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Epiphytic bryoflora of the Atlas and Antiatlas Mountains, including a synthesis of the distribution of epiphytic bryophytes in Morocco

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SUMMARY

The epiphytic bryoflora of the Atlas and Antiatlas Mountains is catalogued, resulting in a list of 65 taxa (63 mosses and 2 liverworts). Twenty-eight new records are reported: four are new to northern Africa, one is new to Morocco and 23 are regional novelties. In addition, a synthesis of the distribution of epiphytes in Morocco is presented, with distributional maps for the main taxa. Five groups of taxa have been established on the basis of their distribution: widely distributed taxa, Rif taxa, Rif and Middle Atlas taxa, Atlas taxa and taxa with localized occurrences. From these distributional patterns, it can be inferred that the occurrence of epiphytic bryophytes is mostly influenced by climatic conditions.

KEYWORDS: Bryophyte flora, epiphytes, distribution, northern Africa, distributional maps.

INTRODUCTION

Morocco is a mountainous country situated in the western Mediterranean basin. Because of its geographical situation, mountainous nature and large size, it is full of contrasts and variations, which makes it a biogeographically interesting area. Despite this interest, its bryoflora has not been deeply studied. In the middle of the 20th century, F. Jelenc and S. Jovet-Ast focused their studies respectively on the mosses and the liverworts of northern Africa (Jelenc, 1955, 1967; Jovet-Ast, 1955, 1956a, b). Thereafter, interest in Moroccan bryophytes decreased, and only in recent years have Spanish bryologists from the universities of Murcia and Autónoma de Madrid undertaken studies in this area. Data on several poorly known areas were increased by inventories, including studies on the bryophytes of the Rif mountains (Jiménez *et al.*, 2002a, b; Draper *et al.*, 2003, 2005), the Antiatlas (Cano *et al.*, 2002) and the Toubkal mountain in the High Atlas (Ros *et al.*, 2000). This paper is intended to supplement existing knowledge of the epiphytic bryophyte flora, by cataloguing these species in the Atlas and Antiatlas mountains and synthesizing information on their distributions in the whole of Morocco.

STUDY AREA

The Atlas and Antiatlas mountains constitute, together with the plain called Meseta, the Atlasic lands, which occupy most of the country (Fig. 1). These lands have their western border on the Atlantic coast and their eastern one in the high basins of the Muluya and Ziz rivers. From north to south, they comprise the territory between the Sebou and Drâa rivers. Within these limits, Tazzeka mountain is floristically similar to the Rif mountains (Draper *et al.*, 2005). The Meseta has not been included in this study, since it is flat low-lying land that has been traditionally dedicated to agriculture, and lacks well-preserved forests.

The Atlas mountains include the Middle and the High Atlas ranges. The materials of the former are mostly siliceous, although calcareous and volcanic outcrops appear at the lowest altitudes of the northern slopes. The highest mountain in the Middle Atlas is Bu-Naceur (3340 m), which lies in the eastern part. The High Atlas is basically calcareous, although in the highest part, in and around Toubkal mountain (4167 m), schists with granite intrusions and volcanic materials appear. The Antiatlas mountains are acidic and include two ancient volcanic massifs: Siroua (3304 m) and Sarhro (2712 m) (Boudy, 1948; Nègre, 1959; Despois & Raynal, 1975).

Morocco has a Mediterranean climate, although different influences cause great variations. Proximity to the ocean softens the climate all along the Atlantic coast, while proximity to the Sahara Desert restricts the establishment of the vegetation in the south-eastern areas. Most of the rainfall is provided by the Atlantic winds that produce rains on contact with the mountains, so the eastern parts are

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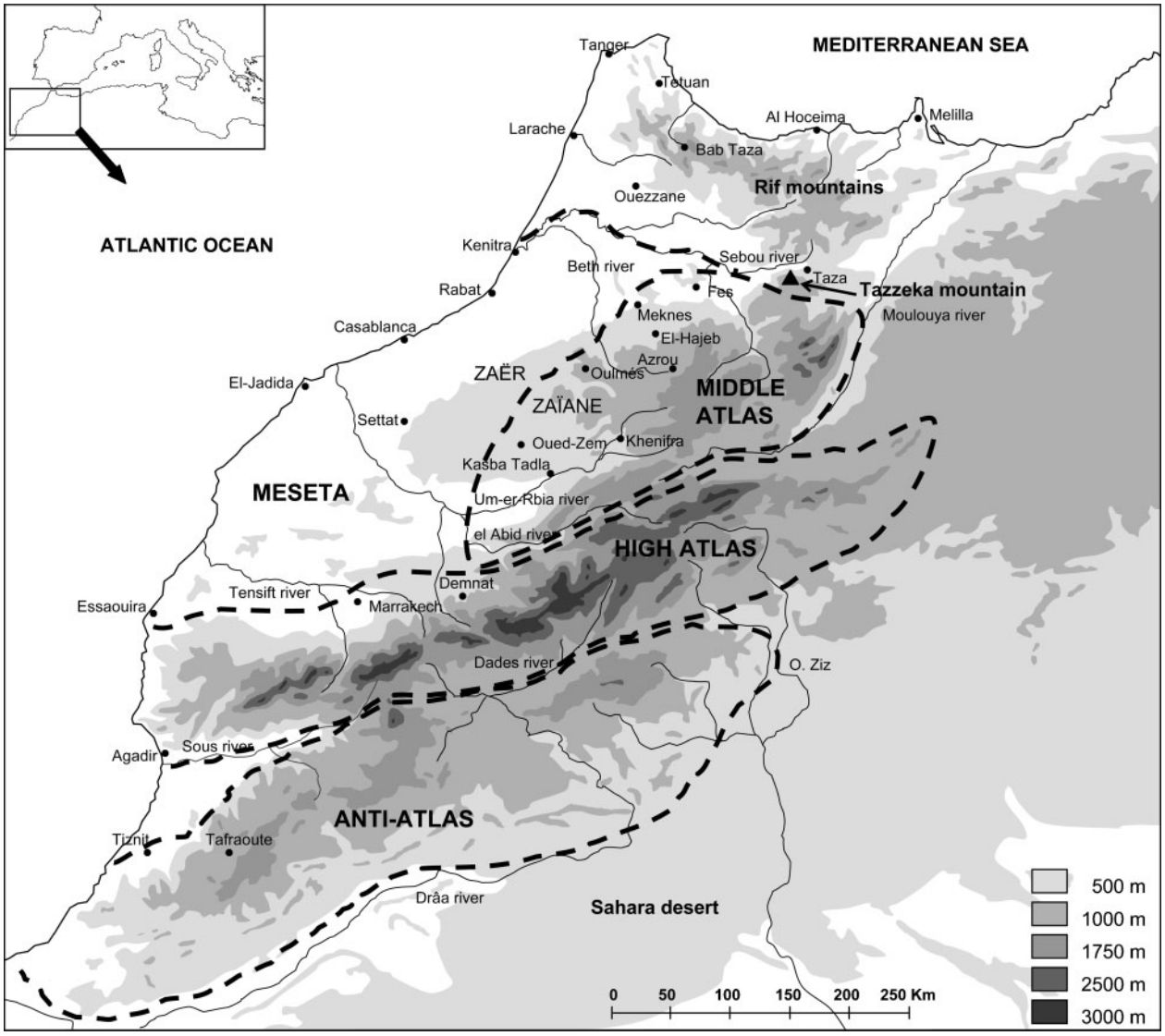

Figure 1. Location of the study area.

drier than the western ones. In addition, precipitation is moderated by latitude (decreasing from north to south) and altitude (in general, rainfall increases with height, although conditions are usually xeric at the summits). Thus, annual precipitation in the study area varies from around 150 mm in the western Antiatlas to >1100 mm in Ifrane (central Middle Atlas). These climatic variations allow the differentiation of five types of Mediterranean climate in Morocco (Fig. 2): arid, semi-arid, subhumid, humid and high mountain (Emberger, 1930a, b; Daget, 1977).

Variety in substrata and climatic features in the study area favours the presence of several different types of forests (Fig. 3). Under arid conditions, steppes of *Artemisia herba-alba* Asso and *Stipa tenacissima* Loefl. ex L. appear and, only in the most oceanic areas *Argania spinosa* (L.) Skeels with *Pistacia atlantica* Desf. and, exceptionally, *Tetraclinis articulata* (Vahl) Mast. form forests, in which epiphytic bryophytes do not occur. The semiarid Mediterranean climate is developed in three forms in Morocco: oceanic, temperate and cold, and to each form corresponds a different type of vegetation. Under oceanic semiarid conditions the forests are dominated, depending on the substratum, by *Tetraclinis articulata*, *Pinus halepensis* Mill., *Quercus rotundifolia* Lam. or, exceptionally, *Quercus suber* L. In temperate semiarid conditions the most abundant species is *Juniperus phoenicea* L., while in cold semiarid climates *Juniperus thurifera* L. subsp. *africana* (Maire) Gauquelin, Idrissi & Lebreton is the dominant tree. The epiphytic stratum is usually poorly developed in most of the semiarid forests, although many of the epiphytes that grow in these environments are biogeographically interesting. In areas under a subhumid Mediterranean climate, the forests are mostly dominated by *Quercus suber*, although this species is locally substituted near the coast by *Juniperus phoenicea* and *Tetraclinis articulata*, and in continental areas by *Quercus rotundifolia*, *Pinus pinaster* Aiton, *Cedrus atlantica* (Endl.) Carrière (in the south-eastern Middle Atlas) and *Juniperus thurifera* subsp. *africana* (in the High

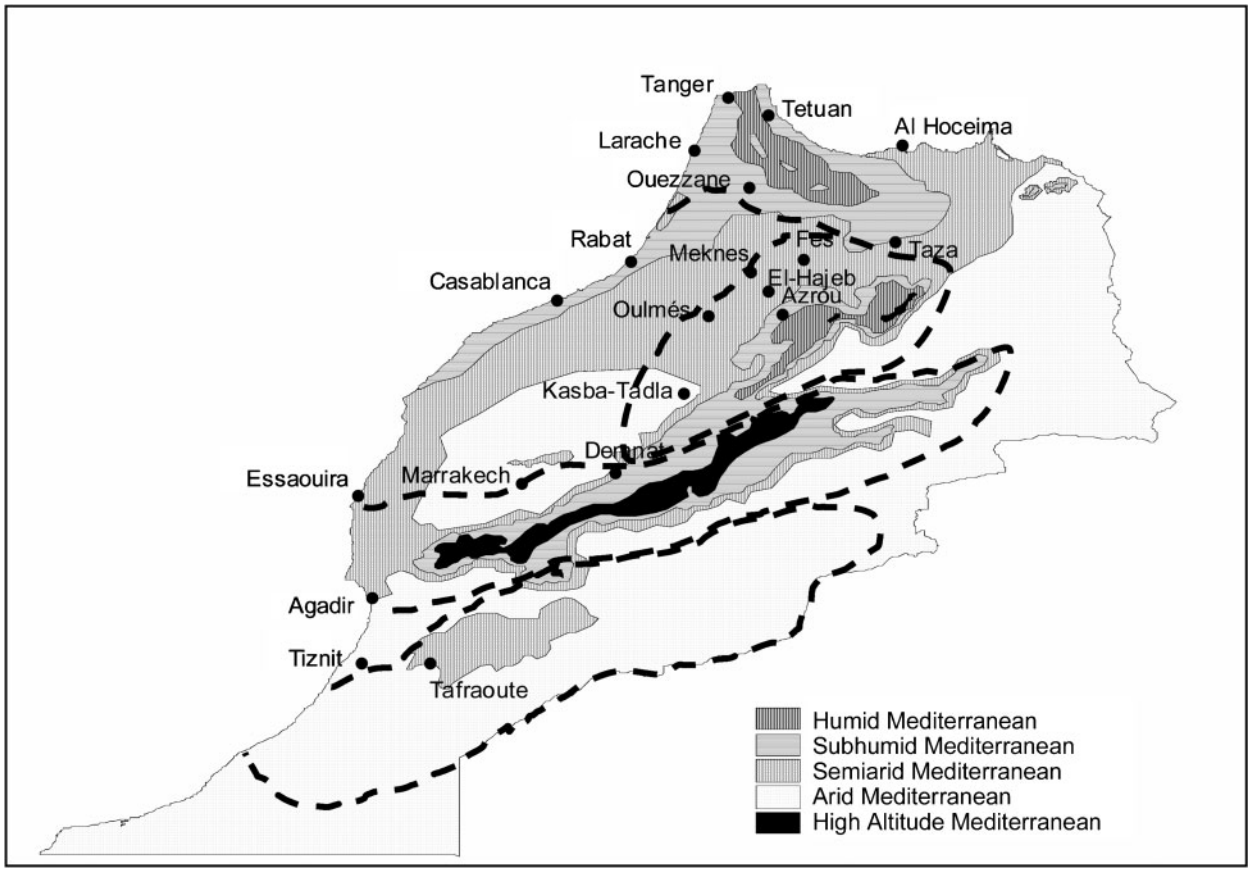

Figure 2. Types of Mediterranean climate in Morocco, after Emberger (1930a, b).

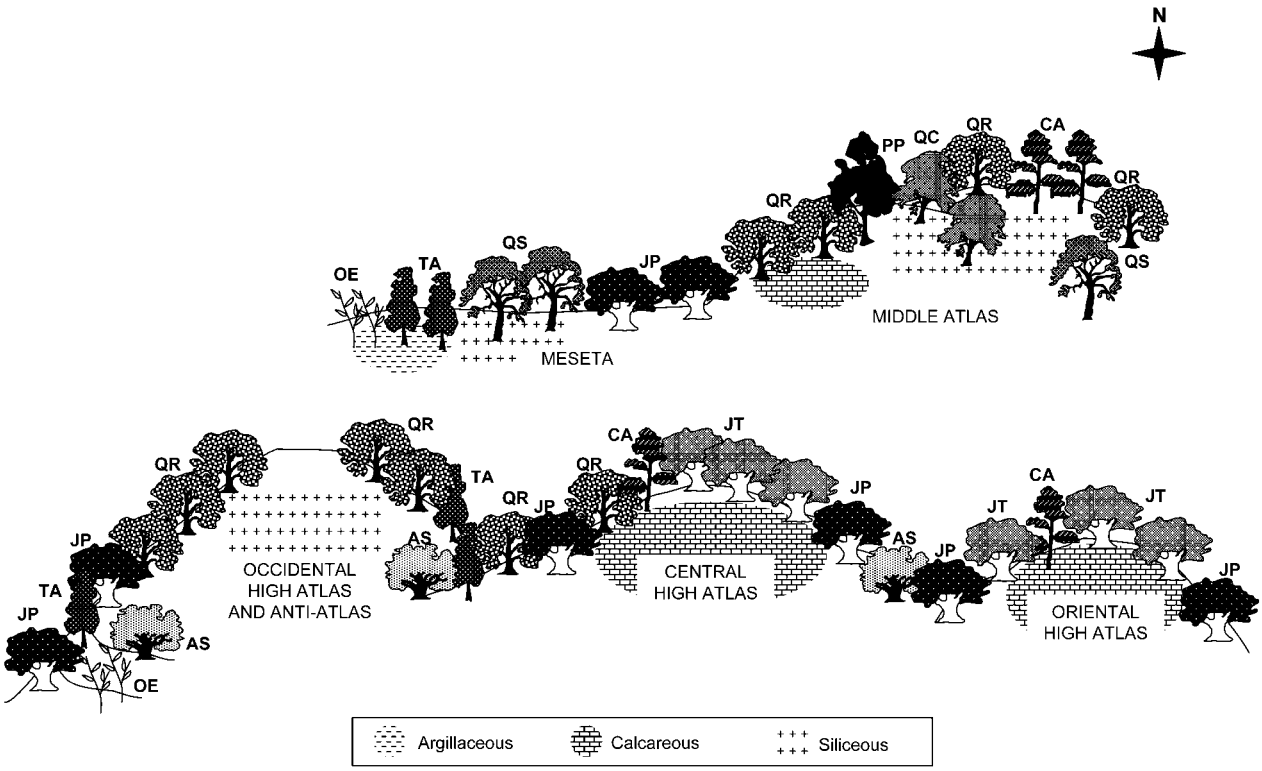

Figure 3. Schematic representation of types of forest in the study area, according to their location on the mountain slopes: AS, *Argania spinosa*; CA, *Cedrus atlantica*; JP, *Juniperus phoenicea*; JT, *Juniperus thurifera*; OE, *Olea europaea*; PP, *Pinus pinaster*; QC, *Quercus canariensis*; QR, *Quercus rotundifolia*; QS, *Quercus suber*; TA, *Tetraclinis articulata*.

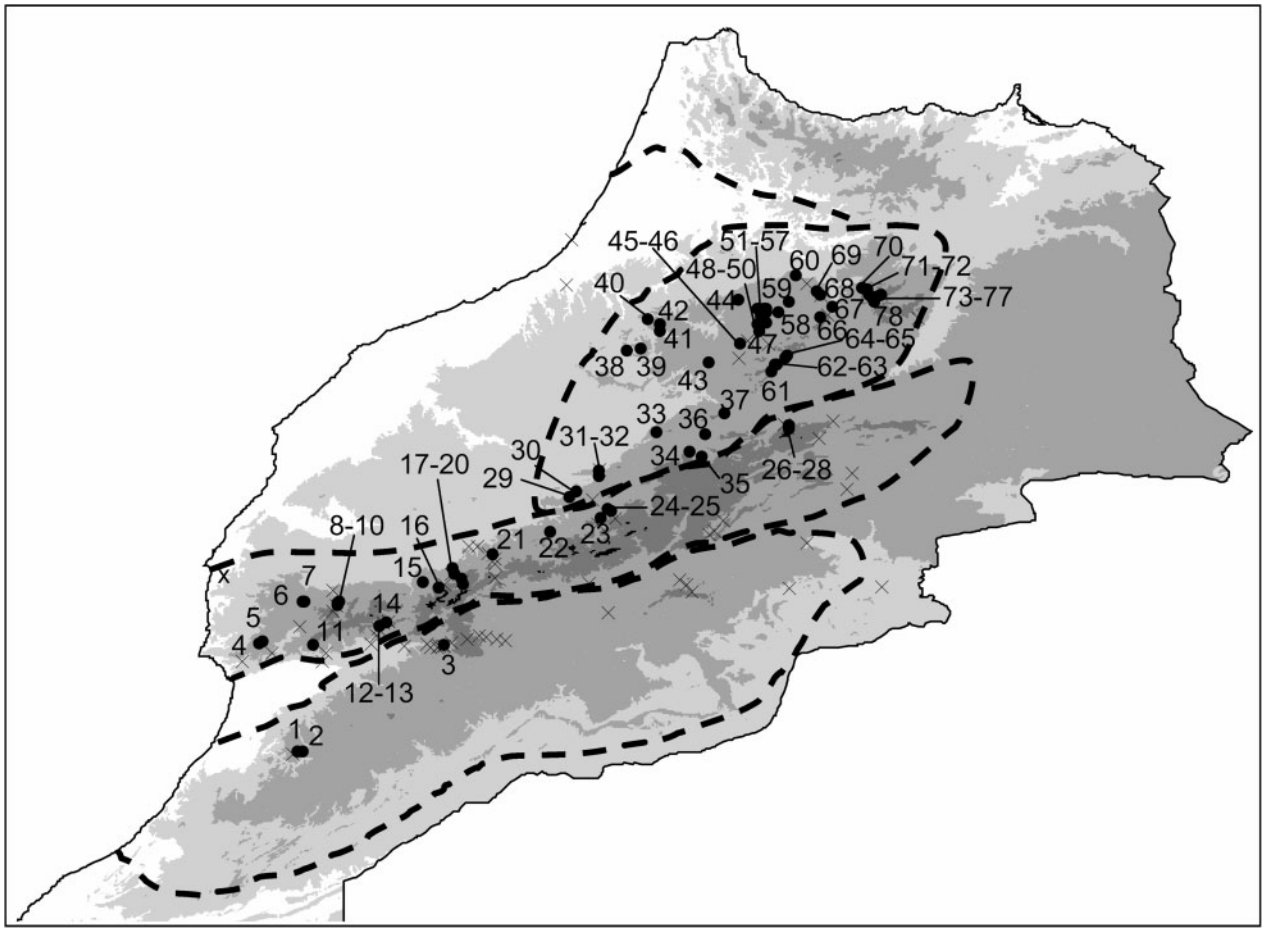

Figure 4. Situation of the sampling sites. Locality numbers appear in Appendix 1, × indicates localities explored which have no epiphytes.

Atlas). The epiphytic stratum in these forests is usually well developed, both in oceanic and continental areas. The humid Mediterranean climate in the Atlasic lands is restricted to montane altitudes of the Middle Atlas, where the forests are dominated by *Pinus pinaster*, *Quercus canariensis* Willd. and *Cedrus atlantica* and also have a well-developed epiphytic stratum. The high mountain Mediterranean climate usually features strong winds and its characteristic vegetation consists of meadows and thorny bushes. In this environment, *Juniperus thurifera* subsp. *africana* and *Quercus rotundifolia* sometimes grow scattered, with few epiphytic bryophytes.

Methodology

Field work was carried out between 1994 and 2004 in 146 localities, but epiphytic bryophytes were found in only 78 of them (Fig. 4 and Appendix 1). Wherever epiphytic bryophytes were available, samples of 20×20 cm were taken from tree bases and trunks on all types of phorophytes.

The affinity of taxa for bark in Morocco has been studied on the basis of local occurrence on different substrata (bibliographic data and field observations) and is mentioned for each taxa in the catalogue. Classes based on the groups established by Mazimpaka & Lara (1995) were defined as follows: 'customary epiphytes', which include strict epiphytes and facultative epiphytes preferentially found on bark; 'cortico-saxicolous', which include facultative epiphytes that colonize both bark and rock in the same way; 'indifferent', for taxa that occur similarly on bark, rock and soil; and 'preferentially not corticolous', for bryophytes that occasionally appear on bark but are commoner on other substrata.

Distributional maps for all the epiphytic taxa recorded in the country, including those of previous catalogues (Draper *et al.*, 2005), were made using ArcView GIS 3.2 (Figs 5–9). Maps for the taxa appearing in fewer than 5% of the localities sampled in Morocco are only shown for customary epiphytes.

Bryophyte Catalogue

The bryophytes found in the Atlasic lands are presented in alphabetical order in the following list. The nomenclature is based on Ros, Cano & Guerra (1999), with the exceptions of the genera *Didymodon* Hedw. (Jiménez, 2004), *Orthotrichum* Hedw. (Cortini Pedrotti & Lara, 2001), *Syntrichia* Brid. (Gallego, 2002), *Tortella* (Lindb.) Limpr. (Puche, 2004) and *Tortula* Hedw. (Cano, 2004). For each taxon, the sites where it has been recorded are given (the

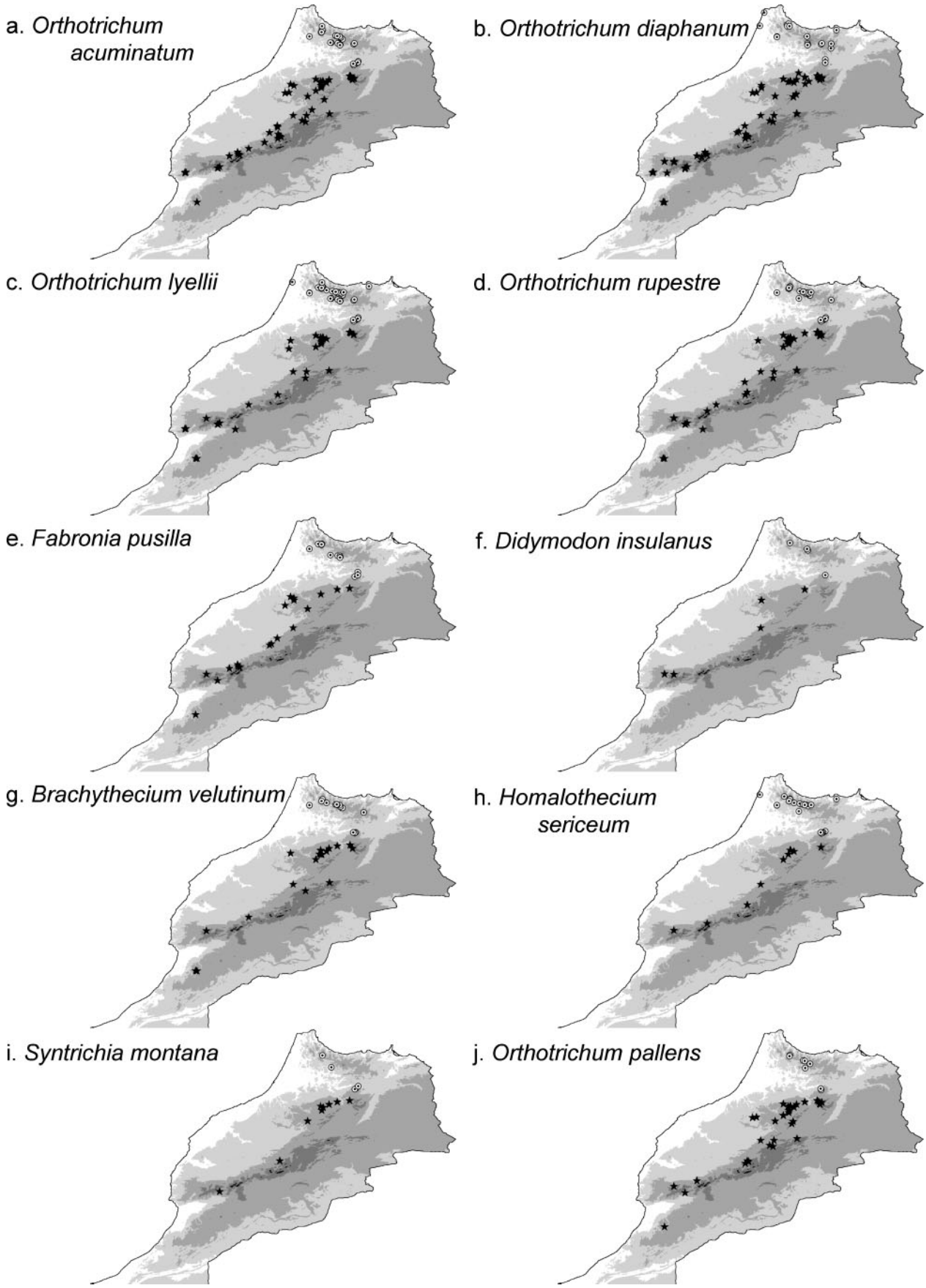

Figure 5. Distribution maps of widely distributed taxa. Stars indicate reports given in the present study, circles indicate bibliographic reports.

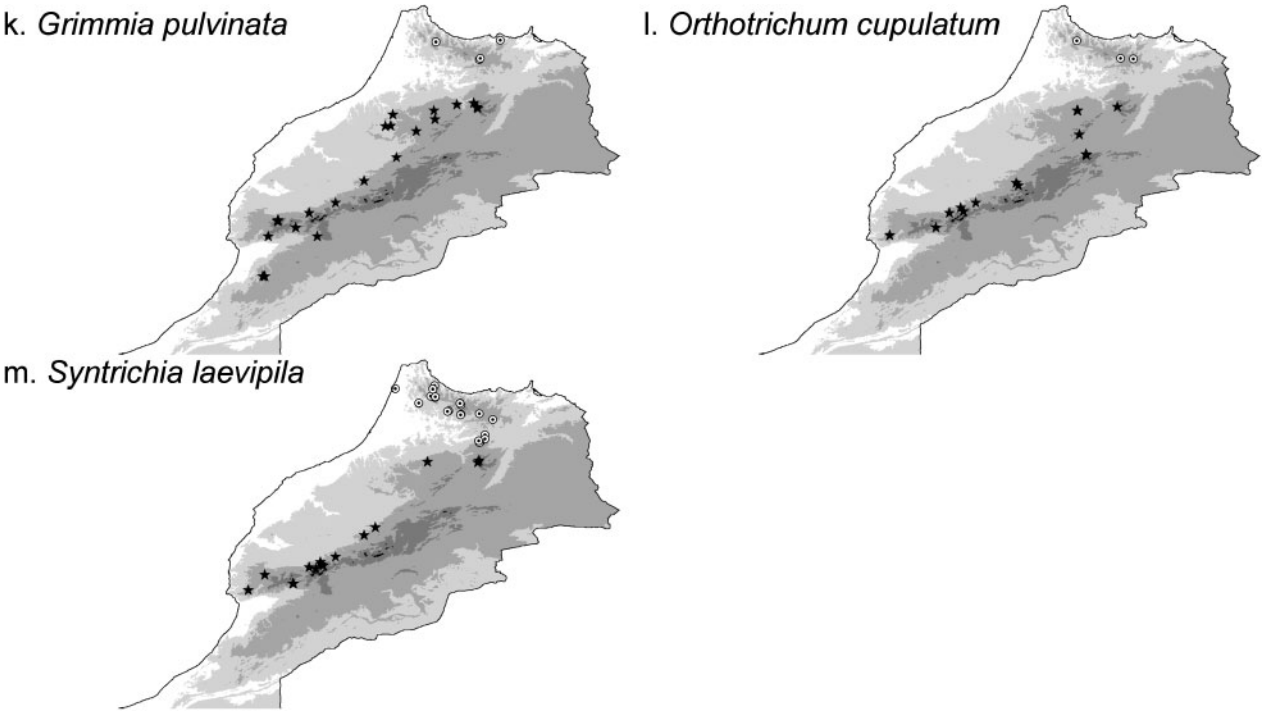

Figure 5. Continued.

locality numbers appear in Appendix 1), as well as its reproductive state (Pr, propaguliferous; F, fertile with gametangia but lacking sporophytes; Fr, with sporophytes), the affinity for bark and a description of the tree stratum occupied in the study area. Distribution in Morocco, altitudinal preferences and other interesting data are given when appropriate. Chorological novelties are marked with *** when new to northern Africa, ** when new to Morocco and * for regional novelties.

Marchantiophyta

Frullania dilatata (L.) Dumort. – 40. Customary epiphyte. Middle Atlas, on bases of *Quercus suber*, 1050 m.

****Porella platyphylla*** (L.) Pfeiff. – 19, 50. Cortico-saxicolous. High Atlas, on trunks and bases of *Quercus rotundifolia*, 1200 m; Middle Altas, on trunks of *Ilex aquifolium* L., 1700 m. Previously recorded from the Rif mountains and the Middle Atlas (Jelenc, 1955, 1967; Garilleti, Lara & Mazimpaka, 1997b; Draper *et al.*, 2005), new to the High Atlas mountains.

Bryophyta

Antitrichia californica Sull. – 33, 38, 40, 42, 45^{Fr}, 49, 56. Cortico-saxicolous. Middle Atlas, on bases and trunks of different phorophytes in forests between 800 and 1650 m.

Barbula unguiculata Hedw. – 1^{Fr}, 4^{Fr}, 12, 13, 15, 21, 43. Preferentially not corticolous. Antiatlas, on bases of *Crataegus monogyna* Jacq. and *Quercus rotundifolia*, 1600 m; High Atlas, on bases and trunks of *Q. rotundifolia* and bases of *Juniperus oxycedrus*, between 1200 and 2100 m; Middle Atlas, on bases of *Q. rotundifolia* and *Olea europaea* L., 1100 m.

****Brachythecium dieckei*** Roll – 34, 50, 74^{F}. Indifferent. Middle Atlas, on bases of *Quercus rotundifolia*, between 1480 and 1700 m. Previously recorded from the Rif (Draper *et al.*, 2005) and High Atlas (Ros *et al.*, 2000) mountains, new to the Middle Atlas.

Brachythecium velutinum (Hedw.) Schimp. – 1^{F}, 2, 9, 21^{Fr}, 27, 33^{F}, 35^{F}, 40, 45, 46, 49, 50^{Fr}, 51^{Fr}, 52, 58^{Fr}, 59, 69, 71, 78^{Fr}. Indifferent. Antiatlas, on bases of *Quercus rotundifolia* between 1600 and 1900 m; High Atlas, on bases of *Q. rotundifolia* and *Juniperus oxycedrus* L. between 1500 and 2000 m; Middle Atlas, on different phorophytes, generally on their bases, in forests between 1050 and 1950 m.

Bryum capillare Hedw. – 38, 39, 40, 41, 50^{Fr}, 51, 58, 69. Preferentially not corticolous. Middle Atlas, on *Quercus rotundifolia*, *Q. suber* and *Q. canariensis*, generally on their bases, between 800 and 1750 m.

Ceratodon purpureus (Hedw.) Brid. – 14, 31. Preferentially not corticolous. High Atlas, on bases of *Quercus rotundifolia*, 1850 m; Middle Atlas, on bases of *Pistacia lentiscus* L., 1300 m.

Dicranoweisia cirrata (Hedw.) Lindb. – $40^{Pr,Fr}$, $46^{Pr,Fr}$, 50^{F}. Customary epiphyte. Middle Atlas, on *Quercus suber* and

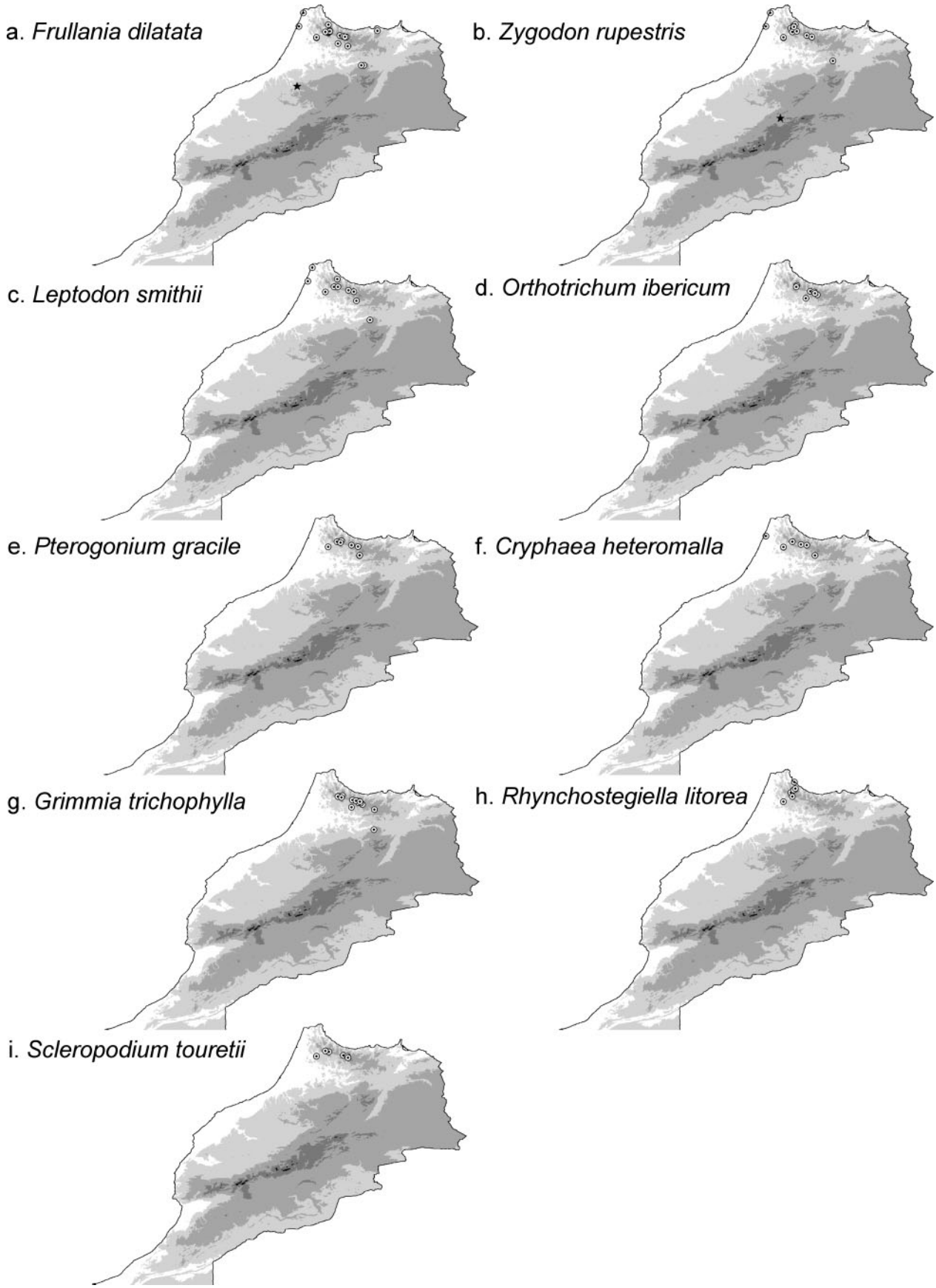

Figure 6. Distribution maps of Riffian taxa. Stars indicate reports given in the present study, circles indicate bibliographic reports.

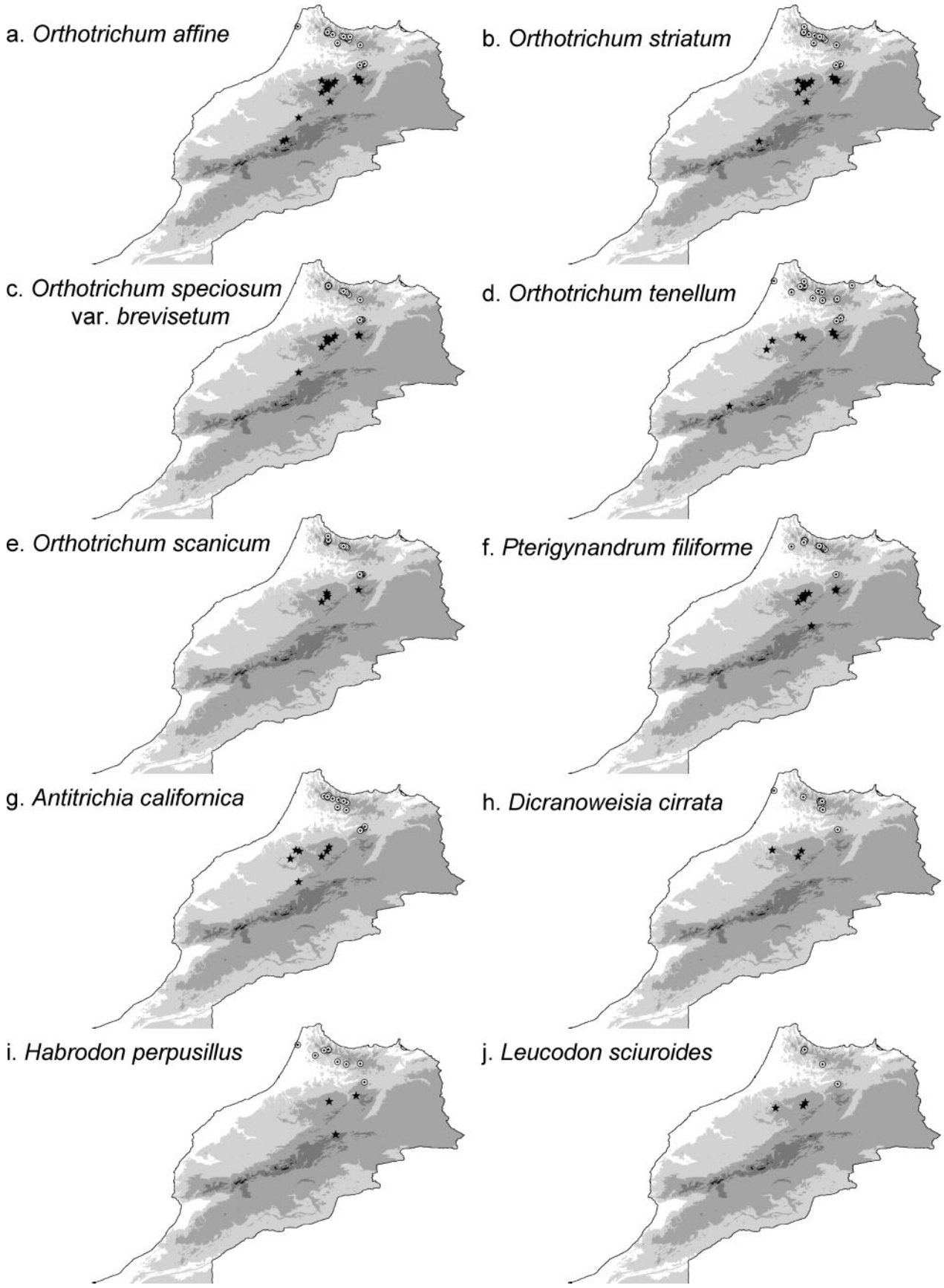

Figure 7. Distribution maps of Rif and Middle Atlas taxa. Stars indicate reports given in the present study, circles indicate bibliographic reports.

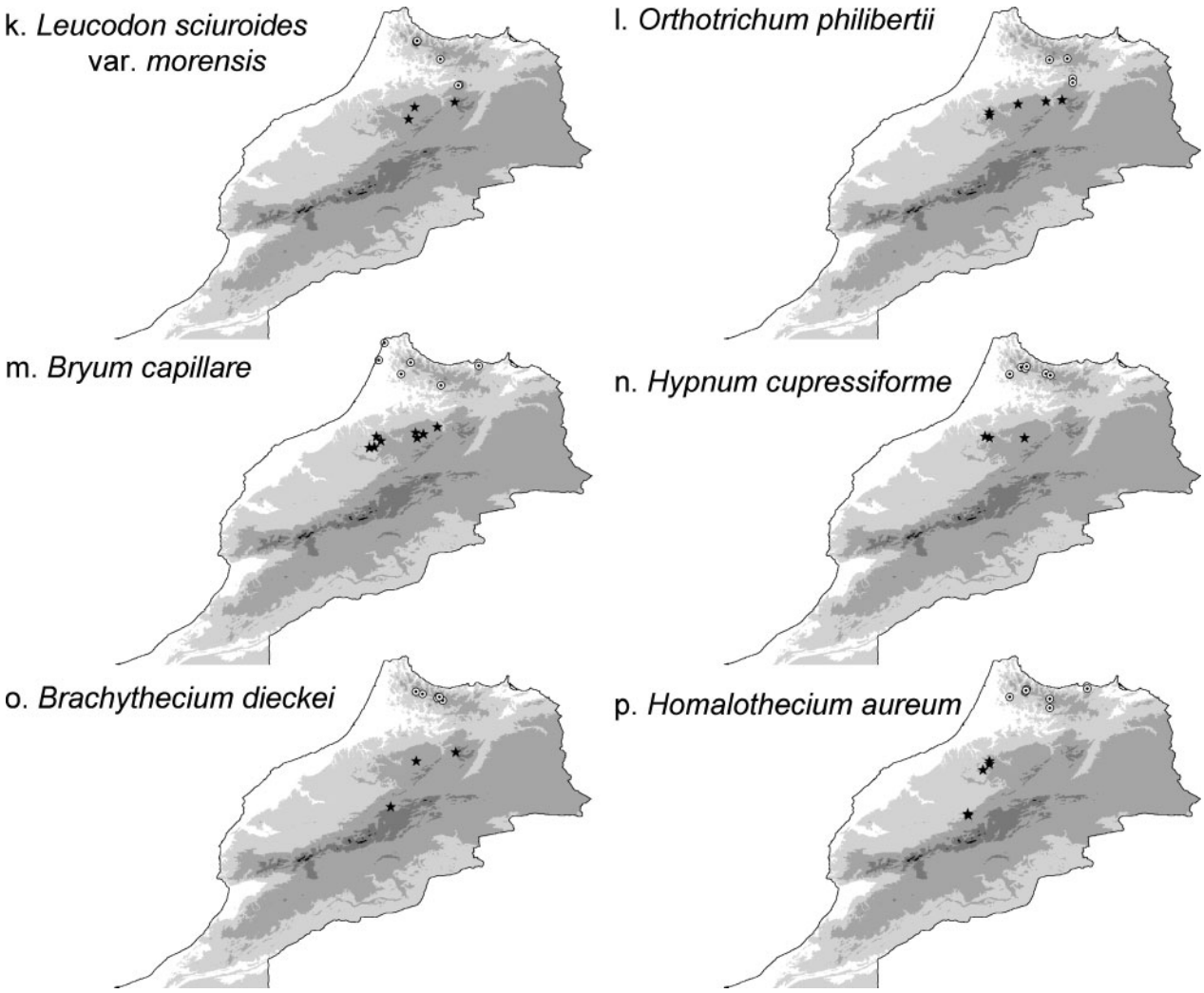

Figure 7. Continued.

Cedrus atlantica, generally on their bases, between 1050 and 1950 m.

Didymodon australasiae (Hook. & Grev.) R.H.Zander – 28^{Fr}. Preferentially not corticolous. High Atlas, on bases of *Cedrus atlantica*, 2100 m.

Didymodon insulanus (De Not.) M.O.Hill – 6, 9, 33, 41, 69^{F}. Preferentially not corticolous. High Atlas, on bases of *Quercus rotundifolia* and *Tetraclinis articulata*, between 1200 and 1900 m; Middle Atlas, on bases of *Q. rotundifolia* and *Q. canariensis*, between 1000 and 1475 m.

Didymodon vinealis (Brid.) R.H.Zander– 7, 9, 41^{F}. Preferentially not corticolous. High Atlas, on bases of *Quercus rotundifolia* and *Juniperus phoenicea*, between 1250 and 1900 m; Middle Atlas, on bases of *Q. rotundifolia*, 1000 m.

****Fabronia pusilla*** Raddi – 1, 8^{Fr}, 12^{Fr}, 15^{Fr}, 17^{Fr}, 18^{Fr}, 19^{Fr}, 29^{Fr}, 30^{Fr}, 31^{Fr}, 33, 38^{Fr}, 40^{Fr}, 41^{Fr}, 42^{Fr}, 43^{Fr}, 52^{Fr}, 69, 70^{Fr}. Customary epiphyte. Antiatlas, on bases of *Crataegus monogyna*, 1600 m; High Atlas, on bases and trunks of different phorophytes, especially *Quercus rotundifolia*, *Juniperus phoenicea* and *Tetraclinis articulata* between 1000 and 2000 m; Middle Atlas, on bases and trunks of different phorophytes, especially *Q. rotundifolia* and *Q. suber* between 700 and 1550 m. Previously recorded from the Rif, Middle Atlas and Antiatlas mountains (Jelenc, 1955; Cano *et al.*, 2002; Draper *et al.*, 2005), new to the High Atlas.

****Fissidens taxifolius*** Hedw. – 70. Preferentially not corticolous. Middle Atlas, on bases of *Quercus rotundifolia*, 1200 m. Previously recorded from the Rif and Antiatlas mountains (Jelenc, 1955, 1967), new to the Middle Atlas.

Grimmia laevigata (Brid.) Brid. – 21, 40^{F}. Preferentially not corticolous. High Atlas, on trunks of *Quercus suber*, 1500 m; Middle Atlas, on trunks of *Q. suber*, 1050 m.

Grimmia pulvinata (Hedw.) Sm. – 1, 2^{F}, 3, 8, 9, 10, 11^{Fr}, 14, 15, 21^{Fr}, 29, 33, 38^{Fr}, 39^{F}, 40^{F}, 43^{Fr}, 47^{Fr}, 51^{Fr}, 69^{Fr}, 70^{Fr},

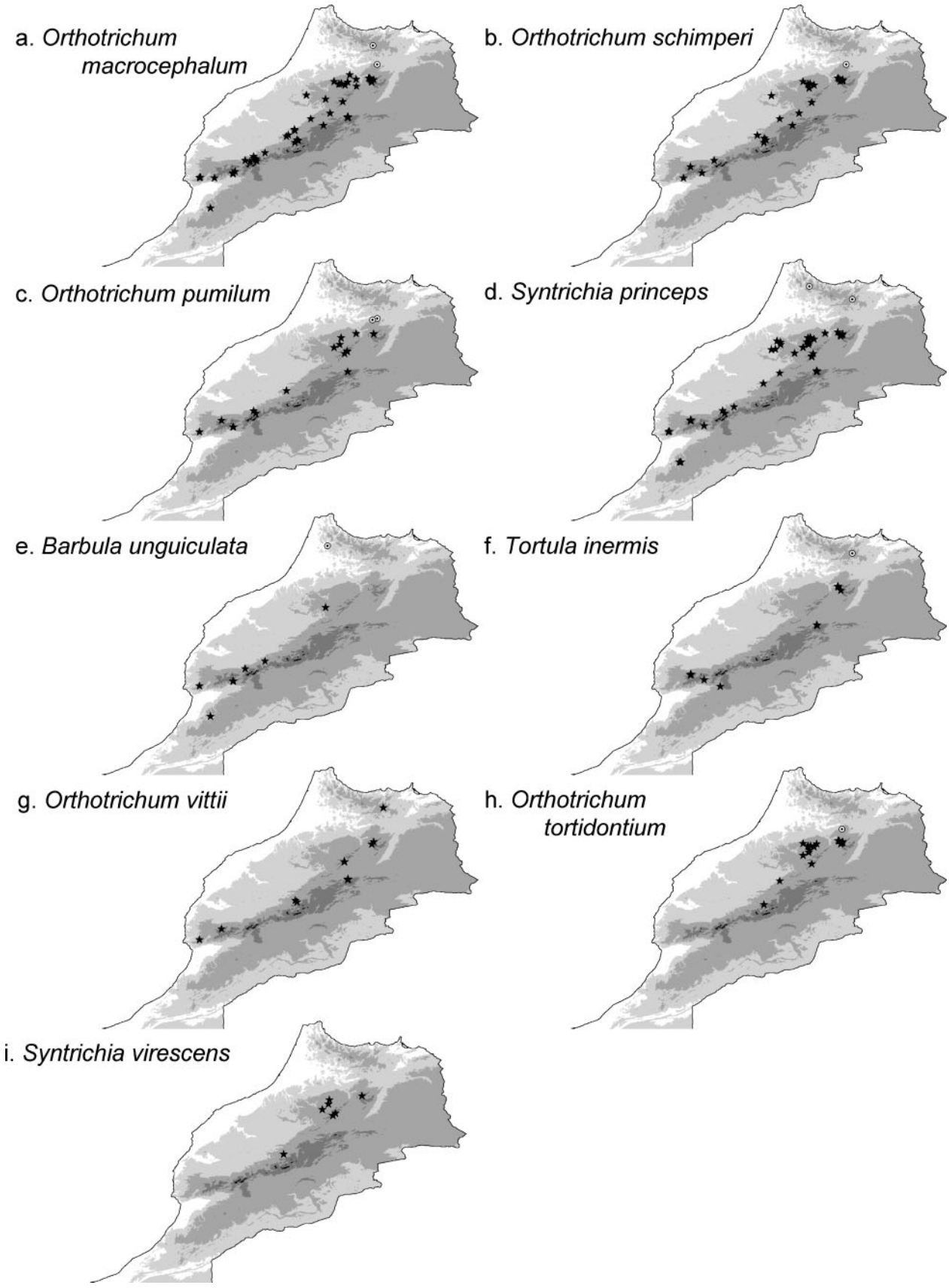

Figure 8. Distribution maps of Atlasic taxa. Stars indicate reports given in the present study, circles indicate bibliographic reports.

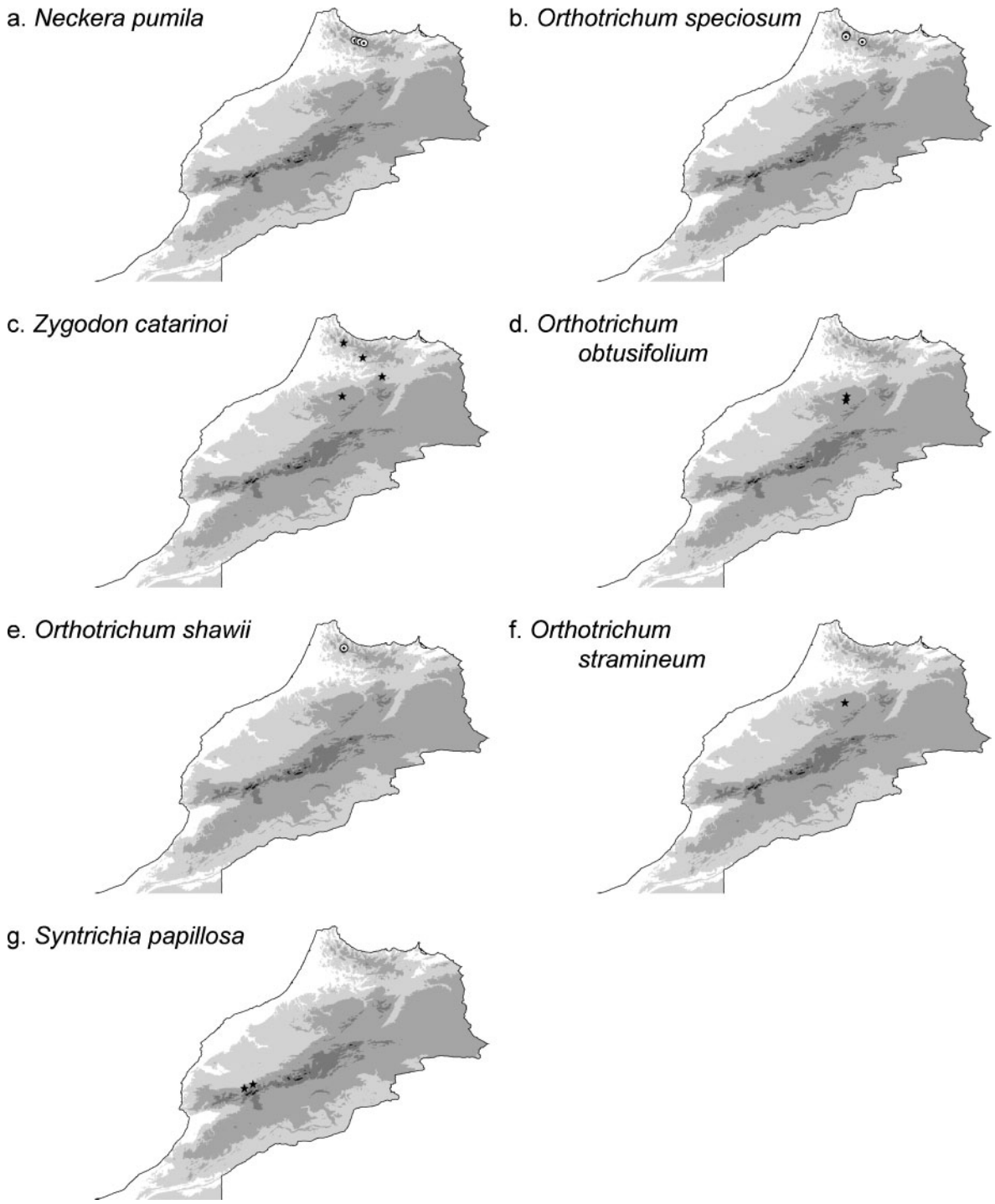

Figure 9. Distribution maps of taxa with localized occurrences. Stars indicate reports given in the present study, circles indicate bibliographic reports.

74, 78[Fr]. Preferentially not corticolous. Antiatlas, on bases of *Quercus rotundifolia*, *Crataegus monogyna* and *Juniperus oxycedrus* between 1600 and 1900 m; High Atlas, on different phorophytes, especially on bases of *Q. rotundifolia*, between 1200 and 1900 m; Middle Atlas, on different phorophytes, especially on bases of *Q. rotundifolia*, between 800 and 2050 m.

Habrodon perpusillus (De Not.) Lindb. – 27, 56, 70[Pr]. Customary epiphyte. High Atlas, on bases of *Quercus rotundifolia*, 2000 m; and Middle Atlas, on bases and trunks of *Q. rotundifolia*, between 1200 and 1500 m. Previously recorded from the Rif and Middle Atlas mountains (Garilleti *et al.*, 1997b; Draper *et al.*, 2005), new to the High Atlas.

Homalothecium aureum (Spruce) H.Rob. – 31, 32, 39, 41, 42. Preferentially not corticolous. Middle Atlas, on bases of *Quercus rotundifolia* and *Pistacia lentiscus* between 950 and 1450 m.

Homalothecium philippeanum (Spruce) Schimp. – 71. Preferentially not corticolous. Middle Atlas, on bases of *Quercus rotundifolia*, 1500 m.

Homalothecium sericeum (Hedw.) Schimp. – 8, 19, 24, 33, 45, 49, 50, 51, 52, 55, 56, 57, 58, 76. Indifferent. High Atlas, on bases of *Quercus rotundifolia* and *Fraxinus dimorfa* Cosson & Durieu, between 1200 and 1750 m; Middle Atlas, on bases and trunks of different phorophytes, especially on *Q. rotundifolia*, between 1475 and 1850 m.

Hypnum cupressiforme Hedw. – 40, 42, 49. Indifferent. Middle Atlas, on bases of *Quercus canariensis* and *Q. rotundifolia*, and trunks of *Acer monspessulanum* L., *Q. suber* and *Q. rotundifolia*, between 950 and 1625 m.

Leucodon sciuroides (Hedw.) Schwägr. var. ***sciuroides*** – 41, 49, 57. Customary epiphyte. Middle Atlas, on bases of *Quercus rotundifolia* and trunks of *Q. rotundifolia* and *Acer monspessulanum*, between 1000 and 1625 m.

Leucodon sciuroides (Hedw.) Schwägr. var. ***morensis*** (Schwägr.) De Not. – 45, 51, 73. Customary epiphyte. Middle Atlas, on bases of *Quercus canariensis* and bases and trunks of *Q. rotundifolia*, between 1300 and 1680 m.

****Orthotrichum acuminatum*** H.Philib. – 2^{Fr}, 4^{Fr}, 5^{Fr}, 12^{Fr}, 13^{Fr}, 14^{Fr}, 15^{Fr}, 17^{Fr}, 18, 19^{Fr}, 21^{Fr}, 22^{Fr}, 23^{Fr}, 24^{Fr}, 25^{Fr}, 27^{Fr}, 29^{Fr}, 31^{Fr}, 32^{Fr}, 33^{Fr}, 34^{Fr}, 35^{Fr}, 36^{Fr}, 37^{Fr}, 38^{Fr}, 39^{Fr}, 40^{Fr}, 42^{Fr}, 43^{Fr}, 44^{Fr}, 45^{Fr}, 46^{Fr}, 47^{Fr}, 49^{Fr}, 50^{Fr}, 51^{Fr}, 52^{Fr}, 53^{Fr}, 54^{Fr}, 55^{Fr}, 56^{Fr}, 58^{Fr}, 59^{Fr}, 61^{Fr}, 70^{Fr}, 71^{Fr}, 72^{Fr}, 73^{Fr}, 74^{Fr}, 75^{Fr}, 76^{Fr}, 77^{Fr}, 78^{Fr}. Customary epiphyte. Antiatlas, on bases and trunks of *Quercus rotundifolia*, 1900 m; High Atlas, on bases and trunks of different phorophytes, especially on *Q. rotundifolia* and *Juniperus oxycedrus*, between 1000 and 2090 m; Middle Atlas, on bases and trunks of all types of phorophytes, especially on *Q. rotundifolia*, between 800 and 2170 m. Previously recorded from the Rif and Middle Atlas mountains (Jelenc, 1955; Lara, Garilleti & Mazimpaka, 1996; Garilleti *et al.*, 1997b; van der Pluijm, 2001; Draper *et al.*, 2005), new to the Antiatlas and High Atlas.

****Orthotrichum affine*** Brid. – 23^{Fr}, 25^{Fr}, 33^{Fr}, 44^{Fr}, 45^{Fr}, 46^{Fr}, 47^{Fr}, 49^{Fr}, 50^{Fr}, 51^{Fr}, 52^{Fr}, 53^{Fr}, 54^{Fr}, 55^{Fr}, 56^{Fr}, 57^{Fr}, 58^{Fr}, 59^{Fr}, 61^{Fr}, 70^{Fr}, 74^{Fr}, 75^{Fr}, 76^{Fr}, 78^{Fr}. Customary epiphyte. High Atlas, on bases and trunks of *Quercus rotundifolia* around 1900 m; Middle Atlas, on all types of phorophytes, generally on trunks, between 1200 and 2170 m. Previously recorded from the Rif and Middle Atlas mountains (Jelenc, 1955, 1967; Lara *et al.*, 1996; Garilleti *et al.*, 1997b; Draper *et al.*, 2005), new to the High Atlas.

Orthotrichum cupulatum Brid. – 5^{Fr}, 14^{Fr}, 15^{F}, 18, 19^{Fr}, 21^{Fr}, 23^{Fr}, 24^{Fr}, 26^{Fr}, 27^{Fr}, 55^{Fr}, 56^{Fr}, 61^{Fr}, 75^{Fr}. Preferentially not corticolous. High Atlas, on different phorophytes, especially on bases of *Quercus rotundifolia*, between 1200 and 2170 m; Middle Atlas, on bases and trunks of *Q. rotundifolia* and *Fraxinus angustifolia* Vahl, between 1500 and 2170 m.

****Orthotrichum diaphanum*** Brid. – 1^{Fr}, 2^{Fr}, 4^{Fr}, 5^{Fr}, 6^{Fr}, 7^{Fr}, 8^{Fr}, 9^{Fr}, 10^{Fr}, 11^{Fr}, 12^{Fr}, 13^{Fr}, 14, 15^{Fr}, 16, 17^{Fr}, 18^{Fr}, 19^{Fr}, 23^{Fr}, 24, 25^{Fr}, 26^{Fr}, 27^{Fr}, 29^{Fr}, 30^{Fr}, 31^{Fr}, 33, 34^{Fr}, 35^{Fr}, 36^{Fr}, 38^{Fr}, 39^{Fr}, 41^{Fr}, 42^{Fr}, 43^{Fr}, 44^{Fr}, 52^{Fr}, 54^{Fr}, 55^{Fr}, 56^{Fr}, 58^{Fr}, 59^{Fr}, 60^{Fr}, 62, 63^{Fr}, 64, 65^{Fr}, 66^{Fr}, 67^{Fr}, 68^{Fr}, 69^{Fr}, 70^{Fr}, 71^{Fr}, 72^{Fr}, 73, 74^{Fr}, 75, 76, 77^{Fr}, 78^{Fr}. Customary epiphyte. Antiatlas, on bases of *Crataegus monogyna* and bases and trunks of *Quercus rotundifolia*, between 1600 and 1900 m; High Atlas, on bases and trunks of different phorophytes, between 1000 and 2600 m; Middle Atlas, on bases and trunks of different phorophytes, between 700 and 2100 m. Previously recorded from the Rif and Middle Atlas mountains (Jelenc, 1955, 1967; Draper *et al.*, 2005), new to the Antiatlas and High Atlas.

****Orthotrichum lyellii*** Hook. & Taylor – 1^{Pr}, 2, 3^{Pr}, 4^{Pr}, $5^{Pr,Fr}$, 9^{Pr}, 12^{Pr}, 13, 14^{Pr}, 21^{Pr}, 23^{Pr}, 28^{Pr}, $33^{Pr,Fr}$, 35^{Pr}, 36, 39^{Pr}, $40^{Pr,Fr}$, $44^{Pr,Fr}$, $45^{Pr,Fr}$, $46^{Pr,Fr}$, 47^{Pr}, 49^{Pr}, $50^{Pr,Fr}$, 51^{Pr}, 52^{Pr}, 54^{Pr}, 56^{Pr}, 57, 58^{Pr}, $70^{Pr,Fr}$, 71^{Pr}, 72^{Pr}, 76^{Pr}. Customary epiphyte. Antiatlas, on bases and trunks of *Quercus rotundifolia*, between 1600 and 1900 m; High Atlas, on bases and trunks of *Q. rotundifolia*, *Juniperus oxycedrus* and *Cedrus atlantica*, and on trunks of *Q. suber*, between 1500 and 2100 m; Middle Atlas, on bases and trunks of different phorophytes, between 1050 and 2050 m. Previously recorded from the Rif, Middle and High Atlas mountains (Jelenc, 1955, 1967; Lara *et al.*, 1996; Garilleti *et al.*, 1997b; Draper *et al.*, 2005), new to the Antiatlas.

****Orthotrichum macrocephalum*** F.Lara, Garilleti & Mazimpaka – 1^{Fr}, $4^{Pr,Fr}$, 5^{Fr}, 11^{Fr}, 12^{Fr}, 13^{Fr}, 14^{Fr}, 15^{Fr}, 16^{Fr}, 17^{Fr}, 18^{Fr}, 19^{Fr}, 20^{Fr}, 21, 23^{Fr}, 24^{Fr}, 25^{Fr}, 26^{Fr}, $27^{Pr,Fr}$, 28, 29^{Fr}, 30, 31^{Fr}, 32^{Fr}, 33^{Fr}, 35^{Fr}, 37^{Fr}, 39, 43^{Fr}, 44^{Fr}, 51^{Fr}, 52^{Fr}, $54^{Pr,Fr}$, 55^{Fr}, $56^{Pr,Fr}$, 58^{Fr}, 59^{Fr}, 60^{Fr}, 61^{Fr}, 66^{Fr}, 69^{Fr}, 70^{Fr}, 71^{Fr}, 73^{Fr}, 74^{Fr}, 77^{Fr}, 78^{Fr}. Customary epiphyte. Antiatlas, on bases of *Crataegus monogyna*, 1600 m; High Atlas, on bases and trunks of different phorophytes, between 1000 and 2600 m; Middle Atlas, on bases and trunks of different phorophytes, between 700 and 2170 m. Previously recorded from the Rif and Middle Atlas mountains (Garilleti, Lara & Mazimpaka, 1997a; Draper *et al.*, 2005), new to the Antiatlas and High Atlas.

******Orthotrichum obtusifolium*** Brid. – 50^{Pr}, 54^{Pr}. Customary epiphyte. Middle Atlas, on bases and trunks of *Quercus rotundifolia*, *Q. canariensis* and *Ulmus minor* Mill., around 1700 m. This subcontinental species is widely distributed in Europe, Asia and north America (Düll, 1985, 1992; Lewinsky, 1993). This report is the first one for northern Africa.

Orthotrichum pallens Bruch ex Brid. – 2^{Fr}, 8^{Fr}, 12^{Fr}, 15^{Fr}, 23^{Fr}, 24^{Fr}, 25^{Fr}, 27^{Fr}, 33^{Fr}, 34^{Fr}, 35^{Fr}, 36^{Fr}, 38^{Fr}, 39^{Fr}, 43^{Fr}, 44^{Fr}, 45^{Fr}, 46^{Fr}, 47^{Fr}, 49^{Fr}, 50^{Fr}, 51^{Fr}, 52^{Fr}, 54^{Fr}, 55^{Fr}, 56^{Fr}, 58^{Fr}, 59^{Fr}, 61^{F}, 62^{Fr}, 69^{Fr}, 70^{Fr}, 72^{Fr}, 74^{Fr}, 77^{Fr}, 78^{Fr}. Customary epiphyte. Antiatlas, on bases and trunks of *Quercus rotundifolia*, 1900 m; High Atlas, on bases and trunks of different phorophytes, especially on *Q. rotundifolia*, between 1200 and 2025 m; Middle Atlas, on bases and trunks of different phorophytes, between 800 and 2170 m. Previously recorded from the Rif mountains (Draper *et al.*, 2005), new to the Atlas mountains.

Orthotrichum philibertii Venturi – 41^{Fr}, 42^{Fr}, 44^{Fr}, 69^{Fr}, 70^{Fr}. Customary epiphyte. Middle Atlas, on bases and trunks of *Quercus rotundifolia*, between 950 and 1680 m. Previously recorded from the Rif mountains (Draper *et al.*, 2005), new to the Atlas mountains.

Orthotrichum pumilum Sw. – 4^{Fr}, 8^{Fr}, 12^{Fr}, 13^{Fr}, 18^{Fr}, 19^{Fr}, 28^{Fr}, 29^{Fr}, 46^{Fr}, 47^{Fr}, 54^{Fr}, 63^{Fr}, 64^{Fr}, 65^{Fr}, $69^{Pr,Fr}$, 77^{Fr}. Customary epiphyte. High Atlas, on bases and trunks of *Quercus rotundifolia*, *Juniperus oxycedrus*, *J. phoenicea* and *Cedrus atlantica*, between 1000 and 2100 m; Middle Atlas, on different phorophytes, generally on trunks, between 950 and 2100 m. Previously recorded from the Rif and Middle Atlas mountains (Jelenc, 1955; Draper *et al.*, 2005), new to the High Atlas.

Orthotrichum rupestre Schleich. ex Schwägr. – 1^{Fr}, 2^{Fr}, 3, 8^{Fr}, 9^{Fr}, 12^{Fr}, 13^{Fr}, 14^{Fr}, 19^{Fr}, 21^{Fr}, 23^{Fr}, 24^{Fr}, 27^{Fr}, 28^{Fr}, 31^{Fr}, 33^{Fr}, 35^{Fr}, 36^{Fr}, 40^{Fr}, 44^{Fr}, 45^{Fr}, 46^{Fr}, 47^{Fr}, 49^{Fr}, 50^{Fr}, 51^{Fr}, 52^{Fr}, 53^{Fr}, 54^{Fr}, 56^{Fr}, 57^{Fr}, 58^{Fr}, 69^{Fr}, 70^{Fr}, 71^{Fr}, 72^{Fr}, 74^{Fr}, 76^{Fr}, 77^{Fr}, 78^{Fr}. Cortico-saxicolous. Antiatlas, on bases of *Juniperus oxycedrus* and *Crataegus monogyna* and bases and trunks of *Quercus rotundifolia*, between 1600 and 1900 m; High Atlas, on bases and trunks of different phorophytes, especially on bases of *Q. rotundifolia*, between 1200 and 2100 m; Middle Atlas, on bases and trunks of different phorophytes, between 1050 and 2100 m.

Orthotrichum scanicum Grönvall – 46^{Fr}, 49^{Fr}, 50^{Fr}, 52^{Fr}, 53^{Fr}, 74^{Fr}. Customary epiphyte. Middle Atlas, on trunks of *Quercus rotundifolia*, *Ilex aquifolium*, *Acer monspessulanum*, *Q. canariensis* and *Sorbus torminalis* (L.) Crantz, between 1550 and 1950 m.

Orthotrichum schimperi Hammar – 9^{Fr}, 11^{Fr}, 12^{Fr}, 15^{Fr}, 23^{Fr}, 24^{Fr}, 30^{Fr}, 33^{Fr}, 35^{Fr}, 37^{Fr}, 38^{Fr}, 44^{Fr}, 50^{Fr}, 51^{Fr}, 52^{Fr}, 54^{Fr}, 58^{Fr}, 61^{Fr}, 70^{Fr}, 72^{Fr}, 75^{Fr}, 76^{Fr}, 77^{Fr}. Customary epiphyte. High Atlas, on bases and trunks of *Quercus rotundifolia* and trunks of *Juglans regia* L. and *Fraxinus dimorfa*, between 1200 and 2025 m; Middle Atlas, on different phorophytes, generally on trunks, between 700 and 2170 m. Previously recorded from the Rif and Middle Atlas mountains (Jelenc, 1955; Draper *et al.*, 2005), new to the High Atlas.

Orthotrichum speciosum Nees in Sturm. var. ***brevisetum*** F. Lara, Garilleti & Mazimpaka – 33^{Fr}, 46^{Fr}, 49^{Fr}, 50^{Fr}, 51^{Fr}, 52^{Fr}, 57^{Fr}, 58^{Fr}, 59^{Fr}, 74^{Fr}, 78^{Fr}. Customary epiphyte. Middle Atlas, on bases and trunks of different phorophytes, between 1475 and 1950 m. This recently described variety is basically known from the Rif mountains and south-eastern Spain, and has been also detected in Algeria and Sicily (Draper *et al.*, 2003). The records in the Middle Atlas mountains confirm the allopatric distribution with var. *speciosum*, which sparsely occurs in the Rif mountains but has not been found in the Atlasic ranges.

****Orthotrichum stramineum*** Hornsh. ex Brid. – $52^{Pr,Fr}$. Customary epiphyte. Middle Atlas, on trunks of *Quercus rotundifolia*, 1550 m. This suboceanic species is widely distributed in Europe, north America and south-western Asia (Düll, 1985). In northern Africa it is known from Algeria (Ros *et al.*, 1999). This report is the first one for Morocco.

Orthotrichum striatum Hedw. – 23^{Fr}, 44^{Fr}, 45^{Fr}, 46^{Fr}, 49^{Fr}, 50^{Fr}, 51^{Fr}, 52^{Fr}, 55^{Fr}, 58^{Fr}, 59^{Fr}, 61^{Fr}, 70^{Fr}, 74^{Fr}, 76^{Fr}, 77^{Fr}, 78^{Fr}. Customary epiphyte. High Atlas, on trunks of *Quercus rotundifolia*, 1950 m; Middle Atlas, on *Q. rotundifolia*, *Q. canariensis*, *Cedrus atlantica*, *Ilex aquifolium* and *Sorbus torminalis*, generally on trunks, between 1200 and 2170 m. Previously recorded from the Rif and Middle Atlas mountains (Jelenc, 1967; Lara *et al.*, 1996; Garilleti *et al.*, 1997b; Draper *et al.*, 2005), new to the High Atlas.

Orthotrichum tenellum Bruch ex Brid. – 21^{Fr}, 38^{Fr}, 40^{Fr}, $44^{Pr,Fr}$, 52^{Fr}, 70^{Fr}, 71^{Fr}, 78^{Fr}. Customary epiphyte. High Atlas, on trunks of *Quercus rotundifolia*, 1500 m; Middle Atlas, on *Q. rotundifolia* and *Q. suber*, generally on trunks, between 800 and 1850 m.

Orthotrichum tortidontium F. Lara, Garilleti & Mazimpaka – 23^{Fr}, $33^{Pr,Fr}$, 44^{Fr}, 46^{Fr}, 47^{Fr}, 50^{Fr}, 51^{Fr}, 52^{Fr}, 56^{Fr}, 58^{Fr}, 59^{Fr}, 61^{Fr}, 71^{Fr}, 72^{Fr}, 76^{Fr}, 77^{Fr}, 78^{Fr}. Customary epiphyte. High Atlas, on trunks of *Quercus rotundifolia*, 1950 m; Middle Atlas, on bases and trunks of different phorophytes, between 1200 and 2170 m. Previously recorded from the Rif and Middle Atlas mountains (Lara *et al.*, 1996; Draper *et al.*, 2005), new to the High Atlas.

Orthotrichum urnigerum Myrin – 4^{Fr}, 5^{Fr}, 77^{Fr}. Cortico-saxicolous. High Atlas, on bases of *Juniperus oxycedrus* and *Quercus rotundifolia*, around 1600 m; Middle Atlas, on trunks of *J. oxycedrus*, 2100 m. Previously recorded from the Middle Atlas mountains (Jelenc, 1955), new to the High Atlas.

*****Orthotrichum vittii*** F. Lara, Garilleti & Mazimpaka – 4^{Fr}, 9^{Fr}, 23^{Fr}, 24, 27^{Fr}, 28^{Fr}, 62^{Pr}, 63, 77^{Fr}, 78^{Fr}. Customary epiphyte. High Atlas, on different phorophytes, especially on trunks of *Juniperus oxycedrus* and bases of *Quercus rotundifolia*, between 1640 and 2100 m; Middle Atlas,

generally on trunks of *J. thurifera*, between 1850 and 2100 m. It has also been recently found in the eastern Rif mountains (Berkane mountain, UTM grid 30SVD2242), on bases of *Q. rotundifolia*, 1450 m. This species is basically known from *J. thurifera* forests above 900 m in the Iberian Peninsula (Lara *et al.*, 1999). These reports are the first ones for northern Africa, where it is also mostly found in *J. thurifera* forests.

Pleurochaete squarrosa (Brid.) Lindb. – 10. Preferentially not corticolous. High Atlas, on bases of *Juniperus oxycedrus*, 1400 m. Because of its small leaves (less than 3 mm long) that are reflexed when moist, but not squarrose, this plant probably belongs to the var. *maroccana* Jelenc (Thériot & Trabut, 1930; Jelenc, 1954), that has only been reported from Morocco (Jelenc, 1955).

Pottia starckeana (Hedw.) Müll. Hal. – 3. Preferentially not corticolous. Antiatlas, on bases of *Juniperus oxycerus*, 1750 m.

****Pterigynandrum filiforme*** Hedw. – 28, 45, 46^{Pr}, 47^{Pr}, 49, 50^{Fr}, 57, 58, 76, 78. Cortico-saxicolous. High Atlas, on bases of *Cedrus atlantica*, 2100 m; Middle Atlas, on different phorophytes, generally on their bases, between 1625 and 2050 m. Previously recorded from the Rif and Middle Atlas mountains (Jelenc, 1955, 1967; Lara *et al.*, 1996; Draper *et al.*, 2005), new to the High Atlas.

****Rhynchostegium confertum*** (Dicks.) Schimp. – 38, 57. Preferentially not corticolous. Middle Atlas, on bases of *Quercus rotundifolia*, between 800 and 1600 m. Previously recorded from the Rif and High Atlas mountains (Braun-Blanquet, 1954; Jelenc, 1955; Draper *et al.*, 2005), new to the Middle Atlas.

Schistidium confertum (Funck) Bruch & Schimp. – 78^{Fr}. Preferentially not corticolous. Middle Atlas, on bases of *Juniperus thurifera*, 1850 m.

Schistidium singarense (Schiffner) Lazarenko – 70^{Fr}. Preferentially not corticolous. Middle Atlas, on bases of *Quercus rotundifolia*, 1200 m.

****Sematophyllum substrumulosum*** (Hampe) E.Britton – 48. Indifferent. Middle Atlas, on bases of *Cedrus atlantica*, around 1600 m. Previously recorded from the Rif mountains (Jelenc, 1955; Draper *et al.*, 2005), new to the Atlas mountains.

****Syntrichia laevipila*** Brid. – 4^{Fr}, 6^{Pr}, 12, 13, 15^{Pr,F}, 16, 17^{Fr}, 18^{Fr}, 19^{F}, 21^{F}, 29^{Fr}, 32, 44^{Pr,Fr}, 76, 78^{F}. Customary epiphyte. High Atlas, on bases and trunks of different phorophytes, especially on *Juniperus oxycedrus* and *Quercus rotundifolia*, between 1500 and 2600 m; Middle Atlas, on bases and trunks of *Tetraclinis articulata* and *Q. rotundifolia* and bases of *Cedrus atlantica* and *J. thurifera*, between 950 and 1850 m. Previously recorded from the Rif and Middle Atlas mountains (Jelenc, 1955, 1967; Draper *et al.*, 2005), new to the High Atlas.

Syntrichia montana Nees. – 14, 24, 43, 50^{F}, 51^{Fr}, 57, 59, 69^{F}, 70^{F}. Preferentially not corticolous. High Atlas, on bases of *Quercus rotundifolia* and trunks of *Fraxinus dimorfa*, between 1725 and 1850 m; Middle Atlas, on bases and trunks of different phorophytes, especially on *Q. canariensis*, between 1100 and 1700 m.

******Syntrichia papillosa*** Jur. – 15^{Pr}, 18^{Pr}. Customary epiphyte. High Atlas, on bases and trunks of *Quercus rotundifolia*, *Juniperus phoenicea* and *Tetraclinis articulata*, between 1000 and 1200 m. Following Düll (1984), this species was present in North Africa, but Ros *et al.* (1999) considered its presence doubtful because no literature report was known. Such a presence is confirmed with the present records.

Syntrichia princeps (De Not.) Mitt. – 1^{Fr}, 2^{Fr}, 4^{Fr}, 5^{F}, 8^{F}, 9^{Fr}, 10^{F}, 14^{F}, 18^{F}, 19^{Fr}, 21, 26, 27, 28, 31, 33^{F}, 38^{Fr}, 39^{F}, 40^{F}, 41^{Fr}, 42^{Fr}, 43^{Fr}, 45, 46, 47, 49^{F}, 50^{F}, 51, 52^{F}, 55, 56^{Fr}, 58^{F}, 61^{Fr}, 62, 69, 70^{Fr}, 75, 76^{F}, 77^{F}, 78^{F}. Indifferent. Antiatlas, on bases of *Quercus rotundifolia* and *Crataegus monogyna*, between 1600 and 1900 m; High Atlas, on different phorophytes, especially on bases of *Q. rotundifolia*, between 1000 and 2100 m; Middle Atlas, on bases and trunks of different phorophytes, especially on *Q. rotundifolia*, between 800 and 2170 m.

Syntrichia virescens (De Not.) Ochyra – 23, 46, 50, 54, 63, 65^{Fr}, 77. Cortico-saxicolous. High Atlas, on *Fraxinus angustifolia*, 1950 m; Middle Atlas, on different phorophytes, generally on trunks, between 1675 m and 2100 m.

Tortella flavovirens (Bruch) Broth. – 30. Preferentially not corticolous. Middle Atlas, on bases of *Olea europaea*, 700 m.

Tortella humilis (Hedw.) Jenn. – 69^{F}. Preferentially not corticolous. Middle Atlas, on bases of *Quercus rotundifolia* and *Phyllirea angustifolia* L., 1180 m.

****Tortella inflexa*** (Bruch) Broth. – 69^{F}. Preferentially not corticolous. Middle Atlas, on bases of *Quercus rotundifolia*, 1180 m. Previously recorded from the Rif mountains (Jelenc, 1955), new to the Atlas mountains.

Tortella tortuosa (Hedw.) Limpr. var. ***fragilifolia*** (Jur.) Limpr. – 31, 33, 69^{Fr}. Preferentially not corticolous. Middle Atlas, on bases of *Phyllirea angustifolia*, *P. latifolia* L., *Quercus rotundifolia* and *Pistacia lentiscus*, between 1180 and 1475 m.

Tortula atrovirens (Sm.) Lindb. – 7^{Fr}, 18^{Fr}. Preferentially not corticolous. High Atlas, on bases of *Juniperus phoenicea*

and trunks of *Tetraclinis articulata*, between 1000 and 1250 m.

Tortula inermis (Brid.) Mont. – 3, 8^{F}, 9^{Fr}, 10, 14^{F}, 26^{Fr}, 27^{Fr}, 70^{F}, 71^{Fr}, 78^{F}. Preferentially not corticolous. Antiatlas, on bases of *Juniperus oxycedrus*, 1750 m; High Atlas, on *Quercus rotundifolia*, *J. oxycedrus* and *Fraxinus dimorfa*, generally on bases, between 1400 and 2000 m; Middle Atlas, on bases and trunks of *Q. rotundifolia* and *J. thurifera*, between 1200 and 1850 m.

Tortula subulata Hedw. – 50^{Fr}. Preferentially not corticolous. Middle Atlas, on bases of *Cedrus atlantica* and *Quercus rotundifolia*, 1700 m.

Weissia controversa Hedw. – 70^{Fr}. Preferentially not corticolous. Middle Atlas, on bases of *Quercus rotundifolia*, 1200 m.

****Zygodon catarinoi*** C.García, F.Lara, Sérgio & Sim-Sim – 51^{Pr}. Customary epiphyte. Middle Atlas, on bases of *Quercus canariensis* and trunks of *Q. rotundifolia*, 1500 m. This recently described species (García *et al.*, 2006) has been found in different forests in the Iberian Peninsula and Morocco, including three localities in the Rif and Tazzeka mountains (Jbel Bouhalla, UTM grid 30SUD0486; Jbel Tifelloust, UTM grid 30SUD5438; and Jbel Tazzeka, UTM grid 30SVC0477), where it had been previously reported as *Zygodon rupestris* (Draper *et al.*, 2005).

Zygodon rupestris Schimp. ex Lorentz – 36. Customary epiphyte. Middle Atlas, on trunks of *Quercus rotundifolia*, 1850 m. Previously recorded from the Rif mountains (Jelenc, 1955; Draper *et al.*, 2005), new to the Middle Atlas.

Discussion

Representation of moss families

The forests of the Atlas mountains feature an epiphytic bryophyte flora composed of 65 taxa, of which two (3%) are liverworts and 63 (97%) are mosses. The liverworts belong to two families (Jubulaceae and Porellaceae) and the mosses to 13, according to Crandall-Stotler & Stotler (2000) and Buck & Goffinet (2000), respectively. Among these mosses, 78% are acrocarpous and 22% are pleurocarpous. The Orthotrichaceae is the most frequent family (20 taxa of *Orthotrichum* and two of *Zygodon*) and contributes nearly 70% of the species that are customary epiphytes. This agrees with its importance in the epiphytic communities throughout the Mediterranean basin (Lara, Garilleti & Mazimpaka, 1994; Lara & Mazimpaka, 2001), and is concordant with our own observations in the Rif mountains (Draper *et al.*, 2003, 2005). The Pottiaceae is the next most frequent family (19 taxa), although most of its members occur only as facultative epiphytes. The importance of this family in the Atlasic lands, as well as the occurrence of four taxa of Grimmiaceae, is probably due to severe aridity making trunks and rocks ecologically similar. This leads to the enrichment of the epiphytic bryophyte communities with some preferentially saxicolous xerophytes, as has been found in other xeric environments (Vitt, 1981; Albertos *et al.*, 2005). Contrarily, the presence of other facultative taxa like Brachytheciaceae (six taxa), Bryaceae (one taxon), Fissidentaceae (one taxon) and Ditrichaceae (one taxon), is related to the especially favourable moisture conditions that can occur on tree bases.

Distribution of epiphytes in Morocco

With the publication of this catalogue, there is now sufficient knowledge of the epiphytic bryophytes of Morocco to discuss the distributional patterns for the 93 species at present reported (Draper *et al.*, 2003, 2005). Taxa are not homogeneously distributed throughout the country: 78% grow as epiphytes in the Rif mountains, which also exhibit the largest number of exclusive taxa (29); 64% grow in the Middle Atlas (eight of them exclusive to these mountains); 38% grow in the High Atlas (four exclusive taxa), and only 14% in the Antiatlas (only one exclusive). In addition, the proportion of localities with epiphytes dramatically decreases towards the south. This fall both in number of species and bark colonization rate is closely related to the climatic profile of Morocco, which features an aridity gradient southwards. The climatic differences also lead to variations in species distributions, and it is possible to establish five distribution patterns (Figs 5–9): I, widely distributed taxa; II, Rif taxa; III, Rif and Middle Atlas taxa; IV, Atlas taxa; and V, taxa with localized occurrences.

I. **Widely distributed taxa.** The most widely distributed epiphytes in Morocco are: *Orthotrichum acuminatum*, *O. diaphanum*, *O. lyellii*, *O. rupestre* and *Fabronia pusilla* (Fig. 5a–e). All of them are common epiphytic mosses throughout the Mediterranean basin, and, in Morocco, they appear similarly distributed in the different mountain ranges. Their frequency is presumably indicative of the predominantly temperate conditions of the forests with a well-developed epiphytic stratum, both with warm temperatures and available environmental humidity. Another species homogeneously distributed in all the mountain ranges in Morocco (although less frequent) is *Didymodon insulanus* (Fig. 5f), which is a facultative epiphyte that only sporadically grows on bark. Finally, there are some species that are also widely distributed in Morocco and appear in most of the mountain ranges, although they show preferences for a particular area. Thus, *Brachythecium velutinum*, *Homalothecium sericeum* and *Syntrichia montana* (Fig. 5g–i), are more frequent in the Rif and the

Middle Atlas mountains, while in the southern mountains they mostly grow on tree bases. *Orthotrichum pallens* (Fig. 5j) is a Mediterranean continental species which is specially frequent in the forests of the Middle Atlas. *Grimmia pulvinata* and *Orthotrichum cupulatum* (Fig. 5k, l), more xerophytic, are more frequent in the Atlas mountains. Finally, *Syntrichia laevipila* (Fig. 5m) is rare in the humid forests of the Middle Atlas, but it is frequent both in the High Atlas and in the more disturbed forests of the Rif mountains.

II. **Rif taxa.** Some common epiphytes in the Mediterranean basin, such as *Frullania dilatata*, *Zygodon rupestris*, *Leptodon smithii* (Hedw.) F.Weber & D.Mohr, *Orthotrichum ibericum* F.Lara & Mazimpaka, *Pterogonium gracile* (Hedw.) Sm. and *Cryphaea heteromalla* (Hedw.) D. Mohr. (Fig. 6a–f), are found in the Rif mountains, and some of them only reach the Atlasic lands in Tazzeka mountain, which has been proved to be floristically linked to the Rif range, both by its vascular and its bryophytic flora (Valdés *et al.*, 2002; Draper *et al.*, 2005). The absence of these species in other Atlasic mountains may be due to the hard climatic conditions of the southern mountains. In addition to these taxa, the facultative epiphytes *Grimmia trichophylla* Grev., *Rhynchostegiella litorea* (De Not.) Limpr. and *Scleropodium touretii* (Brid.) L.F.Koch (Fig. 6g–i), are able to colonize bark in the humid mountains of the Rif range, but do not grow on trunks in the Atlas mountains.

III. **Rif and Middle Atlas taxa.** Several epiphytic bryophytes are restricted to the northern mountain ranges, and grow both in the Rif and in the most humid parts of the Atlas mountains. Among these species, the most frequent are *Orthotrichum affine*, *O. striatum*, *O. speciosum* var. *brevisetum*, *O. tenellum*, *O. scanicum*, *Pterigynandrum filiforme*, *Antitrichia californica*, *Dicranoweisia cirrata* and *Habrodon perpusillus* (Fig. 7a–i), but *Leucodon sciuroides*, *L. sciuroides* var. *morensis* and *O. philibertii* (Fig. 7j–l) also show this type of distribution. All are mesophytic taxa that become scarce in the southern mountains and gradually disappear due to drier climatic conditions. In addition to these taxa, some species such as *Bryum capillare*, *Hypnum cupressiforme*, *Brachythecium dieckei* and *Homalothecium aureum* (Fig. 7m–p), which are indifferent or preferentially not corticolous taxa, are frequent in these mountains, where they especially grow on tree bases.

IV. **Atlas taxa.** In contrast to the pattern of distribution shown by the taxa of groups II and III, some species are bound to the Atlasic mountain ranges. Among these species, *Orthotrichum macrocephalum*, *O. schimperi*, *O. pumilum* and *Syntrichia princeps* (Fig. 8a–d), are the most frequent, but also *Barbula unguiculata*, *Tortula inermis* and *O. vittii* (Fig. 8e–g) are mostly found in the Atlas mountains. All are relatively xerophytic species whose presence in the Atlas mountains is favoured by the dry climatic conditions. In addition, *Orthotrichum tortidontium* and *Syntrichia virescens* are almost exclusive to the Middle Atlas mountains (Fig. 8h–i), where humidity is relatively high but temperatures are cooler than in other mountain ranges of Morocco (Fig. 2).

V. **Taxa with localized occurrences.** The remaining bryophytes are scarce as epiphytes in the Moroccan mountains, where they have been recorded in $<5\%$ of the localities sampled. This is the case of some customary epiphytic taxa like *Neckera pumila* Hedw., *Orthotrichum speciosum* Nees in Sturm. var. *speciosum*, *O. obtusifolium*, *O. shawii* Wilson in Schimp., *O. stramineum*, *Zygodon catarinoi* and *Syntrichia papillosa* (Fig. 9a–g), which are at the southern border of their distribution range and are therefore only found locally in the study area. In addition, several facultative epiphytes that preferably grow on soil or rocks, and only colonize trees under specially favourable conditions, are found locally in the habitat studied. The favourable conditions for these taxa could be due either to the mildness of the climate or to its aridity (Vitt, 1981; Albertos *et al.*, 2005). The first of these cases has been observed in some areas of the Rif and the Middle Atlas mountains subject to oceanic influence, where some mesic plants that are normally saxicolous or terricolous, such as *Rhynchostegium confertum* or *Sematophyllum substrumulosum*, find a suitable habitat on trunks. In other cases, as has been observed in the High Atlas and Antiatlas mountains, aridity makes trunks and rocks ecologically similar, which favours the presence on trees of xerophytic cortico-saxicolous taxa that are usually found on rocks, such as *Grimmia laevigata*.

Conclusions

The different types of distribution among epiphytes suggest that the occurrence of epiphytic bryophytes in Morocco is mostly influenced by climatic conditions, which progressively become drier southwards and from west towards east. Moisture generally favours the presence of epiphytes, and the epiphytic bryophyte communities are usually richer in the humid forests of the northern ranges than in the southern mountains. Aridity leads to a progressive impoverishment of the epiphytic communities, and also to changes in their composition. Thus, in the Rif and Middle Atlas mountains, epiphytic communities are mostly dominated by customary Mediterranean epiphytes with oceanic preferences, such as *Orthotrichum lyellii*, *O.*

striatum and *O. rupestre*. These species are progressively substituted in the southern mountains by xerophytic customary epiphytes like *Orthotrichum diaphanum*, *O. acuminatum* or *O. macrocephalum*. In addition, changes in atmospheric humidity influence the distribution of the facultative epiphytes. In the Rif and Middle Atlas, epiphytic communities are enriched with mesic taxa rarely found on trunks. In contrast, aridity in the High Atlas and Antiatlas mountains increases the stressfulness of the habitat studied, and a substitution of mesic species by cortico-saxicolous xerophytes of Pottiaceae and Grimmiaceae takes place.

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Appendix 1

A list of the sites studied

1. ANTI-ATLAS, Tizi-n'Tagounit, 29RMN9398, 1600 m, on *Quercus rotundifolia* and *Crataegus monogyna*.
2. ANTI-ATLAS, Lekst mountain, 29RMN9798, 1900 m, on *Quercus rotundifolia*.
3. ANTI-ATLAS, Siroua mountain, 29RPP1298, 1750 m, on *Juniperus oxycedrus*.
4. HIGH ATLAS, Touchka mountain, 29RMP6199, 1640 m, on *Juniperus oxycedrus*.
5. HIGH ATLAS, Touchka mountain, 29RMQ6400, 1600 m, on *Quercus rotundifolia*.
6. HIGH ATLAS, P40 road, passed the cross to Bouaboute and Imi-n'Tanoute, 29RMQ9737, 1200 m, on *Tetraclinis articulata*.
7. HIGH ATLAS, way up to Tichka from Imi-n'Tanoute, northern slope, 29RMQ9838, 1250 m, on *Juniperus phoenicea* and *Tetraclinis articulata*.
8. HIGH ATLAS, way up to Tichka from Imi-n'Tanoute, 29RNQ2536, 1750 m, on *Quercus rotundifolia*.
9. HIGH ATLAS, way up to Tichka from Imi-n'Tanoute, 29RNQ2635, 1900 m, on *Quercus rotundifolia*.
10. HIGH ATLAS, way up to Tichka from Imi-n'Tanoute, 29RNQ2738, 1400 m, on *Juniperus oxycedrus*.
11. HIGH ATLAS, near Tamsoult, 29RNP0597, 1500 m, on *Juglans regia*.
12. HIGH ATLAS, Tizi-n'Test, southern slope, 29RNQ5914, 2025 m, on *Quercus rotundifolia*.
13. HIGH ATLAS, Tizi-n'Test, northern slope, 29RNQ5915, 2090 m, on *Quercus rotundifolia*.
14. HIGH ATLAS, Tiz-n'Test, northern slope, 29RNQ6519, 1850 m, on *Quercus rotundifolia*.
15. HIGH ATLAS, near Asni, 29RNQ9356, 1200 m, on *Quercus rotundifolia*, *Juniperus phoenicea*, *Tetraclinis articulata* and *Pistacia lentiscus*.
16. HIGH ATLAS, Toubkal National Park, Oukaimeden, Tizi-n'Tizrag, 29RPQ0752, 2600 m, on *Juniperus thurifera*.
17. HIGH ATLAS, Ourika valley, Arhbalou, 29RPQ1964, 1000 m, on *Fraxinus angustifolia* and *Populus nigra*.
18. HIGH ATLAS, Ourika valley, 29RPQ1769, 1000 m, *Tetraclinis articulata*, *Juniperus phoenicea* and *J. oxycedrus*.
19. HIGH ATLAS, Ourika valley, past Oulmes, 29RPQ2460, 1200 m, on *Quercus rotundifolia* and *Juniperus phoenicea*.
20. HIGH ATLAS, Setti Fatma, 29RPQ2655, 1500 m, on *Juglans regia*.
21. HIGH ATLAS, Toufliht, 29RPQ5083, 1500 m, on *Quercus suber*, *Q. rotundifolia* and *Juniperus oxycedrus*.
22. HIGH ATLAS, near Tifni, on the road to Imi-n'Ifri, 29RPR9605, 1500 m, on *Quercus rotundifolia*.
23. HIGH ATLAS, way up to Azourki mountain, northern slope, between Âït Mhmed and Agouti, 29RQR3519, 1950 m, on *Quercus rotundifolia*.
24. HIGH ATLAS, way up to Azourki mountain, northern slope, near Âït Mhmed, 29RQR4128, 1725 m, on *Fraxinus dimorfa*.
25. HIGH ATLAS, way up to Azourki mountain, northern slope, between Âït Mhmed and Tamda, 29RQR4425, 1900 m, on *Quercus rotundifolia*.
26. HIGH ATLAS, canyon in the entrance of Jaffar circle, 30SUB1904, 1900 m, on *Fraxinus dimofa* and *Juniperus oxycedrus*.
27. HIGH ATLAS, Jaffar circle, 30SUB2002, 2000 m, on *Quercus rotundifolia* and *Fraxinus dimorfa*.
28. HIGH ATLAS, Jaffar circle, 30SUB1902, 2100 m, on *Cedrus atlantica*.
29. MIDDLE ATLAS, near Ouzoud, 29RQR1138, 950 m, on *Tetraclinis articulata*.
30. MIDDLE ATLAS, Ouzoud gorges, 29SQR1544, 700 m, on *Olea europaea*.
31. MIDDLE ATLAS, road from Afourer to Azilal, 29SQR3363, 1300 m, on *Pistacia lentiscus* and *Quercus rotundifolia*.
32. MIDDLE ATLAS, 12 km from Afourer to Bin el Oidane, 29SQR3459, 1450 m, on *Quercus rotundifolia*.
33. MIDDLE ATLAS, Tizi-n'Âït-Ouira, 29SQS7800, 1475 m, on *Quercus rotundifolia* and *Q. canariensis*.
34. MIDDLE ATLAS, near Cherket, 30STA4081, 1480 m, on *Buxus sempervirens* and *Quercus rotundifolia*.
35. MIDDLE ATLAS, Cherket, 30STA4977, 1550 m, on *Quercus rotundifolia* and *Buxus sempervirens*.
36. MIDDLE ATLAS, Arhbala, 30STA5398, 1850 m, on *Quercus rotundifolia*.
37. MIDDLE ATLAS, Tanout ou Fillet pass, 30STB6918, 2070 m, on *Quercus rotundifolia*.
38. MIDDLE ATLAS, near Moulay Bouazza, 29SQS5277, 800 m, on *Quercus rotundifolia*.
39. MIDDLE ATLAS, past Moulay Bouazza, 29SQS6378, 1100 m, on *Quercus rotundifolia*.
40. MIDDLE ATLAS, past Oulmes, 29SQS6807, 1050 m, on *Quercus suber* and *Q. rotundifolia*.
41. MIDDLE ATLAS, 10 km from Oulmes, 29SQS7896, 1000 m, on *Quercus rotundifolia*.

42. MIDDLE ATLAS, fountain in Oulmes, 29SQT7802, 950 m, on *Quercus rotundifolia*.
43. MIDDLE ATLAS, 27 km north from Kenifra, 30STB5865, 1100 m, on *Quercus rotundifolia*, *Tetraclinis articulata* and *Pistacia lentiscus*.
44. MIDDLE ATLAS, Ifrane, El-Hajeb road, 30STC8322, 1200 m, on *Quercus rotundifolia*.
45. MIDDLE ATLAS, Azrou, Afenouir lake, 30STB8283, 1680 m, on *Quercus rotundifolia*, *Cedrus atlantica* and *Juniperus oxycedrus*.
46. MIDDLE ATLAS, Azrou-Afenouir, S.E. from Afenouir lake, 30STB8283, 1950 m, on *Quercus rotundifolia*, *Cedrus atlantica* and *Juniperus oxycedrus.*
47. MIDDLE ATLAS, Hebri mountain, 30STB9893, 2050 m, on *Cedrus atlantica* and *Quercus rotundifolia*.
48. MIDDLE ATLAS, 4 km from Azrou to Marrakech, 30STC8901, on *Cedrus atlantica*.
49. MIDDLE ATLAS, Azrou, Midelt road, 30STC9701, 1625 m, on *Quercus rotundifolia*, *Ilex aquifolium* and *Sorbus torminalis*.
50. MIDDLE ATLAS, Azrou, Gouraud cedar wood, 30STC9901, 1700 m, on *Cedrus atlantica*, *Quercus canariensis* and *Q. rotundifolia.*
51. MIDDLE ATLAS, Ifrane, Jaaba forest, 30STC9714, 1500 m, on *Quercus canariensis* and *Q. rotundifolia*.
52. MIDDLE ATLAS, Ifrane, 30STC9814, 1550 m, on *Quercus rotundifolia.*
53. MIDDLE ATLAS, 9 km on the road from Ifrane to Azrou, 30STC9907, on *Quercus canariensis*.
54. MIDDLE ATLAS, Ifrane, 30SUC0215, 1675 m, on *Ulmus minor.*
55. MIDDLE ATLAS, Ifrane, des Vierges gorges, 30SUC0215, 1500 m, on *Fraxinus angustifolia* and *Quercus canariensis*.
56. MIDDLE ATLAS, Ifrane, des Vierges gorges, 30SUC0314, 1500 m, on *Fraxinus angustifolia* and *Quercus rotundifolia*.
57. MIDDLE ATLAS, Ifrane, 30SUC0411, on *Quercus rotundifolia* and *Cedrus atlantica*.
58. MIDDLE ATLAS, Vallée des Roches, near Ifrane, 30SUC1310, 1750 m, on *Quercus rotundifolia*, *Cedrus atlantica* and *Acer monspessulanum*.
59. MIDDLE ATLAS, from Sefrou to Ifrane, 30SUC2121 1600 m, on *Quercus rotundifolia*.
60. MIDDLE ATLAS, Sefrou city, 30SUC2744, on *Celtis australis*.
61. MIDDLE ATLAS, Zad pass, 30SUB0655, 2170 m, on *Quercus rotundifolia* and *Cedrus atlantica*.
62. MIDDLE ATLAS, Aguelmame de Sidi Ali, 30SUB1062, 2100 m, on *Juniperus thurifera* and *J. oxycedrus*.
63. MIDDLE ATLAS, from Timahdite to Midelt, 30SUB1163, 1990 m, on *Juniperus thurifera*.
64. MIDDLE ATLAS, from Timahdite to Boulemane, 30SUB1970, 2050 m, on *Juniperus thurifera*.
65. MIDDLE ATLAS, from Timahdite to Midelt, before Aguelmame de Sidi Ali, 30SUB1869, 2000 m, on *Juniperus thurifera*.
66. MIDDLE ATLAS, from Boulemane to Ifrane, 30SUC4605, 1250 m, on *Buxus sempervirens*.
67. MIDDLE ATLAS, from Skoura to Tazouta, near Skoura, 30SUC5615, 895 m, on *Juniperus phoenicea*.
68. MIDDLE ATLAS, from Tazouta to Sefrou, near Tazouta, 30SUC4627, 1085 m, on *Pistacia lentiscus*.
69. MIDDLE ATLAS, from Tazouta to Sefrou, 30SUC4429, 1180 m, on *Quercus rotundifolia* and *Phyllirea angustifolia*.
70. MIDDLE ATLAS, on the way up to Taffert, 30SUC8033, 1200 m, on *Quercus rotundifolia*.
71. MIDDLE ATLAS, on the way up to Taffert, 30SUC8231, 1500 m, on *Quercus rotundifolia*.
72. MIDDLE ATLAS, on the way up to Taffert, 30SUC8331, 1650 m, on *Quercus rotundifolia*.
73. MIDDLE ATLAS, Bou Iblane mountain, between Tizi-n'Tiskine and Taffert, 30SUC8426, 1300 m, on *Quercus rotundifolia*.
74. MIDDLE ATLAS, Taffert, 30SUC8723, 1630 m, on *Quercus rotundifolia*.
75. MIDDLE ATLAS, near Taffert, 30SUC8823, 1700 m, on *Fraxinus angustifolia*.
76. MIDDLE ATLAS, Taffert, 30SUC9124, 1850 m, on *Cedrus atlantica*, *Quercus rotundifolia* and *Juniperus oxycedrus*.
77. MIDDLE ATLAS, Bou Iblane, passed Taffert, 30SUC9426, 2100 m, on *Juniperus thurifera*, *J. oxycedrus* and *Quercus rotundifolia*.
78. MIDDLE ATLAS, from Bou Iblane mountain to Talzemt, 30SUC8919, 1850 m, on *Juniperus thurifera*, *Quercus rotundifolia* and *Cedrus atlantica*.

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