica*, with *H. cedretorum* occurring exclusively south of the straits of Gibraltar on the high mountains of Morocco and Algeria, and *H. paivae* confined to Galicia and northern parts of Portugal, i.e., the northwest corner of the Iberian Peninsula.

In conclusion, our results provide unambiguous evidence for the diversification of this genus within the western Mediterranean, especially the Iberian Peninsula and adjacent northern Africa. The diversification of plants in this area is still poorly understood and bluebells may well provide an excellent example to help unravel evolutionary patterns and processes, including refugia and migration routes, in this highly biodiverse region. This study adds to a rapidly growing body of studies exploring the diversification of plants in the western Mediterranean especially the Iberian Peninsula (e.g., Thompson, 2005; Albaladejo & Aparicio, 2007; De Heredia & al., 2007; Pardo & al., 2008). Some studies of the evolution of western Mediterranean plant diversity point to several crucial events, late Oligocene rifting of continental microterranes, the Messinian salinity crises at the Miocene-Pliocene boundary (5.96–5.33 million year ago [Ma]), the establishment of a Mediterranean climate at the Late Pliocene (3.2–2.8 Ma), and sea level changes during the Pleistocene glaciation cycles (Hsü & al., 1977; Krijgsman & al., 1999; Hewitt, 2000; Loget &

Van den Driessche, 2006; Hampe & Petit, 2007; Magri & al., 2007). The deeper splits in the phylogeny of bluebells may be correlated either with the opening of the Strait of Gibraltar in the Early Pliocene inducing a vicariance pattern, with sister clades occurring in North Africa and the Iberian Peninsula, or the large-scale desiccation of the Mediterranean during the Messinian crisis, whereas the younger splits have been caused by Pleistocene glaciation cycles. The differences in the flowering time between the North African and western European taxa underline the importance of the adaptation to moisture regimes especially summer droughts (Linder, 2003). Future studies will focus on inferring the timing of bluebell diversification using molecular clock approaches.

Infrageneric classification. —Two distinct floral morphologies, patent versus campanulate corollas, exist within *Hyacinthoides* (Fig. 1). Based on this, taxa within *Hyacinthoides* have been segregated into two broad groups, either at subgeneric rank (Speta, 1987) or sometimes even with generic status, e.g., Salisbury (1866). Speta (1987) recognised the subgenus *Hyacinthoides*, comprising only *H. non-scripta* and *H. hispanica* and introduced the subgenus *Somera* (Salisb.) Speta containing *H. italica*, *H. reverchonii*, *H. aristidis*, *H. kabylica*, *H. lingulata*, *H. vincentina* and *H. mauritanica*. Ortiz & Rodríguez-Oubiña (1996) recognised the additional taxon *H. paivae* that had previously been misidentified as both *H. hispanica* and more often *H. italica*. *Hyacinthoides paivae* possessed patent tepals but also showed a degree of fusion of the filaments to the tepals, a character only otherwise seen in members of subgenus *Hyacinthoides*, and this discovery challenged the validity of the split at subgeneric level. Thus, Ortiz & Rodríguez-Oubiña (1996) consequently downgraded the subgenera to the rank of section. The position of *H. kabylica*, here treated as a synonym of *H. cedretorum* (syn. *H. hispanica* subsp. *algeriensis*—see below) called further doubt on the use of these characters. This taxon has a regular non-campanulate corolla, showing little differentiation between inner and outer tepals, and little fusion of the filaments to the tepals (*Somera* features) but is otherwise morphologically and genetically closely aligned, if not nested within, the broad *H. hispanica* (*Hyacinthoides*) clade. Pfosser & Speta (1999) argued that the major dichotomy within the genus resolved

by their phylogenetic study gave support to the validity of the subgeneric treatment, however, the dichotomy they recovered, and which is congruent with the first major split in our tree, does not segregate all of the patent (*Somera*) from the campanulate flowered (*Hyacinthoides*) taxa. Their own data would have necessitated a major re-circumscription of sections *Somera* and *Hyacinthoides* to address this evidence and their conclusion consequently has no support.

Our phylogenetic results do not support a split into the subgenera/sections *Somera* and *Hyacinthoides* but instead suggest a division of three lineages, of which one corresponds to some extent to the section *Hyacinthoides*. The first lineage comprises the eastern clade, with the western Maritime Alps species *H. italica* and three North African species *H. aristidis*, *H. ciliolata*, and *H. lingulata*. The second lineage belongs to the western clade and is formed by three species, *H. flahaultiana*, *H. mauritanica* and *H. reverchonii*, occurring either in North Africa or the southern Iberian Peninsula. The third lineage comprises four species with a mainly Iberian occurrence *H. cedretorum*, *H. hispanica*, *H. non-scripta*, *H. paivae*. We can find no morphological characters that adequately circumscribe the primary groupings revealed by the cpDNA data. Taking into account the more complex phylogeny and the lack of apomorphic characters distinguishing these three clades, we suggest the rejection of previously circumscribed infrageneric taxa.

Nomenclatural considerations: *Hyacinthoides* Heister ex Fabricius (1759) versus *Hyacinthoides* Medikus (1791). — The more widespread and long-cultivated woodland taxa recognised initially by Linnaeus within his genus *Hyacinthus* have had a chequered taxonomic history. Initially linked to the genus *Scilla*, these species, with their paired bracts, have been recognised under many novel generic names. For over a century most authors used *Endymion* Dumort. (1827) until Rothmaler (1944) resurrected the name *Hyacinthoides* (1759), first coined by Heister. This initially met little favour and indeed the later name was proposed for conservation over the earlier, but after an initial inconclusive vote (Pichi-Sermolli, 1954: 113) and a resubmission (Dandy, 1969) this move was rejected. The question as to who was first to validate Heister's pre-Linnaean name has also divided opinion. Stearn (1990) was of the view that "although cited from P.C. Fabricius, *Enumeratio methodica Plantarum Horti Medici Helmstadiensis*, 2 (1759) [it] was not validly published there, since neither this nor Heister's *Systema Plantarum generale* (1748) provides any generic description or diagnosis." He concluded that first valid publication of the name *Hyacinthoides* was thus by Medikus (1791) (not 1793 as cited by Stearn, p. 190). Several authors have subsequently followed Stearn in this generic attribution, (e.g. Speta, 1987; Juan, 2002; Rix, 2004, etc.). Stearn is correct in that neither Heister (1748) nor Fabricius (1759) provide an effective diagnosis—the latter using only the phrase "*floribus albis, coeruleis, rubentibus*", although this would arguably constitute descriptive matter that satisfies Art. 32.1. The second edition of Fabricius' work (1763) gives a more extensive account which outlines his concept of the genus and its distribution:

"Hyacinthoides *Heister*. Ind. 1732. / Hyacinthus corollis campanulatis sexpartitis apice revolutis / L. Sp. 1. non scriptus *Dodon*. Coronar. 172. *Histor. Lugd*. II. 1507 / Corolla coerulea, rubente & alba variat. Anglia & Europa calidior."

Although merely quoting verbatim Linnaeus (1753) description for *H. non-scriptus*, this could be taken as a generic diagnosis, pre-dating Medikus' (1791) validation. However, as Dandy (1969) noted, this is in any case irrelevant, as "*Hyacinthoides* Heister ex Fabricius is validated by implicit reference to Heister's pre-Linnaean work (Nom. Pl. 27. 1741) where *Hyacinthoides* is defined as a genus distinguished from *Hyacinthus* by the character of the perianth".

Selection of a generitype for *Hyacinthoides* Heist. ex Fabr. — Although listed by *Index Nominum Genericorum* (Farr & al., 1959; Farr & Zijlstra, 1996+) as without a designated type, Rothmaler (1944) in his resurrection of *Hyacinthoides* Heist. ex Fabr. clearly states, "Der Typus ist:

H. hispanica (Mill. em. Baker) Rothm., nov. comb. – *Scilla hispanica* Mill. p.p., em. Baker. – *Endymion campanulatus* Parl. – *H. racemosa* Medic."

Although this is not then clearly differentiated from the remaining list of *Hyacinthoides* species he recognised, the latter are not fully alphabetical in order and we feel that it was his clear intention to select *H. hispanica* as generitype. His selection can only be superseded under Art. 10.2, if "it can be demonstrated that the selected type is not conspecific with any of the material associated with the protologue". While all of the references cited by Fabricius (1763) clearly relate to *H. non-scripta*, the work cited by Heister (1741) is *Hortus Cliffortianus*, p. 125 (Linnaeus, 1738). Three sheets of original material are held at BM (BM 000558524-6) and although previously identified as *H. non-scripta* it is our opinion that the material either unambiguously represents *H. hispanica* (BM000558524 – 3rd and 4th from the left), or in the other cases this, or more probably *H. ×massartiana*. It is perhaps relevant to note that the only change Linnaeus made to the descriptive phrase used in *Hortus Cliffortianus* when compiling his (1753) *Species Plantarum* and describing *Hyacinthus non-scriptus*, was the addition of the words "apice revolutis"—a key character distinguishing *non-scripta* from *hispanica*. We therefore believe that Rothmaler's designation cannot be superseded and must be upheld. Rothmaler's selection has priority over that of *Hyacinthus non-scriptus* published by Pichi-Sermolli (1954: 113).

The generic name *Endymion* Dumort. has also, according to *Index Nomimum Genericorum*, never been formally typified, but *E. nutans* (Sm.) Dumort. was cited as type in the 1954 proposal to conserve the name (Pichi-Sermolli, 1954: 113) and this appears to the earliest selection. Dumortier (1827) recognised three species within his new genus: *E. nutans*, based on Smith's *Scilla nutans*; *E. cernuus*, based on Linnaeus' *Hyacinthus cernuus* and *E. patulus* based on Desfontaines' *Hyacinthus patulus*. *Endymion cernuus* was lectotypified by a specimen representing *H. non-scripta* 'Rosea' by Stearn (1990) but which, from the protologue, clearly also included plants we would now refer to *H. hispanica*, whereas *E. patulus* (a replaced synonym for Lamarck's illegitimate homonym

H. amethystinus) is an even more ambiguous name usually considered synonymous with *H. hispanica* but which may also relate to plants now named *H. ×massartiana*. Smith (in Sowerby, 1797), in publishing *Scilla nutans*, justified the change of epithet by saying "*Nutans* expresses an essential part of its specific character, and any thing is better than *non-scriptus*" and cited *Hyacinthus non-scriptus* L. as a synonym. *Scilla nutans* is thus illegitimate and automatically typified under Art. 7.5 of the *ICBN* by the type of *Scilla non-scripta* L. (≡ *H. non-scripta* (L.) Rothm.). The choice of *S. nutans* thus provides the least ambiguous element by which *Endymion* could be typified. The ultimate type of *Endymion* Dum. is therefore Herb. Linn. No. 438.1. (LINN), the lectotype of *H. non-scriptus* L, selected by Stearn (1990: 188).

The status of *Hyacinthoides lingulata* (Poir.) Rothm. var. *ciliolata* (Pomel) Batt. — Our study revealed an initial split discriminating two clades. The predominantly autumn-flowering North African *H. lingulata* clade comprising *H. aristidis* and *H. lingulata* sensu lato (s.l.), which is sister to the spring-flowering *H. italica*, from the French Riviera and northern Italy. The sister clade comprises all other species, which are spring-flowering and distributed predominantly in western Europe, with some taxa also in North Africa. Jordan in Jordan & Fourreau (1903) recognised many new species in this group, subsequently treated by Maire (1958) as infraspecific taxa within *H. lingulata*, of which var. *ciliolata* was arguably the most distinct. The pairing of this taxon with *H. aristidis*, as opposed to *H. lingulata*, in the majority of the recovered trees, suggested a re-assessment of its status and affinities was necessary. While the foliage of *H. aristidis*—two, rarely three, short, almost spathulate leaves with a channelled sheathing base, differs from that of *H. lingulata* s.l. (including var. *ciliolata*) with four, to many, narrowly-lingulate, rather flat-based leaves, *H. lingulata* var. *ciliolata* does share some floral characters with *H. aristidis* as opposed to *H. lingulata* sensu stricto (s.str.). The style is proportionately longer in *aristidis*/*ciliolata* than in *lingulata*, where it is noticeably shorter than the ovary. In addition *aristidis*/*ciliolata* produces a maximum of two seeds per ovule, whereas *H. lingulata* s.str. may produce up to four. Further work is clearly needed on this group to establish additional distinguishing characters and to re-assess critically the taxa recognised by Jordan. *Hyacinthoides aristidis* and *H. lingulata* var. *ciliolata* occur at the eastern extremity of the genus' North African range in Tunisia and Algeria, overlapping in range in the latter with *H. lingulata* s.str. *Hyacinthoides lingulata* then extends exclusively westwards to the Atlantic coast of Morocco.

Although represented by only few examples in this study there is sufficient evidence to support the recognition once again of Pomel's (1874) *Scilla ciliolata* at specific rank. This combination has not previously been made in *Hyacinthoides* and the necessary new combination is therefore made below. Pomel's material is now held in MPU and P and we have selected a sheet from Pomel's herbarium "broussailles, Oran, St. Louis", *Pomel*, MPU 005973 (MPU) as lectotype as it unambiguously matches the protologue. Another collection which could be considered has been divided, the lower portion

(MPU 005972) with Pomel's label is in Montpellier, the upper (P00083324), with a label by(?) Maire and an incorrect collection date [1892] is in Paris; they can be considered isotypes.

"*Hyacinthoides italica*" in Iberia and the status of *H. vincentina* (Link & Hoffmanns.) Rothm. — Schousboe described *Hyacinthoides mauritanica* in 1800, from the north-westernmost tip of Morocco close to Cap Spartel, where it still occurs (specimens: *Jury & al. 13302* = BM000540750 = BB 336). In northern Morocco it is known only from low altitude in the Tanger region (Juan, 2002), although it is cited by earlier authors (Maire, 1958) as also occurring at higher altitudes in the Anti-Atlas, and it is from here that most plants under this name are in cultivation (see however *H. flahaultiana* below). The taxon was incorrectly listed as a Moroccan endemic by Juan (2002); the realisation that plants from Portugal, which had previously been treated as *H. italica* in most major floristic accounts, e.g., Tutin & al. (1980), were in fact synonymous with this North African species was made by Ortiz & al. (1999) although, much earlier, Grey (1938) had suggested the synonymy of *mauritanica* with what was then referred to as *Scilla vincentina*. The status of that narrow endemic taxon, thought to be restricted to the south-westernmost tip of the Algarve, has always been contentious. Heywood in Tutin & al. (1980) suggested it should be accorded no more than varietal status within *H. italica*, differing only in its anther colour and smaller stature. Franco & Rocha Afonso (1994) realised that Portuguese plants were not synonymous with *H. italica* and created a subspecies (subsp. *transtagana*) of *H. vincentina* to accommodate the larger, darker-flowered plants from further north on the Portuguese coast. Upon equating these plants with *H. mauritanica*, a name which pre-dates *vincentina* as a specific epithet by three years, Ortiz & al. (1999) made the necessary novel combination—*H. mauritanica* subsp. *vincentina*, although it is clear from their key that they saw considerable overlap in the majority of the distinguishing characters; only leaf curvature with marginal undulation was considered discretely diagnostic.

The plants of Sagres in the Cape St. Vincent area, the *locus classicus* for *H. vincentina*, occur in shallow soils in open areas among *Cistus*-dominated scrub over limestone. In this they differ from the typical seasonally inundated habitats occupied elsewhere by *H. mauritanica* in its Portuguese range, although populations on flushed and slumping slopes and seasonally damp cliff-top depressions, e.g., at Zambujeira do Mar, ca. 55 km to the north, sit ecologically and morphologically intermediate. As a consequence of fieldwork associated with this phylogenetic study, it has become obvious that all of the previously stated diagnostic characters (pollen colour, tepal colour, scape height, leaf form) vary continuously. Similarly, at the cpDNA sequence level, no differences could be detected and we therefore conclude that the recognition of *vincentina* at even varietal level is not justified. *Hyacinthoides vincentina* (Link & Hoffmanns.) Rothm. should therefore be regarded as a taxonomic synonym of *H. mauritanica* (Schousb.) Speta.

ced *Hyacinthoides flahaultiana* (Emb.) Rumsey — The cpDNA phylogeny revealed that plants previously regarded as *H. mauritanica*, all accessions of *H. mauritanica* and *H. flahaultiana* in this study, fell into two distinct clades. One, exclusively

including all of the material investigated from Southern Morocco (BB 256, C05, C87), was sister to the Spanish narrow endemic *H. reverchonii*. Together these were then sister to *H. mauritanica* s.str. (including *H. vincentina*) from Northern Morocco (BB 336) and Portugal (BB 179, 184, 264). In the light of this a morphological re-assessment was made of the rather limited material available. *Hyacinthoides* was first recorded from the Anti-Atlas mountains by Emberger (1935), who described plants from the Kerdous area as a new taxon, under the name *Scilla flahaultiana* Emb. Maire (1958) reduced this into synonymy under *S. mauritanica*. Subsequent collections, several of which have been maintained in cultivation by specialist bulb growers, have also centred on the Kerdous valley, between Tirhmi and Tizourhane (specimens: *Salmon & Fillan 65*; *Salmon, Bird & Lovell 19* = BB C05, the latter a white flowered form). The plant has also been recorded from the valley of Azour Ighallen, N.W. of Tafraoute (Maire, 1958) and most recently has been collected on Jbel Imzi, ca. 40 km NE of Anezi (specimens: *Jury & al. 20599* = BB 256). Ecologically these plants differ from the North Moroccan/Lusitanian in that all grow at altitudes over 1000 m, on dry terra rossa soils, in scrub under degraded *Argania* woodland, as opposed to growing close to sea-level in seasonally damp, usually sandy soils, in very open communities dominated by graminaceous forbs and ruderal herbs. Morphologically the Anti-Atlas plants show greater similarities to *H. italica* than to *H. reverchonii* and differ from both in their long-acuminate leaf tips and more globose bulbs, characters otherwise unique to *H. mauritanica* in the genus. The Anti-Atlas material however, would appear to differ from that species in the form of its inflorescence, particularly noticeable post-anthesis. *Hyacinthoides mauritanica*, like *H. reverchonii*, generally has a relatively few-flowered inflorescence which becomes sub-corymbose through the elongation and erection of the lowermost peduncles. The Anti-Atlas plants show a denser, more spicate inflorescence, in which the lower peduncles do not markedly elongate and are borne just a little above horizontal post-anthesis. On the basis of the DNA evidence, ecological and morphological differences and discrete geographical ranges, we believe that the Anti-Atlas plants are worthy of specific rank and accordingly a new combination for Emberger's name is necessary; this is made below. There are two available potential types gathered on the same day by Emberger, each with different habitat details amalgamated in the protologue. We here select MPU 006090 (MPU) as lectotype "Anti-Atlas: Rocailles siliceuses près Kerdous, 1000–1200 m, 28.4.1934"; we have chosen this over MPU 006089 (MPU), "Anti-Atlas occidental: Forêt d'Arganix degradées aux environs de Kerdous, Maroc, 1200 m, 28.4.1934" as the protologue states an altitude of 1000–1100m which better fits the former.

The specific status of *Hyacinthoides hispanica*. —Kerguélen (1993) proposed that, because of their morphological similarity, *H. hispanica* and *H. non-scripta* should be regarded as subspecies of the same species, the earliest epithet for which obviously being that of Linnaeus (1753). As a consequence the morphologically and genetically more variable Iberian plant would become *H. non-scripta* subsp. *hispanica*. The apparent abundance and ease with which introgressive hybridisation between the native *H. non-scripta* and the introduced *H. hispanica* has occurred in British gardens and urban surrounds would, if

substantiated, suggest a close relationship. The extent, to which similar hybridisation events have occurred currently, or anciently, in the central sierras of Spain where the two taxa are currently most nearly sympatric and where study of local floras (Cebolla Lozano & Rivas Ponce, 1994) shows discrimination to be problematic, remains to be elucidated. It is clear from our cpDNA phylogeny, however, that these two taxa are well resolved as sister to one another with good support values and this argues for their recognition at specific rank. The identity of the "Spanish Bluebell" as treated in British floras (Stace, 1997) with *H. hispanica* has recently been questioned as material falls beyond the extremes of the morphological range given within the native range of the species. The recovery of a British example within the broad *H. hispanica* clade makes clear that further work is needed to resolve these questions, but also demonstrates that from cpDNA evidence alone these horticultural forms do not form a discrete or distinct unit. Our cytological data shows that the plants from one British population are triploid (J. Squirrell, unpub. data), a condition not yet documented in wild Spanish populations (Speta, 1987). Further work is clearly needed to elucidate the origin and spread of these triploid entities, which have presumably been selected for their size and vigour, and to determine to what extent they are morphologically diagnosable, or indeed reproductively isolated from diploid populations. We have therefore chosen at this stage not to attempt to formally taxonomically recognise the different cytotypes. Should this become necessary the difficulty of assigning a ploidy level to the lectotype would need to be addressed, most probably through epitypification. We can find no previous formal lectotypification of *Hyacinthoides hispanica*, although the Miller specimen we have selected here (Miller "Dict. No. 8, 1768" BM 000893729 (BM) has previously been annotated as both the type of *S. hispanica* Miller as well as that of *S. campanulatus* Ait.

The status of *Hyacinthoides paivae*. —The only taxon for which the cpDNA data do not provide clear support through monophyly is the recently described *H. paivae* S. Ortiz & Rodr.-Oubiña. This northwestern Iberian endemic, which has been much confused with both *H. italica* and *H. hispanica* in the past, occupies an intermediate position between the *Somera* type and *Hyacinthoides* type flower forms and might therefore have been predicted to appear as sister to the *hispanica–non-scripta* clade, or basal to it. Its position(s) as derived from within *hispanica* suggest the possibility that its floral form may result from a reversion to a more ancestral state, some support for which is provided by the position of *H. cedretorum* (syn. *H. hispanica* subsp. *algeriensis*), that also possesses a more regular, open corolla with reduced filament to tepal fusion. *Hyacinthoides paivae*, *H. non-scripta* and *H. hispanica* are apparently currently sympatric in northwest Spain, although this is uncertain given the comparatively recent description of the first (Ortiz & Rodríguez-Oubiña, 1996) and past misidentifications. In any case contact zones may have occurred in the past, which through hybridisation might act to confuse a phylogeny produced from a uniparentally-inherited marker such as the plastid. Further work utilising nuclear DNA markers, or a co-dominant marker system such as allozymes, which sample all genomes, may be necessary to resolve the morphological/

molecular conflict identified here. Until such work is completed we prefer to maintain *H. paivae* as a species as it has a distinct geographical range and is morphologically discrete. The accession MA438768, representing the isolated populations in the Sierra de la Demanda region (Burgos and La Rioja) groups with *H. paivae* accessions in the cpDNA phylogeny. Whereas the *trnCD* sequence matches *H. paivae* and other cpDNA regions are unique (*atpB*) or match *H. hispanica*, it seems to be more closely related to *H. non-scripta* on morphological features. Based on our dataset we therefore cannot place it into any lineage of the *H. non-scripta*/*H. hispanica* clade [W2]. Further studies are currently being carried out to elucidate the phylogeographic history of populations in this region.

The correct name and status of *Hyacinthoides hispanica* subsp. *algeriensis*. — All records of *Hyacinthoides hispanica* in North Africa (e.g., Juan, 2002 refers to the plant which has been treated by later authors as a variety (Maire, 1958) or latterly as a subspecies (Förther & Podlech, 2002) of that species, under the epithet *algeriensis*, first coined by Battandier (1880) for a variety of *Endymion patulus* (Desf.) Dumort. Some authors have, however, accorded the taxon specific rank as *Hyacinthoides kabylica* (Speta, 1987; Ortíz & Rodríguez-Oubiña, 1996). The first validly published name at specific rank is, however, *Endymion cedretorum*, described by Pomel (1874) for plants from Djebel Endate in Algeria.

Morphologically this taxon is very distinctive. It possesses strongly revolute tepals to which the filaments are fused to less than a quarter of the tepal's length (Fig. 1); there are little or no distinctions between the inner and outer tepals in this respect and the filaments are sub-equal in length. These characters have suggested a placement within subgenus *Somera* (Speta, 1987), although it is clear from our study that this taxon's affinities are clearly within the broad *hispanica* clade where it forms a discrete monophyletic unit; the small amount of variation noted being between High Atlas (BB 074) vs. Middle Atlas and Rif material.

This delicate spring-flowering taxon is widely but sparsely distributed along the high mountain chains of North Africa, where it grows from ca. 1400 to 2700 m altitudes, generally under *Cedrus* or *Abies*. It is recorded from north-east Algeria (Jijel province), westwards to the Rif of northern Morocco, where it has recently been re-discovered (Carine & al., 2006), and south through the Atlas Mountains. Plants from the High-Atlas, where it grows on open, but sheltered rock ledges, often in quite nitrophilous conditions, have coarser growth, paler flowers with less reflexed tepals and, in the populations from the Oukaimeden area and the Col du Tichka, creamy-yellow anthers and pollen, whereas typically the anthers and pollen are dark purplish-blue. Our cytological data suggest that material from throughout the Moroccan range is, uniquely within the genus, tetraploid (*n* = 16). As mentioned above, the presence of other polyploid (3*x*) lineages within the *hispanica* clade are known, although their morphological differences are more quantitative than qualitative in nature. Given the tetraploid taxon's allopatry and distinctive floral form, we suggest this is best recognised as a species. The earliest available epithet at this level has not been transferred to *Hyacinthoides* and that combination is now made here. A lectotype

is here selected (MPU 005974) from Pomel's original syntype material, now distributed between Montpellier and Paris.

When the cpDNA dataset alone is considered, the recognition of this taxon at specific level (and that of *H. paivae*) does render *H. hispanica* paraphyletic; further work is needed to test this using a wider range of molecular markers.

■ TAXONOMIC TREATMENT

Hyacinthoides Heist. ex Fabr., Enum. 2. 1759 – Type (designated by Rothmaler in Feddes Repert. Spec. Nov. Regni Veg. 53: 15. 1944): *H. hispanica* (Mill.) Rothm.
= *Usteria* Medik., Act. Acad. Theod. Palat. 6. Phys.: 480. 1790 (non Willd. 1790) ≡ *Hylomenes* Salisb., Gen. Pl.: 26. 1866 – Type: *U. hyacinthiflora* Medik.
= *Hyacinthoides* Medik. in Ann. Bot. (Usteri) 2: 9. 1791 – Type: *H. racemosa* Medik.
= *Endymion* Dumort., Fl. Belg.: 140. 1827 – Type (designated by Pichi-Sermolli in Taxon 3: 113. 1954): *Endymion nutans* Dumort., Fl. Belg.: 140. 1827 (≡ *Scilla nutans* Sm., nom. illeg. ≡ *Hyacinthus non-scriptus* L.) ≡ *Agraphis* Link, Handbuch 1: 166. 1829 (type designated by Pfeiffer, Nom. 1: 82. 1873) ≡ *Lagocodes* Raf., Fl. Tellur. 2: 24. 1837 (Rafinesque indicated as type "1 *Lag. nutans* Raf. *S do Sm. DC.* [which he equated with] *S. cernua* L. *Hyacinthus cernuus* et *H. nonscriptus* L.").
= *Somera* Salisb., Gen. Pl.: 26. 1866 – Type: *S. italica* (L.) Salisb., Gen. Pl.: 27. 1866 (*Scilla italica* L.; *Hyacinthoides italica* (L.) Rothm.).
= *Apsanthea* Jord. in Jordan & Fourreau, Icon. Fl. Eur. 2: 40. 1903 – Type (designated by Speta in Phyton (Horn) 26: 288. 1987): *A. serotina* Jord. in Jordan & Fourreau, Icon. Fl. Eur. 2: 40. 1903.

1. *Hyacinthoides aristidis* (Coss.) Rothm. in Feddes Repert. Spec. Nov. Regni Veg. 53: 15. 1944 ≡ *Scilla aristidis* Coss. in Bull. Soc. Bot. France 5: 104. 1858 ≡ *Endymion aristidis* (Coss.) Chouard in Bull. Mus. Hist. Nat. (Paris), Ser. 2, 2: 703. 1930 – Type: "in provincia Cirtensi, in monte Djebel Edough haud procul ab urbe Bône ab amicissimo A. Letourneaux inventa" (?P, not seen).

2. *Hyacinthoides cedretorum* (Pomel) Rumsey, **comb. nov.** ≡ *Endymion cedretorum* Pomel, Nouv. Mat. Fl. Atl.: 384. 1874 ≡ *Scilla hispanica* var. *cedretorum* (Pomel) Maire in Mém. Soc. Sci. Nat. Maroc 7: 153. 1924 – Lectotype (designated here): Dj. Endate, (Tienet-el-Kad) 5 Mai 1860, *Pomel*, MPU 005974 (MPU).
= *Scilla kabylica* Chabert in Bull. Soc. Bot. France 56: 477. 1909 ≡ *Endymion kabylicus* (Chabert) Chouard in Ann. Sci. Nat., Bot., Ser. 10, 13: 287. 1931 ≡ *Hyacinthoides kabylica* (Chabert) Rothm. in Feddes Repert. Spec. Nov. Regni Veg. 53: 15. 1944 – Type: Algeria, in Kabyliae rupestribus calcareis nemorosis regionis subalpinae, ca. 1700 m.s.m. Djebel Magris, *Reverchon*, Plantes d'Algerie 1898 no. 356 (?B not seen).

= *Endymion patulus* var. *algeriensis* Batt. in Bull. Soc. Bot. France 27: 164. 1880 ≡ *Hyacinthoides hispanica* subsp. *algeriensis* (Batt.) Förther & Podlech in Sendtnera 7: 86. 2002 – Type: "djebel Mouzaïa, à 1400 mètres; Teniet el Haad, forêt de Cèdres", *Battandier*, MPU 007151 (MPU).

3. *Hyacinthoides ciliolata* (Pomel) Rumsey, **comb. nov.** ≡ *Scilla ciliolata* Pomel, Nouv. Mat. Fl. Atl.: 385. 1874 ≡ *Scilla lingulata* var. *ciliolata* (Pomel) Batt., Fl. Algérie Tunisie: 334. 1905 ('1902') – Lectotype (designated here): "broussailles, Oran, St. Louis", *Pomel*, MPU 005973 (MPU); isotypes P 00083324(P); MPU 005972 (MPU); syntype: Oran, Tlemsen, Pomel, Oct. 1854, MPU No. 005971 (MPU).

4. *Hyacinthoides flahaultiana* (Emb.) Rumsey, **comb. nov.** ≡ *Scilla flahaultiana* Emb. in Bull. Soc. Sci. Nat. Maroc 15: 175. 1935 – Lectotype (designated here), Anti-Atlas: Rocailles siliceuses près Kerdous, 1000–1200 m, 28.4.1934 MPU 006090 (MPU); isotype, Anti-Atlas occidental: Forêt d'Arganix degradées aux environs de Kerdous, Maroc, 1200 m, 28.4.1934, *Emberger* MPU 006089 (MPU).

= *Hyacinthoides mauritanica* sensu auct. Maroc., non *H. mauritanica* (Schousb.) Speta.

5. *Hyacinthoides hispanica* (Mill.) Rothm. in Feddes Repert. Spec. Nov. Regni Veg. 53: 15. 1944 ≡ *Scilla hispanica* Mill., Gard. Dict., ed. 8: x. 1768 ≡ *Endymion hispanicus* (Mill.) Chouard ≡ *Scilla campanulata* Ait., Hort. Kew 1: 444. 1789 ≡ *Agraphis campanulata* (Ait.) Link Handb.1: 166. 1829 ≡ *Endymion campanulatus* (Ait.) Parl., Fl. Ital. 2: 488. 1852 ≡ *Hyacinthoides non-scripta* subsp. *hispanica* (Mill.) Kerguélen, Index Synonym. Fl. France: XIII. 1993 – Lectotype (designated here): Herb. Miller "Dict. No. 8, 1768", BM 000893729 (BM).

= *Hyacinthus amethystinus* Lam., Encycl. 3(1): 190. 1789, non L. Sp. Pl. 1: 317. 1753 ≡ *Hyacinthus patulus* Desf., Tabl. École Bot.: 26. 1804 ≡ *Scilla patula* (Desf.) DC., Fl. Franç., ed. 3, 3: 211. 1805 ≡ *Endymion patulus* (Desf.) Dumort., Fl. Belg.: 140. 1827 ≡ *Agraphis patula* (Desf.) Rchb., Fl. Germ. Excurs.: 106. 1830 ≡ *Hyacinthoides patula* (Desf.) Rothm. in Feddes Repert. Spec. Nov. Regni Veg. 53: 15. 1944. "cultivée depuis long-temps au Jardin du Roi" [Paris] – Type: not designated.

= *Hyacinthoides racemosa* Medik. in Ann. Bot. (Usteri) 2: 9. 1791. Cultivated at Mannheim Botanic Garden – Type: not designated.

6. *Hyacinthoides italica* (L.) Rothm. in Feddes Repert Spec. Nov. Regni Veg. 53: 15. 1944 ≡ *Scilla italica* L., Sp. Pl.: 308. 1753 ≡ *Somera italica* (L.) Salisb., Gen. Pl.: 27. 1866 ≡ *Endymion italicus* (L.) Chouard in Bull. Mus. Hist. Nat. (Paris), Ser. 2, 2: 702. 1930 – Lectotype (designated by van Raamsdonk in Feddes Repert. 108: 105. 1997): Herb. Linn. No. 429.1 (LINN).

= *Scilla bertolonii* Duby, Bot. Gall. 1: 465. 1828 – Type: "circa Nicaeam" (?BERN, not seen).

7. *Hyacinthoides lingulata* (Poir.) Rothm. in Feddes Repert. Spec. Nov. Regni Veg. 53: 15. 1944 ≡ *Scilla lingulata* Poir., Voy. Barbarie 2: 151. 1789 ≡ *Endymion lingulatus* (Poir.) Chouard in Ann. Sci. Nat., Bot., Ser. 10, 13: 287. 1930 – Type: "Foliis lineari-lingulatis, floribus spicatis, bracteis pedunculo longioribus … côté des Nadis" (?P, not seen).

= *Apsanthea serotina* Jord. in Jordan & Fourreau, Icon. Fl. Eur. 2: 40. 1903 – Type not designated: "Algeria: circa Guelma" (?LY, not seen).

= *Apsanthea oligantha* Jord. in Jordan & Fourreau, Icon. Fl. Eur. 2: 40. 1903 – Type not designated: "Algeria: Circa Oran" (?LY, not seen).

= *Apsanthea propera* Jord. in Jordan & Fourreau, Icon. Fl. Eur. 2: 41. 1903 – Type not designated: "Algeria: Bône" (?LY, not seen).

= *Apsanthea micrantha* Jord. in Jordan & Fourreau, Icon. Fl. Eur. 2: 41. 1903 – Type not designated: "Algeria: Bône" (?LY, not seen).

= *Apsanthea melanocarpa* Jord. in Jordan & Fourreau, Icon. Fl. Eur. 2: 41. 1903 – Type not designated: "Algeria: Bône" (?LY, not seen).

8. *Hyacinthoides mauritanica* (Schousb.) Speta in Phyton (Horn) 26(2): 288. 1987 ≡ *Scilla mauritanica* Schousb., Iagttag. Vextrig. Marokko: 168. 1800 – Type: Morocco, Shibil Kibir Mt., *Schousboe s.n.* (?C, not seen).

= *Scilla vincentina* Link & Hoffmanns. in Neue Schriften Ges. Naturf. Freunde Berlin 4: 17. 1803 ≡ *Endymion vincentinus* (Link & Hoffmanns.) Chouard in Bull. Mus. Hist. Nat. (Paris), Ser. 2, 2: 703. 1930 ≡ *Hyacinthoides vincentina* (Link & Hoffmanns.) Rothm. in Feddes Repert. Spec. Nov. Regni Veg. 53: 15. 1944 ≡ *Hyacinthoides mauritanica* subsp. *vincentina* (Link & Hoffmanns.) S. Ortiz, Buján & Rodr.-Oubiña in Pl. Syst. Evol. 217: 172. 1999 – Type: "Cap St. Vincent in Portugal" (?B, not seen).

= *H. vincentina* subsp. *transtagana* Franco & Rocha Afonso, Nova Fl. Portug. 3, 1: 72. 1994 – Holotype: Algarve: Lagos, pr. de Bensafrim, nos arrelvados húmedos, alt. ca. 110m, *B. Rainha 5332*, 4 Apr. 1962 (LISE 66231).

9. *Hyacinthoides non-scripta* (L.) Chouard ex Rothm. in Feddes Repert. Spec. Nov. Regni Veg. 53: 15. 1944 ≡ *Hyacinthus non-scriptus* L., Sp. Pl.: 316. 1753 ≡ *Scilla festalis* Salisb., Prodr. Chapel-Allerton: 242. 1796 (nom. illeg.) ≡ *Scilla nutans* Sm. in Sowerby & Smith, Engl. Bot. 6: t. 377. 1797 (nom. illeg.) ≡ *Scilla non-scripta* (L.) Link & Hoffmanns. in Neue Schriften Ges. Naturf. Freunde Berlin 4: 19. 1803 ≡ *Endymion nutans* Dumort., Fl. Belg.: 140. 1827 (nom. illeg.) ≡ *Agraphis nutans* Link., Handb. 1: 166. 1829 (nom. illeg.) ≡ *Endymion non-scriptus* (L.) Garcke, Fl. Nord u. Mittel Deutschl.: 322. 1849 – Lectotype (designated by Stearn in Ann. Mus. Goulandris 8: 188. 1990): Herb. Linn. No. 438.1 (LINN).

= *Hyacinthus cernuus* L., Sp. Pl.: 317. 1753 ≡ *Scilla cernua* (L.) Hoffmanns. & Link in Neue Schriften Ges. Naturf. Freunde Berlin 4: 19. 1803 ≡ *Endymion cernuus* (L.) Dumort., Fl. Belg.: 140. 1827 – Lectotype (designated by

Stearn in Ann. Mus. Goulandris 8: 191. 1990): Herb. Linn. No. 438.3 (LINN).

10. *Hyacinthoides paivae* S. Ortiz & Rodr. Oubiña. in Pl. Syst. Evol. 202: 113. 1996 – Type: Spain, La Coruña, Dumbría, Montes de Pineda, grassland. 2. IV. 1994. *Louzan 319* (holotype: SANT; isotypes: BM, COI, K, LOU, MA, MAF, SANT).

11. *Hyacinthoides reverchonii* (Degen & Hervier) Speta in Phyton (Horn) 26(2): 288. 1987 ≡ *Scilla reverchonii* Degen & Hervier in Magyar Bot. Lapok 5: 7. 1906 ≡ *Endymion reverchonii* (Degen & Hervier) Breistr. in Bull. Mens. Soc. Linn. Lyon 23: 130. 1954 – Type: Sierra de la Cabrilla, E. Reverchon Exsicc. 1905, No. 1392 (holotype? BP, not seen; isotype: BM).

Hybrids

Hyacinthoides ×massartiana Geerinck in Belg. J. Bot. 129: 83. 1996 (***Hyacinthoides non-scripta*** (L.) Chouard ex Rothm. × ***H. hispanica*** (Mill.) Rothm.) – Type: Belgique, Région de Bruxelles-Capitale, Watermael-Boitsfort, parc Tournay-Solvay (Case IFBL: E4.46.24), bord d'etang de la Woluwe, 6/5/1995. *Geerinck-Coutrez 7617* (holotype: BR; isotype: LG).

= "***Hyacinthoides ×variabilis***" P.D. Sell, Fl. Gr. Brit. 5: 268. 1996, non rite publ. (Art. 32.1(d) & Art. H.10.1).

■ KEY TO THE SPECIES OF *HYACINTHOIDES*

1 Stamen fused to external tepal over at least 1/4 of tepal length **2**
1 Stamen fused to external tepal for less than 1/4 of tepal length **4**
2 Outer stamens fused to tepal for over 70% of stamen length, corolla narrowly tubular, with strongly reflexed tepal tips. . . . . *H. non-scripta*
2 Outer stamens fused to tepal for less than 70% of stamen length; corolla campanulate, tepal tips not, or only slightly reflexing. **3**
3 Internal and external stamens of differing lengths, the external >7 mm, corolla campanulate at anthesis. . . . . *H. hispanica*
3 Internal and external stamens sub-equal, the external <7 mm, corolla with tepals ± patent at anthesis . . . *H. paivae*
4 Tepals revolute at anthesis, usually >12 mm long . . . . *H. cedretorum*
4 Tepals ± patent at anthesis, <12 mm long **5**
5 Leaves long acuminate, bulb ± globose to conical **6**
5 Leaves obtuse to acute tipped, bulb ovoid, pyriform, rarely sub-spherical **7**
6 Inflorescence sub-corymbose to racemose, pedicels elongating in fruit, becoming erect to erecto-patent . . . .*H. mauritanica*

6 Inflorescence a lax to dense short raceme, pedicels not markedly elongating and horizontal to sub-erect in fruit . . . .*H. flahaultiana*
7 Pedicels shorter than, or equalling tepal length, flowers October–March, leaves lingulate-spathulate. **8**
7 Pedicels exceeding tepal length, flowers March–May, leaves linear-lanceolate **10**
8 Leaves 2(–3), sub-erect, keeled below, spathulate. . . . . *H. aristidis*
8 Leaves (3–)5–10, procumbent to ascending, not conspicuously keeled below, lingulate. **9**
9 Inflorescence opening from top, locules with up to 4 seeds. . . . . *H. lingulata*
9 Inflorescence opening from base, locules 2-seeded . . . . *H. ciliolata*
10 Tepals >7 mm long, pale at base, intense blue-mauve above, leaves wine-red just below ground level . . . . *H. reverchonii*
10 Tepals usually <7 mm long, ± pale blue throughout, leaves not conspicuously pigmented below . . . .*H. italica*

■ ACKNOWLEDGEMENTS

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Appendix. Voucher information and GenBank accession numbers given for samples used in this study. The number after the second hyphen in a voucher, e.g., "-01", indicates the individual in a sampled population.

Voucher (FJR = F.J. Rumsey; JCV = J.C. Vogel; JS = J. Squirrell; MG = M. Grundmann; SO = S. Ortiz; SWA = S.W. Ansell), country, political subdivision (BB code, GenBank accession numbers: *atpB-rbcL* IGS, *trnC-ycf6*, *trnH-psbA* IGS, *trnL-trnF* region, *trnG-trnR* region). BB codes refer to voucher specimens at BM. Other herbaria included in BB code. Detailed voucher data available on request.

H. ARISTIDIS: *Ray Cobb s.n.*, Algeria (cult.) (**BB-334-01**, FJ232722, FJ269130, FJ423302, FJ423232, FJ423374) — Oberösterreichisches Landesmuseum Linz, cult. nr. 51786, Algeria (cult.) (**BB-335**, FJ232723, FJ269131, FJ423303, FJ423233, FJ423375); *H. CEDRETORUM*: *FJR & S.L. Jury s.n*, Morocco, Mid Atlas (**BB-073**, FJ232759, FJ269170, FJ423342, FJ423270, FJ423414) — *S.L. Jury & al. 19594*, Morocco, High Atlas (**BB-074-01**, FJ232760, FJ269171, FJ423343, FJ423271, FJ423415) — *Ait Lafkih & al. 126*, Morocco, Rif Mts. (**BB-142-01**, FJ232761, FJ269172, FJ423344, FJ423272, FJ423416) — *FJR s.n.*, Morocco (cult.) (**BB-C01**, FJ232762, FJ269173, FJ423345, FJ423273, FJ423417); *H. CILIOLATA*: Chelsea Physic Garden CPG 6-97-7912, Tunisia (cult.) (**BB-C88**, FJ232719, FJ269127, FJ423299, FJ423229, FJ423371) — *M. Salmon SL253*, Tunisia (cult.) (**BB-C90**, FJ232720, FJ269128, FJ423300, FJ423230, FJ423372) — *M. Salmon SL263*, Tunisia (cult.) (**BB-C91**, FJ232721, FJ269129, FJ423301, FJ423231, FJ423373); *H. FLAHAULTIANA*: *S.L. Jury & T.M. Upson s.n.*, Morocco, Anti-Atlas (**BB-256**, FJ232731, FJ269142, FJ423314, FJ423243, FJ423386) — *M. Salmon SBL19*, Morocco, Anti-Atlas (cult.) (**BB-C05**, FJ232730, FJ269141, FJ423313, FJ423242, FJ423385) — Chelsea Physic Garden CPG 491-99, Morocco, Anti-Atlas (cult.) (**BB-C87**, FJ232732, FJ269143, FJ423315, FJ423244, FJ423387); *H. HISPANICA*: *Cecilia Durães s.n.*, Portugal, Aveiro (**BB-029-01**, FJ232738, FJ269149, FJ423321, FJ423250, FJ423393) — *MG & FJR s.n.*, Portugal, Faro (**BB-185-01**, FJ232739, FJ269150, FJ423322, FJ423251, FJ423394) — *MG & FJR s.n.*, Portugal, Faro (**BB-188-01**, FJ232765, FJ269176, FJ423348, FJ423276, FJ423420) — *MG & FJR s.n.*, Portugal, Faro (**BB-189-01**, FJ232740, FJ269151, FJ423323, FJ423252, FJ423395) — *L. Farrell s.n.*, Portugal, Setúbal (**BB-193-01**, FJ232741, FJ269152, FJ423324, FJ423253, FJ423396) — *MG & FJR s.n.*, Spain, Cáceres (**BB-204-01**, FJ232742, FJ269153, FJ423325, FJ423254, FJ423397) — *MG & FJR s.n.*, Spain, Salamanca (**BB-207-01**, FJ232766, FJ269177, FJ423349, FJ423277, FJ423421) — *MG & FJR s.n.*, Spain, Salamanca (**BB-210-01**, FJ232743, FJ269154, FJ423326, FJ423255, FJ423398) — *MG & FJR s.n.*, Spain, Salamanca (**BB-212-01**, FJ232744, FJ269155, FJ423327, FJ423256, FJ423399) — *JS s.n.*, United Kingdom, London (**BB-236-01**, FJ232758, FJ269169, FJ423341, FJ423269, FJ423413) — *MG & FJR s.n.*, Portugal, Sesimbra (**BB-261-01**, FJ232745, FJ269156, FJ423328, FJ423257, FJ423400) — *MG & FJR s.n.*, Portugal, Setúbal (**BB-262-01**, FJ232746, FJ269157, FJ423329, FJ423258, FJ423401) — *MG & FJR s.n.*, Portugal, Portalegre (**BB-268-01**, FJ232747, FJ269158, FJ423330, FJ423259, FJ423402) — *MG & FJR s.n.*, Spain, Badajoz (**BB-270-01**, FJ232748, FJ269159, FJ423331, FJ423260, FJ423403) — *MG & FJR s.n.*, Spain, Huelva (**BB-271-01**, FJ232749, FJ269160, FJ423332, FJ423261, FJ423404) — *MG & FJR s.n.*, Spain, Huelva (**BB-273-01**, FJ232750, FJ269161, FJ423333, FJ423262, FJ423405) — *MG & FJR s.n.*, Spain; Badajoz (**BB-275-01**, FJ232767, FJ269178, FJ423350, FJ423278, FJ423422) — *MG & FJR s.n.*, Spain, Sevilla (**BB-276-01**, FJ232751, FJ269162, FJ423334, FJ423263, FJ423406) — *MG & FJR s.n.*, Spain, Córdoba (**BB-282-01**, FJ232752, FJ269163, FJ423335, FJ423264, FJ423407) — *MG & FJR s.n.*, Spain, Córdoba (**BB-284-01**, FJ232753, FJ269164, FJ423336, FJ423265, FJ423408) — *MG & FJR s.n.*, Spain, Málaga (**BB-301-01**, FJ232768, FJ269179, FJ423351, FJ423279, FJ423423) — *MG & FJR s.n.*, Spain, Granada (**BB-316-01**, FJ232754, FJ269165, FJ423337, FJ423266, FJ423409) — *E. Alonso & E. de Paz s.n.*, Spain, León (**BB-LEB080798**, FJ232755, FJ269166, FJ423338, FJ423267, FJ423410) — *F. Llamas & al. s.n.*, Spain, León (**BB-MA526921**, FJ232757, FJ269168, FJ423340, FJ423268, FJ423412) — *SO & I. Pulgar s.n.*, Portugal, Viseu (**BB-SANT27643**, FJ232769, FJ269180, FJ423352, FJ423280, FJ423424); *H. ITALICA*: *SWA & E. Sagona s.n.*, Italy, Liguria (**BB-286-01**, FJ232710, FJ269117, FJ423289, FJ423220, FJ423361) — *SWA & E. Sagona s.n.*, Italy, Piedmont (**BB-288-01**, FJ232711, FJ269118, FJ423290, FJ423221, FJ423362) — *SWA & E. Sagona s.n.*, France, Provence-Alpes-Côte d'Azur (**BB-293-01**, FJ232712, FJ269119, FJ423291, FJ423222, FJ423363) — *SWA & E. Sagona s.n.*, France, Provence-Alpes-Côte d'Azur (**BB-294-01**, –, FJ269120, FJ423292, –, FJ423364) — Royal Hort. Soc. Wisley no. 20060810*A, United Kingdom (cult.) (**BB-C45**, FJ232713, FJ269121, FJ423293, FJ423223, FJ423365); *H. LINGULATA*: *S.L. Jury 12639*, Morocco, Haut Ouerrha (**BB-337**, FJ232715, FJ269123, FJ423295, FJ423225, FJ423367) — *S.L. Jury 12624*, Morocco, Zerhoun (**BB-338**, FJ232716, FJ269124, FJ423296, FJ423226, FJ423368) — *M. Salmon SF281*, Morocco, Mohammedia (**BB-C92**, FJ232717, FJ269125, FJ423297, FJ423227, FJ423369) — *M. Salmon SBL41*, Morocco, Wilaya de Meknes (cult.) (**BB-C93**, FJ232718, FJ269126, FJ423298, FJ423228, FJ423370) — *S.L. Jury 15677*, Morocco, Quezzane (**BB-MA611036**, FJ232714, FJ269122, FJ423294, FJ423224, FJ423366); *H. MAURITANICA*: *MG & FJR s.n.*, Portugal, Faro (**BB-179-01**, FJ232727, FJ269137, FJ423309, FJ423240, FJ423381) — *MG & FJR s.n.*, Portugal, Setúbal (**BB-184-01**, FJ232728, FJ269138, FJ423310, FJ423239, FJ423382) — *MG & FJR s.n.*, Portugal, Évora (**BB-264-01**, FJ232729, FJ269139, FJ423311, FJ423240, FJ423383) — *S.L. Jury 13302*, Morocco, Tánger (**BB-336**, –, FJ269140, FJ423312, FJ423241, FJ423384); *H. NON-SCRIPTA*: *FJR & A. Paul s.n.*, Spain, La Coruña (**BB-121-01**, FJ232733, FJ269144, FJ423316, FJ423245, FJ423388) — *FJR & A. Paul s.n.*, Spain, Lugo (**BB-135-01**, FJ232734, FJ269145, FJ423317, FJ423246, FJ423389) — *MG s.n.*, Belgium, Wallonisch Brabant (**BB-159-01**, FJ232735, FJ269146, FJ423318, FJ423247, FJ423390) — *JCV s.n.*, United Kingdom, Kent (**BB-177-01**, FJ232736, FJ269147, FJ423319, FJ423248, FJ423391) — *R. Arias s.n.*, Spain, León (**BB-LEB079550**, FJ232737, FJ269148, FJ423320, FJ423249, FJ423392); *H. PAIVAE*: *FJR, SO & A. Paul s.n.*, Spain, La Coruña (**BB-127-01**, FJ232763, FJ269174, FJ423346, FJ423274, FJ423418) — *R.I. Louzán s.n.*, Spain, La Coruña (**BB-MAF150573**, FJ232764, FJ269175, FJ423347, FJ423275, FJ423419); *H. REVERCHONII*: *MG & FJR s.n.*, Spain, Jaén (**BB-323-01**, –, FJ269132, FJ423304, –, FJ423376) — *MG & FJR s.n.*, Spain, Jaén (**BB-324-01**, –, FJ269133, FJ423305, FJ423234, FJ423377) — *MG & FJR s.n.*, Spain, Jaén (**BB-328-01**, FJ232724, FJ269134, FJ423306, FJ423235, FJ423378) — *MG & FJR s.n.*, Spain, Jaén (**BB-332-01**, FJ232725, FJ269135, FJ423307, FJ423236, FJ423379) — *M. Salmon s.n.*, Spain, Jaén (cult.) (**BB-C06**, FJ232726, FJ269136, FJ423308, FJ423237, FJ423380); *Hyacinthoides* **sp.**: *J. Arizaleta & al. s.n.*, Spain; La Rioja (**BB-MA438768**, FJ232756, FJ269167, FJ423339, –, FJ423411); **OUTGROUP TAXA**: *Autonoe latifolia*: *M. Salmon SBL13*, Morocco, Anti-Atlas (cult.) (FJ232702, FJ2691089, FJ423281, FJ423212, FJ423353); *Autonoe maderensis*: RBGE no 20022079, Portugal, Madeira (cult.) (BM000904046, FJ232703, FJ269110, FJ423282, FJ423213, FJ423354); *Brimeura amethystina*: RBGE cult. (FJ232704, FJ269111, FJ423283, FJ423214, FJ423355); *Muscari comosum*: *MG & FJR s.n.*, Portugal, Faro (BM000904044, FJ232705, FJ269112, FJ423284, FJ423215, FJ423356); *Oncostema peruviana*: *FJR*, ex hort., unlocalised (BB-C07, FJ232706, FJ269113, FJ423285, FJ423216, FJ423357); *Pfosseria bithynica*: *FJR*, ex hort., unlocalised (BB-C08, FJ232707, FJ269114, FJ423286, FJ423217, FJ423358); *Scilla siberica*: *FJR*, ex hort., unlocalised (FJ232708, FJ269115, FJ423287, FJ423218, FJ423359); *Tractema monophylla*: *MG & FJR s.n.*, Portugal, Faro (FJ232709, FJ269116, FJ423288, FJ423219, FJ423360).