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HESPEROCODON, A NEW GENERIC NAME FOR *WAHLENBERGIA HEDERACEA* (CAMPANULACEAE): PHYLOGENY AND CAPSULE DEHISCENCE

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The European species *Wahlenbergia hederacea* (L.) Rchb. (Campanulaceae) is molecularly distant from the remainder of the wahlenbergioids, and its inclusion with them renders the tribe Wahlenbergieae Endl. (1838) non-monophyletic. Additional support for this conclusion may be derived from its gross morphological characteristics, which are essentially campanuloid. However, although not strictly identical to that of *Wahlenbergia* Schrad. ex Roth, the capsule dehiscence mechanism of *W. hederacea* is still fundamentally wahlenbergioid and differs from the majority of campanuloids. Several genera such as *Feeria* and *Jasione*, which are intermediate between typical wahlenbergioids and typical campanuloids, have similar capsule characteristics, and it is postulated that *Wahlenbergia hederacea*, together with these 'transitional' genera, are all relatively ancient components of a campanulaceous palaeoflora of the early Tertiary of Eurasia. The wahlenbergioid type of dehiscence is considered to be a plesiomorphic character whereas the diverse campanuloid types of dehiscence mechanisms are derived under conditions of intense selection. It is suggested that *Wahlenbergia hederacea* is probably most closely related to, and ancestral to, the rapunculoid lineages of *Campanula* s.l. that subsequently evolved over much of Eurasia and North America. Consequently, *Wahlenbergia hederacea* should be classified in the Campanuloideae and the new generic name *Hesperocodon* Eddie & Cupido *gen. nov.* is proposed.

Keywords. Campanulaceae, campanuloid, capsule morphology, dehiscence mechanisms, loculicidal, Lusitanian, phylogeny, poricidal, valvate, wahlenbergioid.

Introduction

Recent molecular investigations of the Campanulaceae (Eddie *et al.*, 2003; Cupido, 2009; Haberle *et al.*, 2009; Roquet *et al.*, 2009; Prebble *et al.*, 2011) have shown that the European species *Wahlenbergia hederacea* (L.) Rchb. is distant from the remainder of the wahlenbergioids, and its inclusion with them renders the tribe Wahlenbergieae Endl. (Endlicher, 1838) non-monophyletic (Fig. 1). These findings prompted a re-investigation of the morphology of this species and we conclude that, based on

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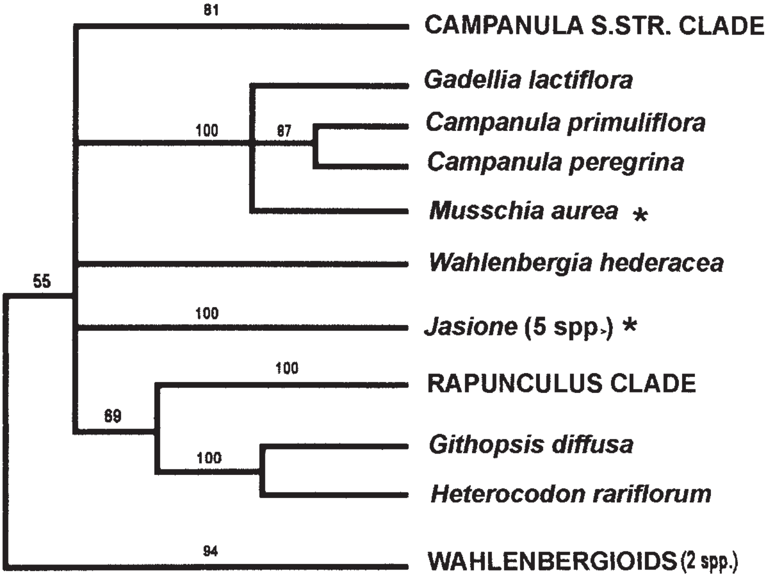

FIG. 1. Strict consensus of 2629 most parsimonious trees of selected taxa of the Campanulaceae based on ITS sequence data, showing the topological position of *Wahlenbergia hederacea* (*Hesperocodon hederaceus* comb. nov.) in a polytomy with the two major campanuloid clades and the 'transitional' taxa (indicated by asterisks). The wahlenbergioid outgroup comprises *Craterocapsa congesta* and *Roella ciliata*. Numbers above branches are bootstrap percentages for 1000 replicates. After Eddie *et al.* (2003).

both molecular and morphological evidence, *Wahlenbergia hederacea* is best included in the Campanuloideae. Thus, its inclusion in the Wahlenbergieae is also unsustainable and its removal from *Wahlenbergia* Schrad. ex Roth necessitates a new generic name (Lammers, 2007). [Note: Eddie *et al.* (2010) treated the Campanulaceae as a separate family from the Lobeliaceae and Cyphiaceae. Their recommendation was to divide the Campanulaceae into three subfamilies: Campanuloideae, Canarinoideae and Wahlenbergioideae. This treatment will be formalised in a future publication. In this scheme, their 'Wahlenbergioideae' will be very similar in composition, but not identical to, Wahlenbergieae Endl., and will include both Wahlenbergioideae Kolak. and Prismatocarpoideae Kolak.]

Wahlenbergia hederacea is first mentioned by Bauhin (1596) under the synoptic phrase *Campanula Cymbalariae folio* (De Candolle, 1830: 141), which was later expanded by Tournefort (1700) as *Campanula Cymbalariae foliis vel folio hederaceo*. It was included in the first edition of *Species Plantarum* by Linnaeus (1753) as *Campanula hederacea* but was subsequently transferred to *Wahlenbergia* by Reichenbach (1827), a move adopted by De Candolle (1830), who included it within his *Wahlenbergia* sect. *Aikinia*. A glance at other 19th-century works suggests that occasionally there has been some doubt about *Wahlenbergia hederacea* being included in *Wahlenbergia*. For example, it was treated as a separate genus by Roth (1827)

(*Schultesia* Roth *nom. illeg.*) and by Fourreau (1869) (*Aikinia* Salisb. ex Fourr. *nom. illeg.*), or included as part of the genus *Roucela* Dumort. (Dumortier, 1822).

Throughout the Campanulaceae, primary generic characters depend upon fruit structure (Hilliard & Burtt, 1973). The classification of *Wahlenbergia hederacea* in the Wahlenbergieae rests largely on the mode of dehiscence of the capsule, which is reported to be loculicidal by valves above the calyx lobes (De Candolle, 1830), a mode commonly found in many of the wahlenbergioids, particularly *Wahlenbergia* (Clapham *et al.*, 1962; Rix, 2004). However, the dehiscence mechanism of *Wahlenbergia hederacea* is not strictly identical to that of *Wahlenbergia* (Fig. 2A). In *Wahlenbergia*, the sclerenchymatous septa (the 'Dehiscenzkörper' of Feer, 1890) bend outwards hygroscopically, splitting the capsule apex and forming a crown-like structure with 2–5 points depending on the species (Fig. 2B) (von Brehmer, 1915: fig. 3, p. 23; fig. 6, p. 29; Thulin, 1975), whereas in *W. hederacea* the capsule is membranous, the septa are not sclerenchymatous, and the valves do not form a pointed crown.

At maturity the corolla is deciduous and the tumescent apex of the ovary (*pars superior*), together with the remnant base of the style, ruptures along lines of weakness to form three valves in line with the locules. Yet, the whole mechanism is still essentially wahlenbergioid and the septa may play a role (if somewhat reduced) in the rupture of the ovary apex. The mechanism is probably homologous with that of

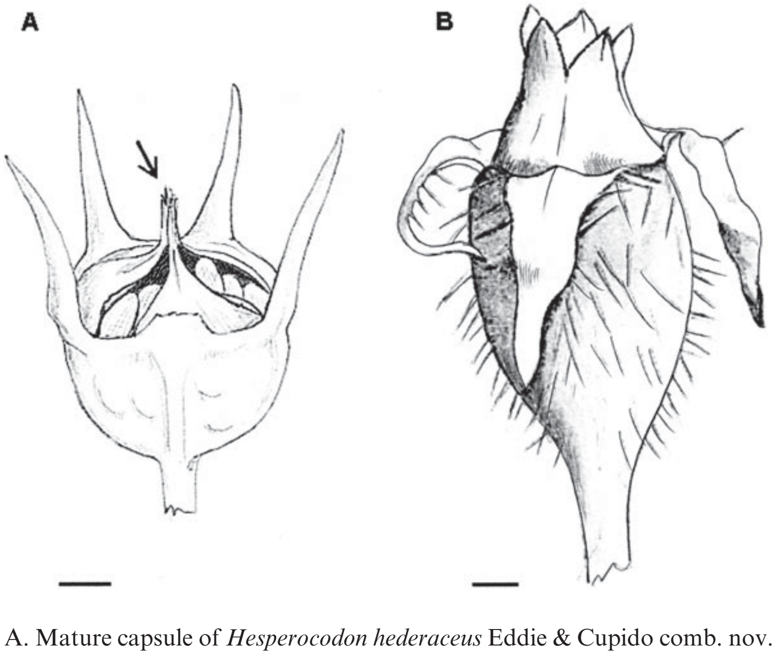

FIG. 2. A. Mature capsule of *Hesperocodon hederaceus* Eddie & Cupido comb. nov. showing rupture of the ovary apex (*pars superior*), with the seeds visible inside. Nearest calyx lobe removed. Arrow shows attached style base. Scale bar = c.0.25 mm. Modified from Stella Ross-Craig, *Drawings of British Plants*, Part XIX, plate 4(C) (1963); B. Mature capsule of *Wahlenbergia capensis* (L.) A.DC. showing the 5-pointed crown of the ovary apex. Scale bar = c.1 mm. From a photograph, Kirstenbosch Botanic Gardens, South Africa, i 2012 (W.M.M.E.).

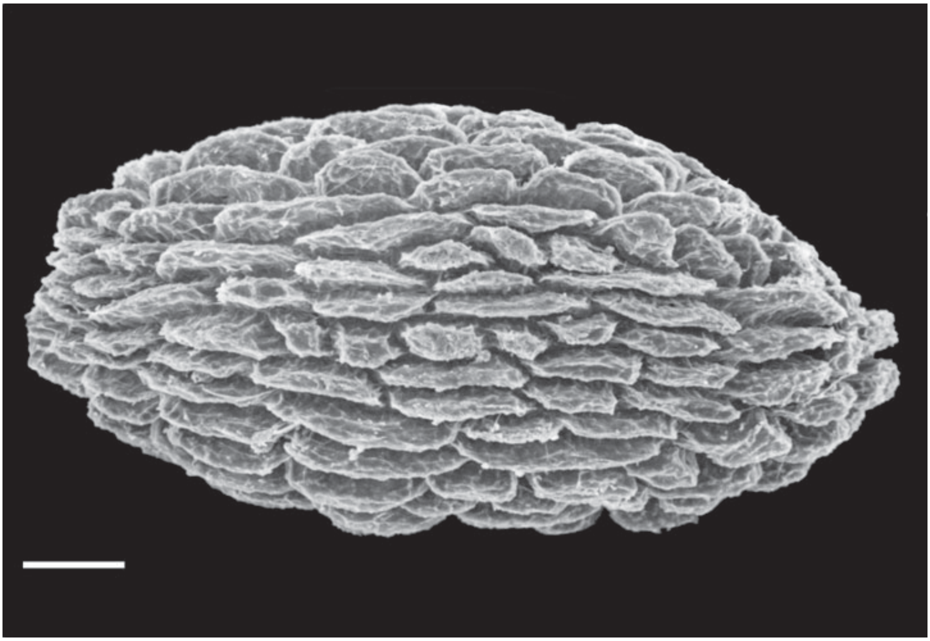

FIG. 3. Seed of *Hesperocodon hederaceus* Eddie & Cupido comb. nov. showing the wedge-shaped hilum and the coarsely verrucate testa, each cell of the reticulum with a conspicuously raised lumen. Scale bar = 100 µm. Electronmicrograph No. 8139, University of Reading, viii 1984 (W.M.M.E.). Sample from the Royal Botanic Garden, Kew: No. 266-6626609.

Wahlenbergia, but it is decidedly unlike the capsule of *Edraianthus*, which opens by irregular rupture of the *flattened* ovary apex. According to Kolakovsky (1986, 1987), the rupture of the capsule apex in *Edraianthus* is achieved by means of the axicorn, which performs a similar function on the hypanthial walls of *Campanula* spp., and is, therefore, very different from the mechanism found in *Wahlenbergia*. *Edraianthus* has also traditionally been associated with the wahlenbergioids (De Candolle, 1830; Endlicher, 1838; Bentham, 1876; Schönland, 1889; Kovanda, 1978; Takhtajan, 1987) but molecular investigations (Eddie *et al.*, 2003; Cosner *et al.*, 2004; Stefanović *et al.*, 2008), and growth and seedling morphology (Shulkina *et al.*, 2003), have now shown *Edraianthus* to be a core component of the European Campanuloideae, as was intimated by Hilliard & Burtt (1973). Fedorov (1972) and Kolakovsky (1987) also included this genus in the tribe Campanuloideae based on its overall morphology.

Apical dehiscence mechanisms are to be found in at least three other genera of the Campanulaceae: *Jasione* L., *Feeria* Buser and *Githopsis* Nutt., which, on the basis of molecular analyses, may have distant affinity with *Wahlenbergia hederacea*, although all are radically different genera and none is generally thought to be closely related to it. These genera are discussed below, principally in order to highlight the diversity of capsule morphology within the Campanulaceae and the degree of convergence that has resulted in apparent taxonomic confusion and mis-classification.

Jasione and *Feeria* both possess loculicidal valvate dehiscence mechanisms that, indeed, *are* reminiscent of *Wahlenbergia*. Following De Candolle (1830), who classified it in a subtribal group (unnamed) that included *Wahlenbergia*, *Jasione* has traditionally been classified as belonging to the tribe Wahlenbergieae (Endlicher, 1838) or subtribe Wahlenbergiinae [as Wahlenberginae] (Schönland, 1889), whereas *Feeria angustifolia* (Schousb.) was originally included in the genus *Trachelium* L. in the Campanuloideae Burnett (1835) by Schousboe (1800), and transferred to the monotypic genus *Feeria* by Buser (1894). Its position next to *Trachelium* in the Campanuloideae has subsequently been maintained, mostly on account of the supposed resemblance of their inflorescences to each other despite radical differences in capsule dehiscence mechanisms. *Feeria* dehisces loculicidally and distally by three apical valves, which form a 3-pointed crown, whereas *Trachelium* dehisces laterally and proximally by rupture of the hypanthial walls at the base of each sulcus. Although the chromosome number of *Feeria* ($2n = 34$) and its geographical distribution in the western Mediterranean also supports association with *Trachelium* ($2n = 32, 34$), its overall inflorescence morphology equally resembles *Jasione* ($2n = 12, 14, 18, 24, 36, 48, 60$), although the latter lacks a terminal flower. The majority of *Jasione* species are also western Mediterranean in distribution, so it may ultimately prove to have greater affinities with *Jasione*, as was shown by Olesen *et al.* (2012). The western North American genus *Githopsis* ($2n = 18, 20, 36, 38, 40$) also has apical dehiscence by irregular rupture and was included by Schönland (1889) in his subtribe Wahlenbergiinae [as Wahlenberginae], but, as Morin (1983) astutely observed, 'Except for its mode of capsule dehiscence, which is no more like that of Wahlenbergieae than it is like that of Campanuleae, *Githopsis* fits well into Campanuleae.'

The form of the mature capsule in diverse lineages of Eurasian bellflowers seems to be under intense selection pressure and may be an insular/montane phenomenon associated with a loss of dispersibility and portioned seed release. For example, tardy dehiscence and/or irregular rupture of the capsule has apparently evolved independently in the *Campanula* s.str. clade (Eddie *et al.*, 2003) among several of the endemic species and segregates of *Campanula*/*Edraianthus* in the Balkan mountains and the Aegean region (e.g. *Halacsyella parnassica* (Boiss. & Spruner) Janch., *Petkovia orphanidea* (Boiss.) Stef., *Campanula sartorii* Boiss. & Heldr., *C. incurva* Aucher ex A.DC.), plus species in *Campanula* sect. *Quinqueloculares* Phitos, and in Anatolia (e.g. *C. ptarmicifolia* Lam. and *C. scoparia* (Boiss. & Hausskn.) Damboldt) (Hartvig, 1991; Eddie, 1997).

In general, throughout the Campanulaceae, there also seems to be a correlation between mode of dehiscence and inflorescence structure. The '*Protoedraianthus*' group of *Edraianthus* (Lakušić, 1988), which has both poricidal and loculicidal modes occurring in the same individual plants (Stefanović *et al.*, 2008), may allow us to determine the factors that have precipitated the evolution of different dehiscence modes. This may be illustrated by *Edraianthus tarae* Lakušić (= *Protoedraianthus tarae* Lakušić *nom. inval.*), which has dichasia (rarely polychasia) composed of one central (sub-)sessile flower and several lateral flowers found at the tips of relatively long pedicels. As a consequence of their respective positions, the central fruits open apically, as in other *Edraianthus* spp., while the pedicellate fruits open laterally, reminiscent of those typically found in *Campanula* (Stefanović *et al.*, 2008). Another type of seed presentation mechanism (secondary presentation) is found in *Campanula glomerata*, which is superficially very similar to *Edraianthus* and also has an inflorescence surrounded by an involucre of bracts. In this species the lateral pores of the capsules are proximal and the seeds collect on the subtending bracts before finally being dispersed by wind (Leins & Erbar, 2010).

The departure from typical wahlenbergioid characteristics in *Wahlenbergia hederacea* inevitably invites speculation about its relationships. On a cursory inspection, it may be considered vaguely similar in habit and general appearance to *Wahlenbergia procumbens* (L.f.) A.DC. or even *Prismatocarpus sessilis* Eckl. ex A.DC. In his seminal monograph of 1830, Alphonse de Candolle stated: '*Manifeste in genere Wahlenbergia Schrad. locanda est, prope W. procumbentem*', but any notion of a relationship with living wahlenbergioids is soon dispelled, for *W. hederacea* is most unlike the majority of the Wahlenbergieae in almost all aspects of floral and, especially, vegetative morphology. In recent studies using ITS and *trn*L-F molecular markers (Cupido, 2009), *Wahlenbergia procumbens* and *Prismatocarpus sessilis*, although both are isolated morphologically from other South African species, were shown to be well-supported components of the wahlenbergioid clade.

In marked contrast, *Wahlenbergia hederacea* is essentially campanuloid in both floral and vegetative characteristics. The long pedicels, floral morphology, and foliage recall *Peracarpa* Hook.f. & Thomson more than any other taxon and they also share certain similarities in habit and habitat. *Wahlenbergia hederacea* is a 'boundary-layer' plant of rainy, windswept habitats where it threads its way through patches of moss and short grass, and it is possible that the long pedicels are an adaptation to aid seed dispersal. A similar function for the long pedicels of *Peracarpa* may also be postulated. Their pollen is similar, being of low relief and with very short spinules (Eddie, 1984), but both genera are also characterised by marked differences in capsule and seed morphology, dehiscence mechanisms and chromosome number. *Peracarpa* ($2n = 28, 30$) has a torulose, membranous capsule that splits irregularly at the base, and more elongate seeds with lengthwise compressed reticula. [Note: The mode of capsule dehiscence in *Peracarpa* is probably not homologous with the lateral ruptures which characterise the majority of species of non-rapunculoid *Campanula* (= *Campanula* s.str. clade of Eddie *et al.*, 2003).]

Wahlenbergia hederacea also distantly resembles several of the European isophylloid campanulas, particularly in vegetative morphology, but the flowers are most similar to those of North American rapunculoid species such as *Campanula aparinoides* Pursh ($2n = 34$), *C. californica* (Kellogg) A.Heller, as well as *C. robinsiae* Small and the California annuals (*C. exigua* Rattan ($2n = 34$) and *C. angustiflora* Eastw. ($2n = 30$), etc.). Many of these North American species also have a predilection for damp habitats. A possible relationship between *Wahlenbergia hederacea* and these taxa, as well as with genera such as *Heterocodon* Nutt., and the Chinese *Homocodon* D.Y.Hong

(Hong, 1980; Hong & Ma, 1991), should be examined more closely, although existing molecular data suggest otherwise. Surprisingly, *Homocodon* is apparently not as closely related to the North American *Heterocodon* as their morphology implies, but, based on molecular data, is in fact closer to *Adenophora* (Lu *et al.*, 2007; Zhou *et al.*, 2012), whereas, also based on molecular data, *Peracarpa* is allied to both *Heterocodon* and *Githopsis*. In spite of these new findings, all these lineages belong to the *Rapunculus* clade (Zhou *et al.*, 2012). The chromosome number of *Wahlenbergia hederacea* ($2n = 36$, Gadella, 1966), its topological position on molecular cladograms, unusual seed morphology (Fig. 3), and geographical distribution should make us wary of a facile assumption of a close relationship with these rapunculoid lineages.

All molecular studies place *Wahlenbergia hederacea* more or less between the core campanuloids and core wahlenbergioids, along with genera such as *Jasione* and *Musschia* Dumort. These two genera were called 'transitional taxa' by Eddie *et al.* (2003), implying that they were, in a sense, neither proto-typically campanuloid nor wahlenbergioid. In a study by Roquet *et al.* (2009), using combined *rbc*L and *trn*L-F data, *Wahlenbergia hederacea* forms part of an unresolved polytomy involving *Jasione* and *Feeria*, plus several southern hemisphere wahlenbergioid taxa. Similarly, in a combined four-gene study of Olesen *et al.* (2012), *Wahlenbergia hederacea* also formed part of a clade with both *Jasione* and *Feeria*, albeit with 87% bootstrap support. In the ITS studies of Eddie *et al.* (2003) and in the three-gene study of Haberle *et al.* (2009), *Feeria* occupied a clade comprising *Azorina vidalii* (H.C.Watson) Feer, *Campanula edulis* Forssk. and *C. mollis* L. Therefore, the relationships of *Wahlenbergia hederacea* and the 'transitional taxa' are still not fully resolved and should be further investigated by fine-honing molecular analyses using a diversity of sequence data, in addition to refined morphological examination.

If we retain classical Linnaean categories, which are characterised solely by the properties shared by their members, then studies of chloroplast genome rearrangements suggest that *Jasione* is best treated as campanuloid and should be classified accordingly (Cosner *et al.*, 2004) (for an interesting discussion on categories, see Lakoff, 1987). We recommend that *Wahlenbergia hederacea* also be included in the Campanuloideae and its phylogenetic position based on molecular results be regarded as co-basal within this lineage. On consideration of the distribution of the 'transitional taxa', including both *Feeria* and *Wahlenbergia hederacea*, we hypothesise that they are *all* relatively relictual in the Mediterranean Basin, Macaronesia and western Europe, and are likely to be very old elements of the Campanulaceae as a whole. This conclusion is corroborated by all molecular investigations of these taxa to date (Eddie *et al.*, 2003; Haberle *et al.*, 2009; Roquet *et al.*, 2009, etc.). Therefore, it may be descended from a proto-campanuloid component of a palaeoflora that occupied the North Atlantic region of Eurasia in early Tertiary times prior to the evolution and spread of the rapunculoid lineages of *Campanula* in Eurasia and North America. From this perspective, the capsule dehiscence mechanism should be regarded as a plesiomorphic character. As yet, we have no concrete evidence for the actual age of the early branching events in the evolutionary history of the Campanulaceae despite the tone of recent claims (e.g. Roquet *et al.*, 2009; Olesen *et al.*, 2012), but our current research indicates that the age of the Campanulaceae is much older than current estimates (Eddie & Cupido, in prep.). Leaving aside biogeographic, phylogenetic and ecological conjecture, *Wahlenbergia hederacea* requires a new generic name. Consequently we propose the following:

Taxonomic Treatment

Hesperocodon Eddie & Cupido, **gen. nov.**

Herb with affinities in Campanulaceae, but somewhat resembling *Anagallis tenella* (Primulaceae) in habit.

Leaves almost peltate, resembling tiny juvenile leaves of *Hedera helix* (Araliaceae). Flowers more or less nodding, often appearing partially closed at night or after rain. Corolla tubular-campanulate with three prominent purplish veins extending from the tube to the base of each lobe. Filaments broadened at the base, long and tapering, with long, downward-pointing awl-like unicellular hairs on the margins of the lower half, but filaments not forming a nectar-dome. Pollen oblate-spheroidal, tri-zonoporate, with low surface relief and few small spinules; 26 μm equatorial diameter. Ovary swelling at the apex at maturity. Capsules dehiscing above the calyx by apical rupture. Seeds few (c.12–15), relatively large (0.6 mm long), ovate, flattened; seed-coat coarsely verrucate. – Type species: *Campanula hederacea* L.

Hesperocodon hederaceus (L.) Eddie & Cupido, **comb. nov.** – *Campanula hederacea* L., Sp. Pl. 1: 169 (1753). – *Campanula hederifolia* Salisb., Prodr. Stirp. Chap. Allerton 127 (1796) as 'hederaefolia', *nom. illeg.* – *Wahlenbergia hederacea* (L.) Rchb., Icon. Bot. Pl. Crit. 5: 47 (1827). – *Schultesia hederacea* (L.) Roth, Enum. Pl. Phaen. Germ. 1: 690 (1827). – *Roucela hederacea* (L.) Dumort., Fl. Belg. 58 (1827). – *Campanula pentagonophylla* Vuk., Linnaea 26: 325 (1854), *nom. illeg.* – *Valvinterlobus filiformis* Dulac, Fl. Hautes-Pyrénées 459 (1867), *nom. illeg.* – *Aikinia hederacea* (L.) Fourr., Ann. Soc. Linn. Lyon (n.s.) 17: 112 (1869). – *Campanopsis hederacea* (L.) Kuntze, Revis. Gen. Pl. 2: 379 (1891). – *Cervicina hederacea* (L.) Druce, Fl. Berkshire 324 (1898). – *Wahlenbergia hederifolia* Bubani, Fl. Pyren. 2: 18 (1899), *nom. illeg.* – Type: *Löfling* s.n. Herb. Linn. No. 221.77 (lecto LINN, designated here). **Fig. 4.**

Hesperocodon hederaceus (ivy-leaved bellflower) has few unambiguous features that can be used as a basis for a new generic name. The specific epithet is adequate, although the tiny leaves only superficially resemble those of ivy. We have based the name *Hesperocodon* on its unique Atlantic distribution, the prefix 'Hespero' being derived from the Greek word *έσπερος* (hesperos) for 'western', and the suffix *κωδων* (codon), for 'bell'. Since the generic name is masculine, the specific epithet now becomes '*hederaceus*'. The name *Hesperocodon* was used by Webb & Berthelot (1844) for a section of the genus *Specularia* Heister ex A.DC. (= *Legousia* Durande), but priority does not extend across different levels in the taxonomic hierarchy.

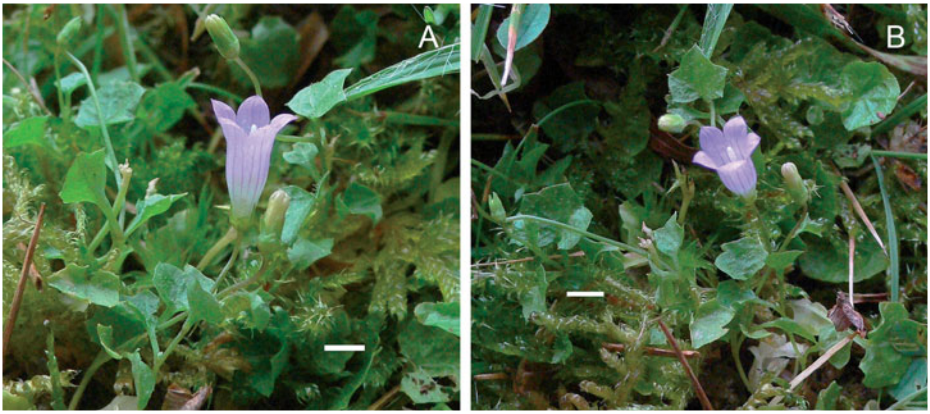

FIG. 4. *Hesperocodon hederaceus* comb. nov. A. Side-view of corolla showing tubular-campanulate shape and coloured veins on the outside of tube reaching to the corolla lobes. Scale bar = 0.5 cm; B. View showing flower in 'male' phase, coloured veins inside tube, whitish pollen, and ivy-like leaves. On short grass and moss, Poltalloch, Argyll, Scotland, 23 viii 2012 (W.M.M.E.).

Distribution and habitat. Hesperocodon hederaceus has an odd distribution from sea level to about 485 m along the Atlantic seaboard of western Europe from Spain and Portugal to the Netherlands and Germany, and a predilection for wet, windswept acidic heathlands, and bogs, mossy or grassy areas bordering streams and flushes, or *Salix* carrs and woodland clearings. It is frequently naturalised on mossy lawns. At the height of the glacial maximum, approximately 20,000 years ago, it presumably was relictual in western France and the Iberian Peninsula. From a historical perspective its distribution can be described as 'Oceanic southern-temperate type' or Lusitanian. Several other species have similar distribution patterns, including *Erica mackaiana* Bab., *E. ciliaris* L. and *Daboecia cantabrica* (Huds.) C.Koch (Ericaceae), *Pinguicula grandiflora* Lam. (Lentibulariaceae) and *Saxifraga hirsuta* L. (Saxifragaceae) (Ingrouille, 1995). The highly localised distribution of *Wahlenbergia hederacea* in the British Isles, particularly in western Ireland and southwest Scotland, may have resulted from random re-colonisation events following the retreat of the ice, although the species has been declining in the British Isles during much of the 20th century due to habitat loss (Preston *et al.*, 2002). There is no evidence of this species ever having occurred in North Africa or Macaronesia and it is unlikely, as has been recently suggested, that it is a relictual component of an Afroalpine flora (Rix, 2004). Virtually nothing is known of its biology. In cultivation it displays some self-compatibility (Eddie, pers. obs.) and its persistence in small patches in scattered localities is, in all likelihood, linked to its capacity for vigorous vegetative reproduction. The genetics of its scattered populations would be interesting for future investigation and for their conservation (Kay & John, 1995).

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