Hygrohypnum (Amblystegiaceae, Bryopsida) in the Iberian Peninsula

Gisela OLIVÁN\textsuperscript{a}\textsuperscript{*}, Esther FUERTES\textsuperscript{b} and Margarita ACÓN\textsuperscript{c}

\textsuperscript{a}Departamento de Biología Vegetal I, Facultad de Biología, Universidad Complutense de Madrid, E-28040 Madrid, Spain \ (giselaolivan@hotmail.com)

\textsuperscript{b}Departamento de Biología Vegetal I, Facultad de Biología, Universidad Complutense de Madrid, E-28040 Madrid, Spain \ (efuertes@bio.ucm.es)

\textsuperscript{c}Departamento de Biología (Botánica), Facultad de Ciencias, Universidad Autónoma de Madrid, É-28049 Madrid, Spain \ (margarita.acon@uam.es)

\textbf{Abstract} – The genus \textit{Hygrohypnum} Lindb. is studied for the Iberian Peninsula, based mainly on herbarium specimens kept in BM, PC, S and the main Iberian herbaria. Eight species of \textit{Hygrohypnum} occur in the Iberian Peninsula: \textit{Hygrohypnum cochlearifolium}, \textit{H. duriusculum}, \textit{H. eugyrum}, \textit{H. luridum}, \textit{H. molle}, \textit{H. ochraceum}, \textit{H. smithii} and \textit{H. styriacum}. Of these, \textit{H. eugyrum} and \textit{H. cochlearifolium} are considered to be extinct in the Iberian Peninsula. \textit{Hygrohypnum alpestre} and \textit{H. polare} are definitively excluded from the Iberian bryophyte flora, since its occurrence at present or in the past could not be confirmed. Only the occurrence of \textit{Hygrohypnum ochraceum} has been confirmed for Portugal. Keys, descriptions, illustrations, SEM photographs and distribution maps of the species of \textit{Hygrohypnum} in the Iberian Peninsula are provided.

\textit{Hygrohypnum} /Amblystegiaceae /Iberian Peninsula /flora /taxonomy /distribution

\section*{INTRODUCTION}

\textbf{Taxonomic history of Hygrohypnum}

The generic name \textit{Hygrohypnum} was introduced by Lindberg (1872) to replace the illegitimate name \textit{Limmobium} used by Schimper (1853), who was the first to treat the genus as separate from the broadly conceived \textit{Hypnum} Hedw. However, the generic concept of \textit{Hygrohypnum} was not very clear at that time, as it was not for many other pleurocarpous genera, that were being segregated from \textit{Hypnum} at the same time as the technical advances in microscopy progressed, allowing the usage of new morphological characters. This yielded numerous changes of taxonomic status and the coming and going of taxa from one genus to another during decades. For instance Lindberg (1879) and Kindberg (1897) reduced \textit{Hygrohypnum} to unranked subdivisions of \textit{Amblystegium} Schimp., \textit{Calliergon} (Sull.) Kindb. respectively, and Limpricht (1904) considered it as a subgenus of \textit{Hyponym}.

It was not until Brotherus (1908) published the treatment of the Musci in the first edition of “Die Natürlichen Pflanzenfamilien” that \textit{Hygrohypnum}
became widely used. Besides, he pointed out that *Hygrohypnum* was not as close to *Hypnum* as it was to the genera included in the Amblystegiaceae, at that moment still considered to be a subfamily of Hypnaceae, but which would be later elevated to the rank of family (Brotherus, 1923). Since then *Hygrohypnum* was generally accepted to belong to the family Amblystegiaceae, and many taxa were described within it. Thus, Wijk *et al.* (1962) compiled 60 specific and subspecific taxa published under *Hygrohypnum*.

During the seventies two works shed light on this obscurely circumscribed genus. Jamieson (1976) carried out an exhaustive worldwide revision of *Hygrohypnum*, using a large number of morphological and anatomical characters never employed before in this context. He retained only 16 species in *Hygrohypnum* and reduced many subspecies and varietal names to synonyms, although he did not relocate most of the excluded taxa. At the same time Kanda (1976), in a revision of the Amblystegiaceae from Japan, split the genus into *Hygrohypnum* and *Pseudohygrohypnum* Kanda, on the basis of costa structure and habitat preferences, and placed these in a new subfamily of the Amblystegiaceae, the Hygrohypnoideae Kanda. The subfamily name Hygrohypnoidea had been already introduced by Szafran (1961), although it was invalid because of the lack of Latin description. Szafran (1961) placed the genera *Hygrohypnum*, *Scorpidium* and *Calliergon* in this family, and subdivided the genus *Hygrohypnum* in two sections, sect. *Lurida* and sect. *Dilatatae*. The latter was invalidly published and validated later by Ochyra (1983).

However, and despite these works, the circumscription of *Hygrohypnum* remained unclear, and many species were later described in this genus or transferred to it (e.g. Crum, 1985; Delgadillo *et al.*, 1995; Frahm, 1996; Nishimura, 1985; Sharp & Crum, 1994; Vohra, 1980). Therefore the checklist of mosses of Crosby *et al.* (1999) still presents 33 species remaining in the genus, although many of them, especially those from Central and South America, have been transferred to other genera (e.g. Buck, 1997; Ochyra, 1991, 1999a,b; Ochyra & Sharp, 1988). Basically the species left in the genus are those that were previously recognized by Jamieson (1976), all of them with Holartic distribution, with the exception of *Hygrohypnum luridum* (cf. Bartram, 1949; Enroth & Ignatov, 1999; Hedenäs, 2003).

Jamieson himself, after circumscribing *Hygrohypnum*, concluded his thesis saying that he believed the genus was polyphyletic. This hypothesis was later confirmed by Hedenäs (1998), who carried out phylogenetic analyses employing 74 morphological and anatomical characters from 93 species representing the Thuidiaceae, the temperate Hypnaceae and the Amblystegiaceae, including 10 species of *Hygrohypnum*.

The polyphyly of *Hygrohypnum* is also supported by recent phylogenetic studies of the family Amblystegiaceae in the broad sense based on molecular data (Vanderpoorten *et al.*, 2001), and on molecular and morphological data (Vanderpoorten *et al.*, 2002), which show that this family is polyphyletic and contains the family Amblystegiaceae *s.str.* and Calliergusonaceae (Kanda) Vanderpoorten *et al.*, and that some species of *Hygrohypnum* belong to the Amblystegiaceae *s.str.*, while some others could belong to the Calliergusonaceae.

Ignatov and Ignatova (2004) have made great nomenclatural changes in the genus *Hygrohypnum*. Only *Hygrohypnum luridum* was kept in the genus, while *H. alpestre* and *H. cochlearifolium* were transferred to the genus *Ochryrea* Váňa, which had already been placed in the family Amblystegiaceae and suggested to be closely related to *Hygrohypnum* (Stech & Frahm, 2001). Two species, *H. ochraceum* and *H. duriusculum*, were transferred to a new genus, *Hygrohypnella*.
Ignatov & Ignatova, belonging to a newly proposed family, Scorpidiaceae Ignatov & Ignatova, together with Scorpidiun, Limprichtia, Hamatocaulis, and Sanionia. \textit{Hygrohypnum subeugyrum} was transferred to \textit{Pseudohygrohypnum} Kanda, belonging to the family Pylaisiaceae Schimp., along with Breidleria, Calliergonella, Callicladium, Stereodon, Ptlium, Homomallium, and Pylaisia.

The phylogeny of \textit{Hygrohypnum} has been recently reconstructed based on ITS1-2, \textit{trnL-trnF} and \textit{atpB-rbcL} sequences (Oliván et al., 2006), showing good support for two major clades within the genus, one with \textit{H. styriacum} and \textit{H. luridum} (the type of the genus), which seems to be part of the Amblystegiaceae \textit{s.str.}, and the other one containing the rest of species of \textit{Hygrohypnum} grouped in three well supported clades, that seem to be somehow related with Calliergonaceae. However, although it is clear that \textit{Hygrohypnum} is polyphyletic, and there seems to be four groups within it, the relationships with other closely related taxa remain unclear. Therefore, in our opinion, it is risky at this point to carry out drastic nomenclatural changes in \textit{Hygrohypnum}, before further analyses are performed. For this reason we keep a conservative position in this work and follow Jamieson’s taxonomic treatment of the genus \textit{Hygrohypnum}.

**History of \textit{Hygrohypnum} in the Iberian Peninsula**

From the middle to the end of the nineteenth century several taxa of \textit{Hygrohypnum}, corresponding to 8 currently recognized species of the genus were reported from the Iberian Peninsula in the literature. These species are [nomenclature after Jamieson (1976) and Crosby et al. (1999)]; \textit{Hygrohypnum alpestre}, \textit{H. cochlearifolium}, \textit{H. durutisculum}, \textit{H. luridum}, \textit{H. molle}, \textit{H. ochraceum}, \textit{H. smithii} and \textit{H. polare}. \textit{Hygrohypnum lusitanicum} (Schimp.) Corb., which now belongs to \textit{Platyhypnidium} as \textit{Platyhypnidium lusitanicum} (Schimp.) Ochyra & Bednarek-Ochyra, was also reported from the Iberian Peninsula. Besides these taxa, \textit{Hygrohypnum eugyrum} was more recently reported from Asturias, northern Spain (Simó & Vigón, 1977).

The checklist of mosses of Spain (Casas, 1981) listed the 9 species of \textit{Hygrohypnum} mentioned above. This list was reduced to 8 in a later checklist (Casas, 1991), after the exclusion of \textit{Hygrohypnum alpestre}. \textit{Hygrohypnum styriacum} is the last species in the genus to be incorporated to the Iberian flora (Rams & Oliván, 2006). Table 1 summarizes the first records for the 10 species of \textit{Hygrohypnum} cited in the literature for the Iberian Peninsula.

The main goals of the present study have been: (1) to assess the status of the Iberian specimens of \textit{Hygrohypnum} in the light of modern taxonomic works and to establish which species occur in the studied area, (2) to determine the current distribution and ecology of \textit{Hygrohypnum} species in the Iberian Peninsula, (3) to provide descriptions and illustrations of Iberian \textit{Hygrohypnum}, in order to fill in the gap due to the lack of a complete Iberian bryophyte flora.

**MATERIAL AND METHODS**

This revision is based mainly on herbarium material from BM, PC, S and the main Iberian herbaria (BCB, FCO, GDAC, LISU, MA, MACB, MAF, MUB, PAMP, SALA, VAB, VIT), and on material collected by the authors in the course of this study, which are now deposited at MACB.
Table 1. Species of Hygrohypnum reported from the Iberian Peninsula in the literature, bibliographic reference to the first records and locality of collection.

<table>
<thead>
<tr>
<th>Species</th>
<th>Bibliographic reference</th>
<th>Locality</th>
</tr>
</thead>
<tbody>
<tr>
<td>H. alpestre</td>
<td>Colmeiro (1867)? Casas (1981)</td>
<td>Sierra Nevada Pyrenees</td>
</tr>
<tr>
<td>H. cochlearifolium</td>
<td>Schimper (1876)</td>
<td>Pyrenees</td>
</tr>
<tr>
<td>H. duriusculum</td>
<td>Höhnel (1895)</td>
<td>Sierra Nevada</td>
</tr>
<tr>
<td>H. eugyrum</td>
<td>Simó &amp; Vigón (1977)</td>
<td>Cantabrian Range (Asturias)</td>
</tr>
<tr>
<td>H. luridum</td>
<td>Spruce (1849) Colmeiro (1889) Henriques (1889)</td>
<td>Spanish Pyrenees Sierra de Gredos</td>
</tr>
<tr>
<td>H. molle</td>
<td>Höhnel (1895)</td>
<td>Sierra Nevada</td>
</tr>
<tr>
<td>H. ochraceum</td>
<td>Leresche &amp; Levier (1880) Boulay (1884) and Jeannernat &amp; Renauld (1885)</td>
<td>Sierra de Gredos Spanish Pyrenees</td>
</tr>
<tr>
<td>H. smithii</td>
<td>Boulay (1884)</td>
<td>Spanish Pyrenees</td>
</tr>
<tr>
<td>H. styriacum</td>
<td>Rams &amp; Oliván (2006)</td>
<td>Sierra Nevada</td>
</tr>
<tr>
<td>H. polare</td>
<td>Allorge &amp; Casas (1976)</td>
<td>Spanish Pyrenees</td>
</tr>
</tbody>
</table>

About 500 specimens were examined, of which 260 were Iberian. Due to the large number of revised specimens belonging to Hygrohypnum ochraceum, H. luridum and H. duriusculum, abridged lists, including only one specimen per province (being Andorra considered too as a province), are provided for these taxa. Full lists can be requested from the authors. A number of 110 morphological and anatomical characters have been studied. The descriptions of the gametophytic characters and sexual branches, as well as the habitat descriptions, illustrations and SEM photographs are based on Iberian specimens. The sporophytic characters of Hygrohypnum ochraceum, H. luridum, H. smithii, H. duriusculum and H. molle are also based on Iberian specimens. Those of Hygrohypnum eugyrium and H. cochlearifolium were described from non-Iberian specimens, kept at S and BM, during the visits of one of the authors to these institutions, since there were no sporophytes in any of the studied Iberian specimens. The type specimens kept at S and BM were also checked.

The nomenclatural parts of the taxa treatments include only the names and combinations used in the literature referring to the Iberian Peninsula or present on the labels of the herbarium specimens checked for this study. Full synonymies of each taxon treated here can be found in Jamieson (1976).

The nomenclature follows Crosby et al. (1999) and Jamieson (1976). Authors’s names are abbreviated according to Brummit & Powell (1992).
The threat category for each species of *Hygrohypnum* in the Iberian Peninsula has been evaluated applying the criterion B (restricted area of occupancy, few localities, decline) as defined by the IUCN (2001) and Hallingbäck et al. (1998). The categories used are also those given by the IUCN (2001).

**RESULTS**


**Plants** forming dense or loose tufts, rigid or soft to the touch, older parts denuded or not, frequently with shredded leaves, green, dark green, green-yellowish or brownish, usually medium-sized, sometimes small or large. **Stem** usually prostrate with ascending to erect branches, irregularly branched; stem transverse section with central strand (outside Iberian Peninsula sometimes absent), large and ± thin-walled medullar cells and 1-4 layers of thick-walled cortical cells, with or without hyalodermis; axillary hairs variably abundant (1-8 per leaf axil), with 1-7 hyaline apical cells and 1 or 2 quadrate, shortly rectangular to rectangular and brownish basal cells; pseudoparaphyllia either foliose and broad, or with at least the outer ones filamentose; paraphyllia absent. **Rhizoids** below leaf costa insertion, usually on ventral part of prostrate stems or branches, red-brownish, branched, slightly branched or unbranched, smooth or slightly papillose, variably abundant. **Stem leaves** very variable, straight, curved or falcate, slightly to deeply concave or plane, ovate, broadly ovate, ovate-lanceolate, oblong-elliptic, oblong-ovate, orbicular, rarely lanceolate, size very variable; closely or distantly spaced, sometimes imbricate, erect, erecto-patent to erect-spreadwing; margin usually plane and recurved at base, sometimes recurved throughout, usually entire, sometimes finely denticulate in upper half or with a few teeth near apex; apex various, rounded, obtuse, acute, gradually or abruptly acuminate or apiculate; costa variable, usually short and double or forked near insertion with one or both arms reaching mid-leaf or beyond, other times single, slender or stout, reaching 50-70% of leaf length, rarely percurrent; median lamina cells linear, linear-flexuose, or short and rhombic, usually thin-walled, but sometimes thick-walled, smooth, similar or becoming wider and shorter towards apex, wider, similar, longer, or shorter, towards base, but usually more strongly incrassate, sometimes yellowish to brownish, frequently porose; marginal cells similar to adjacent median lamina cells or shorter and wider, sometimes hyaline with reabsorbed outer cell-walls (outside Iberian Peninsula sometimes longer than median lamina cells); alar cells similar to adjacent cells or differentiated, quadrate, shortly rectangular to rectangular or irregular, inflated or not, hyaline, yellowish to brownish or reddish, usually thin-walled, sometimes ± thick-walled, forming a poorly to well-defined, usually rectangular to ovate group along leaf margin,
excavate or not, decurrent or not. **Branch leaves** similar to stem leaves or slightly larger. **Autoicous** or **Dioicous. Perigonia** lateral on stem, perigonal leaves ovate, abruptly and shortly acuminate, margin entire or slightly denticulate, ecostate. **Perichaetium** lateral on stem; inner perichaetial leaves straight, mostly plicate, ovate-lanceolate, oblong-lanceolate, lanceolate or triangular, erect, margin entire or denticulate in upper part, apex acute or abruptly to gradually and shortly acuminate, costa variable, absent, short and double or single, long and double, single, or forked, upper cells usually smooth, sometimes abaxially prorate; vaginula with paraphyses. **Seta** long, reddish, usually twisted or slightly so, smooth. **Capsule** inclined to horizontal, cylindrical or shortly cylindrical, ± curved, usually contracted below mouth when dry, brownish, smooth, not furrowed when dry. **Exothecial cells** shortly rectangular, quadrate or rounded-hexagonal, thick or thin-walled, smooth, becoming smaller, rounded and usually with more strongly incassate cell-walls towards mouth; stomata at base of capsule, phaneropore. **Separating annulus** usually present, rarely annulus persistent. **Peristome** well developed; exostome yellow or yellow-brownish, lower outside ornamentation cross-striolate, upper outside ornamentation papillose, border widened or not where ornamentation changes from cross-striolate to papillose; endostome hyaline or yellowish, basal membrane high, segments not or narrowly perforate, finely papillose to almost smooth, cilia 1-3 rudimentary to well developed, sometimes absent, nodose. **Lid** conical. **Calyx** ciliate, naked. **Spores** 10.0-25.0 μm, finely papillose.

**Key to the species**

1. Stem with hyalodermis. **Dioicous** .............................. 1. *H. ochraceum*
2. Stem without hyalodermis or outer cortical cells larger and thinner-walled than sub-adjacent cortical cells, but not forming a hyalodermis ................. 2
3. Stem outer cortical cells larger and thinner-walled than sub-adjacent cortical cells. Stem leaf apex gradually acute; margin entire and usually with a few small teeth near apex; costa double, usually reaching 25% of leaf length, rarely up to mid-leaf; alar cells quadrate to rectangular, usually inflated and bright red to red-brownish with age ................. 2. *H. eugrium*
4. Leaves falcate and/or straight within the same specimen; alar cells differentiated, forming a well-defined group. Perichaetium inserted on the stem above perigonia. Capsule without separating annulus 3. *H. luridum*
5. Stem cortical cells uniform. Stem leaf apex apiculate, abruptly and ± shortly acuminate or acute; margin entire; costa single, forked or double, usually reaching mid-leaf or beyond; alar cells undifferentiated or quadrate to shortly rectangular, rarely inflated, hyaline or yellowish-brown with age ................. 4
6. Leaves deeply concave. Outer pseudoparaphyllia filamentose, inner pseudoparaphyllia foliose, narrowly triangular .......................... 5. *H. smithii*
7. Costa slender, short, rarely reaching more than 50% of leaf length, double or forked near insertion, rarely single or forked above ................. 6
6. Leaves concave to plane. Outer and inner pseudoparaphyllia foliose, broad .......................................................... 7

7. Leaves oblong-elliptic to broadly ovate, sometimes orbicular; apex abruptly obtuse or broadly acute, sometimes rounded, rarely apiculate; alar cells rectangular to quadrate or irregular, inflated, thick-walled, forming a well-defined group. Upper cells of perichaetial leaves always smooth. .......................................................... 7. *H. duriusculum*

7. Leaves usually broadly ovate to ovate; apex generally gradually acute; alar cells undifferentiated or a few rectangular, shortly rectangular to quadrate cells, slightly more incrassate than surrounding cells, not forming a differentiated group. Upper cells of perichaetial leaves usually prorate. . . . .......................................................... 8. *H. molle*

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*Figs 1-6, Figs 14-17*


**Plants** forming ± dense tufts, sometimes big mats, soft or slightly rigid to touch, older parts rarely denuded, sometimes with shedded leaves, green-yellowish to brownish, medium-sized to big (4-12(15) cm). **Stem** usually prostrate or ascending, irregularly branched, sometimes almost unbranched, infrequently almost pinnately branched; stem transverse section ± rounded, with central strand, large and thin-walled medullar cells and 2-3 layers of small, thick-walled cortical cells enclosed by a well developed hyalodermis; axillary hairs scarce to moderately abundant (1-2(3) per leaf axil), very long, with (4)5-6(7) hyaline-brownish apical cells and 1-2 quadrate and brownish basal cells; pseudoparaphyllia foliose, broadly triangular to semi-orbicular, with irregular margin. **Rhizoids** below leaf costa insertion, red-brownish, slightly branched or unbranched, smooth, variably abundant. **Stem leaves** variable, straight, curved or falcate, concave to plane, usually ovate-lanceolate to ovate, sometimes broadly ovate or lanceolate, 0.5-0.8 mm wide × 1.2-2.1 mm long; closely or distantly spaced, usually spreading to loosely imbricate; margin plane, minutely denticulate from midleaf to apex, sometimes completely entire; apex acute to gradually acuminate, tip usually blunt; costa variable, even among leaves on same stem, usually long (up to 60% of leaf length) and double or forked near insertion, sometimes long and single, to mid-leaf or beyond; median lamina cells linear, linear-flexuose or fusiform, (4.0)5.0-6.5 µm wide × (30.0)45.0-80.5(100.0) µm long, ± thin-walled, smooth, becoming shorter
Figs 14-21. SEM photographs. 14-17. *Hygrohypnum ochraceum*; 18-21. *Hygrohypnum luridum*. Peristome (14, 18); outside ornamentation of exostome in the region where the ornamentation changes from cross-striolate to papillose (15-20); lower outside ornamentation of exostome (16, 19); detail of the lower outside ornamentation of exostome (17); spore (21).
towards apex and slightly shorter and wider towards base; marginal cells wider or similar to adjacent median lamina cells, becoming shorter towards apex and shorter and wider towards base; alar cells shortly rectangular, quadrate, sometimes linear, thin-walled, hyaline, forming a well-defined, rectangular or ovate group, consisting of 2-3 rows of cells along basal leaf margin, sometimes appearing decurrent due to persistent cells of hyalodermis. **Diocous, Perichaetium** lateral on stem; inner perichaetal leaves straight, plicate, ovate-lanceolate, erect, margin entire or minutely denticate near apex, apex gradually acuminate or acute, costa single, sometimes forked above, reaching mid-leaf or beyond (up to 60%), upper cells linear, ± thin-walled, smooth, becoming wider, linear-rectangular, inflated and thinner-walled towards base; vaginula with paraphyses. **Seta** 1.5-2.5 cm, red, twisted, smooth. **Capsule** typical for genus. **Exothecial cells** quadrate to shortly rectangular, thin-walled, smooth, becoming smaller, rounded and with more incrassate cell-walls towards mouth; stomata few at base of capsule, phaneropore. **Separating annulus** present, 2-3 rows of cells. **Peristome** typical; border of exostome slightly widened where ornamentation changes from cross-striolate to papillose; endostome yellowish, basal membrane high, about 35% of endostome height, segments not or narrowly perforated, finely papillose, cilia 1-3, usually well developed, as long as segments, nodose. Spores 12.0-17.0 μm, finely papillose. Sporophytes rare in Iberian specimens.

**Habitat:** On wet or irrigated rocks in or beside mountain streams. Sometimes beside high mountain lakes or in fens with current water.

**Worldwide distribution:** Common in Europe, Northern and Central Asia, Japan, North America and Greenland (Jamieson, 1976).

**Distribution in the Iberian Peninsula** (Fig. 22): Hygrohypnum ochraceum is widespread in the mountainous areas of the northern half of the Iberian Peninsula, while in the southern half this species occurs only in Sierra Nevada. In the Eurosiberian region of the Iberian Peninsula (the northernmost part of the peninsula, along the coast and including the Galician-Portuguese Massif, Cantabrian Range and the Pyrenees) *H. ochraceum* grows from the low montane to alpine belts (50-1900 m a.s.l.) in the Galician-Portuguese Massif (Orense and Minho) and the Cantabrian Range (Lugo, Asturias, León, Palencia, Cantabria and Basque Country), while in the Pyrenees (Navarra, Lérida and Andorra) this species is restricted to the alpine regions (1700-2367 m a.s.l.). In the Mediterranean region it can be found in the high mountains, between 1500 and 2225 m a.s.l., in the Central Range (Madrid, Segovia, Salamanca, Cáceres and Beira Alta), Iberian Range (Burgos, Soria and Guadalajara) and Penibetic Range (Sierra Nevada in Granada).

**Threat category for the Iberian Peninsula:** Least concern (LC).

**Selected specimens examined:** ANDORRA. 31TCH91, Enrodat, Estany d’Isle, MACB 79071, E. Fuertes & G. Oliván, 2001.

**SPAIN. Ávila:** 30TUk15, Sierra de Gredos, Garganta de las Pozas, MACB, E. Fuertes & Acón, 1997.

**Asturias:** 29TPRH86, Cangas del Narcea, Monte Muniellos, FCO-Brief 2797, M. C. Fernández-Ordóñez, 2002.

**Cantabria:** 30TUN87, Sierra de Peña Sagra, Pozo de la Vega, MACB 75940, G. Olíván & E. Fuertes, 1997.


**Guipúzcoa:** 30TWN87, Elduayen, Valle de Leizarán, presa del río Leizarán, VIT 12548, P. Heras, 1989.

**Lérida:** 31TCH52, Pallars Sobirà, Vall de Cardós, baixant de la Pleta Vella, BCB 49964, Casas & Ruiz, 1998.


**Lugo:** 29TPJ20, Sierra de Xistral, MACB; E. Fuertes, G. Olíván & A. Sallent, 2000.

**Navarra:** 30TXN09, Endarlaza, PC. P. & V. Allorge, 1927. **Orense:** 29TNG83, Parque de Xurés, Puxedo, BCB 47197, Casas, Sérgio & Brugués, 1995.


**Salamanca:** 30TTK65, Hoyamoros, BCB 20619, Elías, 1985. **Soria:** 30TWM14, Covaleda, cascada de la Laguna Negra y Urbión, VIT 5304, P. Heras, 1984.
Fig. 22. Distribution map of *Hygrohypnum ochraceum* in the Iberian Peninsula. ● confirmed occurrence (10 × 10 km square).


Figs 7-13


Plants forming loose tufts, soft to touch, older parts sometimes denuded or with shredded leaves, green-yellowish to brownish, medium-sized (2-5(6) cm). Stem usually prostrate with ascending branches; stem transverse section oval-rounded, with poorly developed central strand, large and thin-walled medullar cells and 3-4 layers of small, thick-walled, red-brownish cortical cells, cells of outer layer slightly larger and thinner-walled; axillary hairs moderately abundant ((1)2-3 per leaf axil), with 1-3 hyaline apical cells and 1 shortly rectangular and brownish basal cell; pseudoparaphyllia foliose, broadly triangular. Rhizoids usually absent. Stem leaves straight or falcate, concave, ovate, ovate-lanceolate, oblong-lanceolate, or lanceolate, usually strongly narrowed at base due to excavate alar groups embracing stem, 0.4-0.7 mm wide × 0.9-1.5 mm long; ± closely spaced, erect-spread to spreading, sometimes loosely imbricate; margin plane or inrolled in upper part, entire, usually with a few small teeth near apex; apex acute, tip blunt or sharp, sometimes appearing virtually apiculate due to inrolled margins in upper part of leaf; costa short and double (up to 25% of leaf length, seldom up to mid-leaf); median lamina cells linear-flexuoese to fusiform,
3.0-5.0 µm wide × 30.0-50.0(60.0) µm long, ± thin-walled, smooth, becoming wider, shorter, rhombic to fusiform and slightly thicker-walled towards apex, similar in shape, thicker-walled, porose and brownish with age towards base; marginal cells similar to adjacent median lamina cells; alar cells quadrate and thick-walled in upper part of alar group, rectangular and thinner-walled at base of group, strongly inflated, hyaline in young leaves, becoming red-brownish to bright red with age, forming very well-defined, ovate-triangular, and usually excavate group, not decurrent. **Autoicus. Perichaetia** lateral on stem above perigonia, inner perichaetal leaves straight, plicate, ovate-lanceolate to lanceolate, erect, margin entire or sinuose, serratulate near apex, apex ± gradually acuminate, costa short (rarely reaching mid-leaf, usually up to 20% of leaf length) and double or absent, upper cells linear, straight, ± thick-walled, smooth, becoming wider, linear-rectangular, inflated and thinner-walled towards base; vaginula with paraphyses. **Seta** 1.5-2.5 cm, red-brownish, twisted, smooth. **Capsule** typical for genus. **Exothecial cells** shortly rectangular, thick-walled, smooth, becoming smaller and rounded towards mouth; stomata few at base of capsule, phaneropore. **Separating annulus** present, consisting of 3 rows of large cells. **Peristome** typical: lower outside ornamentation of exostome strongly cross-striolate, border of exostome wide, widened where the ornamentation changes from cross-striolate to papillose; endostome hyaline-yellowish, basal membrane high, about 45% of endostome height, segments narrowly perforated, papillose to strongly papillose throughout, cilia 2-3, well developed, at least as long as segments or longer, nodose. **Spores** 15.0-20.0 µm, finely papillose. Sporophytes not known from Iberian specimens. **Habitat**: On rocks in or beside mountain springs. **Worldwide distribution**: Scattered in Northern, Western and Central Europe, British Islands, Faeroes, Eastern Asia, Japan and North America (Jameson, 1976). **Distribution in the Iberian Peninsula** (Fig. 23): Only found in one locality, in lowlands of Asturias. **Threat category for the Iberian Peninsula**: Extinct (EX). **Specimens examined**: **SPAIN. Asturias**: 29TPJ81, Villayón, embalse de Arbón, FCO-Brief 2796, E. Vigón, 1974.


*Linnobium palustre* Schimp., Bryol. Eur. 6: 66, 574. 1853, illegitimate, type of earlier name included.

*Hygrohypnum palustre* Loeske, Moosfl. Harz. 319. 1903, illegitimate, type of earlier name included.

**Plants** forming dense tufts, often big mats, soft to touch, older parts rarely denuded, sometimes with shredded leaves, green, green-yellowish to brownish, usually medium-sized (4-6 cm), but sometimes small and slender (1-3 cm). **Stem** usually prostrate, sometimes with ascending to erect branches, irregularly branched; stem transverse section ± rounded, with central strand, large and ± thin-walled medullar cells and 3-4 layers of very thick-walled, yellow-brownish, small cortical cells, without hyalodermis; axillary hairs scarce (1 per leaf axil), with 2-3 hyaline apical cells and 2 shortly rectangular to rectangular, brownish basal cells; pseudoparaphyllia foliose, triangular. **Rhizoids** below leaf costa insertion on ventral part of prostrate stems or branches, red-brownish, slightly branched or unbranched, smooth, variably abundant. **Stem leaves** very variable, straight, curved or falcate, concave, ovate, ovate-lanceolate or oblong-ovate, size very variable 0.4-1.0 mm wide × 0.9-2.5 mm long; closely or distantly spaced, usually erect to erect-spread, sometimes imbricate; margin plane or incurved, especially in upper part of leaf, entire; apex apiculate to abruptly and ± shortly acuminate or acute, sometimes acumen or aciculus channelled; costa variable, even among leaves on same stem, usually long and stout (up to 60-75% of leaf length), sometimes percurrent, infrequently forked or double; median lamina cells variable, long, linear, linear-flexuose, or short and rhombic, (4.0)5.0-6.5(8.5) μm wide × (25.0)45.0-60.5(90.5) μm long, ± thin-walled, smooth, similar or becoming slightly wider and shorter towards apex, towards base slightly shorter and wider, with more strongly incassate cell-walls, yellowish and porose; marginal cells similar to adjacent median lamina cells; alar cells varying from shortly rectangular to quadrate in upper part of group to rectangular and slightly inflated in lower part, usually ± thick-walled and yellowish-brown, forming a well-defined and rectangular or ovate group along basal margin, sometimes excavate, not decurrent. **Autoicus. Perichaetia** lateral on stem or branches above perigonia; inner perichaetial leaves straight, plicate, ovate-lanceolate, erect, margin entire or slightly denticulate near apex; apex shortly acuminate, costa long and single (up to 60% of leaf length) or short and double (35-50% leaf length), upper cells linear, thin-walled, smooth, becoming wider, linear-rectangular and inflated towards base; vaginula with paraphyses. **Seta** 1.2-2.5 cm, red, slightly twisted, smooth. **Capsule** typical for genus, except that it is not always constricted below mouth when dry. **Exothecial cells** shortly rectangular, thin-walled or slightly incassate, smooth, becoming smaller, rounded and with more strongly incassate cell-walls towards mouth; stomata usually abundant at base of capsule, phaneropore. **Separating annulus** absent, 2-3 rows of cells forming a persistent annulus. **Peristome** well developed; exostome yellow-brownish at base, yellow above, lower outside ornamentation cross-striolate, with larger plates than other species.
of genus, upper outside ornamentation papillose, border wide throughout, slightly widened where ornamentation changes from cross-striolate to papillose; endostome yellowish, basal membrane high, about 30-35% of endostome height, segments narrowly perforated, finely papillose, cilia 1-3, usually well developed, as long as segments, nodose. **Spores** 17.5-20.0 µm, finely papillose. Sporophytes common in Iberian specimens.

**Habitat:** On rocks in or beside streams, on wet rocks in gorges and beech woods, rarely on wood. It seems to prefer calcareous substrates, although it has also been collected on siliceous rocks.

**Worldwide distribution:** Widespread in Eurasia and North America. Scattered in Central America (Guatemala) and South America (Colombia and Bolivia) (Hedenäs, 2003). Also reported from New Guinea by Enroth & Ignatov (1999).

**Distribution in the Iberian Peninsula** (Fig. 35): Common in the Eurosiberian region, where it grows from the low montane to alpine belts (60-2000 m a.s.l.) in the Cantabrian Range (Asturias, León, Cantabria, North Burgos and Basque Country), while it is restricted to high altitudes (1000-2000 m a.s.l.) in the Pyrenees (Navarra, Huesca and Gerona). In the Mediterannean region *H. luridum* can be found in scattered localities in the high mountains (970-1800 m a.s.l.) in the Iberian Range (Burgos, La Rioja, Teruel and Cuenca) and Penibetic Range (Sierra Nevada, Granada).

**Threat category for the Iberian Peninsula:** Least concern (LC).


**Figs 29-34**


**Plants** forming ± dense tufts, rigid to touch, older parts sometimes denuded or with shedded leaves, green to green-yellowish, relatively small (1-3 cm). **Stem** usually prostrate or with a few ascending branches, irregularly branched; stem transverse section ± rounded, with central strand, large and thin-walled medullar cells and 1-2 layers of ± thick-walled yellow cortical cells, without hyaloderms; axillary hairs scarce (1 per leaf axil), with 1-3(4) hyaline apical cells and 2 quadrant to shortly rectangular and brownish basal cells; pseudoparaphyllia foliose, triangular to narrowly triangular. **Rhizoids** at base of costa or below leaf costa insertion or scattered on stem, red, unbranched, smooth, ± abundant in prostrate stems. **Stem leaves** straight, concave, ovate, 0.3-0.5 mm wide × 0.7-1.0 mm long; ± closely spaced, erect-spread; margin plane, entire or very weakly denticulate; apex abruptly acuminate, acumen sometimes channelled; costa short
(up to 50% of leaf length), double or forked near insertion, sometimes short and single; median lamina cells shortly linear-flexuose to fusiform, (3.0)5.0–6.2 μm wide × 25.0–37.5(47.5) μm long, thin-walled, smooth, becoming wider, shorter and rhombic towards apex, wider, linear-rectangular and porose towards base; marginal cells slightly shorter and wider; alar cells similar to basal cells or a few shortly rectangular to rectangular and thin-walled cells, but not forming a differentiated group. **Autoicous. Perichaetia** lateral on stem or on short lateral branches at base of stem, among perigonia, inserted very close to them on stem and usually in pairs (one perichaetium and one perigonium together), appearing virtually paroicous; inner perichaetial leaves straight, plicate, oblong-lanceolate to triangular-ovate, erect, margin entire or weakly denticulate near apex, apex abruptly acuminate, costa single, very slender or absent, upper cells linear-rectangular, thin-walled, smooth, becoming elongate-rectangular and slightly inflated towards base; vaginula with paraphyses. Sporophytes not seen, neither in Iberian specimens nor in non-Iberian specimens.

**Habitat:** Small shady hollows on mica schist rocks on boulder-rich ground in alpine glaciers.

**Worldwide distribution:** Rare. According to Hill *et al.* (1994) it has a boreal-montane distribution. It is rare in the mountain regions of Norway, Sweden, Iceland and Britain, and more frequent in the Alps, Tatra and Carpathian Mts. Outside Europe it occurs in North America, along the Rocky Mountains.

**Distribution in the Iberian Peninsula** (Fig. 23): It is only known from one locality in Sierra Nevada (Granada) at 3000 m a.s.l.
Threat category for the Iberian Peninsula: Critically endangered (CR).
Note: According to Jamieson (1976) and Smith (2004) *Hygrohypnum styriacum* is pseudoparicoicus.

Figs 36-40, Figs 46-49


Plants forming ± dense tufts or mats, very rigid to touch, older parts sometimes denuded or with shredded leaves, dark green, brownish in lower parts, relatively small to medium-sized (1-4(7) cm). Stem usually prostrate with ascending branches, usually unbranched in lower and prostrate part of stem and irregularly branched, with numerous ascending branches in upper part of stem; stem transverse section ± rounded, with central strand, large and thin-walled medullar cells and 3-4 layers of thick-walled red-brownish cortical cells, without hyalodermis; axillary hairs abundant (3-5 per leaf axil), with 2-4 hyaline-brownish apical cells and 1-2 quadrate to shortly rectangular and brownish basal cells; outer pseudoparaphyllia filamentose, inner pseudoparaphyllia foliose, broad, triangular or semi- orbicular with irregular margin. Rhizoids below leaf costa insertion in ventral part of prostrate stems or branches, red-brown, slightly branched, smooth, variably abundant. Stem leaves straight, slightly concave, broadly ovate to orbicular, sometimes ovate, 0.6-0.9(1.2) mm wide × (0.6)0.8-1.1(1.3) mm long; ± closely spaced, sometimes loosely imbricate, erect-spreading; margin plane, slightly recurved at base, entire or weakly denticulate, sometimes appearing denticulate due to re-absorption of outer wall of marginal cells; apex rounded or obtuse; costa usually single, up to 65-75% of leaf length, sometimes forked above, always very stout; median lamina cells linear-flexuoso to fusiform, 5.0-7.5 μm wide × 25.0-54.5 (62.5) μm long, thick-walled, smooth, becoming wider, shorter and rhombic to rounded towards apex, longer and wider and with more incrustate walls towards base; marginal cells shorter and wider, rhombic and sometimes hyaline; alar cells rectangular, shortly rectangular or quadrate, thick-walled, forming a vaguely differentiated group, ovate to triangular along basal margin, narrowly and longly decurrent. Autoicos. Perichaetae lateral on stem above perigonia, inner perichaetal leaves straight, plicate, ovate-lanceolate, erect, margin entire or slightly denticulate, apex acute and blunt or acuminate, costa single, almost reaching apex, and strong, upper cells linear-flexuoso, shorter and wider towards margin, ± thick-walled, smooth, becoming linear-rectangular and thin-walled towards base; vaginula with paraphyses. Seta 1.2-1.5 cm, red, slightly twisted, smooth. Capsule typical for genus. Exothecial cells shortly rectangular, thick-
Fig 46-53. SEM photographs. **46-49. Hygrohypnum smithii; 50-53. Hygrohypnum duriusculum.** Peristome (46); outside ornamentation of exostome in the region where the ornamentation changes from cross-striolate to papillose (47, 50); upper outside ornamentation of exostome (48, 52); spore (49, 53); endostome (51).
walled, smooth, becoming smaller and rounded towards mouth; stomata few at base of capsule, phaneropore. **Separating annulus** present, consisting of 2 rows of cells. **Peristome** typical, but exostome teeth narrower than in other species of genus; border of exostome narrow, not widened where ornamentation changes from cross-striolate to papillose; endostome yellowish, basal membrane high, about 45% of endostome height, segments narrowly perforated, papillose above to finely papillose below, cilia 1-2(3), poorly developed, nodose. **Spores** 12.5-17.5 µm, finely papillose. Sporophyte very common in Iberian specimens.

**Habitat:** On rocks in or beside streams or springs, rarely submerged near banks of mountain lakes.

**Worldwide distribution:** Northern Europe, mountainous areas of Central and Eastern Europe, British Islands, Iceland, Greenland, and North America (Jamieson, 1976).

**Distribution in the Iberian Peninsula** (Fig. 54): *Hygrohypnum smithii* is restricted to the alpine region (1850-2200 m) of the Pyrenees (Huesca and Lérida).

**Threat category for the Iberian Peninsula:** Nearly threatened (NT).


**Figs 41-45**


**Isolectotype:** NY.


**Plants** forming loose tufts, very soft to touch, brownish, to medium-sized (2-4 cm). **Stem** usually prostrate with ascending to erect branches, unbranched or irregularly branched; stem transverse section rounded, with central strand, long and thin-walled medullar cells and 1-2 layers (the second one usually incomplete) of thick-walled brownish cortical cells, without hyalodermis; axillary hairs ± abundant (2-3 per leaf axil), with 3-5 hyaline apical cells and 2 rectangular and brownish basal cells; outer pseudoparaphyllia filamentose, inner pseudoparaphyllia folioid, narrowly triangular (consisting of 2 rows of cells at base). **Rhizoids** below leaf costa insertion, brown, unbranched or slightly so, smooth, infrequent. **Stem leaves** straight, deeply concave, broadly ovate to oblong-elliptic or orbicular, 0.6-0.9 mm wide × (0.6)0.7-1.0(1.3) mm long; ± closely spaced, erect-spreading; margin sometimes recurved along whole leaf margin, otherwise plane, entire to sinuose; apex rounded or obtuse, sometimes acute, usually cuculate; costa short (up to 35-50% of leaf length), double or forked near insertion, sometimes short and single or forked above, always slender; median lamina cells linear-flexuose to fusiform, 5.0-6.5 μm wide × 25.0-45.5(50.5) μm long, thin-walled, smooth, becoming wider, shorter and rhombic towards apex, similar to median cells or longer, wider, and linear-rectangular towards base; marginal cells shorter and wider, rhombic and sometimes hyaline, especially in upper half of leaf; alar cells similar to basal cells or sometimes a few short rhombically to quadrate, thin-walled cells forming an indistinctly differentiated and narrowly recurrent group. **Autoicous. Perichaetia** lateral on stem, inner perichaetal leaves straight, plicate, oblong-lanceolate or ovate-lanceolate, erect, margin entire or sinuose, apex acute, costa short and single (up to 50% of leaf length), upper cells linear, ± thin-walled, smooth, becoming wider and longer, with more strongly incrassate cell walls towards base; vaginula with paraphyses. **Seta** 1.0-1.5 cm, reddish, slightly twisted, smooth. **Capsule** typical for genus. **Exothecial cells** shortly rectangular, thick-walled, smooth, becoming smaller and rounded towards mouth; stomata few at base of capsule, phaneropore. **Separating annulus** present, consisting of 2 rows of cells. **Peristome** typical; border of exostome not widened where the ornamentation changes from cross-striolate to papillose; endostome hyaline to yellowish, basal membrane high, 40-45% of endostome height, segments not or narrowly perforated, finely papillose, cilia 2-3, poorly to
well developed, nodose. **Spores** 15.0-20.0 μm, finely papillose. Sporophytes not known from Iberian specimens and very rare in non-Iberian specimens.

**Habitat:** Mountain cold stream banks.

**Worldwide distribution:** Scattered in Northern Europe, mountainous regions of Central Europe, Greenland, and North America (Jamieson, 1976).

**Distribution in the Iberian Peninsula** (Fig. 23): Pyrenees (Huesca). It has not been collected since the end of the nineteenth century.

**Threat category for the Iberian Peninsula:** Extinct (EX).

**Specimens examined:** **SPAIN. Huesca: 31TH02**, Collado de Gregorio cerca del lago, a l'O de la Maladeta, 2900 m, leg. Gouard 1873, BM.

**Note:** According to Jamieson (1976) *Hygrohypnum cochlearifolium* sexuality is unclear. However, some of the non-Iberian specimens examined for this study were autoicous, although the Iberian specimens only had perichaetia.


**Figs 50-53, Figs 55-60**


**Plants** forming ± loose tufts or mats, rigid to touch, older parts usually denuded, green to dark green, medium-sized (2-5(7) cm). **Stem** usually prostrate, sometimes with ascending branches, irregularly branched; stem transverse section elliptical-rounded, with central strand, large and ± thin-walled medullar cells and 3-4 layers of thick-walled yellowish cortical cells, without hyaloderms; axillary hairs abundant (3-5 per leaf axil), with 2-5 hyaline apical cells and 2 quadrate to transversally rectangular (wider than high) and brownish basal cells; pseudoparaphyllia foliose, broad, usually semi-orbicular with irregular margin. **Rhizoids** below leaf costa insertion on ventral part of prostrate stems or branches, red-brown, branched, smooth or slightly papillose, ± abundant. **Stem leaves** straight, slightly concave or plane, weakly plicate, oblong-elliptic to broadly ovate, sometimes almost orbicular, 0.8-1.0(1.2) mm wide × 1.3-1.5 mm long; ± distantly spaced, spreading to erect-spreading, sometimes subsecund; margin plane, narrowly recurved at base, sometimes inrolled when dry, entire to sinuose, sometimes slightly denticulate near apex, usually appearing virtually serrulate due to reabsorption of outer wall of marginal cells; apex abruptly obtuse or broadly acute, with tip blunt, sometimes rounded, rarely apiculate; costa short (33-50% of leaf length), double or forked near insertion, sometimes forked above, producing short
branches, rarely single; median lamina cells linear-flexuose to fusiform, size very variable, even among leaves on same stem, 3.0(5.0)-6.2(7.0) mm wide × 42.5-80.0(105.0) mm long, ± thin-walled, smooth, becoming wider, shorter and rhombic towards apex and wider, ± rectangular, usually brownish or yellowish, thick-walled and porose towards base; marginal cells usually wider and shorter than median lamina cells, sometimes hyaline; alar cells rectangular to quadrate or ± irregular, inflated, thick-walled, forming a well-defined group, ovate to rectangular, sometimes excavate, shortly decurrent. **Autoicous, Perichaetium** lateral on stem above perigonia; inner perichaetial leaves straight, plicate, ovate-lanceolate, erect, margin denticulate in upper third of leaf, apex acute or shortly acuminate, costa absent or weak, single or forked (up to 50% of leaf length), upper cells rhombic to fusiform, ± thick-walled, smooth, becoming rectangular or linear-rectangular and thin-walled towards base; vaginula with paraphyses. **Seta** 1.0-1.3 mm, red, twisted, smooth. **Capsule** typical for genus. **Exothecial cells** shortly rectangular to hexagonal-rounded, thick-walled, smooth, becoming smaller and rounded towards mouth; stomata few at base of capsule, phaneropore. **Separating annulus** present, consisting of 2-3 rows of cells. **Peristome** typical; border of exostome not widened where the ornamentation changes from cross-riolatie to papillose; endostome hyaline to yellowish, basal membrane high, 40-45% of endostome height, segments not or narrowly perforated, finely papillose, cilia 2-3, usually as long as segments, nodose. **Spores** 15.0-20.0 μm, finely papillose. Sporophytes very rare in Iberian specimens.  
**Habitat:*** On rocks in cold, running mountain streams, sometimes on irrigated rocks, or rarer on soil, beside streams or close to small waterfalls. 
**Worldwide distribution:** Widespread in North Europe and mountainous areas of the rest of Europe, Northern, Western, Central and Eastern Asia, Japan, North America, and Greenland (Jamieson, 1976).

**Distribution in the Iberian Peninsula** (Fig. 66): Relatively common in the Pyrenees (Andorra, Lérida, Gerona) from 900 to 2400 m a.s.l. and in the Penibetic Range (Sierra Nevada, Granada), where it occurs at higher altitudes (2750-2900 m a.s.l.). Rare in the montane to alpine belts (700-1600 m a.s.l.) of the Cantabrian Range (Asturias and León), and alpine areas (1200-1650 m a.s.l.) of the Iberian (Soria) and Central Ranges (Madrid).

**Threat category for the Iberian Peninsula:** Least concern (LC).

**Selected specimens examined:** **ANDORRA.** 31TCH71, Riu de la Coma del Forat, BCB 37808, Casas, 1978.  

8. **Hygrohypnum molle** (Hedw.) Loeske, Moosfl. Harz.: 320, 1903.  
**Figs 61-65, Figs 67-70**  
Fig. 66. Distribution map of *Hygrohypnum durianicum* in the Iberian Peninsula. ● confirmed occurrence (10 × 10 km square).


**Plants** forming loose tufts or mats, soft to touch, usually foliose throughout, rarely denuded in older parts, green, yellow-green, dark green to brown in lower parts, medium-sized (3-6(8) cm). **Stem** usually prostrate, sometimes with ascending branches, irregularly branched; stem transverse section elliptical, with central strand, large and ± thin-walled medullar cells and 2-3 layers of thick-walled yellowish or reddish cortical cells, without hyalodermis; axillary hairs abundant (3-6(8) per leaf axil), with 2-3(4) hyaline-brownish apical cells and 2 quadrate to rectangular (higher than wide) and brownish basal cells; pseudoparaphyllia foliose, broad, usually semi-orbicular with irregular margin. **Rhizoids** below leaf costa insertion on ventral part of prostrate stems or branches, red-brown, slightly branched, smooth, variably abundant. **Stem leaves** straight, slightly concave to concave, broadly ovate, sometimes ovate, tapering gradually to apex, (0.7)0.9-1.2 mm wide × 1.3-2.1 mm long; ± closely spaced, loosely imbricate to spreading, infrequently subsecund; margin plane, slightly recurved at base, entire to sinuose in lower half, usually denticulate in upper half; apex gradually acute, with tip blunt;
costa short and double or forked near insertion, usually both branches reaching mid-leaf or beyond, rarely single or forked above; median lamina cells linear-flexuose to fusiform, size ± uniform, 3.7-7.5 μm wide × (25.0)32.5-62.5(70.0) μm long, thin-walled, smooth, becoming wider, shorter and rhombic or short fusiform towards apex and sometimes wider, linear-rectangular, and infrequently more strongly incrassate towards base; marginal cells usually similar to median cells, sometimes wider in upper leaf; alar cells not differentiated or a few rectangular, shortly rectangular to quadrate cells, slightly more incrassate than surrounding cells, not forming a differentiated group, narrowly decurrent. **Autoicous. Perichaetia** lateral on stem above perigonia, inner perichaetial leaves straight, plicate, lanceolate, erect, margin denticulate, at least in upper third of leaf, apex acute, costa absent or weak, single or forked (up to 50% of leaf length), upper cells rhombic to fusiform, ± thick-walled, prorate, becoming linear-rectangular, thin-walled and smooth towards base; vaginula with paraphyses. **Seta** 0.7-1.0 cm, red, twisted, smooth. **Capsule** typical for genus. **Exothecial cells** shorty rectangular to hexagonal-rounded, thick-walled, smooth, becoming smaller and rounded towards mouth; stomata few at base of capsule, phaneropore. **Separating annulus** present, consisting of 2-3 rows of cells. **Peristome** typical; border of exostome not widened where ornamentation changes from cross-striolate to papillose; endostome hyaline to yellowish, basal membrane high, 40-45% of endostome height, segments narrowly perforated, finely papillose, almost smooth, cilia 2-3 usually short, rudimentary, nodose. **Spores** 17.5-25.0 μm, finely papillose. Sporophytes very rare in Iberian specimens.

**Habitat:** On rocks in or beside cold, running mountain streams.
Fig. 71. Distribution map of *Hygrohypnum molle* in the Iberian Peninsula. ● confirmed occurrence (10 × 10 km square).

**Worldwide distribution:** Northern Europe, mountainous areas of Western and Central Europe, British Islands, North America and Greenland (Jamieson, 1976).

**Distribution in the Iberian Peninsula** (Fig. 71): Scattered in the alpine region (1700-2450 m a.s.l.) of the Pyrenees (Lérida and Gerona), in the Cantabrian Range (León) (about 1200 m a.s.l.), and in the Penibetic Range (Sierra Nevada, Granada), where *Hygrohypnum molle* grows at very high altitudes (1600-2880 m a.s.l.).

**Threat category for the Iberian Peninsula:** Vulnerable (VU).


**DISCUSSION**

**Taxonomy**

*Hygrohypnum* species, as many other aquatic mosses, are extremely variable. This is evidenced by the large number of names that Jamieson (1976) synonymized. For instance he reduced to the status of synonyms of *H. luridum* no less than 80 names, and at least 30 names were synonymized with *H. ochraceum*. It seems that slight differences in water regime can induce variation in morphology (Kanda, 1975), at least in some characters such as leaf size, shape and
symmetry, leaf orientation or costa structure. These plastic characters are precisely some of the most commonly used in the traditional taxonomic treatments of pleurocarpous mosses.

Leaf shape and symmetry, leaf orientation or costa structure may be useful for the identification of *Hygrohypnum* specimens at the species level, although they have to be used with caution and always in combination with other less plastic characters. In our experience the most taxonomically useful characters for *Hygrohypnum* species are: presence or absence of a hyalodermis in the stem, differentiation of alar cells and alar groups, number of axillary hairs per leaf axil and number of apical cells per axillary hair, shape of pseudoparaphyllia, sexual condition, proration of upper cells of perichaetal leaves, and presence or absence of a separating annulus in sporophytes.

Attending only to a few plastic characters, as those mentioned above, that were used as key characters in many old taxonomic treatments, Spanish bryologists made many mistakes in the identification of *Hygrohypnum* species and other aquatic or wetland mosses. The most frequently misidentified species in the genus are *Hygrohypnum ochraceum* and *H. luridum*. They have been confused with each other or with other aquatic species, such as *Brachythecium rivulare* Schimp. and *Eurhynchium* species. However, the similarity among them is only superficial, and they can be easily differentiated under a microscope. Table 2 clarifies the differences between *H. ochraceum* and *H. luridum*.

*Hygrohypnum molle* has frequently been confused with *H. duriusculum*. Both species are truly very similar, and the delimitation between them was not clear for a long time. Schimper (1853) synonymized *Hypnum molle* Hedw. with his own species *Limnobium molle* Schimp., but later Wilson (in Schimper, 1860) appreciated a difference between the type specimens of *Hypnum molle* and Schimper's concept of *Limnobium molle*, and decided to give a new name, *Hypnum dilatatum*, for the specimens fitting Schimper's description. Ulterior taxonomic treatments of *Hygrohypnum* (e.g. Nyholm, 1965; Jamieson, 1976) pointed out additional differences between these species and clarified their circumscription. Table 3 provides the characters that differentiate Iberian specimens belonging to *Hygrohypnum duriusculum* and *H. molle*.

Table 2. Differential characters between *Hygrohypnum ochraceum* and *Hygrohypnum luridum*.

<table>
<thead>
<tr>
<th>Character</th>
<th><em>Hygrohypnum ochraceum</em></th>
<th><em>Hygrohypnum luridum</em></th>
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<tbody>
<tr>
<td>Stem transverse section</td>
<td>Hyalodermis present</td>
<td>Hyalodermis absent</td>
</tr>
<tr>
<td>Axillary hairs</td>
<td>1-3 per leaf axil, very long, with 5-6 hyaline-brownish apical cells</td>
<td>1 per leaf axil, short, with 2-3 hyaline apical cells</td>
</tr>
<tr>
<td>Pseudoparaphyllia</td>
<td>Broadly triangular to semi- orbicular</td>
<td>Triangular</td>
</tr>
<tr>
<td>Alar cells</td>
<td>2-3 rows of quadrate to rectangular thin-walled, hyaline cells</td>
<td>Numerous quadrate or shortly rectangular cells, thick-walled and usually yellowish-brown</td>
</tr>
<tr>
<td>Sexuality</td>
<td>Dioicous</td>
<td>Autoicous</td>
</tr>
<tr>
<td>Separating annulus</td>
<td>Present</td>
<td>Absent</td>
</tr>
</tbody>
</table>
Colmeiro (1867) reported *Hygrohypnum molle* as “*Hypnum molle* Dicks.” in Sierra Nevada, and included “*Hypnum alpestre* Sw.” as a synonym of that name. The similarity of *Hygrohypnum molle* and *H. alpestre* was noted in some early works (e.g. Bridel, 1812, 1827; Sprengel, 1827), and even Schimper (1853) illustrated *H. alpestre* with a drawing that actually corresponds to *H. molle*.

In view of the unclear delimitation of *H. molle* at that time, it is not surprising that Colmeiro (1867), and later Casares Gil (1915), considered both species to be synonymous. Nevertheless, no material from Sierra Nevada belonging to *Hygrohypnum alpestre* has been found during this revision, whereas *Hygrohypnum molle* is relatively common in the area. Casas (1981) included *Hygrohypnum alpestre* in the checklist of mosses of Spain, noting that Seró found this species in the Pyrenees (Portarró d’Esport). However, that specimen was later revised by Pierrot and re-identified as *Hygrohypnum molle*, and therefore *Hygrohypnum alpestre* was excluded from the Iberian bryophyte flora (cf. Casas, 1991). Table 4 shows the main differences between *Hygrohypnum alpestre* and *H. molle*.

*Hygrohypnum polare* was recorded from the Spanish Pyrenees (Allorge & Casas, 1976). However, this species is not included neither in the catalogue of bryophytes from the Spanish Pyrenees (Casas, 1986), nor in the Catalanian bryophyte flora (Casas et al., 2001). Therefore, we can only assume that the specimen of *H. polare* recorded by Allorge & Casas (1976) was misidentified and later re-identified, although we could not find that specimen when checking PC or BCB. No other specimen belonging to *H. polare* has been found in any of the herbaria revised for this work. Consequently *H. polare* is excluded from the Iberian bryophyte flora.

The rest of the *Hygrohypnum* species occurring in the Iberian Peninsula are very distinct, and do not present identification problems.

Table 3. Differential characters between *Hygrohypnum duriusculum* and *Hygrohypnum molle*.

<table>
<thead>
<tr>
<th>Character</th>
<th><em>Hygrohypnum duriusculum</em></th>
<th><em>Hygrohypnum molle</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Stem transverse section</td>
<td>2-3 layers of small, thick-walled cortical cells</td>
<td>3-4 layers of small, thick-walled cortical cells</td>
</tr>
<tr>
<td>Leaf shape</td>
<td>Oblong-elliptic to broadly ovate, sometimes orbicular</td>
<td>Usually broadly ovate to ovate</td>
</tr>
<tr>
<td>Leaf apex</td>
<td>Abruptly obtuse or broadly acute, sometimes rounded, rarely apiculate</td>
<td>Usually gradually acute</td>
</tr>
<tr>
<td>Alar cells</td>
<td>Rectangular to quadrate or irregular, inflated, thick-walled, forming a well-defined group</td>
<td>Undifferentiated</td>
</tr>
<tr>
<td>Upper cells of perichaetal leaves</td>
<td>Smooth</td>
<td>Usually prorate</td>
</tr>
</tbody>
</table>
Table 4. Differential characters between *Hygrohypnum alpestre* and *Hygrohypnum molle*.

<table>
<thead>
<tr>
<th></th>
<th><em>Hygrohypnum alpestre</em></th>
<th><em>Hygrohypnum molle</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf shape</td>
<td>Oval to oblong-ovate</td>
<td>Usually broadly ovate to ovate</td>
</tr>
<tr>
<td>Leaf apex</td>
<td>Abruptly acute or apiculate.</td>
<td>Usually gradually acute. Tip plane</td>
</tr>
<tr>
<td>Leaf concavity</td>
<td>Deeply concave</td>
<td>Slightly concave to concave</td>
</tr>
<tr>
<td>Alar cells</td>
<td>Quadrate to rectangular, forming a well-developed group</td>
<td>Undifferentiated</td>
</tr>
<tr>
<td>Upper cells of perichaetal leaves</td>
<td>Smooth</td>
<td>Usually prorate</td>
</tr>
</tbody>
</table>

**Habitat and distribution in the Iberian Peninsula**

*Hygrohypnum ochraceum* and *H. luridum* are the most widespread species of the genus in the Iberian Peninsula, and both occur at a wide range of altitudes (1940 and 2317 m respectively). The same pattern is observed in their global distribution; both are the most widespread species of *Hygrohypnum* in the world. This is likely due to their relatively wider range of habitat preferences. *Hygrohypnum luridum* is the species that is found in the most diverse habitats. It has even been found growing epiphytically in Scotland, which led to the description of a new species *Pictus scoticus* C.C. Towns., which, in our opinion, is no more than an atypical form of *H. luridum*. Considering that *H. luridum* has some sporophytic characters more typical of epiphytic mosses, like the absence of a separating annulus, it is not so strange that *H. luridum* can grow as an epiphyte.

All the specimens from the Central Range previously identified as *Hygrohypnum luridum* were misidentified. It seems that this species prefers calcareous substrata, and maybe that is the reason why it does not grow on the granitic substrata of the Central Range. The occurrence of *Hygrohypnum luridum* in Serra do Bussaco (Portugal) has not been confirmed, since no material from this locality was found in the revised herbaria (see Fig. 35). *H. luridum* was recorded in Serra do Bussaco in 1889, and it has not been collected there again (cf. Alcorge, 1974). Consequently this species is excluded from the Portuguese bryophyte flora, *H. ochraceum* being the only species of *Hygrohypnum* present in Portugal.

*Hygrohypnum duriusculum* and *H. molle* have similar habitat preferences, although *H. molle* occurs above 1200 m a.s.l., while *H. duriusculum* can be found from 700 m a.s.l., which may indicate that *H. duriusculum* is able to live in streams with warmer water than required for *H. molle*. This could explain why *H. molle* is less frequent than *H. duriusculum* in the Iberian Peninsula (see Figs 66, 71).

*Hygrohypnum ochraceum, H. luridum, H. duriusculum, and H. molle* have a distribution pattern that is very common among Iberian bryophyte species. They occur in the alpine regions, above 1200 m a.s.l., in the inland mountainous areas of the Iberian Peninsula, but grow at lower altitudes, sometimes below 100 m a.s.l., in the Cantabrian Range thanks to the Atlantic influence that allows many plants with high humidity requirements to grow at lower altitudes than they do in the more continental interior mountain ranges.
Hygrohypnum cochlearifolium was collected in the Spanish Pyrenees by Gouard in 1873, and described by Schimper (1876) as a new species, Hypnum goulardii Schimp. According to Casares Gil (1915), Gouard collected H. cochlearifolium in two localities in the Pyrenees (Valle de Arán and Collado Gregorio). However, only the material from Collado Gregorio has been found in the herbaria checked during this study. This species has never been collected again in the Iberian Peninsula, and the type specimens of H. goulardii are the only representatives of the species in the area.

Although Hygrohypnum eugyrium was already known in the French Pyrenees since the end of the nineteenth century (Jeanbernat & Renaud, 1885), it has not been found in the Spanish Pyrenees, and the only record for this species corresponds to Simó & Vigón (1977) in the Cantabrian Range (Asturias).

Conservation

According to Sérgio et al. (1994) Hygrohypnum cochlearifolium, H. eugyrium and H. molle are considered species in Spain and the Iberian Peninsula. Hygrohypnum smithii is considered to be rare in Spain and the Iberian Peninsula. Hygrohypnum luridum is extinct in Portugal, and H. polare is extinct in the whole Iberian Peninsula.

Our results disagree with those of Sérgio et al. in the treatment of Hygrohypnum cochlearifolium and H. eugyrium. Both species have only been recorded from one 10 km × 10 km square and one locality, but these records are not recent. H. cochlearifolium was collected in 1873 and H. eugyrium in 1974. Both species should therefore be considered as extinct (EX) in the Iberian Peninsula. Sérgio et al. (1994) listed Hygrohypnum polare as extinct in Spain and the Iberian Peninsula. However, as mentioned above we believe that this species never occurred in the Iberian Peninsula.

So far Hygrohypnum smithii has been recorded in six 10 km × 10 km squares and eleven localities (Fig. 54), all of them in the Pyrenees, agreeing only with the first part of criterion B as defined by Hallingbäck et al. (1998), therefore it cannot be considered as a vulnerable species in the Iberian Peninsula. Besides, the authors have observed that the populations of this species in the Pyrenees are large and usually have sporophytes, which suggests that they are in good condition.

Hygrohypnum styriacum has been very recently recorded for the first time in the Iberian Peninsula (Rams & Oliván, 2006), and therefore it is considered here as critically endangered (CR). However, it is likely that more finds will be made now that its occurrence is known.

Although the situation of some of the species of Hygrohypnum in the Iberian Peninsula is critical, none of them are threatened in Europe as a whole (Schumacker & Martiny, 1995). This is probably due to the marginal geographic distribution of all the populations of Hygrohypnum in the Iberian Peninsula, which form the south-western limit of their distribution area in the Paleartic Region.

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