Characterisation of Holocene plant macrofossils from North Spanish ombrotrophic mires: vascular plants

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SUMMARY

Methods and criteria that were used to identify plant macrofossils from four ombrotrophic mires in northern Spain are presented. Twelve monocotyledon and ten dicotyledon species were recorded. Some were identified from vegetative or reproductive macroremains (*Eriophorum angustifolium, Molinia caerulea, Calluna vulgaris, Erica mackaiana, Erica tetralix, Potentilla erecta*), while others were recognised only by their fruits (*Rhynchospora alba, Carex durieui, Carex echinata, Carex binervis, Carex demissa, Betula alba*), seeds (*Juncus squarrosus, Juncus bulbosus, Luzula multiflora, Narthecium ossifragum, Drosera rotundifolia, Drosera intermedia, Caltha palustris, Daboecia cantabrica*), rhizome fragments with remains of leaves (*Agrostis curtisii*), or twigs with buds and leaves (*Vaccinium myrtillus*). Descriptions of the specific distinctive characters for the plant macrofossils that were recorded are accompanied by illustrations that facilitate their interpretation. Dichotomous identification keys are also provided.

KEY WORDS: bogs, plant macro-remains, rhizomes, leaves, seeds

INTRODUCTION

Vascular plant macrofossils include the remains of all (reproductive and vegetative) plant structures such as leaves, fruits, seeds, wood, roots and rhizomes which are visible to the naked eye (Dickson 1970, Birks & Birks 1980, Warner 1988, Birks 2001) and have been preserved in a variety of depositional environments. They may be found, for example, in lacustrine, fluviatile and salt marsh sediments. In peat deposits, these remains are often well preserved and found in high concentrations.

At present there are no standardised (internationally agreed) identification methods that provide useful and effective criteria for identifying plant macrofossils to family, genus and species levels. Taxonomic studies are mainly carried out using botanical reference collections and palaeobotanical publications. Identification of plant macrofossils by comparison with modern material from reference collections is a task with many difficulties, because the diagnostic characters that are used in the keys for present-day flora (i.e. for modern or fresh specimens) often relate to parts of the vegetative or reproductive apparatus that may not be preserved in the sub-fossil state. Moreover, different intensities of decomposition may lead to macrofossils that differ in shape and size from their modern counterparts. Physical and chemical treatments causing degradation of fresh plant material similar to that experienced during ‘fossilisation’ processes can be very useful in helping to ensure accurate species-level identifications of plant macrofossils.

Another handicap for identifications of vascular plant macrofossils in peat is the shortage of comprehensive descriptions in palaeobotanical publications. Also, these descriptions are often not readily accessible (e.g. Bertsch 1941 in German; Beijerinck 1947 in Dutch; Körber-Grohne 1964 in German; Katz *et al*. 1965, 1977 in Russian; Grosse-Brauckmann 1972, 1974 in German) or restricted to particular taxonomic groups, e.g. *Carex* (Szczepanik-Janyszek & Klimko 1999, Starr & Ford 2001, Jiménez-Mejías & Martinetto 2013), *Eriophorum* (Tucker & Miller 1990) or *Juncus* (Körber-Grohne 1964, Gałka 2009, Sievers 2013). Moreover, the majority of the most prominent publications that contain descriptions or pictures of vascular plant macrofossils are for central and eastern Europe (Grosse-Brauckmann & Streitz 1992, Velichkevich &

Zastawniak 2006, 2008) or for north-west Europe (Mauquoy & van Geel 2007).

Ombrotrophic mires in northern Spain are located near the southern distribution limit for this type of bog in Europe (Pontevedra-Pombal 2002). Their plant cover, both present and past, has peculiar characteristics that differentiate them from similar bogs elsewhere Europe (Fraga *et al*. 2001, Mighall *et al*. 2006, Schellekens *et al*. 2011, Romero-Pedreira 2015). To date, few analyses of plant macrofossils in the peat deposits of northern Spain have been undertaken (Castro *et al*. 2015). Palaeobotanical studies of bogs can deliver important information about past climate change and, thus, can also contribute to improving our understanding of future climate.

The main objective of the research reported here was to comprehensively study the vascular plant macrofossils preserved in four peatlands in northern Spain, with special emphasis on the morphological characters that allow accurate identifications at genus and species levels. We hope that the information presented here will be useful, not only to increase knowledge about European bog palaeofloras, but also to facilitate future studies on plant macrofossil identification. A second part, about bryophyte macrofossils from the same bogs, is in preparation.

METHODS

The study involved four phases, of which the first two were carried out simultaneously.

1. Extraction of plant macrofossils from peat

The sampled bogs (Figure 1, Table 1) were three blanket bogs, namely: Pena da Cadela (PDC, Xistral Mountains) (Castro *et al*. 2015), Borralleiras de Cal Grande (BCG, Buio Mountains) (Pontevedra-Pombal *et al*. 2013) and Zalama (ZAL, Ordunte Mountains) (Souto *et al*. 2014); and one raised bog: Chao de Veiga Mol (CVM, Xistral Mountains) (Pontevedra-Pombal *et al*. 2014).

Peat monoliths were obtained using a Wardenaar corer for the first 100 cm and a Russian corer (diameter 5 cm) for the subsequent parts of the cores, except in the case of Pena da Cadela, where the peat core was obtained by directly sampling fresh sections in newly excavated ditches on a previously undisturbed bog. The cores were sliced into 2 cm thick samples which were stored at 4 °C until analysis.

Plant macrofossils were extracted from the peat samples according to the protocol of Mauquoy *et al*. (2010). Sub-samples of peat (5 cm^3) were digested with 8 % NaOH for 15 minutes and disintegrated

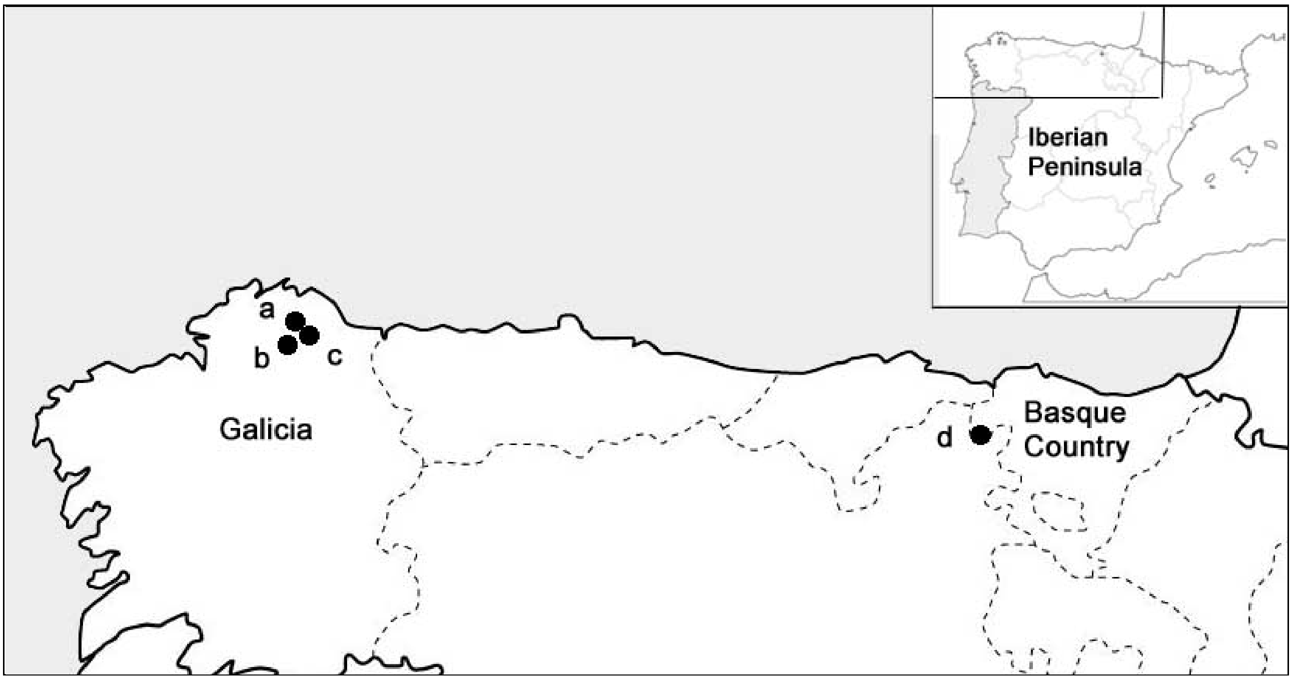

Figure 1. Locations of the sampled bogs: a) CVM (Chao de Veiga Mol), b) PDC (Pena da Cadela), c) BCG (Borralleiras de Cal Grande), d) ZAL (Zalama).

Table 1. Characterisation of the sampled bogs. Climatic data according to *Martínez-Cortizas & Pérez-Alberti (1999) and **Heras (2002). MaT = mean annual temperature, P = annual precipitation, Nps = number of peat samples analysed.

Bog	**Location**	**Altitude** (m a.s.l.)	**Dominant lithology**	**MaT** (°C)	**P** (mm)	**Depth** (cm)	**Nps**
Pena da Cadela	43° 30′ 09″ N / 7° 33′ 01″ W	970	quartzite	*7.5	*1800	183	93
Borralleiras de Cal Grande	43º 35′ 25″ N / 7º 30′ 50″ W	600	quartzite	*11.5	*1400–1600	231	116
Chao de Veiga Mol	43º 32′ 34.4″ N / 7º 30′ 13.41″ W	695	granodiorite	*7.5	*1800	845	187
Zalama	43º 08′ 06.16″ N / 3º 24′ 51.9″ W	1330	quartz sandstones	**7.5	**1600	226	132

using a sieve (0.2 mm mesh). The screened material was transferred to petri dishes and scanned for macrofossils using an Olympus SZ30 binocular microscope. The plant macrofossils were then isolated and stored in 70 % ethanol at 4 °C.

2. Reference collection of current bog flora

Modern plant material (vegetative and reproductive) was gathered from various European bogs, including the four studied here, and used to prepare a reference collection composed of i) herbarium specimens, ii) fruits and seeds and iii) microscope slides.

For herbaceous species, whole plants - including rhizomes and roots - were collected as herbarium specimens. For woody species, samples of shoots, stems, leaves, flowers and fruits were selected for the reference collection. All specimens were identified according to *Flora Ibérica* (Castroviejo *et al*. 1986–2015) and *Flora Europaea* (Tutin *et al*. 1964–1980). Dry, ripe fruits and seeds of the present bog flora were stored in hermetically sealed bottles at 4 ºC.

Sections of the roots, rhizomes, stems and leaves, as well as epidermis samples from vegetative and reproductive organs, were used for microscope slide preparations. In order to simulate the fossil state, dried herbarium samples, fruits and seeds were rehydrated and gently heated in 8 % NaOH solution for five minutes then cleared for immersion in 5 % sodium hypochlorite solution (Locquin & Langedon 1983). This treatment produces a taphonomic effect which facilitates the study of structures, tissues and cells that are more resistant to decomposition. DPX (xylene based mountant) and Hoyer's solution (Anderson 1954) were used for permanent slides.

All reference material (herbarium specimens, fruits, seeds and microscope slides of both modern and fossilised material) has been deposited in the Natural History Museum of the University of Santiago de Compostela.

3. Identification of macrofossils

Plant macrofossils were analysed first under an Olympus SZ30 binocular microscope and then under an Olympus CX40 compound microscope. Most of the macrofossils were identified to species or genus level on the basis of comparisons with reference collection specimens and/or information from bibliographic sources (Grosse-Brauckmann 1972, 1974; Grosse-Brauckmann & Streitz 1992, Mauquoy & van Geel 2007, Tomlinson 1985, Velichkevich & Zastawniak 2006, 2008; Cappers & Neef 2012). The identified macrofossils were photographed with an Olympus SC20 camera, and were also drawn using a *camera lucida* attached to the microscope.

4. Reference collection of plant macrofossils

The identified plant macrofossils were stored in 70 % ethanol at 4 °C, in hermetically sealed bottles arranged according to the following criteria: a) bog of origin; b) peat sample number; and c) species. When different types of macrofossils were identified from the same species, each type was stored in a separate container. Thus, a single species from one peat sample may be represented by several bottles in the reference collection. This collection has also been deposited in the Natural History Museum of the University of Santiago de Compostela.

RESULTS

Most of the macrofossils found in the peat samples were small (0.5–10 mm) and presented different degrees of descomposition. The most common remains were those of herbaceous roots, usually consisting of just an elongated epidermal envelope surrounding a dark single stele, most of which could not be assigned to a particular species because of their limited variability and lack of identifying taxonomic characters.

Wood remains were also abundant and included the roots, stems and twigs of shrubs. These typically consisted of an elongated wood axis with an outer covering of bark, although separate remains of bark and lignified fragments were also frequent. Identification of woody macrofossils was generally very difficult below family level, and only twigs that retained buds or leaves could be identified to species.

While the relatively good preservation status of carpological remains, mature fruits and seeds often allowed identification at species level, leaves were rarely well preserved. The exception was the family Ericaceae, for which we recorded several well preserved (although usually fragmented) leaves.

Identifications were carried out to the lowest possible taxonomic level. Macrofossils of Ericaceae, Cyperaceae and Poaceae were relatively easy to identify at family and genus levels. The major difficulties were at species level, especially among closely related species.

Distinctive characteristics for the 22 macrofossil species recorded are shown, and those appropriate for species identification highlighted, in the Appendix (Tables A1–A4, Figures A1–A7).

We examined rhizomes, achenes and seeds of *Eriophorum angustifolium* (Table A1, Figure A1), as well as achenes of *Carex* species (*C. binervis, C. demissa, C. durieui and C. echinata* (Table A1, Figure A2) and *Rhynchospora alba* (Table A1, Figure A1). We also found rhizomes of *Carex* that we could not assign to particular species (Table A1, Figure A2).

Rhizomes of *E. angustifolium* differ from other Cyperaceae and Poaceae rhizomes, mainly in terms of the shape, size and disposition of root and leaf scars, as well as the frequent pigmentation of some epidermal cells (Table A1, Figure A1).

Achenes of Cyperaceae species can be identified by the characteristics shown in Table A1. It is remarkable that all studied species in this family had similar seeds (Figures A1, A2), while in other monocotyledon families, such as Juncaceae, there are different specific seed morphologies (Table A2, Figure A4).

With regard to dicotyledonous seeds, morphological differences among genera are evident in the Ericaceae although, within the genus *Erica*, the seeds of *E. mackaiana* are similar to those of *E. tetralix* (Table 2.1). Therefore, leaf remains are very useful in distinguishing between these two species (Table A3, Figure A5).

To summarise the diagnostic characteristics for taxa and facilitate their use for species identifications, we have developed dichotomous keys for rhizomes, leaves, and fruits/seeds (Boxes 1–3).

Among the taxa identified, *E. mackaiana* was the most frequent species for all sampled bogs, followed by *Molinia caerulea* and *Eriophorum angustifolium* (Table 3).

Box 1. Dichotomous key for rhizomes.
1. Rhizomes slender, segmented, with notorious scars ……..……………………………………………..…………....2
1. Rhizomes not segmented, with fascicles of leaf basis (Figure A3k).…………………………….………***Agrostis curtisii***
2. Rhizomes with verticillate thread-like fibers (Figure A2w)……………………………......………..….***Carex*** spp.
2. Rhizomes without verticillate thread-like fibers…………………………………………………………..….……3
3. Epidermal cells with straight walls, sometimes strongly pigmented (Figure A1b)…..…***Eriophorum angustifolium***
3. Epidermal cells no pigmented, with undulate walls (Figure A3b)……….……….………………..***Molinia caerulea***

Box 2. Dichotomous key for leaves.
1. Ericoid type, with revolute margins (Figure A5)……..………………..........................……...……......…..….2
1. Other shape ..………………………......…………………………………………….……………….……....……4
2. Leaves with petiole ……………………………..………………………………………………………..........….3
2. Sessile leaves (Figure A5l)…………..……………..………………………..…...……...………......***Calluna vulgaris***
3. Epidermal cells with straight anticlinal walls (Figure6h)……..…………………………….......….…***Erica tetralix***
4. Epidermal cells with anticlinal walls slightly sinuous (Figure6c).……………..……………......…***Erica mackaiana***
4. Leave s with reticulate or palmate venation...5
4. Leaves with parallel venation...6
5. Leaves reticulate. Margins serrulate, glabrous or with glandular hairs (Figure A6b,c)….……....***Vaccinium myrtillus***
5. Leaves (leaflets) with palmate venation, dentate and sparsely hairy (Figure A7b,c)………...….......***Potentilla erecta***
6. Epidermal cells similar in shape and size, sometimes pigmented (Figure A1e)..................***Eriophorum angustifolium***
6. Long rectangular epidermal cells intermixed with very short cells and silica bodies (Figure A3d).....***Molinia caerulea***

Box 3. Dichotomous key for fruits and seeds.

1. Fruits or seeds very small (< 1mm long) … 2
1. Fruits or seeds small (> 1mm long) … 8
2. Seeds with tuberculate ornamentation (Figure A6c,l) … 3
2. Seeds or fruits with other ornamentation … 4
3. Seeds ovate. Outer testa cells with straight walls (Figure A6n) … ***Drosera intermedia***
3. Seeds globose. Outer testa cells with sinuous walls (Figure A6g) … ***Daboecia cantabrica***
4. Seeds with a pore. Testa epidermal cells polyhedral with thick straight walls (Figure A5r) … ***Calluna vulgaris***
4. Seeds without the above characteristics … 5
5. Seeds elliptic to globose. Epidermal cells with sinuous walls (Figure A5d,i) … ***Erica mackaiana/Erica tetralix***
5. Seeds usually fusiform with mamillate apex. Epidermal cells with straight walls (Figures A4a, A6i) … 6
6. Seeds brownish. Epidermal cells over 50µm wide (Figure A6j) … ***Drosera rotundifolia***
6. Seeds yellowish. Epidermal cells generally less than 50µm wide … 7
7. Seeds elliptic, 0.4–0.6 × 0.2–0.35mm (Figure A4a) … ***Juncus bulbosus***
7. Seeds obliquely ovoid to kidney-shaped, 0.7 × 0.4mm (Figure A4d) … ***Juncus squarrosus***
8. Seeds at least 5 times as long as wide … 9
8. Seeds or fruits less than 3 times as long as wide … 10
9. Epidermal cells elongated to polyhedral, about 5 times as long as wide (Figure A6h) … ***Drosera rotundifolia***
9. Epiderma l cells narrowly elongated, about 10 times as long as wide (Figure A4i) … ***Narthecium ossifragum***
10. Caryopsis with longitudinal hilum (Figure A3i) … ***Molinia caerulea***
10. Seeds or fruits without longitudinal hilum … 11
11. Fruits with remains of two translucent wings and the two styles in the apex Figure A7g,h) … ***Betula alba***
11. Seeds or fruits without wings … 12
12. Seeds longitudinally elliptic … 13
12. Fruits ovate, obovate or transversely elliptic … 14
13. Seeds with rounded apex (Figure A7d) … ***Caltha palustris***
13. Seeds with mamillate apex (Figure A4f) … ***Luzula multiflora***
14. Fruit capsule type, with many seeds inside (Figure A5p) … ***Calluna vulgaris***
14. Fruit achene type, with 1 seed inside … 15
15. Achenes ovoid, weakly carinate and surface rugose-ribbed (Figure A7a) … ***Potentilla erecta***
15. Achenes not carinate and surface not rugose-ribbed … 16
16. Achenes biconvex … 17
16. Achenes trigonous or subtrigonous … 18
17. Achenes ovate to trullate. Outer epidermal cells polyhedral with several silica bodies (Figure A2g,h) … ***Carex echinata***
17. Achenes obovate with remains of bristles at the base. Outer epidermal cells rectangular with sinuous walls (Figure A1m,o) … ***Rhynchospora alba***
18. Outer epidermal cells rectangular with sinuous walls and several silica bodies (Figure A1i) … ***Eriophorum angustifolium***
18. Outer epidermal cells polyhedral with straight walls and one central silica body … 19
19. Achenes 2 to 3 mm long (Figure A2l) … ***Carex binervis***
19. Achenes 1 to 2 mm long … 20
20. Achenes 1 to 1.5 mm long (Figure A2r) … ***Carex demissa***
20. Achenes 1.9 to 2 mm long (Figure A2a) … ***Carex durieui***

DISCUSSION

For the mires included in this study, there is a strong concordance between present flora and palaeoflora. The most important past and present families in the Xistral bogs are Ericaceae (*E. mackaiana*), Poaceae (*M. caerulea*) and Cyperaceae (*E. angustifolium* and *Carex* spp.) (Table 3). At Zalama Bog *E. tetralix* replaces *E. mackaiana* due to the particular distributions of these vicariant species (Webb 1955, Nelson & Fraga 1983), *M. caerulea* and *E. angustifolium* are again frequent, and the scarcity of *Carex* macroremains is noteworthy.

When examining the remains of monocotyledons, the colour of the achenes allows a first differentiation between *Carex* and *Eriophorum* because *Carex* achenes are generally yellowish or brown while *Eriophorum* achenes are blackish. Our fossil *Eriophorum* achenes are very similar to modern *E. angustifolium* material from other Spanish localities, but differ from those described by Tucker & Miller (1990) in shape, style persistence and anticlinal walls of the epidermal cells. According to these authors *E. angustifolium* achenes are obovoid to ellipsoid, with style base absent and epidermal cells with straight anticlinal walls; whereas our

Table 3. Relative frequencies (%) of the plant macrofossils identified for each sampled bog (CVM: Chao de Veiga Mol; BCG: Borralleiras de Cal Grande; PDC: Pena da Cadela; ZAL: Zalama) and for all sampled bogs (AVERAGE). In the last column, values for the most frequent species are shown in **bold** type.

TAXON	**Remains**	CVM	BCG	PDC	ZAL	AVERAGE
Eriophorum angustifolium Honck.	Fruits	23.5	44.8	6.5	31.8	**26.7**
	Rhizomes-Leaves	21.9	60.3	8.6	12.9	**25.9**
Rhynchospora alba (L.) Vahl	Fruits	2.1	-	-	-	0.5
Carex durieui Steud. ex Kunze	Fruits	4.2	-	8.6	-	3.2
Carex echinata Murray	Fruits	-	0.9	-	-	0.2
Carex binervis Sm.	Fruits	-	0.86	-	-	0.2
Carex demissa Hornem.	Fruits	-	-	1.1	-	0.3
Carex spp.	Rhizomes	64.2	36.2	48.4	1.52	**49.6**
Agrostis curtisii Kerguélen	Rhizomes-Leaves	-	-	5.4	2.3	1.9
Molinia caerulea (L.) Moench	Fruits	15.0	13.8	1.1	6.8	9.2
	Rhizomes-Leaves	39.0	45.7	77.4	53.0	**53.8**
Juncus squarrosus L.	Seeds	-	0.9	3.2	50.8	13.7
Juncus bulbosus L.	Seeds	21.9	12.9	28.0	-	15.7
Luzula multiflora (Retz.) Lej.	Seeds	-	-	1.1	-	0.3
Narthecium ossifragum (L.) Huds.	Seeds	10.2	-	17.2	1.5	9.6
Ericaceae	Wood	100.0	81.0	61.3	83.3	**81.4**
Calluna vulgaris (L.) Hull	Seeds-Fruits	48.1	1.7	2.2	36.4	**22.1**
	Leaves	12.3	6.9	1.1	37.1	14.3
Daboecia cantabrica (Huds.) K. Koch	Seeds	5.3	-	-	1.5	1.7
Erica tetralix L.	Seeds	-	-	-	28.8	7.2
	Leaves	-	-	-	12.9	3.2
Erica mackaiana Bab.	Seeds	98.9	82.8	54.8	-	**59.1**
	Leaves	93.6	50.0	39.8	-	**45.8**
Vaccinium myrtillus L.	Leaves-Stems	-	-	-	9.1	2.3
Betula alba L.	Fruits	10.2	-	-	-	2.5
Drosera rotundifolia L.	Seeds	21.9	14.7	2.2	3.0	10.4
Drosera intermedia Hayne	Seeds	1.6	-	-	-	0.4
Potentilla erecta (L.) Raeusch.	Fruits-Leaves	-	5.2	0.01	0.8	1.5
Caltha palustris L.	Seeds	-	8.6	2.2	-	2.7

fossilised achenes of *E. angustifolium*, like the modern ones in the reference collection, are usually obovate subtrigonous with the style base persistent and epidermal cells having undulate anticlinal walls. This is in agreement with Bojnanský & Fargasová (2007) and Villar (2008) for modern material. In the case of rhizomes and leaves, the presence of pigmented epidermal cells irregularly distributed in both rhizomes and leaves is a good diagnostic character for *E. angustifolium.* Other morphological and anatomical characters for the rhizomes of this species are in agreement with those previously described by Grosse-Brauckmann (1972).

Identification of *Carex* species on the basis of achene characters is difficult because the interspecific variability is very low. Therefore, it is necessary to take into account a combination of the most useful diagnostic characters (Table A1), as observed by Miller (1997) and Jiménez-Mejías & Martinetto (2013).

Carex durieui is not recorded in bog palaeofloras. At present this species is endemic to the north-west Iberian Peninsula, where it is common in bogs and wet meadows on acid substrates. Descriptions (Table A1) and illustrations (Figure A2 a–c) of fossilised achenes of this species are published for the first time in this article. Many of the rhizomes and leaves that, due to their state of decomposition, we could identify only as *Carex* spp. (Table 3) may belong to *C. durieui*.

Rhynchospora alba was recorded only in the CVM raised bog, where several achenes with perianth bristles were sufficiently well preserved to be identified. Velichkevich & Zastawniak (2006) found fruits of this species in a few central and eastern European palaeofloras, but these were shorter (1.4–1.6 mm) than the CVM ones and lacked bristles. The achenes we recorded are in concordance with the description of Grosse-Brauckmann (1972) and with modern fruits from central and eastern Europe (Bojnanský & Fargasová 2007). Moreover, they are similar to fruits illustrated in Figure 3F of Mauquoy & van Geel (2007).

Among the macroremains of grasses (Poaceae), *M. caerulea* is the dominant species in all of the studied bogs (Table 3). Mostly rhizomes and leaves, but also caryopses, have been identified. It is remarkable that the overall frequency of caryopses in our peat samples was about 9 %, since Grosse-Brauckmann (1972) pointed out that *M. caerulea* caryopses are recorded from central European bogs only in exceptional cases. The macroscopic and microscopic (epidermis) stem morphologies of this species are consistent with the descriptions of Grosse-Brauckmann (1972) and Mauquoy & van Geel (2007). The leaf epidermis has pairs of short cells (one broad and one narrow) intermixed with long cells, which is characteristic for this species. The other grass species, *A. curtisii*, is recorded in peat deposits for the first time here, so the description and illustrations constitute new data for bog palaeofloras.

Fossil *Juncus* seeds are present in all four bogs. *J. bulbosus* seeds at various stages of decomposition are common in the Xistral bogs but absent from Zalama, where *J. squarrosus* seeds were observed in more than 50 % of the peat samples (Table 3). The latter species is scarcer in the Xistral bogs. The distinctive characters for seeds of these species (Table A2) are consistent with those of modern seeds from Europe (Romero Zarco 2010, Bojnanský & Fargasová 2007). Fossilised seeds of both *Juncus* species were previously included in the British palaeoflora (Godwin 1975). Petr (2013) also identified fossil seeds of *J. bulbosus* from central European mires.

Most of the dicotyledonous remains belong to the Ericaceae. Morphological characters like size, shape and ornamentation of *Erica* and *Calluna* seeds from the peat deposits are in agreement with bibliographic data for present-day seeds (Huckerby *et al*. 1972, Fraga 1983, Fraga 1984, Fagundez & Izco 2004 a,b). However, when decomposition processes have destroyed the ornamental elements of the outer seed coat (testa), it is generally very difficult to differentiate between closely related species - as for several *E. tetralix* seeds from Zalama and others belonging to *E. mackaiana* from Xistral. Fortunately, the presence of fossilised leaves and seeds in the same samples has allowed us to overcome these impediments to species identification. For this Ericaceae species, descriptions and illustrations of fossilised vegetative and reproductive structures obtained from peat deposits are also available in several publications (Huckerby *et al*. 1972, Grosse-Brauckmann 1974, Grosse-Brauckmann & Streitz 1992, Mauquoy & van Geel 2007).

Although remains of the other dicotyledonous species identified were much less frequent (Table 3), most of them have been recorded in other European bog palaeofloras (Grosse-Brauckmann 1974, Mauquoy & van Geel 2007). In the case of *Drosera rotundifolia*, the loose-fitting testa of the seeds may remain as the outer envelope or become detached, reducing the external envelope to tegmen. Therefore, in terms of size and shape, the seeds of *D. rotundifolia* exhibit two different external appearances (Figure A6 a–b).

In some cases, changes in the forms of seeds during the degradation processes cause the seeds of different species to develop similar appearances. This is the case for *Narthecium ossifragum*, whose seeds are always observed without the characteristic appendixes, so they look very similar to seeds of *D. rotundifolia* that have retained the testa. Other seeds which may be confused with one another, if they are degraded but have retained elements of their external relief, are those of *Drosera intermedia* and *Daboecia cantabrica*; since both of these species have testa with baculiform ornamentation.

In this article we have paid particular attention to methods and criteria that facilitate the identification of plant macrofossils occurring in peat deposits, because the accurate identification of these remains is vital to achieving accurate palaeoenvironmental reconstructions. On the basis of our results we can conclude that the palaeoflora of bogs in northern Spain present species in common with ombrotrophic mires in other parts of Europe, but also include particular species that make these bogs different from similar peatlands located elsewhere.

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Appendix: Diagnostic characteristics for plant macrofossils found in bog peat in northern Spain.

Table A1. Monocotyledons: Cyperaceae. Nomenclature of achene morphology follows Berggren (1969).

Species	Structure	Shape	Roots and leaves scars	Rhizome epidermal cells	Epidermal cells of the sheath leaves and roots
Eriophorum angustifolium Honck.	Rhizome	Fragments of elongated axis or narrow circular sections, both with roots and leaf remains or scars of them.	Roots: Big circles or projections of irregular distribution. Leaves: Rows of small circles, distributed along the contour of the rhizome (Figure A1a).	Polyhedral, sometimes with varying degrees of pigmentation (Figure A1b).	Leaves: Basal cells quadrangular to rectangular, with straight walls, sometimes pigmented. Upper cells rectangular, with anticlinal walls, weakly undulate, sometimes pigmented (Figure A1c, e). Roots: rectangular, with straight walls, sometimes pigmented (Figure A1g).

Species	Structure	Size (mm)	Shape	Outer pericarp epidermal cells	Pericarp
Eriophorum angustifolium Honck.	Achene	2-3 × 1-1.5	Weakly obovate, subtrigonous, dark brown. Flat ventral face and dorsal convex faces. Apex with the style base persistent. Basis gradually narrowed. Often the pericarp was found open and without the seed inside (Figure A1h).	Rectangular with several silica bodies; anticlinal walls undulate (Figure A1i).	Beneath the epidermis an outer layer of elongate cells oriented longitudinally and one inner layer of elongate cells orientated transversely (Figure A1j).

Species	Structure	Size (mm)	Shape	Apex	Base	Outer pericarp epidermal cells	Inner pericarp cells
Rhynchospora alba (L.) Vahl.	Achene	2-2.5 × 1–1.3	Broadly obovate, biconvex. Surface lustrous, brown yellowish (Figure A1m).	Prolonged, acuminate or mucronate (Figure A1m).	Gradually narrowed with remains of perianth bristles retrorsely barbellate (Figure A1m, p).	Rectangular with sinuous anticlinal walls (Figure A1o).	Longitudinally elongated.

Species	Structure	Shape	Roots and leaves scars	Rhizome epidermal cells
Carex spp.	Rhizome	Fragments of elongated axis with verticillate thread-like fibres and root scars (Figure A2w).	Roots: big circles or projections of irregular distribution. Leaves: rows of fibres that correspond to the leaf nerves, distributed by almost the contour of the rhizome (Figure A2w).	Polyhedral, with straight walls (Figure A2x)

Species	Structure	Size (mm)	Shape	Apex	Base	Outer pericarp epidermal cells
Carex durieui	Achene	1.9–2 × 1–1.3	Trigonous to bicovex, obovate, brown (Figure A2a).	Rounded to flat under the stylopodium (Figure A2a).	Gradually narrowed (Figure A2a).	Polyhedral (30–40 × 25–30 µm) with one central silica body (Figure A2b).
Carex echinata	Achene	1.5–2 × 0.8–1.3	Plano-convex, ovate to trullate. yellowish (Figure A2g).	Obtuse under the stylopodium (Figure A2g).	Sharply narrowed (Figure A2g).	Polyhedral (25–35 × 20–25 µm) with several silica bodies (Figure A2h).
Carex binervis	Achene	2.2–3.2 × 1–1.4	Trigonous, obovate, brown (Figure A2l).	Flat under the stylopodium (Figure A2l).	Gradually narrowed (Figure A2l).	Polyhedral (50–60 × 30–45µm) with one central silica body (Figure A2n).
Carex *demissa*	Achene	1.1–1.5 × 0.9–1.2	Trigonous, broadly obovate, brown (Figure A2r).	Rounded to flat under the stylopodium (Figure A2r).	Gradually narrowed (Figure A2r).	Polyhedral (30–40 × 25–30 µm) with one central silica body (Figure A2s).

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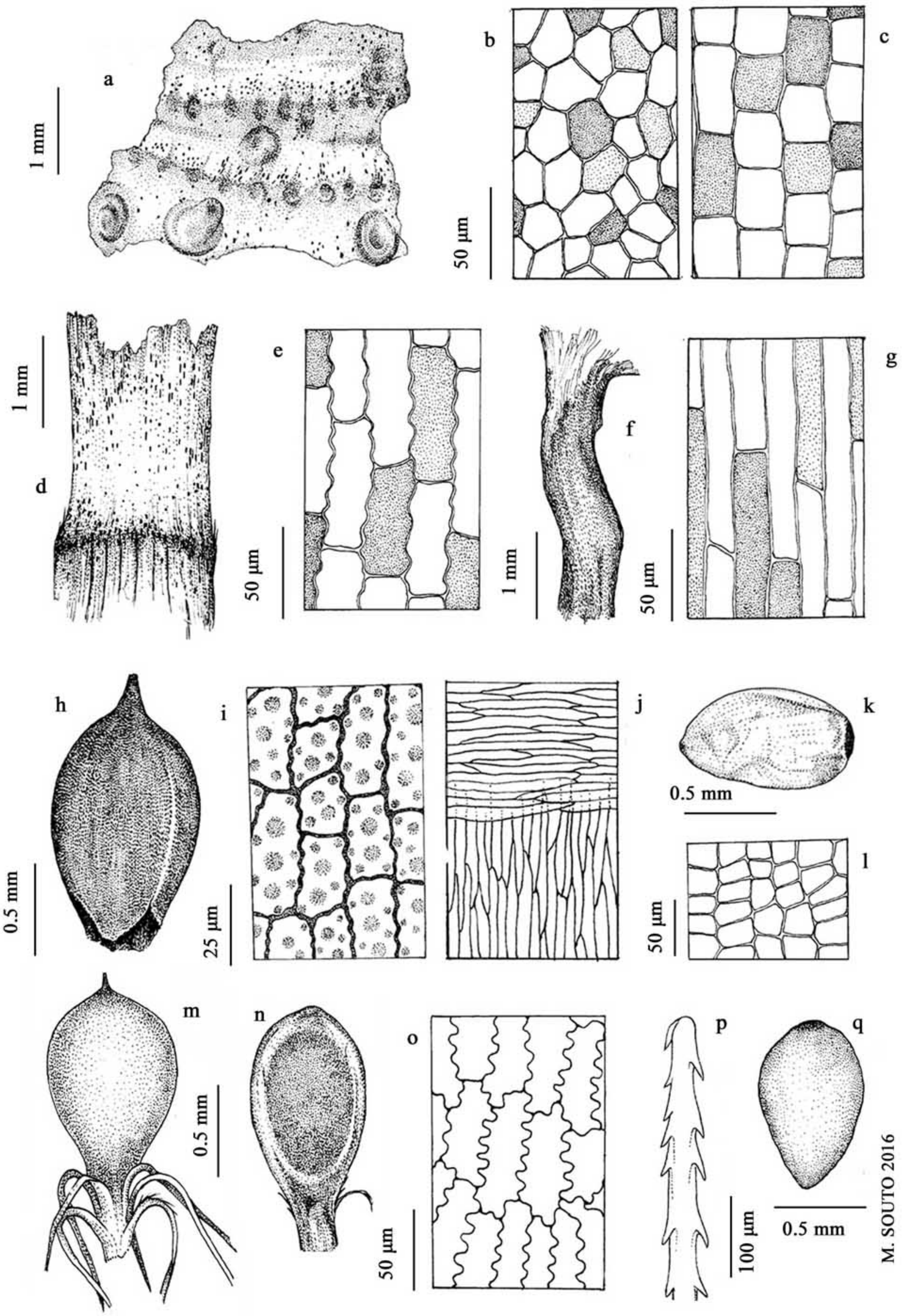

Figure A1. *Eriophorum angustifolium*: a) rhizome fragment with scars of roots and leaves; b) rhizome epidermal cells; c) epidermal cells of leaf base; d) leaf sheath; e) epidermal cells of leaf blade; f) root fragment; g) root epidermal cells; h) achene with persistent style base; i) outer achene epidermal cells; j) pericarp with two layers of elongated cells arranged perpendicularly; k) seed; l) seed testa epidermal cells. *Rhynchospora alba*: m) achene with perianth bristles; n) degraded achene with very thin pericarp surrounding the seed; o) outer achene epidermal cells; p) retrorsely barbed perianth bristle; q) seed.

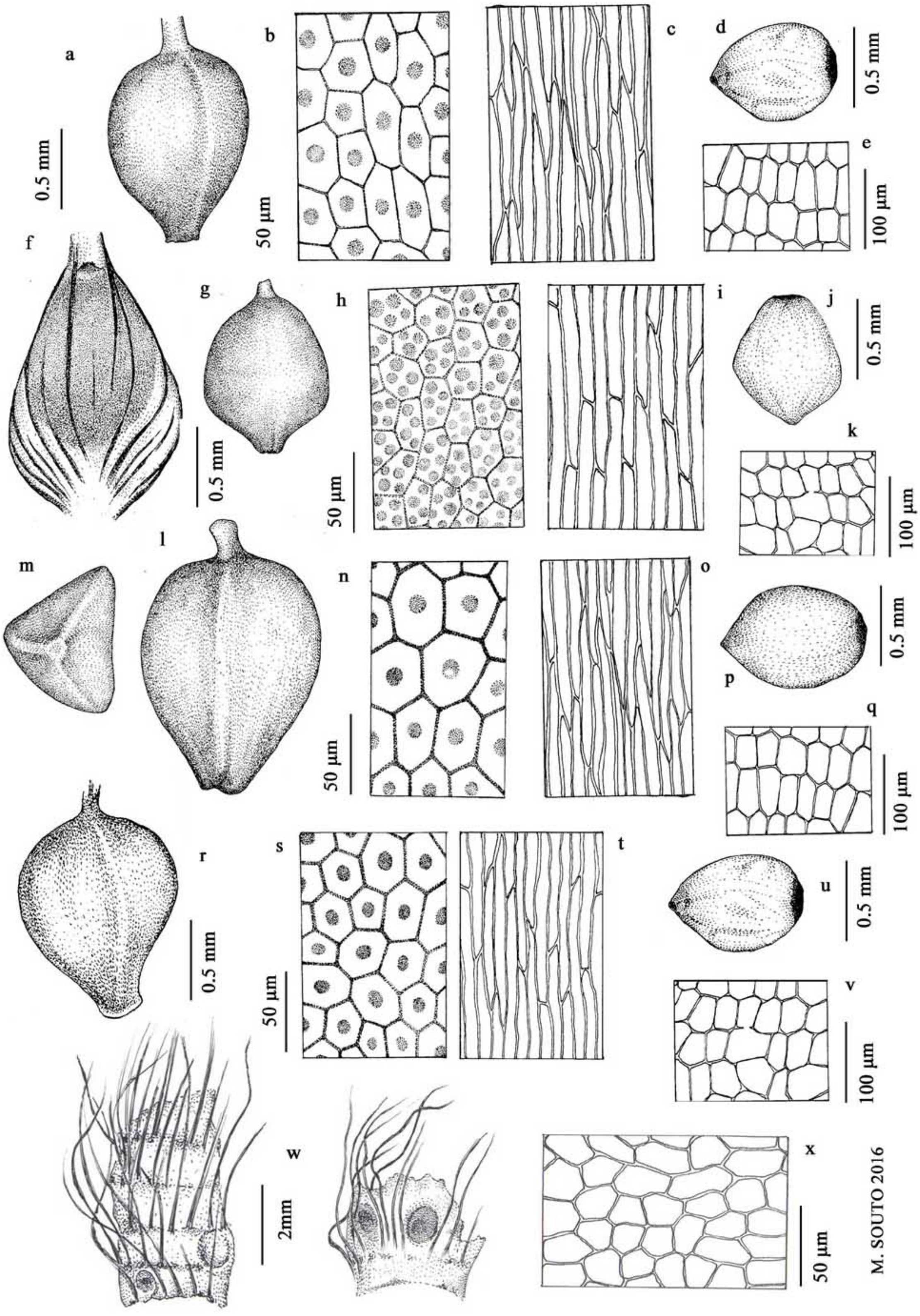

Figure A2. *Carex durieui*: a) achene; b) outer achene epidermal cells; c) inner achene epidermal cells; d) seed; e) seed testa epidermal cells. *Carex echinata*: f) utricule; g) achene; h) outer achene epidermal cells; i) inner achene epidermal cells; j) seed; k) seed testa epidermal cells. *Carex binervis*: l) achene lateral view; m) achene apical view; n) outer achene epidermal cells; o) inner achene epidermal cells; p) seed; q) seed testa epidermal cells. *Carex demissa*: r) achene; s) outer achene epidermal cells; t) inner achene epidermal cells; u) seed; v) seed testa epidermal cells. *Carex* spp.: w) rhizome fragments with root scars and remains of leaves; x) rhizome epidermal cells.

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Table A2. Monocotyledons: Poaceae, Nartheciaceae and Juncaceae. Nomenclature of Poaceae follows Ellis (1979).

Family	Species	Structure	Shape	Roots and leaves scars	Rhizome epidermal cells
Poaceae	*Molinia caerulea* (L.) Moench.	Rhizome	Fragments of elongated axis or narrow circular sections (diameter 2–5 mm). Roots and leaf remains or scars of both, as well as axillary buds, are common (Figure A3a).	Roots: circles or projections of irregular distribution (Figure A3a). Leaves: transversal rows of small circles that correspond to the leaf nerves, distributed along the contour of the rhizome (Figure A3a).	Rectangular to polyhedral with anticlinal walls undulate. Long and short cells are intermixed (Figure A3b).

Family	Species	Structure	Sheath epidermal cells	Blade epidermal cells	Stomatal complex
Poaceae	*Molinia caerulea* (L.) Moench.	Leaf	Long rectangular cells, with undulate anticlinal walls, intermixed with short cells (Figure A3c).	Long rectangular cells, with undulate anticlinal walls, intermixed with pairs of short cells (one broad and one narrow) and silica bodies *Oryza* type (Figure A3d).	Stomata dome-shaped, with rounded subsidiary cells (Figure A3h).

Family	Species	Structure	Size (mm)	Shape	Outer epidermal cells
Poaceae	*Molinia caerulea* (L.) Moench.	Caryopsis	2–2.5 × 0.8–1	Oblong or elliptical, with rafe in the abaxial face (Figure A3i).	Two layers of polymorphic cells, sub-rectangular to polyhedral, with thin walls (Figure A3j).

Family	Species	Structure	Shape	Epidermal cells of sheath leaves
Poaceae	*Agrostis curtisii* Kerguélen	Rhizome	Intravaginal sprouts developed into the sheath leaves, formed by fascicles of leaves in variable number, which are surrounded by remains of sheath leaves (Figure A3k).	The epidermis is very uniform, with rectangular to hexagonal cells of similar sizes and straight anticlinal walls. Some of them with fine hairs or prickles (Figure A3l, m, n).

Family	Species	Structure	Size (mm)	Shape	Epidermal cells of seed coat
Nartheciaceae	*Narthecium ossifragum* (L.) Huds.	Seed	1–2 × 0.2–0.8 (without the external testa appendages of modern material) (Figure A4i).	Narrowly elliptic to fusiform, crushed (Figure A4i).	Double layer of threadlike yellowish cells arranged more or less in parallel (Figure A4j).

Family	Species	Structure	Size (mm)	Shape	Outer epidermal cells	Inner testa cells
Juncaceae	*Juncus bulbosus*	Seed	0.4–0.6 × 0.2–0.35	Narrow elliptic, yellow orange. Hilum prominent and dark (Figure A4a).	Transparent, yellowish, oblong-polyhedral with thin anticlinal walls (Figure A4b).	Strongly pigmented, reddish, oblong-polyhedral (Figure A4c).
	Juncus squarrosus	Seed	0.7 × 0.4	Obliquely ovoid to kidney shaped, red brown. Testa reticulate (Figure A4d).	Yellowish, polyhedral.	Brownish pigmented, polyhedral (Figure A4e).
	Luzula multiflora	Seed	1.4–1.6 × 0.7–0.8	Broadly elliptic, mamillate. Basis with an elaiosome (Figure A4f, g).	Polyhedral with thick anticlinal walls (Figure A4h).	

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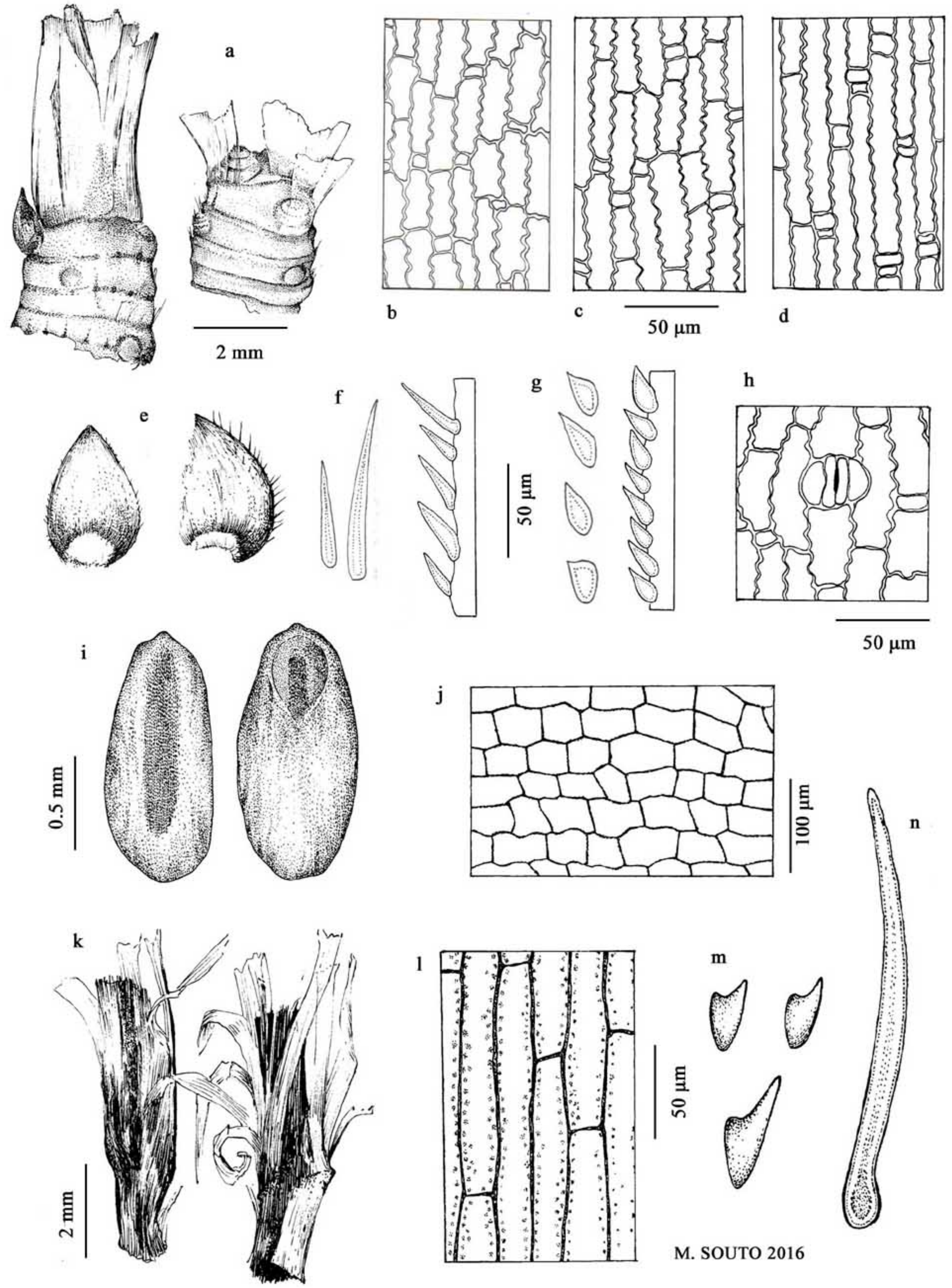

Figure A3. *Molinia caerulea*: a) rhizome fragment with axillary buds and leaf bases; b) rhizome epidermal cells; c) epidermal cells of leaf base; d) adaxial leaf epidermal cells intermixed with silica bodies; e) bud scales; f) bud scale hairs; g) leaf blade hairs; h) leaf blade stomatal complex; i) caryopsis; j) epidermal caryopsis cells. *Agrostis curtisii*: k) rhizome fragments; l) epidermal cells of leaf base; m) leaf prickles (lateral view); n) unicellular leaf hair.

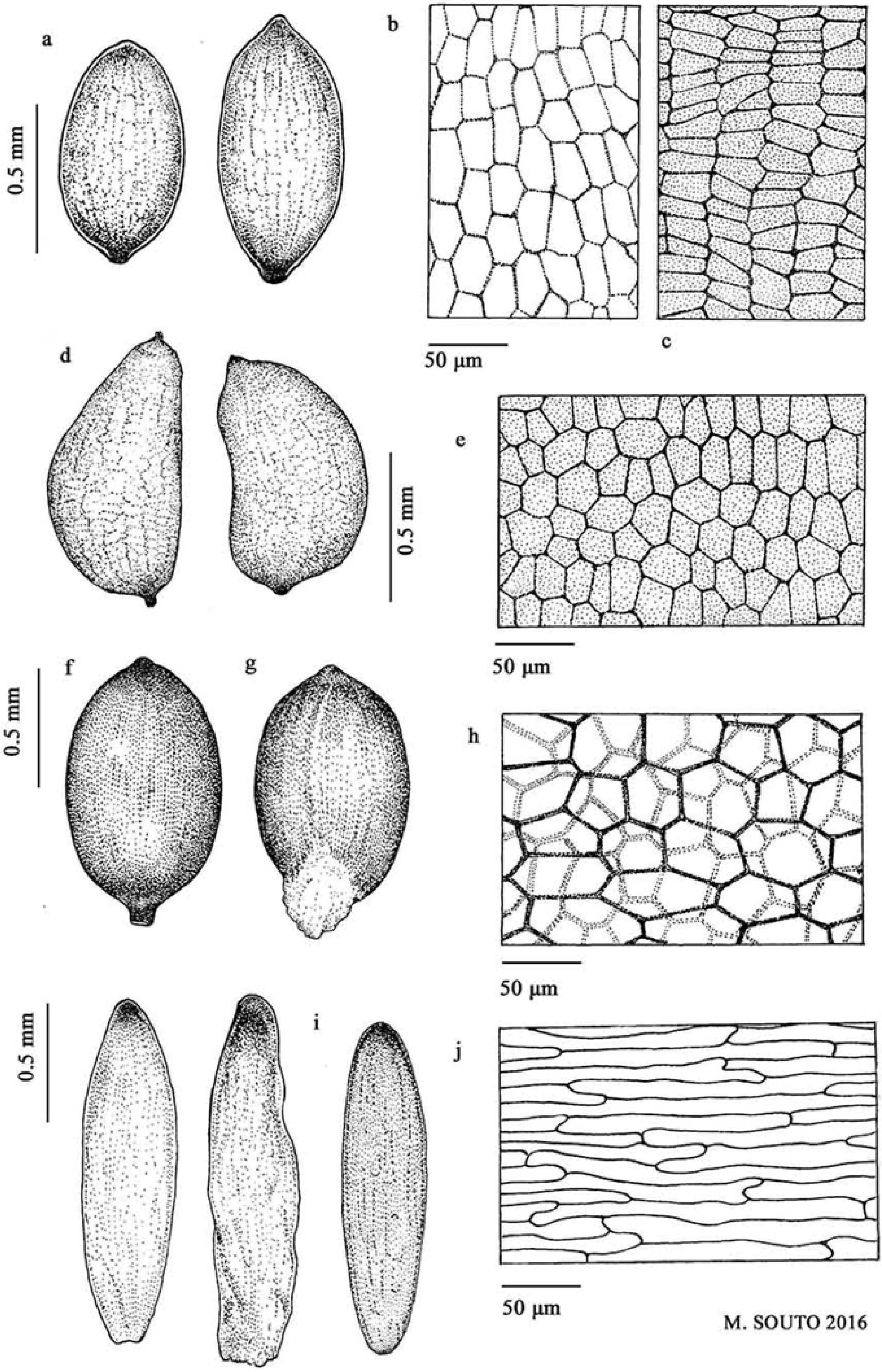

Figure A4. *Juncus bulbosus*: a) seeds; b) seed testa epidermal cells (outer integument); c) seed testa epidermal cells (inner integument). *Juncus squarrosus*: d) seeds; e) seed testa epidermal cells (inner integument). *Luzula multiflora*: f) seed; g) seed with remains of the elaiosome; f) seed testa epidermal cells. *Narthecium ossifragum*: i) seeds without testa (the outer cover is tegmen); j) tegmen epidermal cells.

Table A3. Dicotyledons: Ericaceae and Droseraceae.

Family	Structure(s)	Species	Seed size (mm)	Seed shape	Epidermal testa cells	Fruit
Ericaceae	Seeds, fruits	*Erica mackaiana*	0.3–0.4 × 0.2–0.3	Elliptic to globose. Testa reticulate (Figure A5d).	Jigsaw-puzzle-like with irregular contour, strongly pigmented (Figure A5e).	Capsule subglobose, glabrous, 1.8–2 mm.
		Erica tetralix	0.3–0.4 × 0.2–0.3	Elliptic to globose. Testa reticulate (Figure A5i).	Jigsaw-puzzle-like with irregular contour, strongly pigmented (Figure A5j).	
		Calluna vulgaris	0.5–0.7 × 0.3–0.5	Subglobose to elliptic. Hilium as a circular depression (Figure A5r).	Outer cells strongly pigmented, oblong-polyhedral with thick straight walls and scarce ornamentation (Figure A5s).	Capsule subglobose, 2–3 mm in diameter, style persistent. Remains of perianth are frequent (Figure A5p, q).
		Daboecia cantabrica	0.5–0.8 × 0.5–0.6	Globose. Hilium subterminal and not quite apparent (Figure A6e).	Isodiametric, with irregular contour. Outer periclinal walls with baculiform protuberances (Figure A6f, g).	
			Leaf size (mm)	Leaf shape	Epidermal cells	Stems, twigs
	Leaves, stems	*Erica mackaiana*	2.5–3 × 0.7–1	Oblong-lanceolate with glandular hairs in the margins. Underside broad and easily perceptible (Figure A5b).	Rectangular to polyhedral with irregular contour. Anticlinal walls slightly sinuous (Figure A5c).	With leaves or leaf scars verticillate, in whorls of four (Figure A5a).
		Erica tetralix	2.5–4 × 0.5	Oblong-lanceolate to linear with strongly bended margins. Glandular hairs. Underside very narrow reduced two lines parallel to the midrib (Figure A5g).	Polyhedral with straight anticlinal walls (Figure A5h).	With leaves or leaf scars verticillate, in whorls of four (Figure A5f).
		Calluna vulgaris	1–3 × 1	Sessile, sagittate, glabrous to pilose (Figure A5 l).	Polyhedral with irregular contour (Figure A5m).	With leaves or leaf scars decussate (Figure A5k).
		Vaccinium myrtillus	3–4 × 2	Broadly elliptic or ovate, with reticulate venation. Margin serrulate and glabrous or with remains of glandular hairs (Figure A6b, c).	Polyhedral with irregular contour (Figure A6d).	Twigs 4-angled, glabrous, with alternate buds or scars (Figure A6a).
			Size (mm)	Shape	Testa	Tegmen
Droseraceae	Seeds	*Drosera rotundifolia*	Testa: 1.5 × 0.35 Tegmen: 0.5 × 0.2–0.25	Narrowly elliptic, with two wings or terminal expansions caused by the testa, which is much larger than the tegmen (Figure A6h, i).	Elongated cells with thin walls and longitudinally arranged (Figure A6j).	Brown pigmented cells, rectangular to polyhedral and transversely arranged (Figure A6k).
		Drosera intermedia	0.6–0.75 × 0.45	Ovate with tuberculate ornamentation (Figure A6 l).	Outer periclinal cell walls with baculiform protuberances (Figure A6m, n).	Closely appressed to the testa and the endosperm. Cells hyaline, rectangular to polyhedral (Figure A6o).

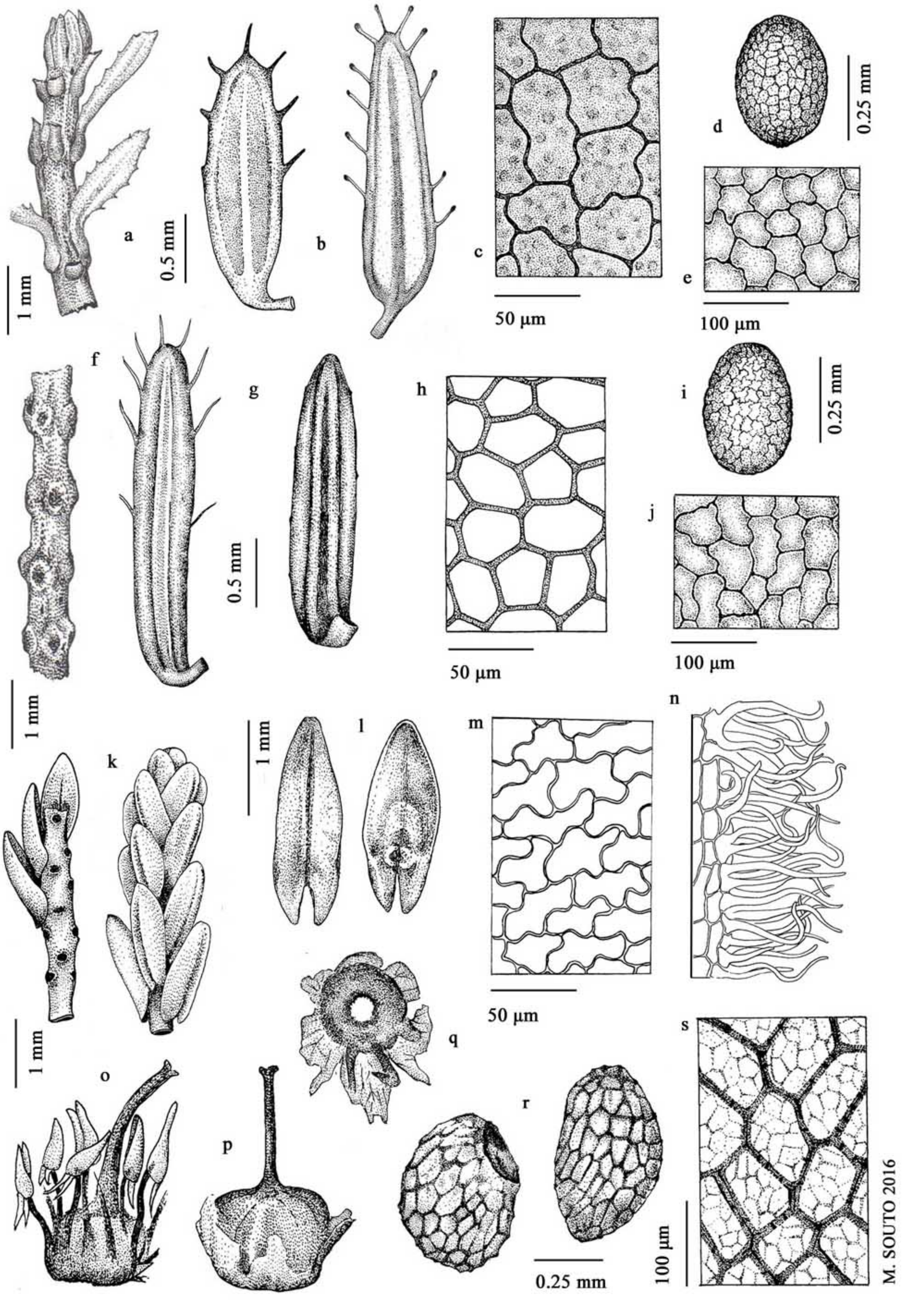

Figure A5. *Erica mackaiana*: a) fragment of twig with leaves; b) leaves; c) epidermal cells of adaxial leaf blade; d) seed; e) seed testa epidermal cells. *Erica tetralix*: f) twig fragment; g) leaves; h) epidermal cells of adaxial leaf blade; i) seed; j) seed testa epidermal cells. *Calluna vulgaris*: k) fragments of twigs with leaves; l) leaves; m) epidermal cells of adaxial leaf blade; n) trichomes of the abaxial leaf blade; o) flower remains; p) capsule with perianth remains; q) perianth remains; s) seed testa cells.

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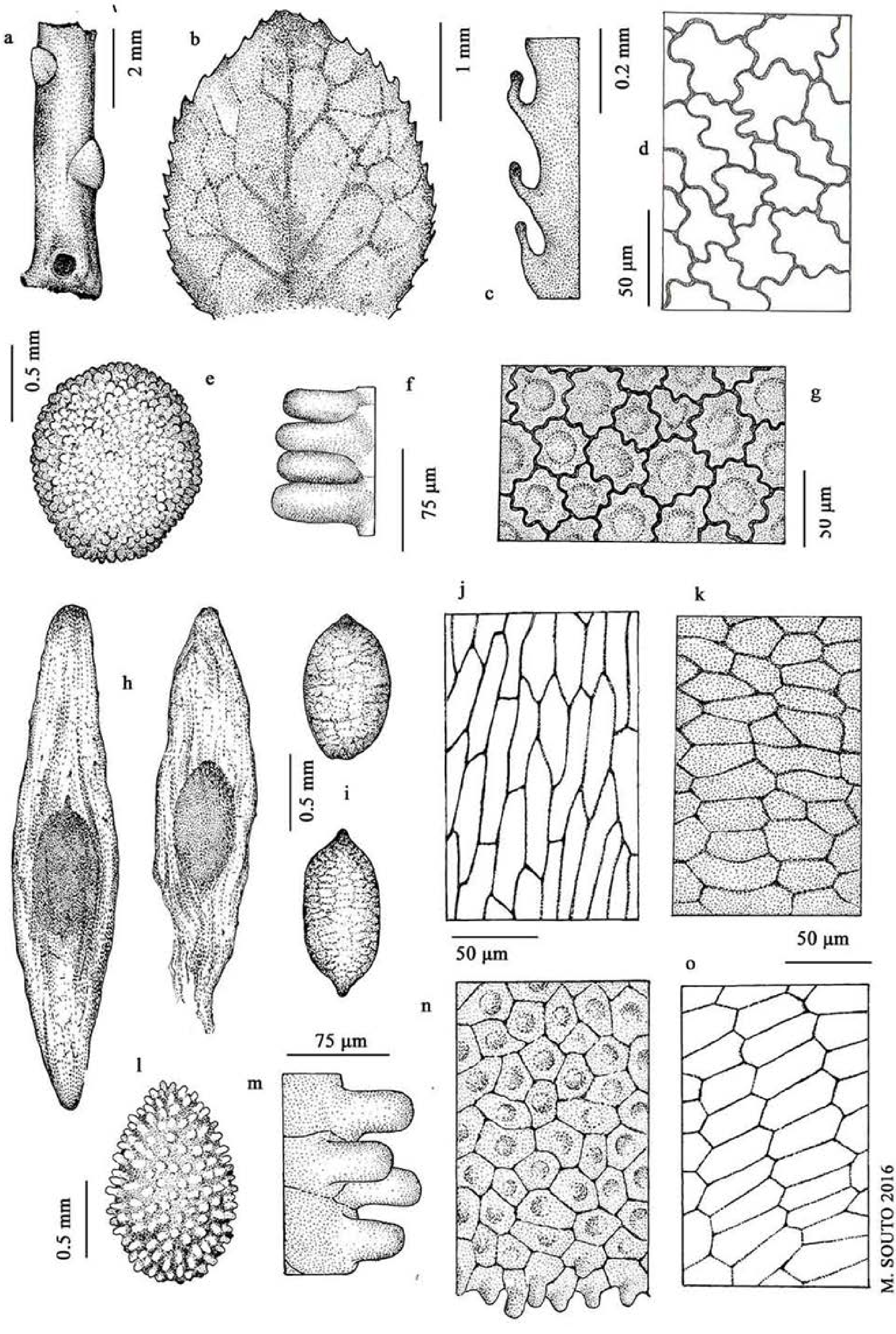

Figure A6. *Vaccinium myrtillus*: a) fragment of twig with alternate buds; b) leaf blade; c) serrulate leaf margin with remains of glandular hairs; d) epidermal cells of adaxial leaf blade. *Daboecia cantábrica*: e) seed; f) testa fragment with baculiform ornamentation; g) seed testa epidermal cells. *Drosera rotundifolia*: h) seeds with testa; i) seeds without testa (the outer cover is tegmen); j) testa epidermal cells; k) tegmen epidermal cells. *Drosera intermedia*: l) seed; m) testa fragment with baculiform ornamentation; n) testa epidermal cells; o) tegmen epidermal cells.

Table A4. Dicotyledons: other families.

Family	Species	Achene	Achene outer epidermal cells	Leaves
Rosaceae	*Potentilla erecta*	1.5–2 × 1.2–1 mm, ovoid, surface rugose-ribbed (Figure A7a).	Polyhedral, small and isodiametric.	Ternate, digitate, leaflets obovate to lanceolate, palmate venation, toothed margins, sparsely hairy (Figure A7b, c).

		Seed size (mm)	Seed shape	Seed, outer epidermal cells
Ranunculaceae	*Caltha palustris*	2 × 0.8–1	Oblong, apex rounded. Lustrous, dark brown to black (Figure A7d).	Polyhedral, reticulate or rugulose (Figure A7e).

		Samara size (mm)	Samara shape
Betulaceae	*Betula alba*	2.5 × 1.2	Elliptic compressed; with two translucent wings and remains of the two styles in the apex. Often they show the embryos and lose their wings (Figure A7g, h).

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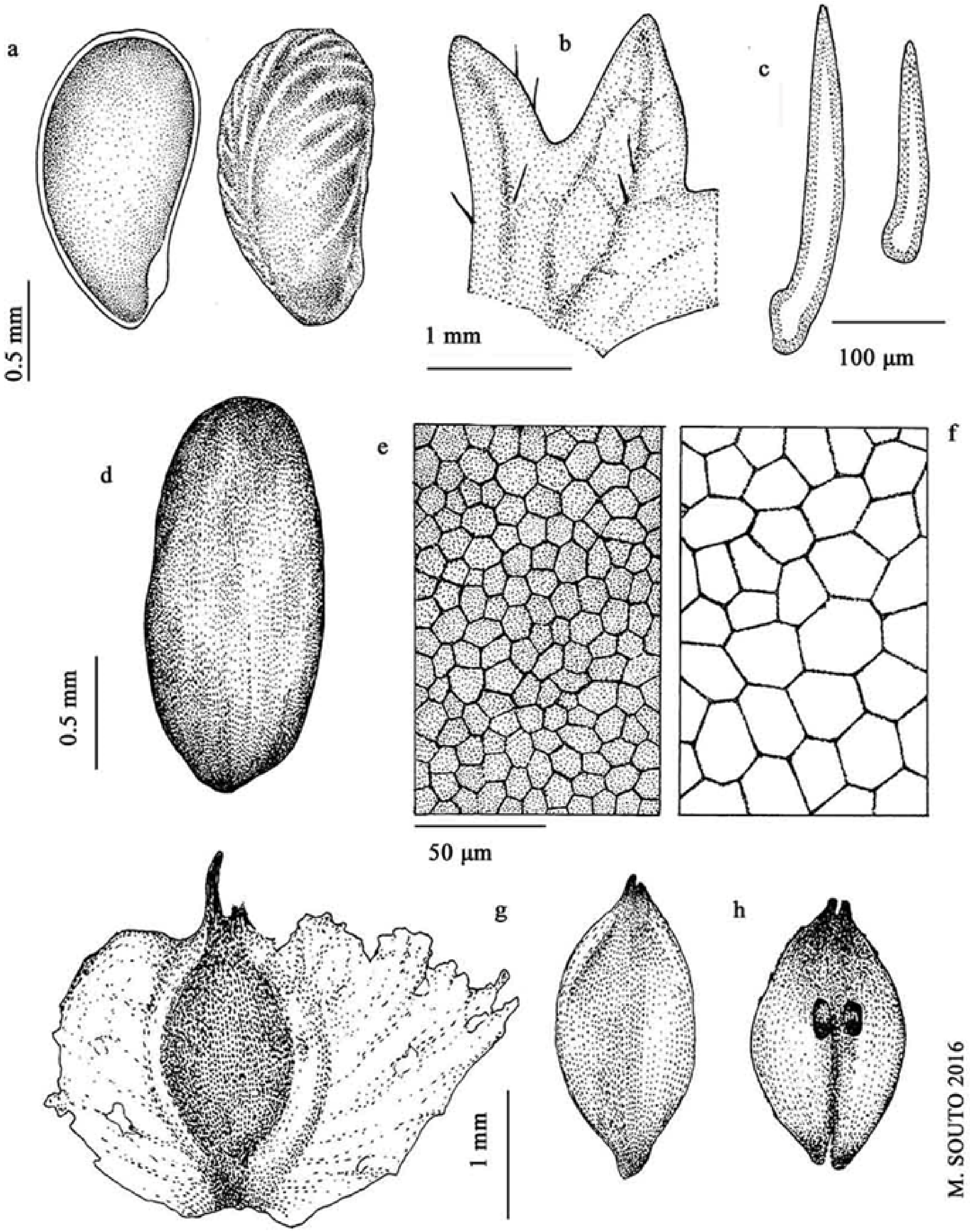

Figure A7. *Potentilla erecta*: a) achenes; b) leaflet fragment; c) leaflet hairs. *Caltha palustris*: d) seed; e) outer testa cells; f) inner testa cells. *Betula alba*: g) fruit with wings (samara); h) fruits which have lost their wings.

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