

# A survey of the epiphytic bryophyte flora of the Rif and Tazzeka Mountains (northern Morocco)

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## SUMMARY

The catalogue of the epiphytic bryophyte flora of the Rif Mountains includes a total of 72 taxa, of which 66 are mosses and six are liverworts. Some new records are provided: *Hypnum resupinatum* and *Tortula israelis*, new to northern Africa, *Antitrichia curtispindula* and *Cryphaea heteromalla*, new to Morocco, and *Dicranoweisia cirrata*, *Isothecium alopecuroides* and *Orthotrichum macrocephalum*, new to the Rif Mountains. Epiphytic communities in the different forest types have been analysed, with the conclusion that altitude and humidity are the main factors that determine their composition. The epiphytic stratum is best developed at the highest altitudes on the Principal chain and Tazzeka Mountain, where taxa of the genus *Orthotrichum* dominate or co-dominate the epiphytic communities: *O. lyellii* and *Antitrichia californica* co-dominate in the montane zones, while *O. speciosum* var. *brevisetum* and *Pterigynandrum filiforme* co-dominate at the highest altitudes. In lower areas, the abundance of epiphytic bryophytes depends on humidity conditions and the presence of a forest canopy. The best preserved forests, where exposed to oceanic winds, are dominated by hygrophilous taxa, such as *Neckera pumila*, *Cryphaea heteromalla* and *Frullania dilatata*, whereas the dry ones are dominated by thermophilous taxa, such as *Orthotrichum tenellum*. Finally, ubiquitous species, such as *Orthotrichum diaphanum* and *Bryum capillare*, are abundant in disturbed forests.

KEYWORDS: Epiphytes, vegetation, mosses, liverworts, northern Africa.

## INTRODUCTION

The Rif Mountains of Morocco extend from the Strait of Gibraltar in the west to the River Moulouya in the east, and have their southern limit in the Sebou basin (Fig. 1). Tazzeka Mountain, which lies to the southeast of the River Sebou, is floristically closer to these mountains than to the Atlas range (Valdés *et al.*, 2002), and has also been included in the study area. Lithologically, the Rif Mountains are formed from a deposit of clay and schists at the tops and northern slopes and from clayey marls on the southern slopes. Additionally, calcareous materials appear to the north of Bab Taza city and on Tazzeka Mountain. The eastern region is formed from marl, slate, sandstone and acidic sedimentary rocks, and the Sebou basin is composed of sands (Boudy, 1948; Nègre, 1959). The whole is subject to a Mediterranean climate softened by its proximity to the Atlantic Ocean. Most of the rainfall is provided by the contact of the humid Atlantic winds with the mountains. Thus, the central and western areas of the Rif range present the highest annual rainfall of Morocco, with 2168 mm on

Bou Hachem Mountain and 1743 mm on Outka Peak. Precipitation gradually decreases at lower altitudes and, to the east, to less than 500 mm. The Atlantic influence is also shown in the moderate temperatures, with an annual average of nearly 17°C (Boudy, 1948).

The variety of rock types and climatic conditions favours the development of a great diversity of plant formations (Fig. 2). The lowest altitudes are covered by *Quercus suber* L. forests on siliceous soils, *Olea europaea* L. woods on clayey soils, *Tetraclinis articulata* (Vahl) Masters groves on calcareous soils and *Pinus halepensis* Miller woods on the poorest soils. At middle altitudes, the evergreen *Quercus ilex* L. subsp. *ballota* (Desf.) Samp. grows mainly on sunny slopes, while on shady slopes it alternates with marcescent (trees whose leaves wither but do not fall off oaks): *Q. faginea* Lam. in the western part, *Q. pyrenaica* Willd. in the central area and *Q. canariensis* Willd. on Tazzeka Mountain. *Abies maroccana* Trabut grows at the uppermost level of the western area, while *Cedrus atlantica* (Endl.) Carrière constitutes the uppermost woods in the central part and on Tazzeka Mountain. Finally, there are also

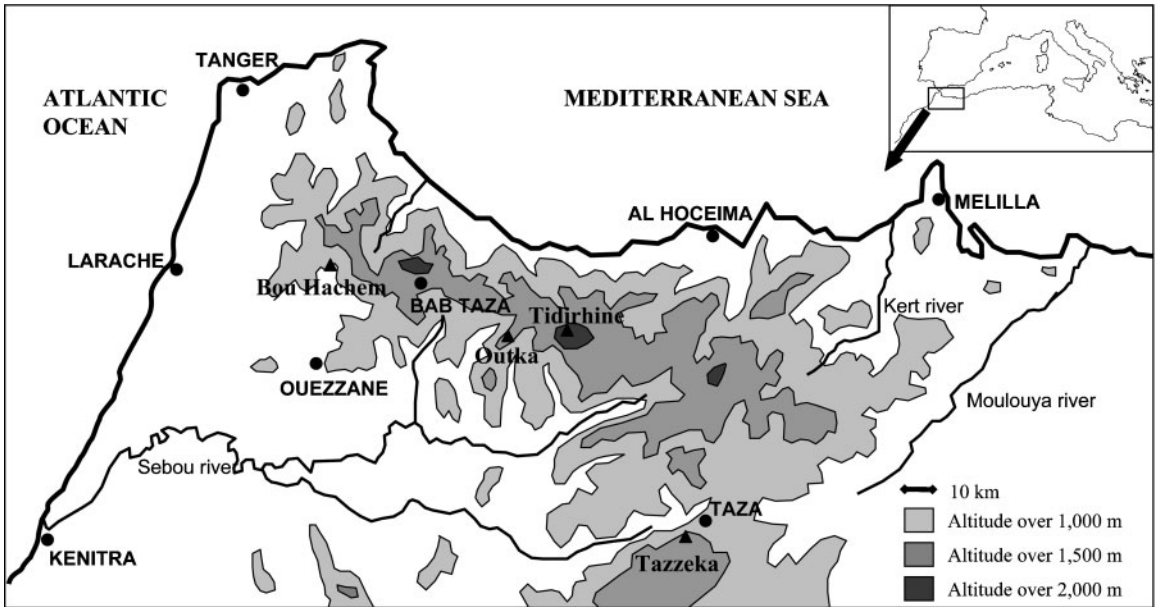


Figure 1. Location of the study area.

plant formations bound to certain edaphic and moisture conditions, like *Prunus lusitanica* L. groves or riparian vegetation (Charco, 1999).

Despite the high interest of this rich area, its bryophyte flora is still little known (Ros, Cano & Guerra, 1999; Cano et al., 2002; Jiménez et al., 2002a, b; Draper et al., 2003). This study aims to increase knowledge of its bryophytes, providing a catalogue of the epiphytic taxa and describing the communities that grow on tree trunks.

METHODOLOGY

Field work was carried out in 96 localities, visited between 1994 and 2002. Epiphytic bryophytes were found in 61 of

these localities, whose geographical details are summarized in the Appendix. Samples of 20 × 20 cm were taken both from the tree bases and trunks on all types of phorophytes in each locality. For a clearer understanding of epiphytic bryophyte ecology and distribution, the study area has been divided into four geographical zones (Ruiz de la Torre, 1957): the Larache sector, the principal chain (including the Tingitane chain, the central Rif and the Al Hoceima sector), the Kert sector and Tazzeke Mountain (Fig. 3). In these areas, localities have been aggregated in groups of similar forest types, as shown in Table 1.

A list of the epiphytic bryophytes found in the study area is presented in alphabetical order in Table 2. Nomenclature

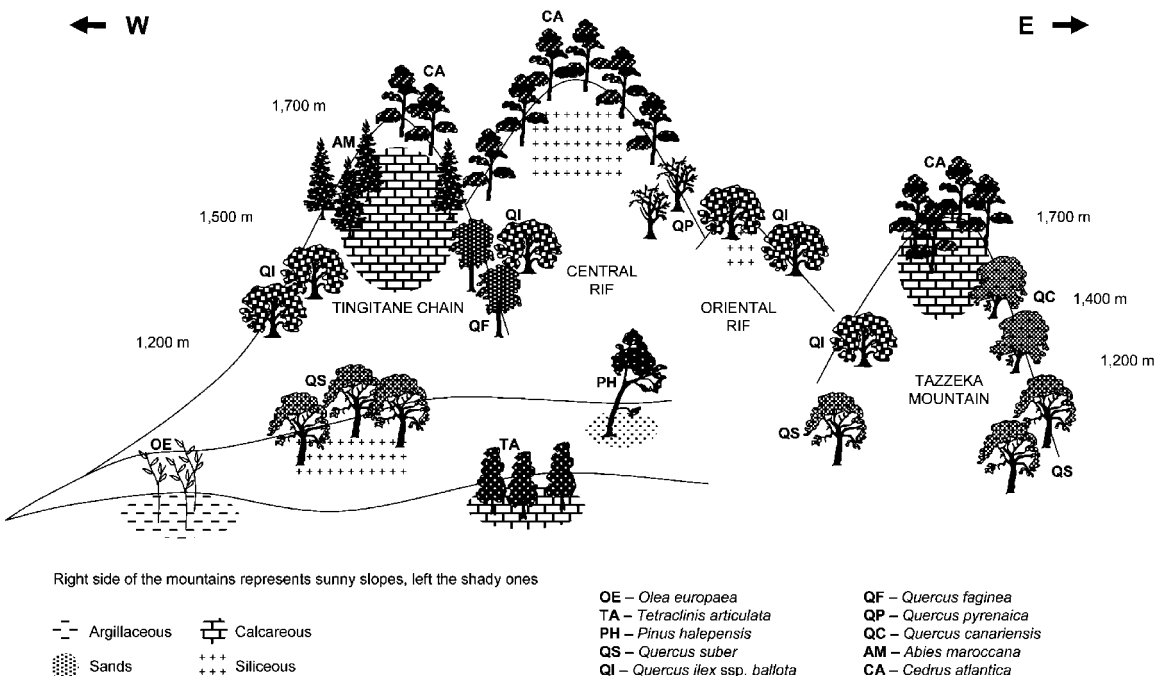


Figure 2. Schematic representation of forest types in the study area, according to their location on the mountain slopes.

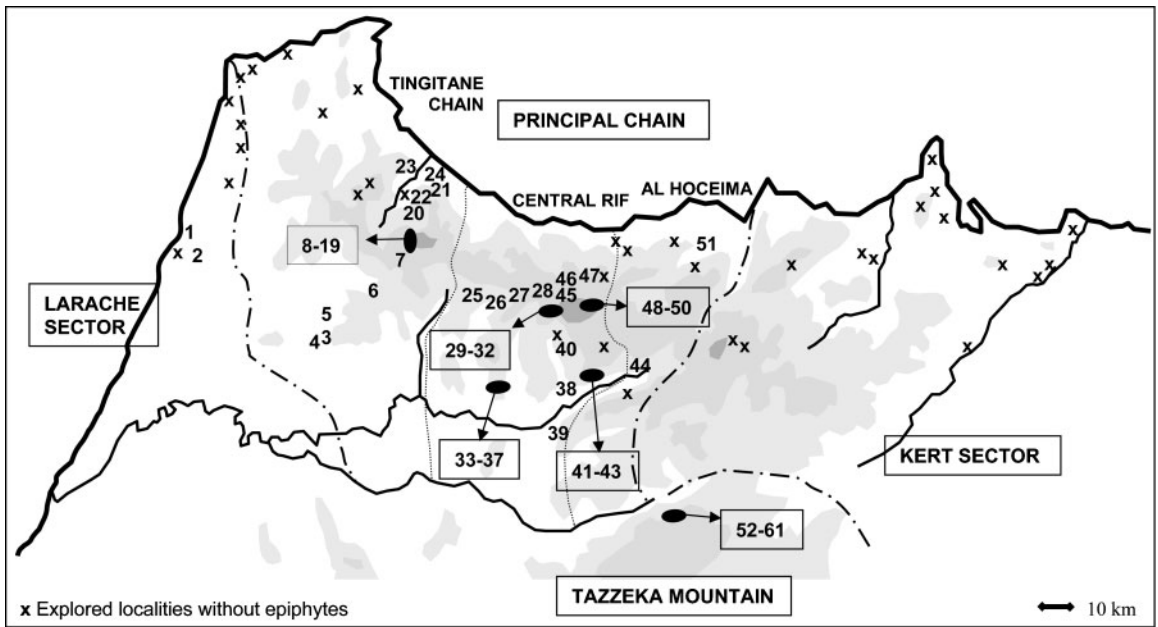


Figure 3. Locations of the sampling sites.

follows Ros, Cano & Guerra (1999), with the exceptions of the genera *Didymodon* Hedw. (Jiménez, 2003), *Schistidium* Bruch & Schimp. (Blom, 1996), *Orthotrichum* Hedw. (Cortini & Lara, 2001), *Syntrichia* Brid. (Gallego, 2002) and *Thamnobryum* Nieuwl. (Stech, Ros & Werner, 2001). Author names follow the world checklist of Crosby *et al.* (1999). Sites where the taxa were recorded are identified in Table 1 and the Appendix.

Taxon abundance has been estimated for each forest type using the Index of Ecological Significance (IES: Lara & Mazimpaka, 1998). The values of this index have been combined in the following classes of abundance: very scarce (<50), scarce (51–100), moderately abundant (101–200), abundant (201–300) and dominant (>301). A correspondence analysis was used to explore bryofloristic relationships among the different forest types. The use of an indirect

unimodal analysis like correspondence analysis is justified because no arch effect was observed and the length of the gradient for axis 1 was around 4 SD (ter Braak & Šmilauer, 1998).

## RESULTS

### Flora

The epiphytic bryophyte flora of the Rif Mountains and Tazzeka is composed of 72 taxa, of which 66 are mosses and six are liverworts (Tables 2 & 3). As usual in the Mediterranean habitats of epiphytes, the genus *Orthotrichum* is the most important, both in number of taxa and abundance (Table 3). The most constant and abundant species in the epiphytic stratum of the Rif

Table 1. Localities aggregated by forest type. Localities with few data are omitted.

Forest type	Geographical zone	Code	Localities
<i>Quercus suber</i> L.	Larache sector	QS1	1, 2
	Western Tingitane chain	QS2	3, 4, 5, 6
	Eastern Tingitane chain	QS3	8, 9
	Central Rif	QS4	25, 33, 34
	Al Hoceima sector	QS5	51
	Tazzeka Mountain	QS6	52, 53
<i>Quercus ilex</i> L. ssp. <i>ballota</i> (Desf.) Samp.	Eastern Tingitane chain	QI1	10, 11
	Al Hoceima sector	QI2	41, 42, 43
	Tazzeka Mountain	QI3	54, 55, 56
<i>Quercus faginea</i> Lam.	Eastern Tingitane chain	QF	12, 13
<i>Quercus pyrenaica</i> Willd.	Central Rif	QP	26, 35, 36, 37
<i>Quercus canariensis</i> Willd.	Tazzeka Mountain	QC	57, 58
<i>Abies maroccana</i> Trabut	Eastern Tingitane chain	AM	14, 15, 16, 17
<i>Cedrus atlantica</i> (Endl.) Carrière	Eastern Tingitane chain	CA1	7, 18, 19
	Central Rif	CA2	29, 30, 32, 46, 49
	Tazzeka Mountain	CA3	59, 60, 61
<i>Pinus halepensis</i> Miller	Central Rif	PH	39
<i>Prunus lusitanica</i> L.	Central Rif	PL	28, 50

**Table 2.** Bryophytes recorded in the Rif and Tazzeke Mountains. Sites are given according to the localities aggregated in Table 1 and numbers in the Appendix. Chorological novelties: \*new to the Rif range; \*\*new to Morocco; \*\*\*new to Northern Africa.

	Localities
<b>Marchantiophyta</b>	
<i>Frullania dilatata</i> (L.) Dumort.	QS1(1, 2); QS2(3, 4, 5, 6); QS3(8); QS4(25, 34); QS5(51); QI1(10, 11); QI2(42); QI3(55); QF(12, 13); AM(14); CA1(18); CA2(46, 49); CA3(59); PL(50); other woods (21, 48)
<i>Lejeunea cavifolia</i> (Ehrh.) Lindb.	QS2(3); other woods (23)
<i>Metzgeria furcata</i> (L.) Dumort.	QS2(3, 5); QS4(25)
<i>Porella platyphylla</i> (L.) Pfeiff.	QF(13); AM(16, 17)
<i>Radula complanata</i> (L.) Dumort.	QS2(3, 4, 5); QS4(25); CA2(49); PL(28, 50)
<i>Radula lindenbergiana</i> Gottsche ex C.Hartm.	QS2(3, 4, 5)
<b>Bryophyta</b>	
<i>Antitrichia californica</i> Sull.	QS2(6); QS3(8, 9); QS4(25, 33); QS6(52, 53); QI1(10, 11); QI2(42); QI3(54, 56); QF(12, 13); QP(26, 35, 36); QC(57, 58); AM(14); CA2(46, 49); PL(50); other woods (45, 48)
** <i>Antitrichia curtispindula</i> (Hedw.) Brid.	QS4(25); CA2(49)
<i>Barbula unguiculata</i> Hedw.	QS2(3)
<i>Brachythecium dieckei</i> Röll	QS3(9); QP(26); CA2(29, 32, 46); other woods (27, 45, 47)
<i>Brachythecium velutinum</i> (Hedw.) Schimp.	QS3(9); QI1(11); QI3(55, 56); QF(12, 13); QC(57); AM(14); CA2(49); CA3(59); PL(50); other woods (31, 47, 48)
<i>Bryum capillare</i> Hedw.	QS1(1, 2); QS2(3); QS5(51); QI2(42); other woods (20)
<i>Ceratodon purpureus</i> (Hedw.) Brid.	QS3(8)
** <i>Cryphaea heteromalla</i> (Hedw.) D.Mohr	QS1(1); QS2(3, 4, 5, 6); QS4(25); QI2(41); QP(26)
<i>Dialytrichia mucronata</i> (Brid.) Broth.	QS2(3, 5); QI2(42)
* <i>Dicranoweisia cirrata</i> (Hedw.) Lindb.	QS1(1); QS3(8); QI2(41); QI3(54, 56); CA2(46, 49); other woods (27, 40, 44, 45, 47)
<i>Didymodon fallax</i> (Hedw.) R.H.Zander	QS5(51)
<i>Didymodon insulanus</i> (De Not.) M.O.Hill	QS6(52); AM(14); other woods (45, 47)
<i>Eurhynchium praelongum</i> (Hedw.) Schimp.	QS2(5); QI1(10); other woods (27)
<i>Fabronia pusilla</i> Raddi	QS2(3, 5, 6); QS3(9); QS4(34); QS6(52); QI1(10, 11); QI2(41, 42, 43); QI3(54, 56); other woods (44)
<i>Grimmia pulvinata</i> (Hedw.) Sm.	QS5(51); QI1(11); PH(39); other woods (38)
<i>Grimmia trichophylla</i> Grev.	QS3(9); QS4(25, 33); AM(14); CA2(32, 46); CA3(59, 60); PH(39); other woods (27, 45, 47, 48)
<i>Habrodon perpusillus</i> (De Not.) Lindb.	QS1(1); QS2(3, 5, 6); QS6(52); QI1(11); QI2(42); QI3(54); QF(12, 13); QP(37); AM(14); PH(39)
<i>Homalothecium aureum</i> (Spruce) H.Rob.	QS2(5); QS3(9); QS5(51); QI1(11); QI2(41); QF(12); AM(14); other woods (45)
<i>Homalothecium sericeum</i> (Hedw.) Schimp.	QS1(1); QS2(3); QS3(9); QS4(25); QI1(11); QI3(54, 55, 56); QF(12, 13); QP(26, 35, 36); QC(57, 58); AM(14, 17); CA1(18); CA2(46, 49); PL(28, 50); other woods (20, 48)
<i>Hypnum cupressiforme</i> Hedw.	QS2(3, 4, 5, 6); QS3(9); QS4(25, 33); QS5(51); QF(12, 13); AM(14); CA2(49); PL(28, 50)
*** <i>Hypnum resupinatum</i> Taylor	QS1(1); QS2(3, 4, 6)
* <i>Isoetecium alopecuroides</i> (Lam. ex Dubois) Isov.	QF(13); CA2(49); PL(28, 50)
<i>Isoetecium myosuroides</i> Brid.	QS2(6); QF(12); PL(50)
<i>Leptodon smithii</i> (Hedw.) F.Weber & D.Mohr	QS1(1, 2); QS2(3, 5, 6); QS4(25); QI2(42); QF(12); CA2(49); CA3(59); PL(50); other woods (23)
<i>Leucodon sciuroides</i> (Hedw.) Schwägr. var. <i>morensis</i> (Schwägr.) De Not.	QF(12, 13); QI2(41); QI3(56); QC(57); AM(14)
<i>Leucodon sciuroides</i> (Hedw.) Schwägr. var. <i>sciuroides</i>	QS3(9); QI2(42); QI3(56); QF(13); AM(14); CA1(18)
<i>Metaneckera menziesii</i> (Hook.) Steere	QF(12, 13)
<i>Neckera pumila</i> Hedw.	QS4(25); CA2(49); PL(28, 50); other woods (48)
<i>Orthotrichum acuminatum</i> H. Philib.	QS2(5); QS3(8, 9); QS4(34); QS6(52); QI1(11); QI2(41, 42); QI3(54, 55, 56); QF(12); QP(37); QC(57, 58); AM(14, 15, 16, 17); CA1(18); CA2(46, 49); CA3(59, 60, 61); PH(39); PL(28, 50); other woods (31, 38, 44, 45, 47, 48)
<i>Orthotrichum affine</i> Brid.	QS1(1); QS3(8); QS4(33); QS6(52); QI1(10, 11); QI3(55); QF(12); QP(26, 36, 37); QC(57, 58); AM(14, 16, 17); CA1(18); CA2(46, 49); CA3(60, 61); PH(39); PL(28, 50); other woods (31, 45, 47, 48)
<i>Orthotrichum cupulatum</i> Brid.	AM(14); other woods (38)
<i>Orthotrichum diaphanum</i> Brid.	QS1(1, 2); QS2(3, 4, 5); QS5(51); QS6(52); QI2(41, 42, 43); PH(39); other woods (22, 23, 38, 47)
<i>Orthotrichum ibericum</i> F. Lara & Mazimpaka	QI1(11); QF(12); QP(37); AM(17); other woods (31, 45, 47, 48)

Table 2. Continued

	Localities
<i>Orthotrichum lyellii</i> Hook. & Taylor	QS1(1); QS2(3, 4, 5, 6); QS3(8, 9); QS4(25, 33, 34); QS5(51); QS6(52, 53); QI1(10, 11); QI2(41, 42); QI3(54, 55, 56); QF(12, 13); QP(26, 35, 36, 37); QC(57, 58); AM(14, 15, 16, 17); CA1(7, 18); CA2(46, 49); CA3(59, 60, 61); PH(39); PL(28, 50); other woods (27, 31, 38, 40, 44, 45, 47, 48)
* <i>Orthotrichum macrocephalum</i> F.Lara, Garilleti & Mazimpaka	QS6(52); PH(39)
<i>Orthotrichum pallens</i> Bruch ex Brid.	QF(12); AM(16); CA2(49); CA3(59,60,61); PL(50); Other woods (31,44,48)
<i>Orthotrichum philibertii</i> Venturi	QS6(52,53); QI2(42); PH(39)
<i>Orthotrichum pumilum</i> Sw.	QC(58); CA3(59,60)
<i>Orthotrichum rupestre</i> Schleich. ex Schwägr.	QS2(3,5); QS3(8,9); QS4(25,33); QS6(52); QI1(10,11); QI3(55,56); QF(12,13); QC(57,58); AM(14,16,17); CA1(18); CA2(32,46,49); CA3(59,60,61); PL(28,50); Other woods (27,31,45,47,48)
<i>Orthotrichum scanicum</i> Grönvall	QS3(8); QI1(11); QI3(55,56); QF(13); QC(57,58); AM(14,15,16,17); CA1(18); CA2(46,49); CA3(60); PL(28,50); Other woods (47,48)
<i>Orthotrichum schimperi</i> Hammar	QS3(8); QS6(53); QI3(54)
<i>Orthotrichum shawii</i> Wilson in Schimp.	QF(12,13)
<i>Orthotrichum speciosum</i> Nees in Sturm.	QS3(8); QI1(11); QI3(55,56); QF(12,13); QC(58); AM(14,15,16,17); CA1(7,18); CA2(46,49); CA3(59,60,61); PH(39); PL(28,50); Other woods (31,47,48)
var. <i>brevisetum</i> F.Lara, Garilleti & Mazimpaka	QF(12); AM(16,17); CA2(49); PL(50)
<i>Orthotrichum speciosum</i> Nees in Sturm.	
var. <i>speciosum</i>	
<i>Orthotrichum striatum</i> Hedw.	QS3(8); QS4(25,33); QS6(52); QI1(10,11); QI3(55,56); QF(12,13); QP(26,36,37); QC(57,58); AM(14,15,16,17); CA1(7,18); CA2(46,49); CA3(59,60,61); PH(39); PL(28,50); Other woods (27,31,45,47,48)
<i>Orthotrichum tenellum</i> Bruch ex Brid.	QS1(1); QS2(3,4,5,6); QS3(8); QS4(34); QS5(51); QS6(52,53); QI2(41,42); QF(12); QC(57,58); AM(14); CA2(49); PH(39); Other woods (38,47,48)
<i>Orthotrichum tortidontium</i> F.Lara, Garilleti & Mazimpaka	QC(58)
<i>Pterigynandrum filiforme</i> Hedw.	QS2(5); QS3(9); QF(13); AM(14,16,17); CA1(7,18,19); CA2(30,32,46,49); CA3(59,60,61); PL(28,50); Other woods (31,45,47,48)
<i>Pterogonium gracile</i> (Hedw.) Sm.	QS2(3,5,6); QS3(9); QS4(25); QI2(41,42); QF(12); AM(14); CA2(46)
<i>Rhynchostegiella litorea</i> (De Not.) Limpr.	QS2(5,6); Other woods (20,21,22,23,24)
<i>Rhynchostegium confertum</i> (Dicks.) Schimp.	QS2(3,5,6); QI2(41)
<i>Schistidium crassipilum</i> H.H.Blom	AM(14)
<i>Scleropodium touretii</i> (Brid.) L.F.Koch	QS2(3,6); QS3(9); Other woods (45,47,48)
<i>Scorpiurium circinatum</i> (Brid.) M.Fleisch. & Loeske	QS1(2); QS2(3,5); Other woods (20,22,23)
<i>Sematophyllum substrunulosum</i> (Hampe) E.Britton	QS1(1); QS2(3,4,5,6); PL(50)
<i>Syntrichia laevipila</i> Brid.	QS1(1); QS2(5,6); QS3(8,9); QS4(33,34); QS6(52,53); QI1(10); QI2(41,42); QI3(54); QC(57,58); CA3(59); PH(39); Other woods (23,45,47)
<i>Syntrichia montana</i> Nees	QS6(52); QI3(55,56); QP(36); AM(14)
<i>Syntrichia princeps</i> (De Not.) Mitt.	QF(12)
<i>Thamnobryum alopecurum</i> (Hedw.) Nieuwl.	QS2(3)
var. <i>maderense</i> (Kindb.) M.Stech, Ros & O.Werner	
<i>Tortella flavovirens</i> (Bruch) Broth.	QS1(2); QS2(4); Other woods (21)
<i>Tortella humilis</i> (Hedw.) Jenn.	QS2(5); Other woods (22)
<i>Tortella tortuosa</i> (Hedw.) Limpr.	AM(14)
*** <i>Tortula israelis</i> Bizot & F.Bilewsky	PH(39)
<i>Tortula subulata</i> Hedw.	Other woods (45,47)
<i>Trichostomum brachydontium</i> Bruch	QS5(51); Other woods (21,24)
<i>Trichostomum crispulum</i> Bruch	Other woods (21)
<i>Weissia controversa</i> Hedw.	QS3(8)
<i>Zygodon rupestris</i> Schimp. ex Lorentz	QS1(1,2); QS2(3,4,5,6); QS4 (25); QI2(41,42); QI3(54); QF(12); AM(14); CA2(49); PL(50); Other woods (20,22,23)

Mountains are *Orthotrichum lyellii*, *O. striatum*, *O. acuminatum* and *O. rupestre*, which grow in all forest types and in more than 50% of the localities sampled. Other frequent taxa, recorded in 25–50% of the localities, usually showed preferences for one forest type: *Orthotrichum tenellum* and *Syntrichia laevipila* were mainly restricted to lower altitude forests; *Antitrichia californica* shows

clear preferences for marcescent *Quercus* forests; while *Pterigynandrum filiforme*, *O. speciosum* var. *brevisetum* and *O. affine* are almost exclusively found in the highest forests (Table 3). *Frullania dilatata*, *Zygodon rupestris*, *Homalothecium sericeum* and *Orthotrichum scanicum* are also frequent in the study area, but with irregular abundances and they do not show preferences for particular



Table 3. Continued

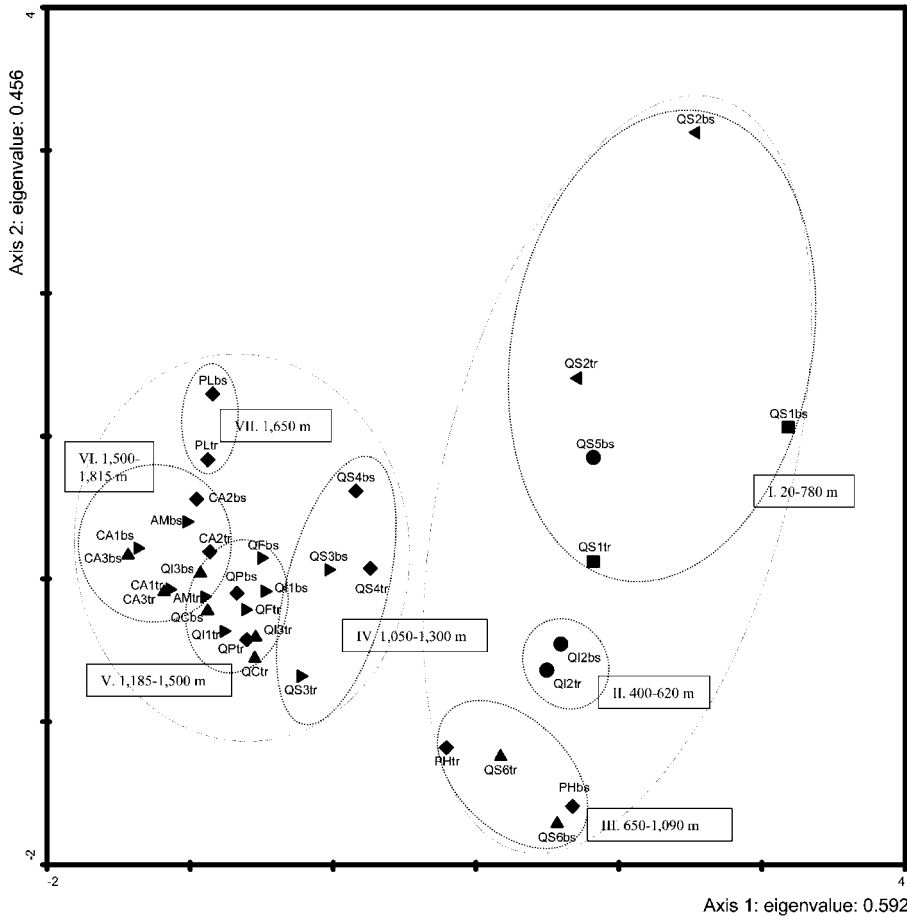
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	bs	tr	bs	tr	bs	tr	bs	tr	bs	tr	bs	tr	bs	tr
<i>O. speciosum</i>	-	-	-	-	-	-	-	-	6	6	17	18	-	9
<i>O. speciosum</i> var. <i>brevisetum</i>	-	-	-	-	12	38	-	-	6	29	184	79	185	279
<i>O. striatum</i>	-	-	-	-	38	83	80	14	27	214	170	226	41	311
<i>O. tenellum</i>	95	70	VS	169	25	74	308	240	MA	S	4	8	161	273
<i>Pterigynandrum filiforme</i>	9	9	96	118	118	118	118	118	118	118	118	118	118	118
<i>Pterogonium gracile</i>	9	9	96	118	118	118	118	118	118	118	118	118	118	118
<i>Rachula complanata</i>	55	30	13	19	17	207	182	35	VS	MA	57	18	27	27
<i>Sematophyllum substrumulosum</i>	36	3	3	3	3	3	3	3	3	3	3	3	3	3
<i>Syntrichia laevipila</i>	107	19	-	MA	47	41	21	-	-	30	44	9	9	9
<i>S. montana</i>	-	-	-	-	-	-	-	-	9	27	VS	VS	6	6
<i>Zygodon rupestris</i>	-	-	-	-	31	70	70	70	70	70	70	70	70	70

forest types. Finally, the remaining taxa are scarce epiphytes in the Rif, growing in less than 25% of the sampled localities and always with low abundances. Among these taxa, *Orthotrichum ibericum*, whose known distribution is basically restricted to the Iberian Peninsula and northern Morocco (Garilleti, Lara & Mazimpaka, 1997), and *O. shawii* and *O. pallens*, representing southern extensions to their previously known ranges (Mazimpaka *et al.*, 2000; Garilleti *et al.*, 2002; Draper *et al.*, 2003), are especially interesting. Taxa of the families Brachytheciaceae and Pottiaceae are also numerous, mostly occurring as facultative epiphytes under favourable moisture conditions (Söderström, 1993; Lara, 1995). Among these, *Tortula israelis*, which was previously known from several localities in the Mediterranean area (Fuentes *et al.*, 1998; Cano, Guerra & Ros, 1996; Cano, Ros & Guerra, 1996; Oliva, 1999), is here newly reported from northern Africa.

Epiphytic bryophytes are not homogeneously developed in the Rif Mountains: bryophytes mostly grow in montane forests of the central and western Rif, while they are scarce in the west at low altitudes and are absent in the easternmost part of the range. Thus, epiphytic communities were found in 73% of the localities visited in the Tingitane chain, where they had a mean cover of 60% in samples of 20 × 20 cm<sup>2</sup>, 89% of the localities in the central Rif, also with 60% mean cover, and at 100% of localities on Tazzeka Mountain, with 70% mean cover. Conversely, only 29% of the localities visited in the Larache and Al Hoceima sectors had epiphytes, with a mean cover of the communities of 27% and 20%, respectively, and no bryophytes were found in this habitat in the Kert sector (Fig. 3). These differences are also reflected in taxon richness: 88% of the recorded bryophytes grew in the Tingitane chain, which also exhibited the largest number of exclusive taxa (15), nearly 70% grew in the central Rif and 41% in Tazzeka Mountain (with four and two exclusive taxa respectively), while only 24% of the bryophytes grew in Larache (with no exclusive taxon) and 16% in Al Hoceima (one exclusive taxon).

#### Epiphytic bryophyte communities

The correspondence analysis ordines the epiphytic communities of the study area as shown in Fig. 4. The horizontal axis, which explains most of the variability, separates communities by altitude into two main groups: communities in forests below 1100 m appear in the right part of the diagram and higher altitude communities in the left one. Forest types above 1100 m in the Rif Mountains gradually follow one another in altitude, and so do their epiphytic communities, which are quite homogeneous and appear close together in the diagram. In contrast, lower altitude epiphytic communities are very heterogeneous and appear scattered along the vertical axis, from cork oak woods in the western Tingitane chain to cork oak and pine tree forests on Tazzeka Mountain. This distribution is a reflection of variation in moisture conditions among the



**Figure 4.** Correspondence analysis ordination of the woods studied: ■, Larache sector; ▶, western Tingitane chain; ▼, eastern Tingitane chain; ◆, central Rif; ●, Al Hoceima sector; ▲, Tazzeke Mountain; I, *Frullania dilatata* epiphytic communities in *Quercus suber* woods; II, *Fabronia pusilla* epiphytic communities in *Quercus ilex* woods; III, *Orthotrichum tenellum* epiphytic communities in *Quercus suber* and *Pinus halepensis* woods; IV, *Orthotrichum lyellii* epiphytic communities in *Quercus suber* woods; V, *Orthotrichum lyellii* and *Antitrichia californica* montane epiphytic communities; VI, *Orthotrichum speciosum* var. *brevisetum* and *Pterigynandrum filiforme* high altitude epiphytic communities; VII, *Isoetecium alopecuroides* epiphytic communities in *Prunus lusitanica* copses.

different areas studied. As a result of the study of the correspondence analysis ordination, seven types of epiphytic bryophyte communities have been described in the Rif Mountains: I, *Frullania dilatata* epiphytic communities in *Quercus suber* woods; II, *Fabronia pusilla* epiphytic communities in *Quercus ilex* woods; III, *Orthotrichum tenellum* epiphytic communities in *Quercus suber* and *Pinus halepensis* woods; IV, *Orthotrichum lyellii* epiphytic communities in *Quercus suber* woods; V, *Orthotrichum lyellii* and *Antitrichia californica* montane epiphytic communities; VI, *Orthotrichum speciosum* var. *brevisetum* and *Pterigynandrum filiforme* high altitude epiphytic communities; VII, *Isoetecium alopecuroides* epiphytic communities in *Prunus lusitanica* copses.

**I. *Frullania dilatata* communities in *Quercus suber* woods** These are developed in *Quercus suber* woods in the western Tingitane chain and the Al Hoceima and Larache areas, and constitute the most heterogeneous of the groups considered. They share the constant presence of *Frullania dilatata* among the dominant taxa and the occurrence of several thermophilous taxa, such as

*Zygodon rupestris*, *Orthotrichum tenellum*, *O. lyellii*, *O. diaphanum* and *Bryum capillare*, but their composition varies according to moisture conditions. Thus, the western Tingitane chain, which receives high precipitation from oceanic winds, shows the richest communities and shelters the most hygrophilous taxa. The physiognomy of tree base communities (QS2bs) in this area is determined by the pleurocarpous *Scorpiurium circinatum* and *Cryphaea heteromalla*, while that of tree trunk communities (QS2tr) is given by *Frullania dilatata*, *Radula complanata* and *Cryphaea heteromalla*. In addition, *Orthotrichum tenellum*, *O. lyellii*, *Hypnum cupressiforme*, *Zygodon rupestris*, *Sematophyllum substrumulosum* and *Leptodon smithii* are constant both on trunks and bases (Table 3). The cork oak woods in the Larache sector are more disturbed and drier, which is reflected in a poorer epiphytic flora, especially on the tree bases. Here the epiphytic communities on both the tree bases (QS1bs) and trunks (QS1tr) contain acrocarpous mosses, such as the ubiquitous *Orthotrichum diaphanum* and *Bryum capillare*, which grow together with *Zygodon rupestris* and *Frullania dilatata*. In addition, *Orthotrichum tenellum* and *O. lyellii* are moderately abundant on tree



trunks, in association with other taxa such as *Leptodon smithii*, *Syntrichia laevipila*, *Orthotrichum affine*, *Homalothecium sericeum* and *Cryphaea heteromalla* (Table 3). In the Al Hoceima sector, epiphytic bryophytes are scarce and have only been found on tree bases (QS5bs), where the communities are dominated by *Frullania dilatata* and *Orthotrichum diaphanum*, which grow together with *Grimmia pulvinata*, *Homalothecium aureum*, *H. sericeum*, *Hypnum cupressiforme*, *Orthotrichum lyellii* and *O. tenellum* (Table 3).

**II. *Fabronia pusilla* communities in *Quercus ilex* woods** *Quercus ilex* woods in the Al Hoceima sector show very homogeneous epiphytic communities both on tree bases (QI2bs) and trunks (QI2tr). The physiognomy of these communities is determined by the pleurocarpous moss *Fabronia pusilla*, which co-dominates the communities with *Syntrichia laevipila* and *Pterogonium gracile*. Other constant taxa are *Orthotrichum lyellii* (especially abundant on tree trunks), *O. diaphanum*, *O. tenellum*, *O. acuminatum*, *Leucodon sciuroides*, *Habrodon perpusillus*, *Antitrichia californica*, *Zygodon rupestris* and *Dialytrichia mucronata* (Table 3). *Orthotrichum philibertii* has only been reported from this community type and from *Orthotrichum tenellum* communities in *Quercus suber* and *Pinus halepensis* woods, which are described below.

**III. *Orthotrichum tenellum* communities in *Quercus suber* and *Pinus halepensis* woods** The third group of epiphytic communities developed at low altitudes, includes those growing in *Quercus suber* woods on Tazzeqa Mountain (QS6) and in a *Pinus halepensis* forest in the central Rif (PH), where epiphytic bryophytes were found only on *Ulmus minor* and *Populus alba*, since under xeric conditions *Pinus halepensis* bark is too acid for bryophyte colonization. The community is characterized by the presence of acrocarpous mosses, among which *Orthotrichum* taxa are the most abundant. Thus, this community is co-dominated by *Orthotrichum tenellum* and *O. lyellii*, which grow together with *Syntrichia laevipila*, *Habrodon perpusillus*, *Orthotrichum acuminatum* and *O. diaphanum* (the last two taxa are especially abundant on tree trunks). The presence of *Orthotrichum macrocephalum* is characteristic, as this drought-tolerant species is exclusive to this community in the study area, and *O. philibertii* has only been found in this community and in *Fabronia pusilla* communities in *Quercus ilex* woods (Table 3).

**IV. *Orthotrichum lyellii* communities in *Quercus suber* woods** *Quercus suber* woods in the eastern Tingitane chain (QS3) and central Rif (QS4) show epiphytic communities dominated by the acrocarpous moss *Orthotrichum lyellii*. This grows with *O. acuminatum*, *O. striatum*, *O. tenellum*, *O. rupestre*, *O. affine*, *Frullania dilatata*, *Antitrichia californica*, *Homalothecium sericeum*, *Syntrichia laevipila* and *Grimmia trichophylla*. In addition, other pleurocarpous mosses such as *Pterogonium gracile*, *Neckera pumila* and *Fabronia pusilla*, characterize tree base communities, where more moisture is available (Table 3).

**V. *Orthotrichum lyellii* and *Antitrichia californica* montane communities** Intermediate altitudes in the Principal chain

and on Tazzeqa Mountain (from 1200 to 1500 m) are characterized by different *Quercus* forest types, according to slope orientation and soil type (Fig. 2). Nevertheless, all these forests show similar epiphytic communities (QI1, QI3, QF, QC and QP; Fig. 4). These communities are basically dominated by the acrocarpous moss *Orthotrichum lyellii* on tree trunks and by the pleurocarpous *Antitrichia californica* on tree bases. Both mosses form communities in which *Orthotrichum striatum*, *O. rupestre*, *O. acuminatum* and *Homalothecium sericeum* are also constant. In addition, *Habrodon perpusillus* is occasional both on tree trunks and bases, *Brachythecium velutinum* usually appears on tree bases, and *Orthotrichum affine*, *O. scanicum*, *O. speciosum* var. *brevisetum* and *Syntrichia laevipila* are common on tree trunks. *Leucodon sciuroides* var. *morensis* dominates locally on *Quercus canariensis* bases and *Metaneckera menziesii* is moderately abundant on *Quercus faginea* bases (Table 3).

**VI. *Orthotrichum speciosum* var. *brevisetum* and *Pterigynandrum filiforme* high altitude communities** Forests above 1500 m in the Principal chain and on Tazzeqa Mountain consist mainly of coniferous trees (Fig. 2), whose epiphytic communities have a rather homogeneous composition regardless of phorophyte type and geographic position. Thus, communities in Spanish fir (AM) and cedar woods in the eastern Tingitane chain (CA1), cedar woods in central Rif (CA2) and cedar woods on Tazzeqa Mountain (CA3) appear grouped in Fig. 4. The communities are dominated by the acrocarpous moss *Orthotrichum lyellii*. Nevertheless, the most characteristic species of these communities are *Orthotrichum speciosum* var. *brevisetum* and *Pterigynandrum filiforme*, orophilous taxa which thrive in mountainous regions and here co-dominate with *Orthotrichum lyellii*, *O. striatum* and *O. rupestre*. In addition, *Orthotrichum affine*, *O. acuminatum*, *Frullania dilatata* and *Homalothecium sericeum* are common and locally abundant, and *Brachythecium velutinum* usually appears on tree bases. Some taxa stand out because of their local importance (Table 3), such as *Orthotrichum pallens* on trunks in cedar woods on Tazzeqa Mountain, *Antitrichia californica* on Spanish fir bases in the Tingitane chain and *Brachythecium dieckii* on bases in cedar woods in central Rif.

**VII. *Isothecium alopecuroides* communities in *Prunus lusitanica* copses** *Prunus lusitanica* forms copses along watercourses in the cedar wood environment. Their epiphytic communities (PL) are similar to those in the surrounding cedar woods, although their microclimatic conditions allow the development of some hygrophilous taxa such as *Isothecium alopecuroides* or *Neckera pumila*. These communities contain different pleurocarpous mosses, among which *Isothecium alopecuroides* is the most important on tree bases, while *Neckera pumila* and *Pterigynandrum filiforme* dominate on tree trunks. In addition, *Hypnum cupressiforme*, *Homalothecium sericeum*, *Orthotrichum lyellii*, *O. rupestre*, *O. affine* and *Radula complanata* are constant. Finally, *Orthotrichum acuminatum*, *Sematophyllum*

*substrumulosum* and *Zygodon rupestris* are usually present both on tree trunks and bases, *Orthotrichum striatum* is frequent on tree trunks and *Brachythecium velutinum* and *Leptodon smithii* are common on tree bases (Table 3).

#### DISCUSSION

Epiphytic bryophyte development is usually dependent on moisture conditions and the state of preservation of native forests (Smith, 1982; Bates, 2000). In the Rif Mountains, the Tingitane chain, the central Rif and Tazzeka Mountain possess the best preserved forests and experience high moisture conditions. By contrast, the Larache sector is a flat area mainly dedicated to agriculture and without well preserved forests. Humidity decreases to the east, leading to a progressive impoverishment in the epiphytic bryophyte flora in Al Hoceima and, finally, to the absence of epiphytic bryophytes in the Kert sector.

The variety of climatic conditions and forest types favours the presence of several types of bryophytic communities. In the most favourable areas, these communities are determined by taxon preferences for a specific altitudinal stage: communities in the forests at high altitude in the Principal chain and Tazzeka Mountain (above 1500 m) are dominated by *Pterigynandrum filiforme* on tree bases and by *Orthotrichum speciosum* var. *brevisetum* on trunks, while *Antitrichia californica* and *O. lyellii* are typical of montane epiphytic communities in the same areas (from 1200 to 1500 m). Epiphytic communities in woods at lower altitudes are more variable, according to moisture conditions and the extent of forest preservation. Thus, *Quercus suber* woods in the humid western Tingitane chain shelter very rich communities, while the same forest type in the degraded Larache and Al Hoceima sectors supports very poor communities dominated by ubiquitous taxa. Community composition also varies according to microclimatic conditions, which explains the differences among the epiphytic communities in *Prunus lusitanica* copses, characterized by the presence of hygrophilous taxa such as *Isothecium alopecuroides* or *Neckera pumila*, from those in the surrounding *Cedrus atlantica* woods.

Some of the epiphytic communities described in the Rif Mountains appear to be closely related to those previously reported from areas of similar ecological conditions on the Iberian Peninsula: *Frullania dilatata* epiphytic communities in *Quercus suber* woods are similar to the ones that grow on *Quercus canariensis* and *Q. suber* in the opposite mountains of Algeciras (Cadiz province), in the south of the Iberian Peninsula (Gil & Guerra, 1981), while the *Orthotrichum lyellii* and *Antitrichia californica* community described in the Rif Mountains at intermediate altitudes is similar to that developing on *Quercus suber* and *Q. ilex* ssp. *ballota* in the Sierra de las Nieves, in the south of the Iberian Peninsula (Guerra, 1982), and on *Quercus pyrenaica* in the Spanish central range (Lara & Mazimpaka, 1994; Lara, Mazimpaka & Garilleti, 1997). Finally, epiphytic *Orthotrichum speciosum* var. *brevisetum* and *Pterigynandrum filiforme* communities described in the Rif Mountains at the highest altitudes are similar to those described

by Guerra (1982) on *Abies pinsapo* Boiss. and *Quercus faginea* in the Sierra de las Nieves, in the south of Spain.

Nevertheless, the communities in the Rif Mountains present some original characteristics related both to the decreasing latitude and to the higher Atlantic influence, especially in the western part of the Rif Mountains. The former implies an increase in altitude of the different forest types and a consequent higher presence of orophilous taxa in the epiphytic communities, while the latter involves more oceanic taxa presence. As an example, intermediate altitude communities in the Rif seem to be more related to those in the Gredos Mountains, which are the most exposed in the Spanish central range to the oceanic influence in winter, and where species like *Orthotrichum acuminatum* and *Antitrichia californica* find their ecological optimum (Lara et al., 1997). The Atlantic influence is still stronger in the Rif range and some drought-tolerant species that are constant in the Gredos range, such as *Orthotrichum tenellum* or *O. ibericum* rarely appear in the Rif Mountains, while other taxa like *Metaneckera menziesii* or *Orthotrichum scanicum* that are locally abundant in the study area, do not grow in the Spanish central range. Epiphytic communities on *Prunus lusitanica* are another interesting case: in the Iberian Peninsula two main groups of epiphytic communities appear, one in the northern forests under Atlantic influence and the other in the inner forests in the Mediterranean region (Calleja et al., 2001). *Isothecium alopecuroides* communities in the Rif Mountains seem to be more related to those described in the Mediterranean region, because both areas are subject to humid microclimates which favour a common floristic composition of their epiphytic communities, and are different from those in the surrounding forests. Nevertheless, the higher altitude of the *Prunus lusitanica* forests in the Rif Mountains implies differences among the dominant taxa in both epiphytic communities: the communities in the Iberian Mediterranean forests are dominated by taxa with oceanic preferences, such as *Metzgeria furcata* and *Frullania dilatata*, while the Rif forests are dominated by *Isothecium alopecuroides* on tree bases and *Neckera pumila* and *Pterigynandrum filiforme* on trunks, subboreal taxa which also dominate or co-dominate the epiphytic communities of the northern forests of the Iberian Peninsula.

Finally, dry conditions appear to determine epiphytic communities, both in the eastern part of the Rif Mountains and in the most disturbed forests at low altitudes, which is reflected in the presence of xerophilous and nitrophilous taxa such as *Orthotrichum diaphanum* and *Syntrichia laevipila*.

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## APPENDIX

## Localities and phorophytes studied

1. Sidi Hassain, 10 km from Larache, 29SQV6606, 200 m, on *Quercus suber*
2. Jbel Dahar Zhirou, Chaka, 30STE3452, 20 m, on *Quercus suber* and *Olea europaea*
3. Loukos affluent valley, near Brikcha, 30STD6869, 145 m, on *Quercus suber* and *Arbutus unedo* L.
4. Gorges between Brickcha and Ouezzane, 30STD6868, 115 m, on *Quercus suber*, *Quercus coccifera* L. and *Pistacia lentiscus* L.

5. Oulad Allah, gorges near Ouezzane, 30STD6868, 150 m, on *Quercus suber* and *Arbutus unedo*
6. Ouara affluent valley, 5 km from Bab Taza, 30STD9386, 450 m, on *Quercus suber* and *Arbutus unedo*
7. Bab Taza: Tala Semtan, 30SUD0687, 1700 m, on *Abies maroccana*
8. Bab Taza: Jbel Bouhalla, S. exposure, 30SUD0183, 1050 m, on *Quercus suber*
9. Bab Taza: Jbel Bouhalla, N. exposure, 30SUD0284, 1100 m, on *Quercus suber*
10. Bab Taza: Jbel Bouhalla, E.–N.E. exposition, 30SUD0285, 1220 m, on *Quercus suber* and *Quercus ilex* ssp. *ballota*
11. Bab Taza: Jbel Bouhalla, 30SUD0385, 1250 m, on *Quercus ilex* ssp. *ballota* and *Quercus faginea* Lam.
12. Bab Taza: Jbel Bouhalla, 30SUD0486, 1300 m, *Quercus ilex* ssp. *ballota* and *Q. faginea*
13. Bab Taza: Jbel Bouhalla, 30SUD0588, 1400 m, on *Quercus ilex* ssp. *ballota*, *Q. faginea* and *Abies maroccana*
14. Bab Taza: Jbel Bouhalla, 30SUD0589, 1500 m, on *Quercus ilex* ssp. *ballota*, *Q. faginea* and *Abies maroccana*
15. Bab Taza: Jbel Bouhalla, clear forest, 30SUD0489, 1595 m, *Abies maroccana*
16. Bab Taza: Jbel Bouhalla, N.–S. valley, 30SUD0590, 1600 m, on *Quercus ilex* ssp. *ballota* and *Abies maroccana*
17. Bab Taza: Jbel Bouhalla, dense forest, 30SUD0590, 1600 m, on *Abies maroccana*
18. Bab Taza: Jbel Bouhalla, 30SUD0490, 1700 m, *Abies maroccana*
19. Bab Taza: Jbel Bouhalla, 30SUD0491, 1800 m, on *Abies maroccana* and *Cedrus atlantica*
20. Dar Akoubaa, Talembote dam, 30STE8901, 300 m, on *Olea europaea* and *Chamaerops humilis* L.
21. Ibouharane, Laou valley, 30SUE0111, 250 m, on *Tetraclinis articulata*
22. Tarhzoute, 30STE9708, 350 m, on *Quercus ilex* ssp. *ballota*
23. Es-Sebt-de-Saïd, Oued Laou road, 30STE9009, 200 m, on *Quercus coccifera*
24. Tamrabete, 30STE9934, 150 m, on *Pinus halepensis* Miller and *Quercus ilex* ssp. *ballota*
25. Tafira, Jbel Tafirane, 30SUD3374, 1300 m, on *Quercus suber*
26. Bab Beren, between Koudiet es Sbaa and Jbel Beni Salah, 30SUD1777, 1400 m, on *Quercus pyrenaica*
27. Tetla Ketama, 30SUD5069, 1450 m, on *Betula pendula* Roth
28. Near Tetla Ketama, 30SUD4870, 1650 m, on *Prunus lusitanica*
29. Ketama, Jbel Tidirhine, dense forest, 30SUD5858, 1720 m, on *Cedrus atlantica*
30. Ketama, Jbel Tidirhine, clear forest, 30SUD5957, 1795 m, on *Cedrus atlantica*
31. Ketama, Jbel Tidirhine, 30SUD6259, 1810 m, on *Salix atrocinerea* Brot. and *Ilex aquifolium* L.
32. Ketama, Jbel Tidirhine, dense forest, good conservation, 30SUD6058, 1815 m, on *Cedrus atlantica*
33. Ghafsäi, Lalla Outka to Jbel Oudka, 30SUD3048, 1130 m, on *Quercus suber*
34. Ghafsäi, Lalla Outka to Jbel Oudka, 30SUD2746, 1300 m, on *Quercus suber*
35. Ghafsäi, Lalla Outka to Jbel Oudka, 30SUD3046, 1310 m, on *Quercus pyrenaica*
36. Ghafsäi, Lalla Outka to Jbel Oudka, 30SUD2947, 1300 m, on *Quercus pyrenaica*
37. Ghafsäi, Lalla Outka to Jbel Oudka, 30SUD3147, 1430 m, on *Quercus pyrenaica*
38. Bou Imechouene, Aknoul to Tahar Souk, 30SUD9543, 850 m, on *Quercus ilex* ssp. *ballota*
39. Maret, 30SUD9241, 1090 m, on *Ulmus minor* Mill. and *Populus alba* L.
40. Hachkor, Koudiat Tighighine, 30SUD4653, 1145 m, on *Quercus suber*
41. Al Haddada, Jbel Tifelloust, 30SUD5439, 400 m, on *Erica arborea* L. and *Myrtus communis* L.
42. Al Haddada, Jbel Tifelloust, 30SUD5438, 585 m, on *Quercus ilex* ssp. *ballota*
43. Al Haddada, Jbel Tifelloust, 30SUD5744, 620 m, on *Nerium oleander* L. and *Pistacia lentiscus*
44. Between Bab Imatene and Bab Jbah, 30SUD4744, 850 m, on *Quercus suber*
45. From Ketama to Azila, near cross to Tawnat, 30SUD5562, 1400 ?m, on *Cedrus atlantica* and *Populus nigra* L.
46. Ketama, Jbel Souk Tahomar, 30SUD5168, 1700 m, on *Cedrus atlantica* and *Quercus ilex* ssp. *ballota*
47. Ketama, Jbel Dedokh, 30SUD5367, 1500 m, on *Cedrus atlantica* and *Quercus coccifera*
48. Ketama, Jbel Bou Bessoui, fountain, 30SUD4271, 1600 m, on *Salix pedicellata* Desf. and *Quercus canariensis*
49. Ketama, Jbel Bou Bessoui, 30SUD4769, 1650 m, on *Cedrus atlantica* and *Quercus ilex* ssp. *ballota*
50. Ketama, Jbel Bou Bessoui, 30SUD4769, 1650 m, on *Prunus lusitanica* and *Ilex aquifolium*
51. Irazzoükene, to Al Hoceima, 30SVD3688, 780 m, on *Quercus suber*
52. Jbel Tazzeke, 30SVC0679, 650 m, on *Quercus suber* and *Quercus ilex* ssp. *ballota*
53. Jbel Tazzeke, 30SVC0578, 1040 m, on *Quercus canariensis*
54. Taza, Jbel Bou Mess'Oud to Jbel Tazzeke, 30SVC0477, 1185 m, on *Quercus ilex* ssp. *ballota*
55. Taza, Jbel Bou Mess'Oud to Jbel Tazzeke, 30SUC9873, 1325 m, on *Quercus ilex* ssp. *ballota*
56. Taza, Bab Bou Idir to Jbel Tazzeke, 30SUC9570, 1425 m, on *Quercus ilex* ssp. *ballota*
57. Taza, Bab Bou Idir to Jbel Tazzeke, 30SUC9369, 1450 m, on *Quercus canariensis*
58. Taza, Bab Bou Idir to Jbel Tazzeke, 30SUC9168, 1500 m, on *Quercus ilex* ssp. *ballota*
59. Taza, Bab Bou Idir to Jbel Tazzeke, 30SUC9172, 1700 m, on *Cedrus atlantica* and *Taxus baccata* L.
60. Taza, Bab Bou Idir to Jbel Tazzeke, 30SUC9072, 1800 m, on *Cedrus atlantica* and *Quercus canariensis*
61. Jbel Tazzeke, 30SUC9070, 1800 m, on *Cedrus atlantica*