Plant Syst Evol (2010) 287:1–17
DOI 10.1007/s00606-010-0284-3

ORIGINAL ARTICLE

Taxonomic revision of European *Apium* L. s.l.: *Helosciadium* W.D.J.Koch restored

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Received: 13 October 2009 / Accepted: 6 March 2010 / Published online: 17 April 2010

Abstract European representatives of *Apium* sensu lato (Apiaceae), and *Apium prostratum* and *Naufraga balearica*, were studied with morphological, fruit anatomical, and palynological methods. Morphometric data were compared with phylogenetic results from previous molecular studies. This confirms that most of the European *Apium* species belong to a separate group corresponding to the previously named genus *Helosciadium*. All these species had previously been formally named as *Helosciadium* species, except for the new combination *Helosciadium bermejoi*, which is formally described here. Molecular studies place *Apium prostratum* and *Naufraga balearica* close to *Apium graveolens*, the type species of *Apium*. Our morphometric results show similarities of *Naufraga* with *H. bermejoi*, but fruit anatomy distinguishes it both from *Helosciadium* and from *A. graveolens*/*prostratum*. The placement of *Cyclospermum leptophyllum* in a separate genus is confirmed. Diagnostic keys to the genera and *Helosciadium* species, and an annotated checklist are given.

Keywords *Apium* · *Helosciadium* · *Cyclospermum* · *Naufraga* · Morphometry · Fruit anatomy · Pollen structure · New combination

Electronic supplementary material The online version of this article (doi:10.1007/s00606-010-0284-3) contains supplementary material, which is available to authorized users.

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Introduction

The genus *Apium* L. in the wide sense (including *Cyclospermum* Lag. and *Helosciadium* W.D.J.Koch, e.g. sensu Wolff 1927; Tutin 1968; Pimenov and Leonov 1993) includes about 20–25 species distributed in both the northern and southern hemispheres. In the northern hemisphere Europe is a centre of diversity, with some European species spreading eastwards into western Asia (Tutin 1968) and southwards into northern and eastern Africa (Tutin 1968; Llorens 1982; Townsend 1989). *Apium* has a complex taxonomic history, with many species having been removed from it over the years only to be replaced by later authors. One of the most far reaching revisions was by Koch (1824) who transferred all the European species of *Apium* other than the type, *A. graveolens*, into his newly described genus *Helosciadium*.

There are now considered to be seven European species belonging to *Apium* sensu lato:

Apium graveolens L., the type species, widely distributed and commonly cultivated for its edible petioles (celery) and tubers (celeriac);

Apium (*Helosciadium*) *nodiflorum* (L.) Lag., widely distributed and notorious for its extreme phenotypic variation;

Apium (Helosciadium) repens (Jacq.) Lag., uncommon and threatened throughout its range;

Apium (Helosciadium) inundatum (L.) Rchb.f., a true aquatic from W Europe and NW Africa;

Apium (Helosciadium) crassipes (W.D.J.Koch ex Rchb.) Rchb.f. endemic to southern Italy, Sicily, Sardinia, Corsica and adjacent parts of North Africa;

Apium (Helosciadium) bermejoi L.Llorens, endemic in the Balearic isles; and

Apium (Cyclophyllum) leptophyllum (Pers.) F.Muell., native to America, but widespread and weedy in Europe and the Tropics.

All seven European species in this group have now been included in molecular phylogenetic studies, showing that *Apium* is polyphyletic. *Apium graveolens* has been included in some of the earliest molecular phylogenetic studies undertaken on the Umbellifer family (Downie and Katz-Downie 1996; Plunkett et al. 1996). This species, the type species of the genus, initially caused confusion as it was placed separate to, and distant from, the other European species included within *Apium* at that time, e.g. *Cyclospermum* (Plunkett et al. 1996) and *Helosciadium* (Downie et al., 2000b). Recent studies have extended the sampling, bringing more rigour to the results and confirming its distant placement to its European congeners. This research also revealed the diminutive Balearic Island endemic *Naufraga balearica* as the closest known relative to *Apium graveolens* (Downie et al. 2000a, b), although this may change when the New World *Apium* species are studied (Spalik et al. 2009). Monospecific *Naufraga* was originally placed in Subfamily Hydrocotyloideae by Constance and Cannon (1967), because of its simplified fruit anatomy, but now this is interpreted as reduction of a more complex fruit type and placement within Subfamily Apioideae is now accepted (Downie et al. 2000b). Currently these two species are grouped in Tribe Apieae with *Ammi*, *Anethum*, *Deverra*, *Foeniculum*, *Petroselinum*, *Ridolfia*, *Sclerosciadium*, and *Stoibrax* (Ajani et al. 2008).

All other European representatives, except *C. leptophyllum*, belong to the genus *Helosciadium.* They form a clearly monophyletic and strongly supported group (100% bootstrap) in recent studies (Hardway et al. 2004; Spalik and Downie 2006; Spalik et al. 2009), and it is now firmly placed in Tribe Oenantheae Dumort. alongside other genera typical of aquatic or wet habitats. This genus now includes all the species included by Wolff (1927) in *Apium* section *Helosciadium* (W.D.J.Koch) Babington, with the exception of the sterile hybrid *A.* x *moorei* (Syme) Druce (*A. inundatum* x *A. nodiflorum*) which is here not recognised as a distinct species (see also Reduron 2007b). Within *Helosciadium* two well-supported sister groups can also be recognised (Hardway et al. 2004; Spalik and Downie 2006):

- Group 1: *H. nodiflorum*, *H. bermejoi* and *H. repens*
- Group 2: *H. inundatum* and *H. crassipes*.

Cyclospermum leptophyllum is the final European species once considered within *Apium*. The generic placement of this distinctive, widespread adventive species has often been controversial. Wolff (1927) placed it within *Apium* in section Cyclospermum (Lag.) DC. whereas Constance (1990) preferred full generic distinction as *Cyclospermum* Lag. Molecular evidence now confirms the distant placement to core *Apium*, and strongly supports recognition in the separate genus *Cyclospermum*. Downie et al. (2001) first suggested that *Cyclospermum* be placed within Tribe Careae Baill, but its assignment to Careae was based on an identification error (Downie et al., unpubl.). Recent studies of additional collections resolve unequivocally that *Cyclospermum* should be placed within Tribe Pyramidoptereae Boiss. (Zhou et al. 2009), and possibly sister group to *Lagoecia cuminoides* (S. Downie, unpubl. data).

In the light of all these studies, it seemed appropriate and informative to investigate whether "classical taxonomical methods" can confirm and strengthen the results of these molecular studies. That is why we undertook a taxonomic revision of European *Apium* s.l., based on morphological, anatomical, and palynological data. In our study we added measurements on *Apium prostratum*, a species from the southern hemisphere, as a control and supplement for *Apium* s.s. Although a complete revision of *Apium* will need extensive sampling of the southern hemisphere species, the taxonomic picture in Europe is now clear, and is summarised below. As a result of this study, we confirm the restoration of the genus *Helosciadium*, with the more recently discovered *A. bermejoi* included in this genus, and the new combination formally described here as *Helosciadium bermejoi* (L. Lorens) Popper & M.F.Watson.

Materials and methods

Morphometry

Sixty-six quantitative morphological traits were measured on 73 herbarium specimens from the herbaria BM, BR, E, K, MA, and RNG and from personal herbarium of J.P. Reduron. The studied material is listed as an Appendix. Specimens were selected to cover the geographical range and morphological variability of the species concerned. The morphological characters studied are listed in Table 1. The character set includes characters most used by past authors in keys and floras to distinguish between the studied taxa. Several other characters were added on the basis of our herbarium studies and field observations. This resulted in a data matrix with 66 quantitative characters (24 are non-metric), from which 12 ratio variables were calculated. Most of the variables relate to vegetative features, but 16 were related to flowers and inflorescences. Because heterophylly is known to occur in some species, a distinction was made between "lower" and "upper" leaves (prefix LO or UP) for measuring variables, depending on their position (basal or apical).

Table 1 Morphological characters and their units or codes

Character (abbreviation used in diagrams)	Units/codes
Stem height (HEIGHT)	cm
Length of the stem (LENGTH)[a]	cm
Diameter of the stem at base (DIAMET)	mm
Number of leaflets (UPLEAFNR, LOLEAFNR)[a]	
Total length of leaf (UPTOTLEAFL, LOTOTLEAFL)[a]	mm
Petiole length (UPPETIOLL, LOPETIOLL)	mm
Leaf sheath length (UPSHEATHL, LOSHEATHL)[a]	mm
Leaf sheath width (UPSHEATHW, LOSHEATHW)[a]	mm
Length of terminal leaflet (UPTLEAFL, LOTLEAFL)[a]	mm
Width of terminal leaflet (UPTLEAFW, LOTLEAFW)[a]	mm
Incision of terminal leaflet (UPTLEAFINC, LOTLEAFINC)	mm
Number of lobes of terminal leaflet (UPTLEAFLOB, LOTLEAFLOB)	
Length of the lowest leaflet (UPLEAFL, LOLEAFL)	mm
Width of the lowest leaflet (UPLEAFW, LOLEAFW)[a]	mm
Petiolule length of lowest leaflet (UPSESSIL, LOSESSIL)[a]	mm
Incision of lowest leaflet (UPLEAFINC, LOLEAFINC)	mm
Peduncle length (PEDUNC)[a]	mm
Number of rays per inflorescence (NRAYS)[a]	
Min/maximum length of rays (LMINRAY, LMAXRAY)	mm
Number of bracts (BRACT)[a]	
Length of bracts (BRACTL)[a]	mm
Min/maximum number of bracteoles (BREOLMIN, BREOLMAX)	
Min/maximum length of bracteoles (BREOLLMIN, BREOLLMAX)[a]	mm
Min/max number of flowers per umbellule (NRFLOMIN, NRFLOMAX)[a]	
Pedicel width (PEDWID)	mm
Habit (CREEP)	1 prostrate, 2 ascending, 3 erect
Rooting at nodes (ROOT)	1 always, 2 half, 3 no
Heterophylly (HETERO)	1 yes, 2 no
Leaf dissection (UPPINNATE, LOPINNATE)	1 pinnate or pinnatifid, 2 bipinnate
Shape of terminal leaflet (UPTLEAFSH, LOTLEAFSH)	3 oblong, 6 elliptic, 7 ovate, 8 obovate, 9 deltoid, 10 circular, 11 rhombic
Dentation of terminal leaflet (UPTLEAFDEN, LOTLEAFDEN)	1 entire, 2 crenate, 3 serrate
Apex shape of terminal leaflet (UPTLEAFAP, LOTLEAFAP)	3 acute, 4 blunt, 5 attenuate
Shape of lowest leaflet (UPLEAFSH, LOLEAFSH)	3 oblong, 6 elliptic, 7 ovate, 8 obovate, 9 deltoid, 10 circular, 11 rhombic
Dentation of lowest leaflet (UPLEAFDEN, LOLEAFDEN)	1 entire, 2 crenate, 3 serrate
Apex shape of lowest leaflet (UPLEAFAP, LOLEAFAP)	3 acute, 4 blunt, 5 attenuate
Incision of bracts (BRACTOOT)	1 entire, 2 toothed, 3 pinnate
Position of bracts (BRACTPOS)	1 appressed to rays, 2 reflexed
Margin of bracteole (BREOLMAR)	1 green, 2 white
Dissection of bracteole (BREOLTOOT)	1 entire, 2 toothed, 3 pinnate
Position of bracteole (BREOLPOS)	1 appressed, 2 reflexed
Anther colour (ANTHCOL)	1 white, 2 greenish white, 3 yellowish, 4 purplish
Degree of compoundness of inflorescence (UMBEL)	1 simple, 2 double

[a] Characters belonging to the minimum character set

The following ratio variables were computed:

- leaf length:width (LO/UPTLEAF for terminal leaflet of lower/upper leaves, LO/UPLEAF for lowest leaflet of lower/upper leaves),
- leaf sheath length:width (LO/UPSHEATH for lower/upper leaves),
- leaf incision:leaf length (LO/UPTLEAFRI for terminal leaflet of lower/upper leaves, LO/UPLEAFRI for lowest leaflet of lower leaves), and
- peduncle length:min/max ray length (PEDMIN/MAX).

The data were analyzed using the software package Systat 8.0 (SPSS, Chicago, IL, USA). For each herbarium sheet several measures were taken whenever possible: some characters were scored per plant, but others are scored for each leaf or inflorescence. Character data were averaged per herbarium collection number, and for some analyses these data were further averaged per taxon. Basic statistics (mean, median, maximum, and minimum values) were computed for each herbarium specimen and for each taxon. Box plots of the mean values were prepared. One-way ANOVA was undertaken for each trait in order to test the significance of the difference of the means between the species. Similarly a Tukey test was used to test the significance of differences between each species. The normality of distribution was tested for each character by comparing their skewness and kurtosis to their relative standard error. The variables BREOLLMIN, BREOLLMAX, NRFLOMIN, and NRFLOMAX were normally distributed, but all other variables had to be transformed. Most variables were log-transformed, but LOSESSIL, UPSESSIL, BRACT, BRACTL, LENGTH, LMAXRAY, BREOLMIN, BREOLMAX, ROOT, HETERO, ANTHCOL, and CREEP were squared. Multicollinearity of the variables was tested in order to respect the model parsimony; Pearson and Spearman correlation coefficients were calculated for pairs of characters for each taxon and for the whole data set. Subsequently a minimum character set was selected with not highly correlated traits (indicated with superscript “a” in Table 1), that was used for discriminant analysis (DA).

In order to identify the most important traits for separating the species principal-component analysis (PCA) was carried out with herbarium specimen collection numbers as operational taxonomical units (OTUs). The significance of the variables for discriminating between the species was further investigated by DA. Both the complete data set with several observations per herbarium specimen and the averaged data set with herbarium collection numbers as OTUs were used for this purpose. DA was also performed on the averaged data set with all metric variables including the ratio variables, as this seemed to improve the results, even if there was multicollinearity between them. Hierarchical cluster analysis (Everitt 1986) was performed also, in order to obtain the relationships between the species based on their morphology. It was carried out with the herbarium collection number as OTUs, and then afterwards with the taxa as OTUs. Several clustering algorithms were used including the average linkage method, the complete linkage method, and Ward’s method, with Euclidean distance as a dissimilarity measure.

Fruit anatomy

Mature fruit samples were taken from the following herbarium specimens; most of which were also included in the morphometic analysis (see Appendix):

A. graveolens	R.H. Bianor 623 (E); E. Dursy & Ch. Schultz s.n. (E); P.A.C. Endress s.n. (E); O. Krebs s.n. (E); J. McNab s.n. (E); C.A. Panckert s.n. (E); T.H.H. von Heldreich s.n. (E)
A. prostratum	Freeman E.D.W. 85/3 (RNG)
C. leptophyllum	G. Bentham & J.D. Hooker 80/56 (E); A. Fleischmann 3047b (E)
N. balearica	R.J.D. McBeath 2760, cultivated in RBG Edinburgh
H. bermejoi	R.N. Lester s.n. (RNG)
H. crassipes	E. Reverchon 97 (E); L. Kralik s.n., 1861, Algeria (E)
H. inundatum	J. Ball s.n., Germany (E); J. Ball s.n., France, Fontainebleau (E); E. Levier s.n., 15/5/1870, Italy, near Pisa (E); Seringe s.n. (E); T.H.H. Von Heldreich s.n. (E)
H. nodiflorum	E. Bourgeau 220 (E); A. Charpin, J. Fernandez Casas & F. Munoz Garmendia 15108 (E); B. Deverall & B. Flannigan 271 (E); E. Reverchon s.n. (E); E. Reverchon 1060 (E); E. Reverchon 1060bis (E)
H. repens	L.F.J.R. Leresche s.n. (E); F. Sennen 817 (E)

Fruits were rehydrated by boiling in water until they sank (about 10 min), then placed in 1 M sodium hydroxide for 12 h. They were then washed in distilled water. Fresh *Naufraga balearica* fruits were collected from a cultivated specimen at RBGE and placed in 50% ethanol for two days.

Fruits were embedded in wax, sectioned and stained on the basis of procedures used by Alex Pridgeon (Royal Botanic Gardens Kew, unpublished), Johansen (1940) and Jensen (1962). The rehydrated fruits were taken through a 50–100% ethanol dehydration series (2 h stages) followed by a 10–100% ethanol:histoclear series. The fruits were left just covered in 100% histoclear and pelted paraffin wax (embedding wax) was added. The samples were kept in an oven at 59°C until the histoclear had completely evaporated (ca. 2 weeks). The fruits were then placed in wax in paper moulds. Once the wax had set, sections were cut at 3–7 μm using a Leitz Wetzler rotary microtome type 1212. Wax ribbons were mounted in distilled water on slides and dried on a slide warmer (43°C for 5 min). Slides were then passed through a 100–50% histoclear:ethanol series (2 min each). The slides were stained for 45 min in a 1% safranin in 50% ethanol solution (this stained lignin red) followed by 1% Alcian blue counter stain for 2 min. The slides were then dehydrated by passing through a 50–100% ethanol series followed by a 10–100% ethanol:histoclear series before mounting in Euparal. These are incorporated into the Umbelliferae fruit slide collection, at E and are available for consultation.

Macerations of the fruits were made so vittae number and longitudinal morphology could be recorded. Mature fruits were placed in a 1 M solution of potassium hydroxide (KOH) and placed in an oven at 59°C for about 10 min. Once the fruits had softened they were placed on slides in a drop of glycerol for 5 min. Under a dissecting microscope, Zeiss Stemmi SV6, they could then be cut on the commissural side using a needle and the seed removed. The vittae are then clearly visible.

Pollen morphology

Pollen was taken from the following herbarium specimens, most of which were also included in the morphometic analysis (see list in Appendix):

A. graveolens	HG Rabyns 5145 (BR); G. de Gottal s.n., 6/1930, Blankenberge, Belgium (BR)
A. prostratum	Freeman E.D.W. 85/3 (RNG); C.C. Pritchard s.n. (BR)
C. leptophyllum	A.F. Lang s.n. (BR); M. Martins 312 (BR)
H. bermejoi	A. Bermejo s.n. (RNG)
H. crassipes	Davis 52175 (E); Ronse 1419 (BR)
H. inundatum	M. Chorley s.n., 6/1982, England, Cumberland, Ennerdale, west end of Ennerdale Water, GR35/088152 (BR); H. Höppner (BR).
H. nodiflorum	J.P.Reduron s.n. (pers. herb.); A. Ronse 742 (BR)
H. repens	R. Trautmann s.n. (BR)
N. balearica	J. Duvigneaud 62E365 (BR)

For pollen preparation, anthers were dissected out from herbarium material and softened in a 1:200 Agepon solution for 30 min. The pollen was isolated by sieving (mesh width 63 μm) after which they were dehydrated (glacial acetic acid) and acetolysed (concentrated sulphuric acid and acetic acid 1:9 for 6 min at 95°C). Pollen grains destined for SEM studies were suspended in ethanol and air-dried on a stub. The length of polar (P) and equatorial (E) axes were measured using SE micrographs, obtained with a Jeol scanning electron microscope type 5800 LV. Measurements were made on three to four pollen grains per specimen, when possible. One-way ANOVA was carried out on the P/E ratio and complemented with Tukey tests in order to investigate significant differences between the species.

Results

Morphometry

Basic statistics and box plots

According to the one-way ANOVA, all traits differ significantly between the species, except the heterophylly and the degree of compoundness of the inflorescence, which are variables with only two states. Arithmetic averages, standard deviations, and minimum and maximum values of several significant morphological traits, and their pairwise statistical significant difference by the Tukey test were computed. Box plots of the means were also drawn for each character in order to illustrate the differences between the species. The basic statistics and a selection of the most significant box plots are shown in an online database. The results according to ANOVA and box plots per trait are discussed together in following paragraphs. The variable numbers indicated between brackets refer to the box plots in the online database.

The plant height (var 1) is a good variable to discriminate between almost all the species, but there is no significant difference between *H. nodiflorum*, *C. leptophyllum*, *A. graveolens*, and *A. prostratum*. The sequence of the species with increasing plant height is: *Naufraga*, *H. bermejoi*, *H. repens*, *H. inundatum*, *H. crassipes*, *C. leptophyllum*, *H. nodiflorum*, *A. graveolens*, and *A. prostratum*. The stem diameter (var 2) separates *H. bermejoi*, *H. repens*, and *Naufraga* individually from all the other species. The number of leaflets per (lower) leaf (var 3) also differentiates between *H. repens*, *Naufraga*, and *A. graveolens* individually versus the other species. The total leaf length of lower leaves (var 4) also distinguishes both *H. repens* and *Naufraga* individually, and *H. crassipes*, *H. inundatum*, and *H. bermejoi* together from the other species. The length of the petiole of lower leaves (var 5) is useful to distinguish *A. graveolens* and *A. prostatum* from other species: they have on average petioles that are longer than 5 cm. Another useful character is the sheath length of the lower leaves (var 6). It is clearly larger in *H. nodiflorum* than in *H. repens*, and is also different in the other *Helosciadium* species and in *Naufraga*. The sheath width (var 7) also separates *H. bermejoi* and *H. repens* from the remaining species. The length of terminal leaflets of lower leaves (var 8) is very useful, because it separates all species individually, except that *Naufraga* and *H. bermejoi* are not significantly different, and *H. inundatum* and *A. prostratum*. Very useful is also the length of the petiolules (var 9): it distinguishes *Helosciadium* from other species, because *Helosciadium* leaflets have no petiolules, except for a few *H. nodiflorum* specimens and for *H. bermejoi*, that has petiolules smaller than 0.4 mm. Thus this character significantly separates *Helosciadium* from other taxa, but within *Helosciadium*, *H. bermejoi* only resembles *H. nodiflorum*. Finally, within the vegetative traits, the length (and to a lesser degree the width) of the lower leaflets of upper leaves (var 10) is significantly different between most of the species.

Several generative traits are also important. The number of bracts (var 11) gives a statistically significant difference between *H. nodiflorum* on one hand, *H. repens* and *H. bermejoi* on the other, and between the remaining species. The box plot of the number of bracts shows that in this group of species only those in *Helosciadium* ever possess bracts: even if bracts are usually absent for *H. inundatum* and *H. crassipes*, exceptionally flowers with one bract can be found. The largest number of bracts is present in *H. repens* (mostly from 4 to 6) and in *H. bermejoi* (mostly 5 or 6). The same is also true for bracteoles, as shown by the box plot of the maximum number of bracteoles (var 12). However, *H. bermejoi* always has no bracteoles. So, with the exception of *H. bermejoi*, the maximum bracteole number reliably distinguishes *Helosciadium* from the other species studied. The (maximum) length of the bracteoles (var 13) defines three groups within *Helosciadium*: *H. bermejoi*, *H. nodiflorum*, and all the remaining species. The peduncle length (var 14) is a good character to distinguish nearly every *Helosciadium* species from the other genera: it is zero in *C. leptophyllum* and *A. prostratum*, and shorter than 0.5 cm in *A. graveolens*. The minimum number of flowers per umbellule (var 15) can also be used to distinguish between species of *Helosciadium*. The ratio peduncle length/minimum ray length is useful to distinguish between *H. repens*, *H. nodiflorum* and *H. crassipes*. The number of rays (var 16) is highest in *H. bermejoi* and allows it to be distinguished from all species except *A. graveolens* and *A. prostratum*; the lowest number of rays is found in *C. leptophyllum*, *H. inundatum*, *Naufraga*, and *H. crassipes*.

It should be noted here that interpretation of the morphology of the inflorescence of *Naufraga balearica* is subject to debate. We have interpreted the inflorescence as consisting of simple umbels borne in the whorl of cauline leaves, as did Constance and Cannon (1967) in the original description of the species. However, it also might be possible to regard the inflorescence as a compound umbel subtended by an involucre of foliaceous bracts. This would change the above mentioned results as to place *Naufraga* closer to *Helosciadium* as far as generative traits are concerned.

Principal-component analysis

The PCA analysis was performed using all the metric variables and resulted in nine components that together explain 88% of the total variance. The first (29%) and second (20%) factors account for nearly 50% of the variance, and they succeed in attributing the specimens to the species (Fig. 1). Most species are well separated, except *H. crassipes* which overlaps with *H. inundatum* and *H. nodiflorum*. The genera are rather well delimited, with a *Helosciadium* cloud in the upper half of the figure, and with *Naufraga* clearly distinguished from *C. leptophyllum* and *A. graveolens/prostratum*. The first factor correlates mainly with plant height, stem diameter, and leaf dimensions (total length, length and width of leaflets, petiole length, and sheath length and width). The second factor correlates negatively with petiolule length and positively with the number and length of bracts and bracteoles, the number of leaflets per leaf, the number of lobes per leaflet, the petiole length of the upper leaves, the peduncle length, and the number of rays per umbel.

Discriminant analysis

Both the complete data and the averaged data per herbarium specimen number showed a good discrimination between the species, but the percentage of correctly

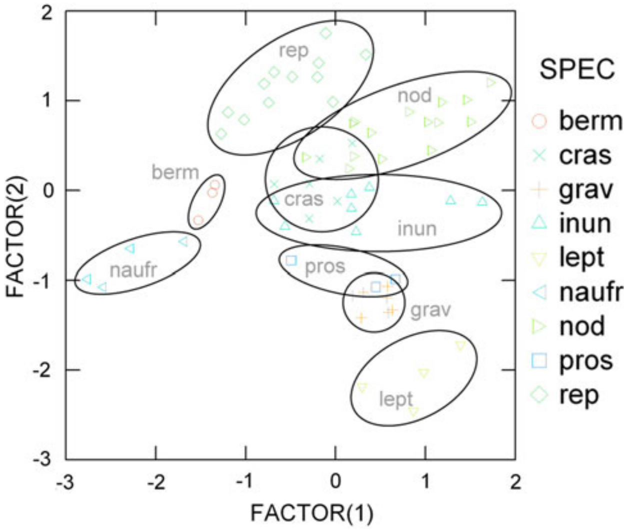


Fig. 1 PCA ordination diagram of 62 specimens and 47 morphological traits

classified plants increased from 98% (95% when jackknifed) to 100% using averaged specimen data (85% for the jackknifed classification matrix). This was further improved to 100% correct classification, and 96% correct when jackknifed, when using all metric variables including the ratio variables. The DA ordination plot is shown in Fig. 2. It gives an even better separation of the species than with PCA. The best discriminated (centroids farthest apart) species is *H. repens*, while the least well separated species is *H. crassipes* from both *H. nodiflorum* and *H. inundatum*, and *A. prostratum* from *A. graveolens* and from *C. leptophyllum*. The generic delimitation of the species, however, does not match these results completely: although most *Helosciadium* are placed together and separate from the other taxa, this is not the case for *H. bermejoi*. On the other hand, *Naufraga* is placed close to *Apium* s.s. (*A. graveolens* and *prostratum*), but also to *Cyclospermum*. This shows that this morphological data set is fit for discriminating between species, but less so for discriminating between genera.

The characters that best discriminate between the species, are more or less the same with or without averaging the data, and with a reduced or complete metric variable list. The trait that was consistently important is the number of bracts (see Table 2* in the online dataset). Other crucial traits for discriminating between the species are: petiolule length; leaflet length, width and (relative) incision of the (upper) leaves; ray length; minimum number of flowers; and stem diameter. These traits were also important contributors to the two main components found by PCA. All traits contributed towards discriminating the species; the exceptions were most of the ratio variables, the number of rays, and the maximum number of flowers.

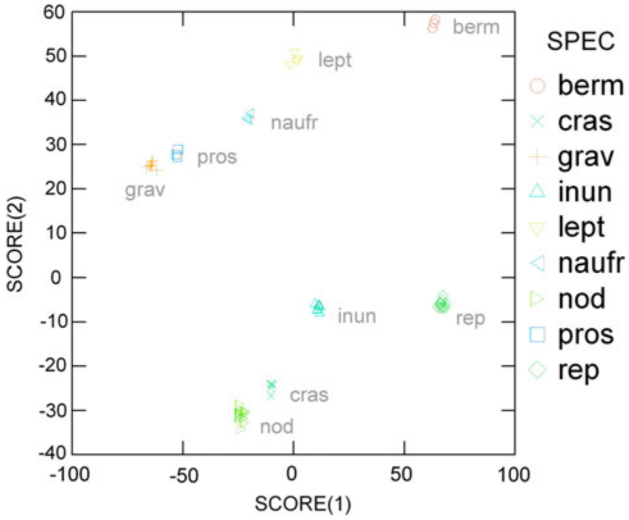


Fig. 2 Discriminant analysis (DA) ordination diagram

Hierarchical clustering

The dendrogram obtained by clustering herbarium specimens of *Helosciadium* using Ward's method is shown in Fig. 3. Because of the limitations of the morphometric data specimens from other genera were not included. The resulting dendrogram has two main branches, the first containing all specimens of *H. nodiflorum* and *H. repens*, the second with all specimens of *H. inundatum* and almost all specimens of *H. bermejoi*, and *H. crassipes*. According to these results, *H. crassipes* and *H. inundatum* are the species pair that are most similar, with *H. bermejoi* next to them. Moreover, *H. repens* and *H. nodiflorum* are also similar to each other.

In this dendrogram most specimens are clustered well together by species. Some specimens are placed within another species, but mostly these fall within a similar taxon, e.g. Kralik 601 (*H. crassipes*) is placed within *H. inundatum*, and Darrah 650, a non flowering specimen of *H. nodiflorum* is placed with *H. repens*. Ronse 697c, that

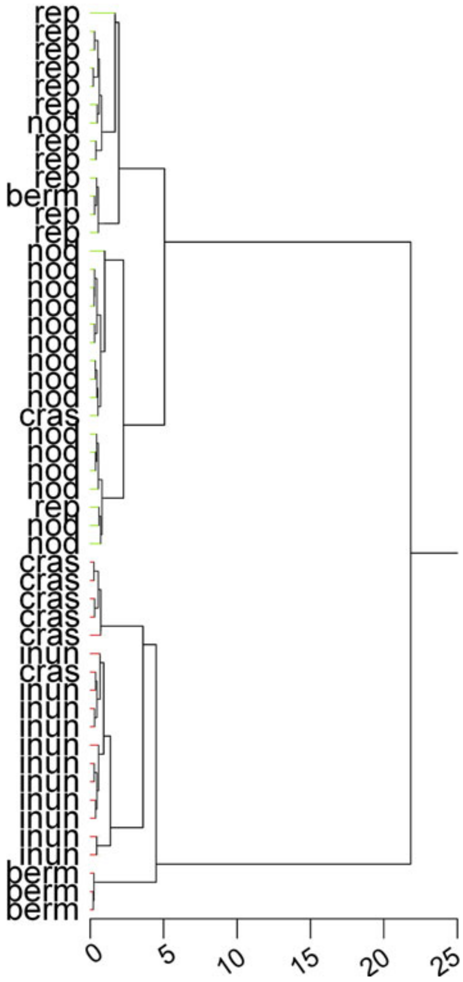


Fig. 3 Dendrogram based on morphological data with herbarium numbers as OTUs

was originally identified as *H. repens,* is placed within *H. nodiflorum*. However, this specimen comes from a mixed *repens*/*nodiflorum* population and subsequent molecular analysis has put it within *H. nodiflorum* (Raspé et al., in preparation). In two cases, specimens are found in more distant clusters, e.g. there is a specimen of *H. crassipes* (Fay 1308) within the *H. nodiflorum* group, and Bermejo s.n., a non flowering specimen of *H. bermejoi* was placed within *H. repens*.

A dendrogram was also prepared with morphological data averaged per taxon. This again resulted in a dendrogram with *H. repens* and *H. nodiflorum* separated from *H. crassipes*, *H. inundatum*, and *H. bermejoi* (Fig. 4).

Fig. 4 **a** Dendrogram based on morphological data with taxa as OTUs. **b** Dendrogram based on morphological data with only taxa of *Helosciadium* as OTUs

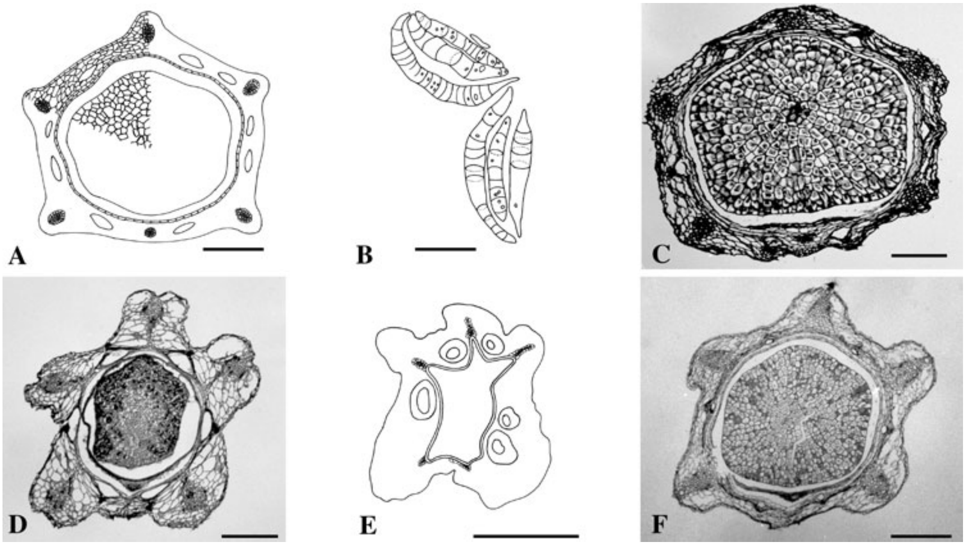
Fruit anatomy

The taxa studied can be divided into four groups based on the characteristics of the transectional anatomy of the mericarps (terminology follows Kljuykov et al. 2004). The number and arrangement of vittae (oil ducts) within the pericarp is often taxonomically useful in Umbelliferae, but these proved uniform across the species investigated because all except *Naufraga balearica* had six primary vittae per mericarp: solitary vittae between each rib (vallecular vittae), and two on the commissure (commissural vittae). However, the distribution of vascular and lignified tissue does seem to be of taxonomic significance, as does the distribution of air cavities.

Apium graveolens (Fig. 5a) mericarp ribs were not particularly prominent as the valleculae are not very narrow or deep. Vascular tissue was present in discrete bundles surrounded by sclerenchyma (collectively referred to here as fibro-vascular bundles), circular-elliptic in cross-section, located under each of the five ribs. Mericarps are variable in the number of vittae as seen in cross-section. Some have the typical vittae arrangement of one vallecular, and two commissural, whereas others have one to five additional smaller vittae alongside those between the ribs. Macerations clearly show that the main vallecular and commissural vittae run unbranched for the length of the fruit, and the additional "dwarf" vittae are very short (Fig. 5b). The inner layer of the mesocarp is lignified and the endosperm is subpentagonal in cross-section. Observations of the New Zealand *Apium prostratum* show it to have the same type of fruit anatomy as *A. graveolens* (see also Arenas and García 1993; Klan 1947).

Helosciadium nodiflorum, *H. repens*, *H. bermejoi*, *H. inundatum*, and *H. crassipes* represent a second type of fruit anatomy. The cross section of the mericarp of

Fig. 5 Anatomical transects of mericarps of European *Apium* s.l. **a** Cross section of the mericarp of *Apium graveolens*. **b** Fruit maceration showing primary and dwarf vittae of *A. graveolens*. **c** Cross section of the mericarp of *Helosciadium crassipes*. **d** Cross section of the mericarp of *Helosciadium inundatum*. **e** Cross section of the mericarp of *Naufraga balearica*. **f** Cross section of the mericarp of *Cyclospermum leptophyllum*



H. crassipes is shown in Fig. 5c; cross sections of other species have already been published by Arenas and García (1993). The ribs are more prominent than the "*graveolens* type", and contain air cavities because of cell collapse as the fruit matures. These air chambers were not so conspicuous in the fruits of *H. crassipes* and *H. bermejoi*, however; this may be partly because of the age of the material available. The mesocarp is proportionally thicker than the "*graveolens* type". The five main fibro-vascular bundles are greatly enlarged, extending deep into each rib, small secretory canals are sometimes present in the ribs (e.g. *H. nodiflorum* and *H. inundatum*, Arenas and García 1993). All the above species have the typical arrangement of primary vittae, but additional dwarf vittae were not seen. When viewed in cross-section the vittae in *H. inundatum* and *H. repens* were rather unusual as occasionally the central "cavity" was stained light blue (not reported by Klan 1947). As vittae in the Umbelliferae are said to be schizogenous in origin (i.e. forming in the intercellular spaces) cellular detail should technically not be present within the vittae. As yet we cannot explain this observation and it merits further anatomical study. Discrete lignified fibro-vascular bundles are positioned above each of the six vittae. A layer of lignified tissue (hypendocarp) also extends between the vittae into a ring surrounding the lignified inner layer of the mesocarp. In *H. inundatum* the smaller fibro-vascular bundles extend around the vittae merging into this layer (Fig. 5d). The endosperm is subterete in cross-section.

Cyclospermum leptophyllum (Fig. 5f) has a fruit anatomy type rather similar to *A. graveolens*, but the epidermis easily separates at maturity, only primary vittae are present, and the fibro-vascular bundles are much larger, deltoid in cross-section, occupying most of the enlarged rib.

The fruit anatomy of *Naufraga balearica* was found to be unique among those studied (Fig. 5e). Although fully mature fruit were not available for study, careful examination of the material enabled interpretation and comparison. The ribs were not particularly prominent, and vascular tissue was restricted to a few vessels below each of the five ribs. In our material only five vittae were present as one of the commissural vittae is apparently missing. Furthermore, unlike most Umbellifers in subfamily Apioideae, the vittae do not stain heavily with safranin. We have found that the vittae are best observed from maceration preparations, and that in cross-section the vittae can be located by the peculiar small, strongly safranin stained regions occurring within the surrounding cells.

Pollen morphology

Micrographs of pollen of the studied species are shown in Fig. 6. All pollen grains are small and belong to the oval type as defined by Cerceau-Larrival (1971), thus they all have a fairly structured tectal surface. This is of the cerebroid type for *A. graveolens*, *A. prostratum*, *C. leptophyllum*, and *Naufraga*, while the *Helosciadium* species have more pronounced, tubular sculptures, especially *H. crassipes* and *H. inundatum*. All *Helosciadium* species have a long ectoaperture, as also does *C. leptophyllum*, whereas it is rather long in *A. graveolens*, *A. prostratum*, and *Naufraga*. Some pollen grains are somewhat thickened at the equator, especially for *A. prostratum* and *A. graveolens*.

Table 2 presents the polar and equatorial axis length of the pollen averaged per species. The P/E values found by other researchers are also given in the last column, these are mainly data from Cerceau-Larrival (1959). The P/E values lie between 1.3 and 1.9, with the mean values mostly around 1.5. On the basis of the mean P/E value there are no significant differences between the species, although *H. repens* and *H. bermejoi* have somewhat smaller values, and *Naufraga balearica* has a larger P/E value. The variability of the P/E values differs between species, with *A. prostratum*, *H. inundatum*, and *Naufraga* having the largest variability, whereas *H. bermejoi* displayed a remarkably small degree of variation. The P/E values that we measured coincide well with the values computed for the same species by Cerceau-Larrival (1959), but she gave only one measure per species. Her value for *A. graveolens* (1.45) coincides with our minimum value found for this species, and her value for *H. inundatum* (1.86) coincides with the maximum value that we measured. The P/E of 1.67 that we found for *Naufraga balearica* lies close to the value of 1.64 that we calculate from the dimensions given by Fridlender (2001). However the pollen dimensions of his Corsican plants are smaller ($P = 11$–12 μm and $E = 7$ μm) than those of plants coming from the type location on the Balearic Islands ($P = 17.4$ μm and $E = 10.5$ μm).

Discussion

One of the main conclusions from previous molecular studies has been the separation of *Helosciadium* from *Apium*. There is also chemical evidence to support this separation (Muckensturm pers. comm. as cited in Reduron 2007a). We found that some morphological characters can also be used to distinguish *Helosciadium* from other taxa, such as the number of bracts and bracteoles and the petiolule length. Bracts and bracteoles only occur in *Helosciadium*, although *H. crassipes* and *H. inundatum* mostly lack bracts and *H. bermejoi* lacks bracteoles. Leaflets are sessile in *Helosciadium*, except in *H. bermejoi* and in some *H. nodiflorum*. *Helosciadium* is rather well separated in PCA ordination diagrams, but in DA ordination *H. bermejoi*

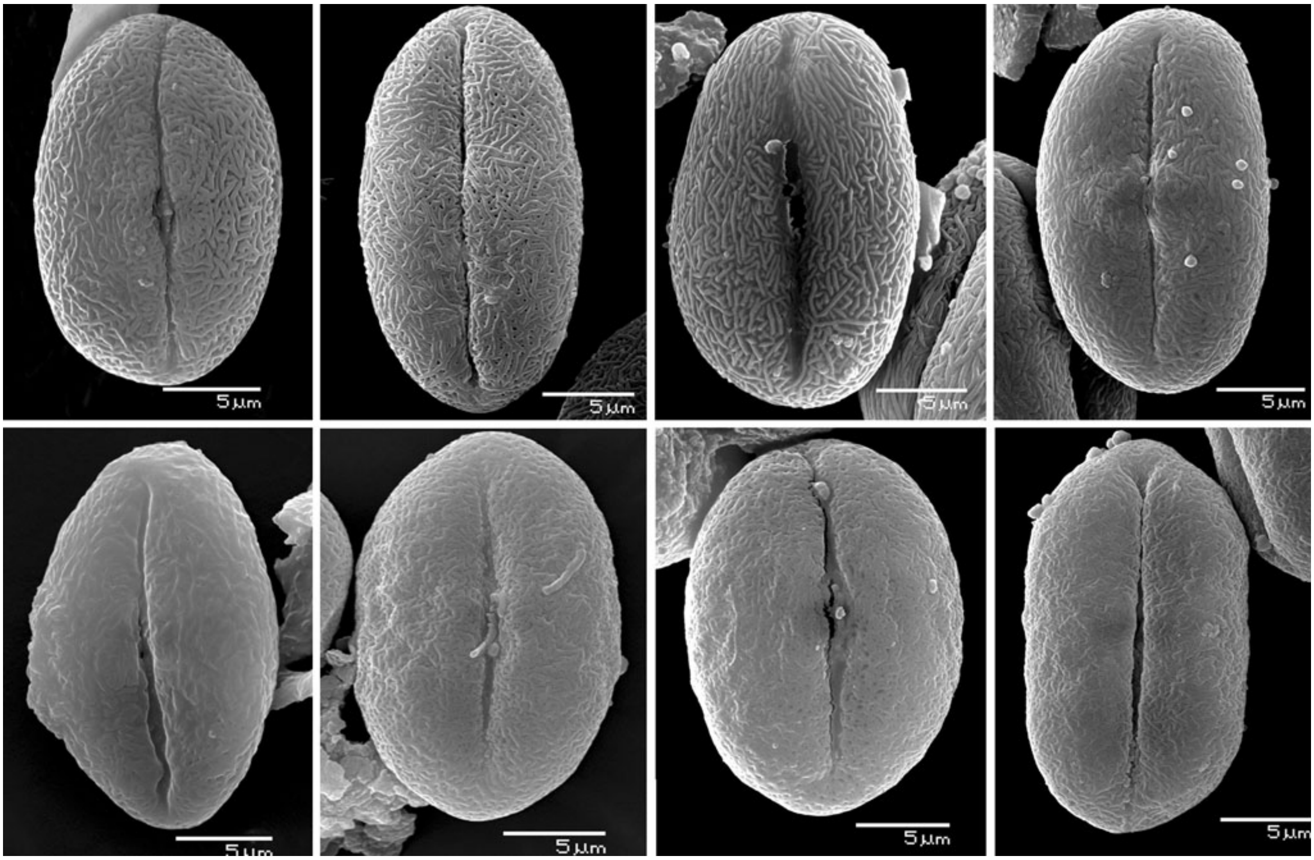


Fig. 6 SEM micrographs of pollen of European *Apium* s.l. **a** *H. bermejoi*, b *H. crassipes*, **c** *H. inundatum*, **d** *H. nodiflorum*, **e** *H. repens*, **f** *A. graveolens*, **g** *A. prostratum*, **h** *C. leptophyllum*

Table 2 Average length (in µm) of polar (P) and equatorial (E) axes of pollen grains of European *Apium* s.l., and their ratio P/E

Species	P	E	P/E (min–max)	P/E other sources
A. graveolens	18.6	12.2	1.54 (1.46–1.68)	1.45
A. prostratum	20.1	13.2	1.55 (1.27–1.93)	
C. leptophyllum	17.2	11.2	1.53 (1.39–1.66)	
H. bermejoi	18.3	12.6	1.46 (1.43–1.48)	
H. crassipes	19.4	12.5	1.55 (1.40–1.71)	1.57
H. inundatum	20.3	13.5	1.52 (1.33–1.86)	1.86
H. nodiflorum	20.5	13.6	1.51 (1.38–1.66)	1.56
H. repens	17.8	13.1	1.37 (1.27–1.49)	
N. balearica	17.4	10.5	1.67 (1.45–1.92)	1.64

is placed separate from the other *Helosciadium* species. Thus on the whole, the chosen morphological data set succeeds only partly in giving generic delimitations, although it enables good distinction between the species.

Most of the morphological traits used in this study have been shown to be useful for discriminating between the sampled species. The two principal components obtained by PCA together explain 88% of the total variance, and the ordination diagram has separated most species well. DA has resulted in a 100% correct classification of the specimens; the DA ordination diagram gives even better separation of the specimens within species. Hierarchical clustering of the herbarium specimens has resulted in a dendrogram clustering the specimens of the same species well together, with only a very few specimens oddly placed. The dendrogram structure supports the presence of the two sister groups that were recognised within *Helosciadium* by molecular studies, *H. nodiflorum* and *H. repens* clustering together in a different group from *H. crassipes* and *H. inundatum*. However, the position of *H. bermejoi* is different, as it was placed with the latter species rather than with *H. nodiflorum* and *H. repens*.

The separate position of *Helosciadium* is supported by fruit anatomy, because they have a distinctive and different mericarp type. The pollen dimensions are not conclusive, but the tectal surface of *Helosciadium* pollen shows more clearly protruding tubular sculptures, instead of more flattened, cerebroid sculptures. The ectoaperture seems to be somewhat longer than in *Apium*.

Apium graveolens and *A. prostratum* are always placed very close to each other by the morphological data, and this is confirmed by their fruit anatomy. Both species show the typical vittae arrangement for umbellifers of one vitta between each rib, and two on the commissure. However, *A. graveolens* sometimes has up to five extra small vittae per vallecula. Similar "dwarf" vittae have also been observed in other taxa (e.g. *Pimpinella anisum*, Lobova and Watson unpublished data), and could be a result of selection for a higher yield of the essential oils produced in the mericarp. On the other hand, similar results were reported by Arenas and García (1993) for the naturally occurring *A. graveolens* var. *butronensis*, a Cantabro–Atlantic endemic, where three vallecular vittae occur. These authors mention that when only one vallecular vitta is present in this species, it takes more than half the intercostal space, as opposed to the smaller vittae in the other *Apium* species (matching *Helosciadium* and *C. leptophyllum*). They also describe the absence of rib secretory ducts in *A. graveolens*, whereas these are present in *C. leptophyllum*, *H. nodiflorum*, and *H. inundatum*, but not visible in *H. repens* and *H. bermejoi*.

Cyclospermum leptophyllum is placed in the neighbourhood of *Apium graveolens* and *A. prostratum* by PCA and clustering of the morphological data, but DA clearly separates it from *Apium*. Its separate position from *Apium* is confirmed by the anatomical characters of its fruit. This accords with the molecular findings, where it is also separated from *Apium* but placed in the tribe Pyramidopterae (Zhou et al. 2009), thus justifying its treatment as a separate genus.

The position of *Naufraga balearica* has been rather mysterious until recent years. After initial inclusion in the Subfamily Hydrocotyloideae, molecular studies have consistently shown that it is very closely related to *Apium graveolens* in the Apioideae. This is also supported by the phytochemical properties of *Naufraga*, as reported by Fridlender (2001). On morphological grounds it is easy to distinguish from the other European species in this group: both PCA and DA separated it well from the other species. By PCA it was placed close to *H. bermejoi*, but DA placed it between *Apium* s.s. (both *A. graveolens* and *A. prostratum*) and *Cyclospermum*. It is distinguished from all other species by fruit anatomy, because it is the only species that does not possess the typical vittae arrangement for Apioideae. In our material we found that it has only one vitta on the commissure instead of two, however, Constance and Cannon (1967) and Reduron (2008) report only four vittae as they found no vittae on the commissural surface.

Diagnostic key to genera

1a	Bracts and/or bracteoles present; mericarps with lignified tissue extending into ribs and above vittae, air chambers present at maturity, ribs prominent	***Helosciadium***
1b	Bracts and bracteoles absent; mericarps with lignified tissue not extending into ribs or present above vittae, air chambers absent, ribs not prominent	**2**
2a	Plants prostrate, <5cm tall; leaves trifoliate to pinnate; mericarp vittae 4 or 5 (absent or only one on the commissure), commissure highly reduced or absent, carpophore absent, endosperm pentagonal in cross-section, vascular tissue reduced often to only one vessel below each rib	***Naufraga***
2b	Plants erect, much larger; leaves pinnate to multipinnate; mericarp vittae 6 or more (two on the commissure), commissure and carpophore present, endosperm subpentagonal in cross-section, fibrovascular tissue prominent below each rib	**3**
3a	Leaf segments not linear; umbels rays 4–13, peduncle mostly distinct (up to 13 mm); mericarps sometimes with 1–5 extra dwarf vittae, fibrovascular tissue elliptic in cross-section	***Apium***
3b	Leaf segments linear; umbels rays 2–3, always sessile; mericarps without extra dwarf vittae, fibrovascular bundles deltoid in cross-section	***Cyclospermum***

Key to species of *Helosciadium*

1a	Plant creeping, stems stoloniferous, rooting at every node; plants less than 30 cm high	**2**
1b	Plant erect or ascending, but not rooting at every node	**4**
2a	Bracts 0–2 (3) per umbel	***H. nodiflorum*var. *ochreatum***
2b	Bracts >3 per umbel	**3**
3a	Plant to 7 cm; bracteoles absent; rays (7–)8–11(–12) per umbel; flower 1 per umbellule	***H. bermejoi***
3b	Plant to 20 (–25) cm; bracteoles present; rays (3–)4–6(–8) per umbel; umbellules many flowered	***H. repens***
4a	Plant to 80 cm; leaves homomorphic; bracteole margins white; rays >3 per umbel	***H. nodiflorum***
4b	Plant to 40 cm; leaves heteromorphic; bracteole margins green; rays 1–3 per umbel	**5**
5a	Plant to 17 cm; rays (1–)2(–3) per umbel; bracteoles (1–)3–4(–6) per umbel; peduncle up to 20× as long as rays; flowers to 8 per umbellule; pedicels not thickened in fruit; styles <stylopodium	***H. inundatum***
5b	Plant to 37 cm; rays 2–5(–7) per umbel; bracteoles (3–)5–6(–8) per umbel; peduncle up to 4× as long as rays; flowers to 16 per umbellule; pedicels thickened in fruit; styles >stylopodium	***H. crassipes***

Annotated checklist of the European species

1. *Helosciadium* W.D.J.Koch, Gen. Pl. Umbell. Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 12: 125. 1824.

=*Heliosciadium* Bluff & Fingerh., Compend. Fl. Germ. 1: 398. 1825.
=*Helodium* Dumort., Fl. belg.: 77. 1827.
=*Heloscia* Dumort., Anal. fam. pl.: 34. 1829.
=*Lavera* Raf., Good book amenit. nat. philad.: 50. 1840.
=*Laoberdes* Raf., Good book amenit. nat. philad.: 50. 1840.
=*Heloschiadium* T.Marsson, Fl. werml.: 83. 1859.
=*Mauchartia* Neck., Elem. bot. 1: 172. 1790. *suppressed name* (ICBN appendix V).
=*Sium* Sect. *Helosciadium* (W.D.J.Koch) Gaudin, Fl. helv. 2: 430. 1828.
=*Helosciadium* Sect. *Mauchartia* DC., Prodr. 4: 104. 1830.
=*Apium* Sect. *Mauchartia* (DC.) Benth. in Benth. & Hook. f., Gen. pl. 1: 888. 1867.
=*Apium* Sect. *Helosciadium* (W.D.J.Koch) Bab., Man. Brit. Bot. ed. 8: 156. 1881.
=*Apium* Subgen. *Helosciadium* (W.D.J.Koch) Drude, in Engl. & Prantl, Pflanzenfam. III 8: 185. 1898.
=*Sium* L., Sp. pl.: 251. 1753. *pro parte*
=*Sison* L., Sp. pl.: 252. 1753. *pro parte*
=*Apium* (L.) Lag., Amen. nat. españ.: 101. 1821. *pro parte*
=*Meum* Mill., Gard. dic. ed. 8. 1768. *pro parte*

Type species: *H. nodiflorum* (L.) W.D.J.Koch (selected by Britton 1918)

Note: *Helosciadium* is here recognised a genus of five species with diversity centred in Europe. When Koch (1824) first erected the genus he included two other species: *H. bulbosum* (Thore) W.D.J.Koch (=*Caropsis verticillatoinundata* (Thore) Rauschert) and *H. lateriflorum* (Link) W.D.J.Koch (=*Cyclospermum leptophyllum*). *Helosciadium* is grouped with *Sium* on the basis of molecular data, however, it can be readily distinguished from this genus as *Sium* has many vittae in each mericarp and a chromosome number $2n = 20$, whereas *Helosciadium* has six vittae per mericarp and $2n = 22$.

1.1. *H. nodiflorum* (L.) W.D.J.Koch, Gen. Pl. Umbell. Nova. 12: 125. 1824.

=*Sium nodiflorum* L., Sp. pl.: 251. 1753 [basionym].
=*Sison nodiflorum* (L.) Brot., Fl. lusit. 1: 423. 1804.
=*Apium nodiflorum* (L.) Lag., Amen. nat. españ: 101. 1821.
=*Helodium nodiflorum* (L.) Dumort. Fl. belg.: 77. 1827.
=*Lavera nodiflora* (L.) Raf., Good book amenit. nat. philad. : 50. 1840.

Lectotype: Herb. Cliff. 98 *Sium 3* (BM) (selected by Jafri, 1985: 78).

Distribution: Native throughout most of Europe (especially the southern and the western part), N. Africa and southern parts of C. and W. Asia; naturalized in parts of N. and S. America.

Note: including var. *ochreatum* (DC.) DC. Prodr. 4: 104 (1830) basionym *Sium repens* var. *ochreatum* DC., in Lamark & De Candolle, Fl. fr. ed. 3. 4: 300. 1805 (see Reduron 2007b, 2009). The infraspecific taxa of *H. nodiflorum* will be covered in detail in a subsequent publication.

1.2. *H. repens* (Jacq.) W.D.J.Koch, Gen. Pl. Umbell. Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 12: 125. 1824.

=*Sium repens* Jacq., Fl. austriac. 3: 34. 1775 [basionym].
=*Apium nodiflorum* subsp. *repens* (Jacq.) Thell. in Hegi, Ill. Fl. Mittl.-Eur. 5: 1150. 1926.
=*Apium repens* (Jacq.) Lag., Amen. nat. españ. 1(2): 101. 1821.
=*Helodium repens* (Jacq.) Dumort., Fl. belg.: 77. 1827.
=*Laoberdes repens* (Jacq.) Raf., Good book amenit. nat. philad.: 50. 1840.

Lectotype: Jacquin, Fl. austriac. 3: t.260. 1775 (***lectotype selected here***)

Distribution: Native to western Europe, parts of central and of southern Europe, and parts of N. Africa.

Note: Jacquin cited no specimens with the original description, and there are no herbarium specimens at the BM that can be linked with this (Banks bought a large amount of Jacquin's material which is now housed at the BM). Jacquin material can also be found in other European herbaria (e.g. AWH, CGE, LIV, OXF, UPS, W), however, we have not managed to trace any original material. We agree with Reduron (2007b) that Jacquin's plate in Flora Austriacae (t. 260) is excellent, detailed, and clear, and we hereby use this plate to typify this species.

1.3. *H. bermejoi* (L.Llorens) Popper & M.F.Watson**, *comb. nov.***

=*A. bermejoi* L.Llorens., Fol. Bot. Misc. 3: 28. 1982 [basionym].

Holotype: (Maó) Menorca, Terrenos marítimos húmedos próximos al Cap Negre. *s.coll. s.n.* (BC Acc. No. 637411)

Distribution: Endemic to Menorca (Spain).

Note: This species is sometimes put close to *Naufraga balearica* by our morphological analyses, rather than with other *Helosciadium* species. It also has low variability of the pollen morphology, which is maybe a narrow island endemic feature.

1.4. *H. inundatum* (L.) W.D.J.Koch, Gen. Pl. Umbell. Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 12: 125. 1824.

=*Sison inundatum* L., Sp. pl.: 253. 1753 [basionym].
=*Sium inundatum* (L.) Lam., Fl. franç. 3: 460. 1778.
=*Hydrocotyle inundata* (L.) Sm. Fl. brit. 1: 290 (1800)
=*Meum inundatum* (L.) Spreng., Sp. umbell.: 114. 1818.
=*Helodium inundatum* (L.) Dumort., Fl. Belg.: 77. 1827.
=*Apium inundatum* (L.) Rchb. f., in Rchb. & Rchb. f., Icon. fl. germ. helv. 21: 9. 1863.

Lectotype: Herb. Linnaeus 356.7 (LINN) (Reduron in Jonsell and Jarvis 2002).

Distribution: Endemic to Europe, mainly western but extending east to Sicily and north to S.E. Sweden.

Note: Hegi (1926) illustrated a mericarp cross-section of this species apparently with three vittae on the commissure, we have not observed this in any of these fruits and suggest that the middle "vitta" is the carpophore vascular bundle. This is supported by the results of Arenas and García (1993).

1.5. *H. crassipes* W.D.J. Koch ex Rchb., Iconogr. bot. pl. crit. t.218 (1825).

=*H. crassipes* W.D.J.Koch, Gen. Pl. Umbell. Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 12: 126. 1824. *nomen nudum.*
=*Sium crassipes* (W.D.J.Koch ex Rchb.) Spreng., Syst. Veg. 4: 120. 1827.
=*Apium crassipes* (W.D.J.Koch ex Rchb.) Rchb.f., in Rchb. & Rchb.f., Icon. fl. germ. helv. 21: 9. 1863.

Lectotype: Sison/Corse, *Helosciadium crassipes*, Salzmann (MPU) (Reduron & Schäfer, in Reduron 2007b).

Distribution: Endemic to Corsica, Sardinia, Sicily and S. Italy, and parts of N. Africa.

2. *Naufraga* Constance and Cannon, Feddes Repert. 74: 1. 1967.

Type species: *Naufraga balearica* Constance & Cannon

2.1. *Naufraga balearica* Constance & Cannon, Feddes Repert. 74: 3. 1967.

Holotype: Pollensa, Mallorca, Baléares. Cala San Vincente, falaise maritime, fissures ombragées et humides: colonisation de dépots de tuf calcaire. *Duvigneaud s.n.,* 22 July 1962 (BM)

Distribution: Endemic to Balearic Islands (Spain) and possibly Corsica.

Note: An unusual monotypic genus, endemic to the Balearic Islands, that has in the past been recorded from Corsica, but the natural population no longer exists there (Fridlender 2001). *Naufraga balearica* has a greatly simplified morphology, and bears some resemblance to another Balearic Island endemic, *Helosciadium bermejoi* (syn. *Apium bermejoi*), with which it shares a similar habitat preference. The fruit anatomy of *N. balearica* is unique amongst those studied and is discussed above, as is the reported chromosome number of $2n = 20$ (Constance et al. 1976). The unusual highly reduced morphology of *Naufraga* and divergence from *A. graveolens* is perhaps a consequence of the extreme isolation, and evolutionary pressure from the littoral habitat. The taxonomic isolation of the genus and its island habitat are reflected in the meaning of its Greek name: shipwrecked sailor.

3. *Apium* L., Sp. pl.: 264. 1753.

=*Carum* L. Sp. pl.: 263.1753. *pro parte*
=*Seseli*.L. Sp. pl.:259. 1753. *pro parte*
=*Sium* L. Sp. pl.:251. 1753. *pro parte*
=*Celeri* Adans., Fam. pl. 2: 498. 1763.
=*Apium* Sect. *Euapium* DC., Prodr. 4: 101. 1830.
=*Helosciadium* (L.) Rojas. Cat. Hist. Nat. Corrient: 65. 1897. *pro parte*
=*Apium* Subgen. *Euapium* (Benth. & Hook.f.) Drude, in Engl. & Prantl, Pflanzenfam. 38: 184. 1898.

Type species: *Apium graveolens* L. *nom. cons. prop.* (*typ. cons. prop.*, Hitchcock and Green 1929; Jarvis 1992; Jarvis et al. 1993.)

Note: Now that the all the European species bar *A. graveolens* are excluded, the centre of diversity of this genus is concentrated in S. America, and comprises approximately 19 S. Hemisphere species with the cosmopolitan weed/escape of cultivation *A. graveolens*. Although we were not able to study the S. Hemisphere members, preliminary results of fruit anatomy and of plant morphology for *A. prostratum* (New Zealand) indicate that it is co-generic with *A. graveolens*. The Australasian *Apium prostratum* exhibits a broad range of variation in habit and leaf morphology, and contains several subspecies and varieties (see Short 1979 for a treatment of the Australian members). The three specimens used in this study belong to *A. prostratum* subsp. *prostratum* var. *filiforme* (A. Rich) Kirk. Further study is needed on the S. Hemisphere *Apium*s to resolve their phylogenetic relationships, and perhaps elucidate the odd disjunction of *Naufraga*.

3.1. *Apium graveolens* L. Sp. pl.: 264. 1753.

=*Seseli graveolens* (L.) Scop., Fl. carn.: 360. 1760.
=*Sium apium* Roth., Tent. fl. germ. 1: 128. 1788.
=*Sium graveolens* (L.) Vest, Man. bot.: 517. 1805.
=*Helosciadium graveolens* (L.) Rojas, Cat. Hist. Nat. Corrient.: 65. 1897.
=*Carum graveolens*(L.) Koso-Pol., Bull. Soc. Nat. Mosc. 1915 *n.s.* 24: 1990.
=*Celeri graveolens* (L.) Britton, Fl. bermuda: 279. 1918.
=*Apium integrifolium* Hayata, J. Coll. Sc. Tokyo, 30: 126. 1911.

Lectotype: Herb. Linnaeus 374.3 (LINN) (selected by Tardieu-Blot 1967)

Distribution: Native to C., S. and E. Europe (often coastal areas), N. Africa, Asia, N. and S. America; widely cultivated and often naturalized in temperate zones.

4. *Cyclospermum* Lag., Amen. nat. españ. 1(2): 101. 1821. *nom. cons.*

=*Sison* L. Sp. pl.: 252. 1753. *pro. parte.*
=*Pimpinella* L. Sp. pl.: 263. 1753. *pro. parte.*
=*Aethusa* L. Sp. pl.: 256. 1753. *pro parte.*
=*Helosciadium* W.D.J.Koch., Gen. Pl. Umbell. Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 12: 125. 1824. *pro parte*
=*Heliosciadium* Sect. *Cyclospermum* (Lag.) DC., Prodr. 4: 105. 1830.
=*Apium* L. Sp. pl.: 264. 1753. *pro parte*
=*Apium* Sect. *Leptocaulis* Benth. & Hook.f. Gen. pl.: 888. 1867. *pro parte*
=*Apium* Sect. *Cyclospermum* (Lag.) H. Wolff, in Engl., Pflanzenreich 90 (4. 228): 53. 1927.

Type species: *Cyclospermum leptophyllum* (Pers.) Sprague ex Britton & Wilson (*typ. cons.*)

Note: *Cyclospermum* as currently understood comprises two S American species and the cosmopolitan weed *C. leptophyllum*. Fruit morphology and anatomy bear some resemblance to *Apium*, although there are other good morphological and cytological characters separating the genera (see key to genera). It would not be surprising if further examination of the S. American *Apiums* results in transfer of some of these to *Cyclospermum*.

4.1. *Cyclospermum leptophyllum* (Pers.) Sprague ex Britton & Wilson, Bot. Porto Rico 6: 52. 1925.

=*Sison ammi* Jacq., Hort. vindob. 2: 95. 1773.
=*Cnidium tenuifolium* Moench, Meth.: 98. 1794. *nomen illegit.*
=*Pimpinella leptophylla* Pers., Syn. pl. 1: 324. 1805 [basionym].
=*Pimpinella lateriflora* Link., Enum. Hort. berol. alt. I.: 285. 1821.
=*Aethusa leptophylla* (Pers.) Spreng., Umbell. prodr.: 22. 1813.
=*Cyclospermum ammi* Lag., Amen. nat. españ. 1(2): 101. 1821.
=*Helosciadium lateriflorum* (Link) W.D.J.Koch., Gen. Pl. Umbell. Nova Acta Phys. Med. Acad. Caes. Leop.-Carol. Nat. Cur. 12: 125. 1824.
=*Helosciadium leptophyllum* (Pers.) DC., Mém. Soc. Nat. Hist. Genève 4: 493. 1829.
=*Apium leptophyllum* (Pers.) F.Muell. ex Benth., Fl. austral. 3: 372. 1866.
=*Apium ammi* Urb., in C. Martius, Fl. bras. 11(1): 341. 1879.
=*Apium ammi* var. *leptophyllum* (Pers.) Chodat & Wilczek, Bull. Herb. Boiss. II. 2: 526. 1902.
=*Cyclospermum leptophyllum* (Pers.) Sprague, Jour. Bot. 61: 131. 1923, *nomen inval.*
=*Apium tenuifolium* (Moench) Thell., in Hegi, Ill. Fl. Mitteleur. 52: 1140. 1926.
=*Apium ammi* var. *genuinum* H. Wolff, in Engl., Pflanzenreich 90 (4.228): 54. 1927.

Holotype: St. Domingo, *Persoon s.n.* (L, Acc. No. 908 255–1068)

Distribution: Native to S. America; naturalized worldwide as a pantropical/warm temperate weed.

Acknowledgments We are most grateful to Mark Newman for his meticulous checking on the complex synonymy and typification; Stephen Downie and Michael Müller for their generous help when working with the molecular data; Sally Rae for assistance in preparing the plates; Frank Van Caekenberghe for the pollen acetolysis and for taking SEM pictures; Jean-Pierre Reduron, Stephen R. Downie, and Krzysztof Spalik for invaluable comments on the manuscript; the personnel of the Conservatoire Botanique National of Mulhouse (France) for providing living material; and the herbaria of Edinburgh (UK) and Madrid (Spain). This research received support from the SYNTHESYS Project http://www.synthesys.info/ which is financed by European Community Research Infrastructure Action under the FP6 "Structuring the European Research Area" Programme. The senior author was funded by a grant by the Trustees of the Royal Botanic Garden Edinburgh.

Appendix

Material examined; the specimens are listed in alphabetical order of the collectors.

Apium graveolens

R.H. Bianor 623, 17/8/1911, Espana, Majorca, Soller, springs (E). *E. Dursy & Ch. Schultz s.n.*, 8/1840, Germany, fossés et prairies près des salines de Dürckheim (Palatinat), Flora Galliae et Germaniae exsiccata 446 (E). *P.A.C. Endress s.n.*, **7**/1831, France, Biarritz, rupes maritimes (E). *O. Krebs s.n.*, **7**/1895, Austria, Wien, im Küchengärten cultiviert (E). *Manucehri 32*, 8/1948, Iran, prov. Kashan, Ghamsar (E). *J. Mc Nab s.n.*, Greece, Corfu (E). *C.A. Panckert s.n.*, Germany, Brandenburg, Salzbrunn bei Treuenbrietzen (E). *Rabyns H.G. 5145*, 19/4/1976, Greece, Crete, Erimoupolis, Sitia (BR). *T.H.H. von Heldreich s.n.*, 20/7/1887, Greece, Attica, in valle Cephissi humidis, pl. exsicc. Florae Hellenicae (E).

Apium prostratum

Freeman EDW 85/3, 12/2/1985, New Zealand, South Otago, N of Nugget Point, exposed dunes, sprawling habit

(RNG). *Gibbons P. 693*, 17/5/1987, Australia, South-Eastern 36°55′S, 139°48′E, 6 km south of Kingston, Butchers Gap Cons. Pk., closed sedge land, scrambling herb, frequent (BR). *Pritchard C.C.*, 11/1/1954, New Zealand, Mason's Bay (BR).

Cyclospermum leptophyllum

G. Bentham & J.D. Hooker 80/56, France, Cévennes (E). *A. Fleischmann 3047b*, Germany, Montefalcone und zwischen Wippach und Heidenschaft, Rchb. Fl. Germ. Novit. 3047b (E). *Lang A.F.*, s.d., Italy, Neapolis (BR). *Marchi P. & B. Martire*, 9/10/1985, Italia, Roma, Universita degli Studi di Roma "La Sapienza", alt. 30 m, University town, unattended lawns (BR). *Martins M. 312*, 7/6/1972, Portugal, Lisboa (Estremadura), Belem, Praça do Imperio, in hortis (BR). *Press J.R. 793*, 4/6/1985, Madeira, Sao Gonçalo, 2 km E of Funchal from EN101 into village, at base of wall in fairly dry earth, quite common (BR).

Helosciadium bermejoi

Bermejo A. s.n., 11/6/1983, Espana, Menorca, Alayor, known only from an area of more or less four hundred square meters (RNG). *A. Bermejo*, Espana, Majorca, grown in Alayor, from the type locality (E). *R.N. Lester s.n.*, 20/8/1983, grown from seed at BG Birmingham University for 4 months, from Espana, Menorca (RNG). *J. Orell s.n.*, 26/7/1986, Espana, Balears, Menorca, Mao, Es cap Negre 31SFE11, pequenos declives de la linea de costa, en suelos de naturaleza fluxoturbidica (MA).

Helosciadium crassipes

Angel Garcia et al. 3885, 7/6/2003, Italia, Sardegna, Cagliari, Gesturi, cercanias del centro didactico, 39°44′36″N 9°7′12″E, 500 m, alcornacal con mirto y lagunas temporales en tabla basaltica (MA). *C. Bicknell & L. Podini*, 24/5/1901, France, Corsica, in paludibus prope Portovecchio (MA). *Davis 52175*, 11/5/1971, Algeria, 7 km W of El Kala (La Calle), edge of dyke, perennial, alt 5–10 m (E). *J.M. Fay 1308*, 1978–1979, Tunesia, parc national d'Ichkeul, marsh, alluvial, loam (E). *L. Kralik 601*, 19/5/1849, France, Corse, Sta Manza près de Bonifacio, marécages maritimes (E). *A. Letourneux & H. de la Perraudière*, 3/6/1861, Algeria, in paludosis ditionis Senhadja Bone inter et Philippeville (E). *E. Reverchon 97*, 1/6/1881, Italia, Sardegna, Tempio, Sta Teresa Gallura, marais de Bancamino (RNG). *Ronse A. 1419*, 10/2006, cultivated, from Conservatoire botanique Mulhouse, originally France, Corse, Musella (BR).

Helosciadium inundatum

Aldosoro s.n., 20/6/1992, Espana, Zamora, Requejo (MA). *Anonymous*, 10/7/1987, Espana, Zamora, Ribadelago, lagunilla, Parque Natural de Lago de Sanabria, 29TPG8166, 1,600 m (MA). *D. Davis & S. Sutton 64358*, 2/6/1979, Italy, Sicily, Messina, ca. 7 km SW of Floresta towards Monte Pojummoru (Nebrodie), ca. 1,300 m (E). *T.H.H. Von Heldreich s.n.*, 20/3/1840, Italia, Sicilia, Panormum, in stagnis montosis prope Panormum, gurgo di Ddingoli sul M. Moarta (E). *F. Gomez Vigide*, 13/6/1988, Espana, La Coruna, Puerto de Son, en la laguna costera de Xuno, 5 m (MA). *E. Rico*, 18/7/1976, Espana, Salamanca, Navasfrias (MA). *Höppner H.*, 21/6/1931, The Netherlands, Maasgebied, Gräben des Koningsveens bei Gennep (BR). *M.S. Romero*, 10/7/1991, Espana, La Coruna, Carbollo, cerca de Brea, en el cauce del rio Rosende, cuenca del Anblons (MA). *Seringe s.n.*, 1700s, Great Britain, Scotland, Kinrosshire, ditch near Auchendinny, Braid Hill, Martler-Bog east of Maw Castle (E). *Turland 856*, 2/5/1995, Greece, Ahaia, coastal region near Kalogria, 33 km W of Patra, alt 0 m, margin of freshwater swamp, somewhat shades (BM). *E. Valdes-Bermejo 11.166 & J. Silva*, 31/7/1987, Espana, Lugo, Cospeito, en las canalizaciones proximas a la laguna, 29TPH 1685 (MA).

Helosciadium nodiflorum

E. Bourgeau 220, 1848, Espana, Santa Cathalina (E). *M.C. Bruno & P.M. Uribe-Echebarria 2074.83*, 29/6/1983, Espana, Burgos, Condado de Trevino, Lanjo, 700 m, UTM 30TWN3124, Manantial calizo, calido (MA). *A. Charpin, J. Fernandez Casas & F. Munoz Garmendia 15108*, 21/8/1978, Espana, Granada, Castril, prope cortijo del Nacimiento, ca. 1,100 m (E). *P. Cousturier*, 1912, France, Corse, Calaciacina, route vers Corte, alt. 700 m (E). *J. Darrah 650*, 17/8/1969, Turkey, Adana, near Hasanbeyli, wet sand, open, vegetative partrs creeping, rooting at nodes (E). *M. de Godos*, 15/7/1993, Espana, Leon, Marrubio, 29TQG0389, aliseda (MA). *B. Deverall & B. Flannigan 271*, 18/7/1956, Espana, Avila, El Arenal, Sierra de Gredos, wet, shades, by stream, 900 m (E). *V.R. Garcia*, 25/7/1977, Espana, Orense, Os Peares, Nogueira de Ramuin, cuneta inundada (MA). *Leadlay & Petty 367*, Portugal, Douro, Lavra (E). *M. Pardo de Santayana 1148 & L. Medina*, 10/8/1999, Espana, Cantabria, San Miguel de Aguayo, arroyo cerca de Sta Maria de Aguayo, 660 m alt. (MA). *Reduron J.P. s.n.*, 4/8/2000, France, Vaucluse, Malaucène (personal herb. J.P.Reduron). *E. Reverchon s.n.*, Espana (E). *E. Reverchon 1060*, 8/1895, Espana, Teruel, Albarracin, lieux humides et herbeux, 1,300 m, rare (E). *E. Reverchon 1060bis*, 7/1904, Espana, Jaen, Barrançon de Valentina, bords des ruisseaux, sur le calcaire, 1,500 m (E).

Ronse A. 742, 3/8/2004, Ireland, Cork, Macroom, in Toone River, 287702, along the river, partly in the water (BR). *A. Somerville*, 13/8/1894, Great Britain, Arran, King's Cove, UC100 (E).

Helosciadium repens

E. Carrillo & L.M. Ferrero, 8/7/2001, Espana, Guadalajara, Checa, Barranco del Cubillo, 30T XK006896, 1,530 m (MA). *LM Ferrero & L. Medina 1456*, 7/8/1997, Espana, Guadalajara, Orea, turbera caliza en el margen del rio de la Hoz Seca, 30TXK0686, 1,500 m (MA). *J.P. Fry 73*, 2/8/1968, Morocco, Middle Atlas, Ras Chedaya, Bab bou Idir, growing in stream, 1,410 m (E). *S.L. Jury 11722, A. Achnal, M. Khanas & LS Springate*, Morocco, Tazzeka, 29 km from Taza on minor road near Bab-Bou-Idir, 34°5′N Long 4°7′W, UTM 30S 396416 3771447, damp flush in *Quercus ilex* forest, abundant on heavily grazed wet area, 1,530 m (MA). *S.L. Jury 17589*, 7/7/1997, Morocco, above Imilchil, on road to Lake Tizlite along El-Ksiba to Imilchil road, damp, heavily overgrazed area by small stream (E). *L.F.J.R. Leresche s.n.*, 19/8/1842, Switzerland, Vaud, au chalet à Gabet au-dessus de Lausanne (E). *G. Mateo*, 18/8/1980, Espana, Soria, entre Morales y Bayubas, WL09, juncales junto al Duero (MA). *Reduron J.P.*, 11/4/2008, France, Haut-Rhin, glaisière de Guewenheim (personal herb. J.P.Reduron). *Ronse A. 697c*, 12/7/2004, Germany, Bayern, Urspring, Viehweide (BR). *F. Sennen 185*, Morocco, Beni-amssrart (MA). *F. Sennen 817*, 21/8/1909, Espana, Aragon, Cella, marécages (E). *Trautmann R. s.n.*, 26/8/1915, Hungary, in scaturiginiibus ad ripam Danubii inter pag. Soroksar et Dunaharaszti infra Budapest (BR).

Naufraga balearica

Dutartre G., 1/6/1981, France, Corse, au sud de Piana, rochers siliceux suintants à Isoetes duriei, etc. (BR). *Duvigneaud J. 62E365*, 22/7/1962, Espana, Majorca, Pollensa (BR). *PDC 12845*, 26/11/1979, seeds from Reading University, Mallorca (E).

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