Characterisation of Holocene plant macrofossils from North Spanish ombrotrophic mires: bryophytes

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SUMMARY

The methods and criteria used for the identification of bryophytes from the peat deposits of four ombrotrophic mires in northern Spain are presented. Two liverworts and fifteen moss taxa were recorded. Twelve were identified to species level, two to genus level (*Polytrichum sp*., *Campylopus sp*.) and another to section level (*Sphagnum* sect. *Acutifolia*). All taxa were identified from their vegetative remains, mainly leaves. Only sporangia of *Sphagnum* species were recorded. Descriptions of the most relevant characters for taxa identifications are shown, accompanied by illustrations that facilitate their interpretation. A dichotomous identification key is also provided.

KEY WORDS: bogs, liverworts, mosses, peat, plant macroremains

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INTRODUCTION

Bryophyte remains frequently constitute an important part of the identifiable peat components which can provide detailed information on the local peat forming vegetation, mainly in conjunction with other plant macrofossils. Bryophytes are more specific indicators of environmental changes along peat cores than vascular plants, because their lack of deep rooting systems means that all sub-fossil remains from the same plant are usually located at the same depth.

Compared to vascular plants, the decomposition rates of mosses are relatively low, most probably due to the existence of recalcitrant cell wall components and secondary metabolites acting as antiherbivore/ compounds. According to Glime (2006), water (low levels of oxygen) seems to be the primary abiotic factor affecting decomposition rate, together with other factors such as pH or temperature and biotic factors such as cell constituents, bryophyte species and available microorganisms. Bryophyte decomposition rates in peat can vary widely (Glime 2006). While Clymo (1965) considered that microorganisms are the chief agents in *Sphagnum* decomposition, Frankland (1974) stated that the acidic conditions in most *Sphagnum* habitats hamper bacterial growth and Dickinson & Maggs (1974) observed that fungi were apparently active, especially in the superficial layers of peat, in the decomposition of the *Sphagnum* leaves. Most of these and other publications on decomposition of peat mosses have been the result of field experimental studies. In general there is a lack of comprehensive information about the different states of decomposition observed in the remains of moss species identified in many palaeobryoflora studies, and this should be corrected in order to facilitate future identifications of sub-fossil bryophytes.

Compared to mosses, the remains of liverworts are much rarer in peat samples due to selective preservation, which causes them to be under-representated in fossil assemblages (Janssens 1983). Few liverwort species have been recorded as macrofossils in peat deposits (Klinger 1968, Grosse-Brauckmann 1974, van Geel 1978, Miller 1984).

Local palaeoflora reconstructions have been based on subfossil moss studies because bryophyte remains are usually preserved in the place where they lived and subsequently died (Dickson 1973 and references therein, Birks 1982). Dickson (1986) and Janssens (1988, 1990) reviewed the literature on palaeoenvironmental reconstructions with fossil bryophytes. Bryophyte macrofossil data have been used to provide water table depth and pH reconstructions (Gorham & Janssens 1992, Mitchell *et al*. 2013). The former forms the basis for palaeoclimate reconstructions using plant macrofossils from rain-fed peat bogs (Rehell & Virtanen 2015). To date, knowledge of bryophyte macrofossils in Spanish peatlands is very scarce (Castro *et al*. 2015).

It is evident that any palaeoecological study requires the fossils to be identified to the lowest possible taxonomic level. According to Birks (1982) "bryophyte remains can be identified in much the same way as modern bryophytes. Careful comparison with accurately determined material, vouched for by herbarium specimens, is essential". Very often, subfossil bryophyte identifications are difficult due to selective decomposition, but there are only few references in the literature to the difficulties encountered by researchers in achieving accurate identifications at genus or species levels. Besides, detailed descriptions and pictures of bryophyte macrofossils are very scarce (Grosse-Brauckman 1974, Janssens 1990, Michaelis 2001, Mauquoy & van Geel 2007). So, in the same way as in a previous article on vascular plant macrofossils (Souto *et al.* 2016), the main objective of this article is to present the moss macrofossils preserved in four peatlands in northern Spain, with special emphasis on the morphological characters that allow accurate identifications to genus and species levels. The two articles together provide a detailed picture of the local palaeoflora of ombrotrophic bogs in northern Spain. The information presented here will be useful not only to increase knowledge about the European bog palaeoflora, but also to facilitate future studies on moss macrofossil identifications.

METHODS

Descriptions of the four studied bogs (Borralleiras de Cal Grande, Chao de Veiga Mol, Pena da Cadela and Zalama), as well as the methods used for peat sampling and extraction of macrofossils, are presented by Souto *et al*. (2016).

Bryophyte macrofossils were examined using an Olympus SZ30 binocular microscope and a high-power light microscope (×400). DPX and Hoyer's solution (Anderson 1954) were used to prepare the microscope slides as permanent wet mounts. An Olympus SC20 camera and a *camera lucida*, both attached to the microscope, were utilised to obtain photographs and drawings. Often, especially when the remains were single *Sphagnum* leaves, cross sections were made to enable careful study of the form and disposition of the leaf cells. The exposure of green cells on the dorsal (convex) and ventral (concave) surfaces of *Sphagnum* leaves can be also observed by constantly changing the microscope focus but, for species identifications, this method is less accurate than the analysis of cross sections.

Bryophyte remains were identified to the lowest possible taxonomic level with the aid of a reference collection, which comprised herbarium specimens and microscope slides of the species which constitute the present-day vegetation of the study sites, as well as additional species encountered on other Spanish and European bogs (see Souto *et al.* 2016 for more detailed information). Keys, descriptions and pictures from bibliographic sources were also consulted (Grosse-Brauckmann 1974, Daniels & Eddy 1990, Paton 1999, Michaelis 2001, Muller *et al.* 2002, Brugués *et al.* 2004, Smith 2004, Casas *et al*. 2006, Mauquoy & van Geel 2007).

Once the macrofossils had been identified they were preserved in 70 % ethanol at 4 °C, in hermetically sealed bottles. The bottles were then arranged according the procedure described by Souto *et al.* (2016) and stored in the Natural History Museum of the University of Santiago de Compostela.

RESULTS

Seventeen macrofossil taxa were recorded. These were two liverwort and twelve moss species, together with three other moss taxa identified to section or genus level (*Sphagnum* sect. *Acutifolia*, *Campylopus* sp. and *Polytrichum* sp.). Single leaves and stems were very common, while large fragments of stems with leaves ($\geq$5mm) were scarce. The distinctive characters are shown in and Figures A1–4 and Tables A1–3 (Appendix).

In weakly decomposed peat the mosses were usually well preserved, facilitating the study of characters for their identification such as shape, size and arrangement of the leaf cells, including those of the central rib. Under more intensive decomposition conditions, most of the remains were only stems (sometimes with leaf scars) or leaf fragments. Under the latter conditions the macrofossils were usually identifiable to genus level only (i.e. *Campylopus* sp., *Polytrichum* sp.), because the diagnostic characters necessary for specific identifications were lacking in highly degraded macrofossils.

For many *Sphagnum* species, extensive fragmentation precluded specific identifications. Thus, *Sphagnum* leaves were often identified to section level only, particularly those belonging to section *Acutifolia*. Likewise, capsules and fragments of stems and branches belonging to the genus *Sphagnum* could not be assigned with certainty to particular species because of the absence of specific diagnostic characters (Figures A2a, b, c, d, f). For this genus, leaf cross sections were usually necessary for accurate specific identifications.

To summarise the diagnostic characteristics and facilitate their use for species determinations, we provide a dichotomous key (Box 1).

Box 1. Dichotomous key for identification of the recorded bryophytes.

1. Leaves arranged strictly in two or three rows (two lateral and one in ventral side) ....2 Liverworts
1. Leaves not strictly arranged in rows..........3 Mosses
2. Leaves with acute apex, mid-leaf cells > 25 µm wide. (Figure A1g, h) ....*Calypogeia sphagnicola*
2. Leaves rounded, mid-leaf cells < 25 µm wide. (Figure A1b, d) ....*Odontoschisma sphagni*
3. More or less entire leaves 4
3. Leaves very degraded and fragmented (rectangular brown-reddish cells) (Figure A4b)..........*Polytrichum* sp.
4. Leaves composed of green and hyaline cells 5
4. Leaves without the above characters …..........11
5. Leaves composed of network of green cells surrounding by hyaline cells with annular thickenings (Figure A2k, l)..........6 (*Sphagnum*)
5. Leaves composed of two layers of hyaline cells and a central layer of chlorophyllose cells (Figure A4o)..........*Leucobryum juniperoideum*
6. Inner walls of hyaline cells papillose (Figure A2n, o)……….........*Sphagnum papillosum*
6. Inner walls of hyaline cells not papillose (Figure A2k, l)…..........7
7. Green cells section triangular to trapezoid (Figure A2g)..........8
7. Green cells section elliptical, fully enclosed between the hyaline cells (Figure A2l)……..........*Sphagnum compactum*
8. Green cells broadly exposed on dorsal surface (Figure A2s)..........9 (*Sphagnum* sect. *Cuspidata)*
8. Green cells broadly exposed on ventral surface (Figure A2g)..........10 (*Sphagnum* sect. *Acutifolia)*
9. Leaves ovate (Figure A2p)……….........*Sphagnum tenellum*
9. Leaves lanceolate, apiculate (Figure A2t)..........*Sphagnum cuspidatum*
10. Margin 1–3 cells wide..........(*Sphagnum* sect. *Acutifolia)*
10. Leaf margins denticulate (Figure A2h)..........*Sphagnum molle*
11. Mid-leaf cells narrow, elongate, strongly sinuose and nodulose (Figure A4g)..........*Racomitrium lanuginosum*
11. Mid-leaf cells without this combination of characters……….........12
12. Mid-leaf cells narrowly elongated, about 10 times as long as wide..........13 (Hypnaceae)
12. Mid-leaf cells rectangular, less than 10 times longer than wide..........14
13. Leaves ovate-triangular, not falcate, with apex obtuse apiculate or sub-cucullate (Figure A3o, q).......... *Calliergonella cuspidata*
13. Leaves narrowly lanceolate, falcate with apex acuminate to filiform (Figure A3k, m)…..*Hypnum cupressiforme* s.l.
14. Mid-leaf cells polyhedral papillose 15
14. Mid-leaf cells rectangular without papillae..........16
15. Leaves lanceolate with margin entire and recurved (Figure A3c)..........*Aulacomnium palustre*
15. Leaves ovate with margins crenulate to denticulate and plane (Figure A3f)..........*Thuidium tamariscinum*
16. Nerve broad, occupying 1/3–1/2 of leaf base width (Figure A4k)..........*Campylopus* sp.
16. Narrower nerve, occupying 1/10 of leaf width (Figure A4h)..........*Dicranum scoparium*

Only *Sphagnum* sect. *Acutifolia* and *Hypnum cupressiforme* were recorded in all four bogs; furthermore, these were the most frequent species across all of the peat cores analysed (Table 1). Of the other taxa identified, *Sphagnum papillosum*, *Sphagnum tenellum*, *Racomitrium lanuginosum* and *Leucobryum juniperoideum* were the only ones with mean frequencies greater than 5 %.

DISCUSSION

Compared to more northern peatlands where *Sphagnum* mosses dominate the flora and are the main peat formers (Dickinson & Maggs 1974, Granath 2012), *Sphagnum* moss macrofossils in the peat stratigraphy investigated in this research were usually less abundant, and vascular plants macrofossils were instead frequently identified (Souto *et al*. 2016). The shortage of bryophytes is remarkable, but it may be due to hydrological alterations (drainage) and land use changes. However, in some samples from Chao de Veiga Mol and Pena da Cadela, bryophyte remains constituted more than 50 % of the peat components. For these samples *Sphagnum* sect. *Acutifolia* and *Hypnum cupressiforme* s.l. were generally the most abundant mosses.

All species recorded as fossils were also found as present-day bryophyte populations. For the mosses,

Table 1. Relative frequencies (%) of the bryophyte macrofossils identified for each core series of the sampled bogs (CVM: Chao de Veiga Mol; BCG: Borralleiras de Cal Grande; PDC: Pena da Cadela; ZAL: Zalama) and for all sampled bogs (AVERAGE).

TAXON	**CVM**	**BCG**	**PDC**	**ZAL**	AVERAGE
Calypogeia sphagnicola	-	-	3.2	-	0.8
Odontochisma sphagni	1.3	-	-	-	0.3
Sphagnum sp.	81.4	-		1.5	23.7
Sphagnum sect. *Acutifolia*	52.1	6.0	32.3	15.9	26.6
Sphagnum molle	-	-	10.8	-	2.7
Sphagnum compactum	0.4	-	18.3	-	4.7
Sphagnum papillosum	33.1	-	22.6	-	13.9
Sphagnum tenellum	21.6	-	12.9	-	8.6
Sphagnum cuspidatum	2.5	-	-	-	0.6
Aulacomiun palustre	3	-	-	3.8	1.7
Thuidium tamariscinum	-	-	2.2	-	0.6
Hypnum cupressiforme	47.9	13.8	5.4	6.8	18.5
Calliergonella cuspidata	-	-	-	5.3	1.3
Polytrichum sp.	-	-	-	6.8	1.7
Racomitrium lanuginosum	5.5	-	24.7	6.1	9.1
Dicranum scoparium	-	-	-	1.5	0.4
Campylopus sp.	-	0.9	-	-	0.2
Leucobryum juniperoideum	11.4	2.6	14	-	7

there was good concordance between the present-day flora and the palaeoflora. Liverworts were very scarce or absent in the cores. This could be due to their poor preservation, which causes their under-representation in subfossil assemblages (Birks 1982, Janssens 1983). In agreement with Grosse-Brauckmann (1974) liverworts do not play a significant role as peat components, compared to the mosses.

Most of the *Sphagnum* remains were single leaves or small branch fragments, so species identifications were often difficult and mainly based on leaf branches because stems with leaves were usually absent. Some branch leaf characteristics such as shape, size, length to width ratio, pores or nature and extent of marginal curling were very useful for identifying *Sphagnum* leaves, but the taxonomic value of these characteristics was frequently insufficient for accurate identification to species or even section level because they did not have precise limits and their ranges overlapped. We examined leaf cross sections whenever possible, as this was the most effective method for studying the shapes and dispositions of chlorophyllose and hyaline cells. In the case of *Sphagnum papillosum*, transverse sections of leaves were not necessary due to the obvious presence of papillae on the internal walls of the hyaline cells.

The abundance of leaves belonging to *Sphagnum* section *Acutifolia* in all four bogs was proved by their triangular photosynthetic cells, broadly exposed on the ventral surface, in transverse section. Among the species belonging to this section only *Sphagnum molle* was identified reliably (in the core from Pena da Cadela), due to the distinctive denticulate leaf margins of this species. The photosynthetic cells of the recorded species of section *Cuspidata* (*Sphagnum tenellum* and *Sphagnum cuspidatum*) were similar to those of the section *Acutifolia* species in that they were triangular in transverse section, but they had opposite arrangement with wider exposure on the dorsal surface of the leaf. Among these species, *Sphagnum tenellum* was distinguished by its shorter leaves. All characters used for identification of the *Sphagnum* species mentioned above, as well as those used for *Sphagnum compactum*, are in agreement with the bibliographic references for subfossil samples (Grosse-Brauckmann 1974, Mauquoy & van Geel 2007) and present-day specimens (Brugués *et al*. 2004, Smith 2004, Casas *et al*. 2006).

After *Sphagnum* section *Acutifolia*, the most frequent and abundant moss in the peat cores was *Hypnum. cupressiforme* s.l., a controversial taxonomic complex which includes a wide range of infraspecific taxa. Within our samples of this species, we could not identify infraspecific taxa with certainty.

The relatively good preservation state of stems with leaves facilitated the identification of some species as *Aulacomnium. palustre, Thuidium. tamariscinum, Calliergonella. cuspidata* and *Racomitrium lanuginosum.* Although, according to Grosse-Brauckmann (1974), *Aulacomnium palustre* leaf cells often have star-shaped lumens due to nodular wall thickenings, we observed in this species that most of the cells had rounded lumens, in agreement with Smith (2004) for present-day material and Mauquoy & van Geel (2007) for subfossil samples.

The *Polytrichum* sp. remains from the Zalama bog are a good example of the selective decomposition process that affects many mosses. As previously noted by Grosse-Brauckmann (1974), the most typical and frequent conservation of *Polytrichum* leaves was as isolated leaf sheath remains, sometimes with small and degraded lamina fragments (Figure A4a). The Zalama leaf remains had brown-reddish cells, much longer than broad at the base of the leaf and approximately trapezoidal at the top (Figure A4c, d).

Finally we wish to emphasise that, although it is often considered that subfossil bryophytes can be identified using methods similar to those employed for modern material (even using the same keys), it is important to know how decomposition processes affect the stems and leaves of different species in order to understand which of the characters preserved in fossilised samples are most valuable for identifying them. For example, one of the most distinctive characters of living *Racomitrium lanuginosum*, commonly used in identification keys, is that each leaf is elongated into a long, decurrent, strongly papillose hyaline point; but in fossilised samples the hyaline point is often lost or very degraded, so the shape of the leaf cells is more useful than the presence or absence of the hyaline leaf point for identifying fossil remains belonging to the genus *Racomitrium*.

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Appendix: Diagnostic characteristics for bryophyte macrofossils.

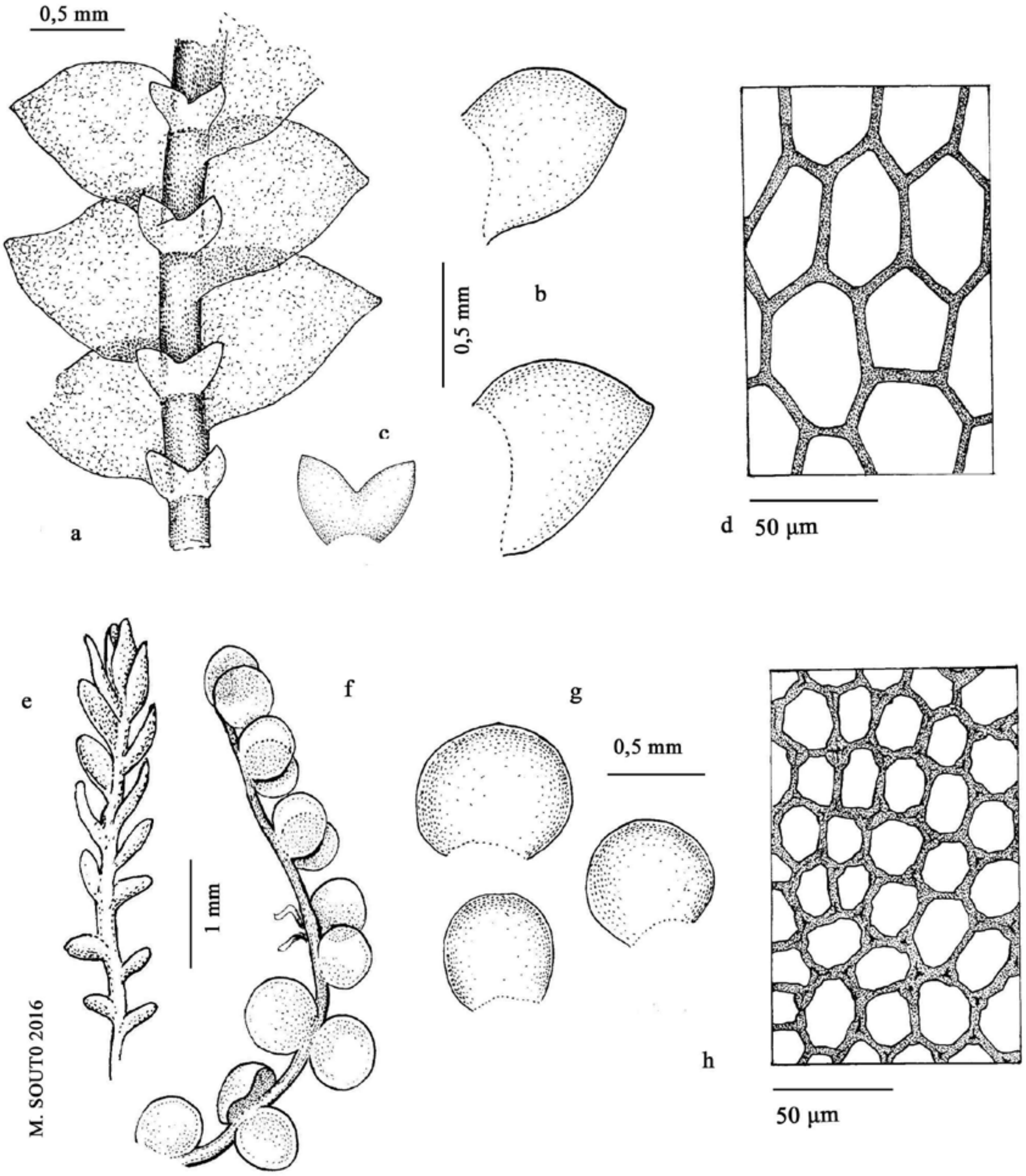

Figure A1. Liverworts. *Calypogeia sphagnicola*: a) fragment of stem, ventral aspect, b) leaves, c) underleaf, d) medium leaf cells; *Odontochisma sphagni*: e) stem apex, dorsal aspect, f) flagelliform stem fragment, lateral aspect, g) leaves, h) medium leaf cells.

Table A1. Diagnostic characteristics for liverworts: stems and leaves (Figure A1).

Species	Arrangement and shape	Mid-leaf cells	Underleaves
Calypogeia sphagnicola (Arnell & J. Perss.) Warnst. & Loeske	Subimbricate. Triangular to ovate-triangular, plane to slightly convex, widest at base and decurrent on ventral side (Figure A1a, b)	> 25 µm wide. Trigones lacking or very small (Figure A1d)	Appressed, bilobed to bifid (Figure A1c)
Odontoschisma sphagni (Dicks) Dumort.	Distant to imbricate. Orbicular to ovate-orbicular, concave, margin narrowly incurved (Figure A1e, f, g)	< 25 µm wide. Trigones large but not bulging (Figure A1h)	Generally absent

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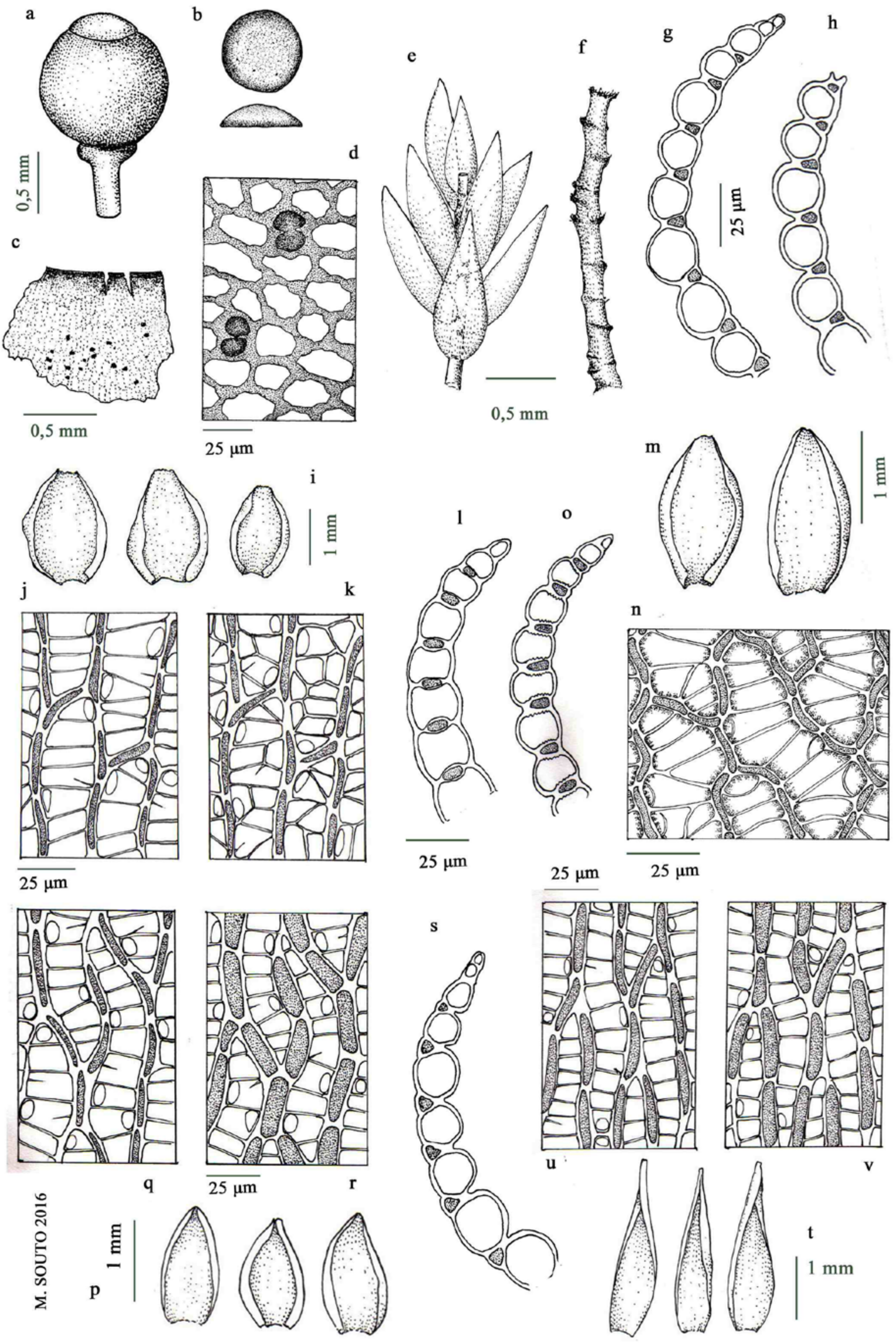

Figure A2. *Sphagnum*. For legend, see next page.

Legend to Figure A2: *Sphagnum* spp.: a) capsule, b) operculum, c) capsule fragment, d) capsule epidermal cells, e) branch with leaves, f) stem fragment without leaves; *Sphagnum* Sect. *Acutifolia*: g) leaf section with green cells exposed on ventral surface; *Sphagnum molle*: h) leaf section with green cells exposed on ventral surface; *Sphagnum compactum*: i) leaves, j) cells at middle of branch leaf on ventral surface, k) cells at middle of branch leaf on dorsal surface, l) leaf section with lens-shaped green cells enclosed between the hyaline cells; *Sphagnum papillosum*: m) leaves, n) cells at middle of branch leaf on ventral surface, o) leaf section with green cells exposed on both surfaces; *Sphagnum tenellum*: p) leaves, q) cells at middle of branch leaf on ventral surface, r) cells at middle of branch leaf on dorsal surface; *Sphagnum cuspidatum*: s) leaf section with green cells exposes on dorsal surface, t) leaves, u) cells at middle of branch leaf on ventral surface, v) cells at middle of branch leaf on dorsal surface.

Table A2. Diagnostic characteristics for mosses*: Sphagnum* spp. branch leaves (Figure A2).

Species	Shape and size (mm)	Apex	Green cells in cross- section
Sphagnum sect. *Acutifolia* (Russow) Schimp.	Ovate to lanceolate 0.8–2 × 0.4–1	Acute or acuminate because of coiling margins	Triangular to trapezoid, broadly exposed on ventral surface (Figure A2g)
Sphagnum molle Sull.	Ovate 1.5–2 × 0.5–0.9 margin denticulate	Acute	Triangular to trapezoid, broadly exposed on ventral surface (Figure A2h)
Sphagnum compactum Lam. & DC	Oblong to ovate 1.8–2.5 × 0.9–1.8 (Figure A2i, j, k)	Rounded or truncate	Elliptical, lens-shaped, fully enclosed between the hyaline cells (Figure A2l)
Sphagnum papillosum Lindb.	Ovate 1.5–2 × 1–1.5 (Figure A2m, n)	Cucullate, scabrous on dorsal face	Elliptical or trapezoidal, with the wider base on ventral surface, but exposed on both surfaces; inner walls of hyaline cells papillose (Figure A2o, n)
Sphagnum tenellum (Brid.) Brid.	Ovate 0.8–1.6 × 0.4–0.8 (Figure A2p, q, r)	Acute because of coiling margins, truncate, smooth on dorsal face	Triangular with the wider base on dorsal surface, but exposed on both surfaces
Sphagnum cuspidatum Hoffm.	Lanceolate 1.6–4 × 0.4–0.6 (Figure A2t, u, v)	Acuminate with an apiculus	Triangular to trapezoid with the wider base on dorsal surface, but exposed on both surfaces (Figure A2s)

Table A3. Diagnostic characteristics for other mosses (Figures A3–4).

Species	Stems	Leaves	Leaf apex	Cells in mid-leaf
Aulacomnium palustre (Hedw.) Schwaegr. var. palustre	With dense brown tomentum (Figure A3a, b)	Lanceolate with nerve ending below the apex; margin recurved, entire to denticulate (Figure A3c)	Acuminate to rounded (Figure A3e)	Irregularly rounded to quadrate with conical papillae; 8–14µm wide (Figure A3d)
Thuidium tamariscinum (Hedw.) Schimp.	Stems regularly 3 pinnate, branches complanate (Figure A3f)	Erecto-patent to concave, ovate, longitudinally ridged, and acute-tipped; nerve strong, ending below the apex; margin crenulate to denticulate (Figure A3f)	Acuminate and denticulate (Figure A3i)	Irregularly rounded to quadrate and unipapillose; 8–10 µm wide (Figure A3h)
Hypnum cupressiforme s.l. Hedw.	Irregularly branched to ± pinnate	Falcate-secund, abruptly narrowed to apex; margin denticulate in the upper part; nerve short or lacking (Figure A3j, k)	Acuminate to filiform (Figure A3k, m)	Thick-walled, linear to vermicular (Figure A3l)
Calliergonella cuspidata (Hedw.) Loeske	Stems and branches cuspidate and complanate (Figure A3n)	Ovate-triangular, nerve lacking; margin entire (Figure A3o)	Obtuse apiculate, sometimes sub-cucullate (Figure A3q)	Thin-walled, 10–18 times as long as wide (Figure A3q)
Polytrichum sp.	Undetermined because only very degraded fragments were recorded	Undetermined because only small leaf fragments and epidermis of leaf bases were recorded, including sheaths attached to stems (Figure A4a, b)	None recorded	In most of the leaf fragments studied, the lower cells were rectangular and brown-reddish and the upper cells square to polygonal (Figure A4c, d)
Racomitrium lanuginosum (Hedw.) Brid.	Densely and irregularly branched	Falcato-secund, lanceolate, long, narrow, nerve stout and long, margins recurved to revolute (Figure A4e, f)	Acuminate to filiform	Sinuose-nodulose rectangular and strongly papillose (Figure A4g)
Dicranum scoparium Hedw.	Covered by dense, whitish tomentum	Lanceolate with notorious nerve, margin entire to dentate (Figure A4h)	Subulate (Fig. 4i)	Rectangular to rhomboidal with thick and brown walls; 15 × 50–60 µm (Figure A4j)
Campylopus sp.	None recorded	Lanceolate, subulate, nerve broad, occupying 1/3–1/2 of leaf base width (Figure A4k)	Undetermined because the only apex remains corresponding to the nerve	More or less rhomboidal, with thick walls (Figure A4l)
Leucobryum juniperoideum (Brid.) Mull. Hal.	Simple, erect (Figure A4m)	Lanceolate, with broad and sheathing base, nerve very broad, occupying almost all the leaf (Figure A4n)	Acute, tubular (Figure A4n)	Rectangular to square, thin-walled (Figure A4o)

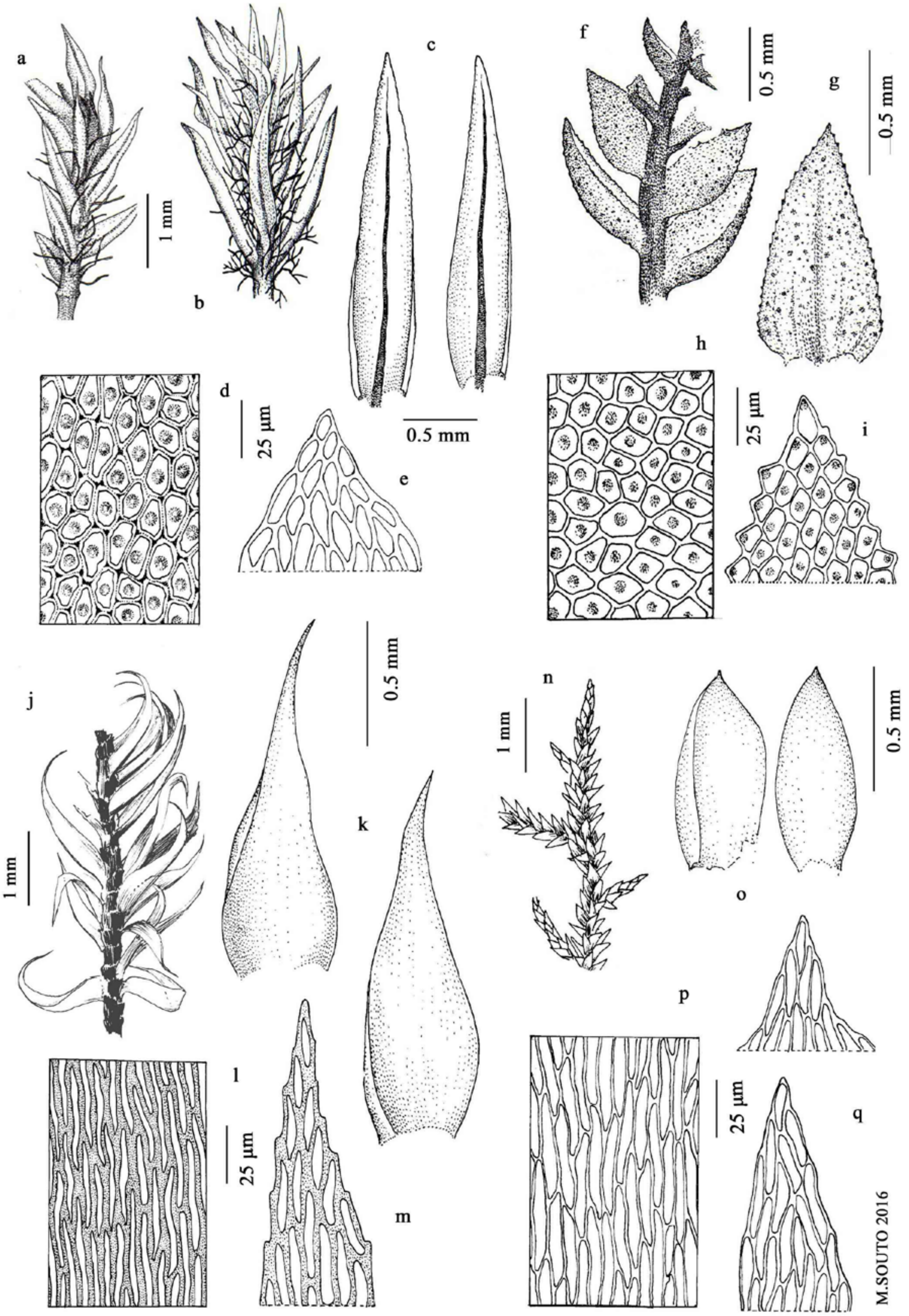

Figure A3. *Aulacomnium palustre*: a, b) fragment of stem with dense tomentum and leaves, c) leaves, d) mid-leaf cells, e) leaf apex; *Thuidium tamariscinum*: f) fragment of stem with leaves, g) leaf, h) mid-leaf cells, i) leaf apex; *Hypnum cupressiforme*: j) shoot fragment, k) leaf, l) mid-leaf cells, m) leaf apex; *Calliergonella cuspidata*: n) branches with leaves, o) leaves, p) mid-leaf cells, q) leaf apex.

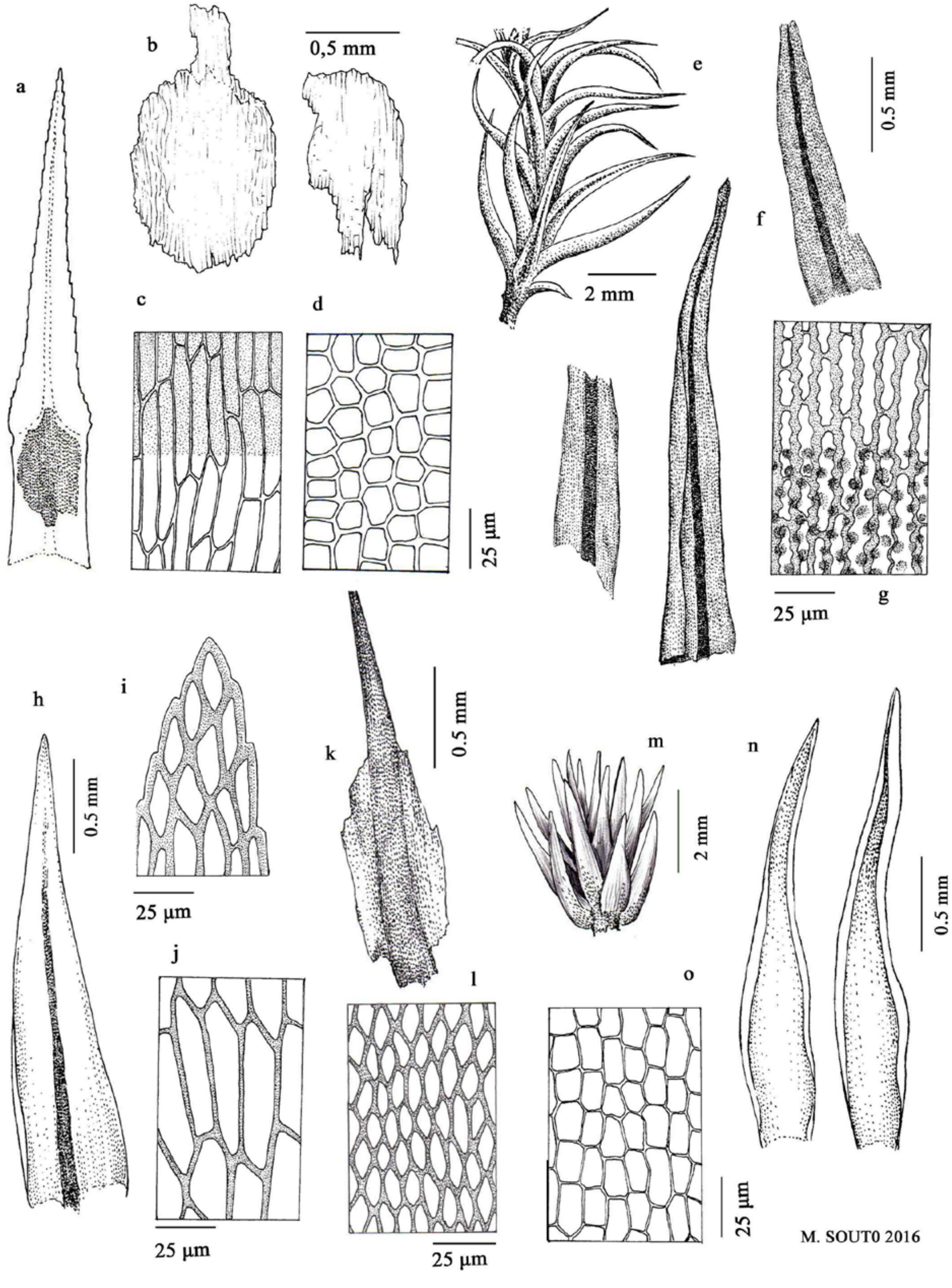

Figure A4. *Polytrichum* sp.: a) reconstruction of a leaf based on one of the studied macrofossils (dark area), b) leaf base fragment, c) cells of leaf base, d) upper cells of a leaf fragment; *Racomitrium lanuginosum*: e) fragment of a branch with leaves, f) leaves, g) mid-leaf cells; *Dicranum scoparium*: h) leaf, i) leaf apex cells, j) mid-leaf cells; *Campylopus* sp.: k) leaf, l) mid-leaf cells; *Leucobryum juniperoideum*: m) stem tip with leaves, n) leaves, o) mid-leaf cells.