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ULRICH DEIL

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Abstract

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The genus *Ptilostemon* is represented in Morocco by four geographically and edaphically vicariant species. This contribution summarizes and expands the knowledge of distribution, ecology and phytosociology for *P. leptophyllus*. The species is endemic to the Central and Eastern Rif Mts, with an outpost in the Tazzeka Mts of the N Middle Atlas. It is strictly acidophilous and colonizes fissures of schist bedrock and moderately moving micascists, mostly in the meso-Mediterranean bioclimate at 1000–1300 m altitude. *P. leptophyllus* occurs in three different communities: (1) *P. leptophyllus*-*Antirrhinum tortuosum* community in the semi-arid, winter-cold Eastern Rif Mts around Tizi Ouzli; (2) *Echium canum*-*Rumex thyrsoides* community in the semi-arid, winter-mild lowlands of the Oued Rhis; (3) *Convolvulus dryadum*-*Silene martyi* community in the subhumid, meso-Mediterranean bioclimate. In all three communities caespitose hemicryptophytes are the predominant life form and Rif endemics such as *P. leptophyllus*, *Convolvulus dryadum*, *Silene martyi* and *S. ibosii* are a prominent chorotype. The pioneer character of other *Ptilostemon* species and the role of the rock environment as an evolutionary trap are discussed.

Key words: rock communities, Asplenietea rupestris, Morocco, evolution, phytochorology, endemism.

Introduction

One reason for the high vascular plant species diversity of the Mediterranean region is the fact that many small mainland areas act as “islands” (Greuter 1991). This is especially the case in mountainous areas, where the edaphic variability is high and where each altitudinal belt offers different bioclimatic conditions. The surrounding areas with another ecological framework act as dispersal barriers. This results in local, endemic plant species, which are restricted to an ecologically defined “island”.

An exceptional rate of endemism is observed on cliffs and screes. The synopsis of European scree communities (Valachovic & al. 1997) shows a strong diversification within the alliances of S Europe. The diagnostic taxa are often geographically vicarious species. This can be either the result of the spatial fragmentation and subsequent speciation of an ancestor taxon widely distrib-

uted across the Mediterranean basin before the Messinian Crisis, or the migration of an ancestor through the Mediterranean region during this event, splitting up later into niche-equivalent geographical vicariants. One example for the latter case is the genus *Ptilostemon*.

The revision of the genus *Ptilostemon* by Greuter (1973) made clear that most species are stenochorous and that their areas of distribution are only rarely overlapping. In many Mediterranean countries such as Morocco, Italy, Greece, Turkey as well as in the Near East, *Ptilostemon* is represented by geographically and edaphically vicariant taxa. In Morocco, four species and two infraspecific taxa occur (Greuter 1973, Fennane & Ibn Tatou 1998, Devesa 2002):

1) *Ptilostemon abylenis* (Maire) Greuter colonizes limestone screes at Jabal Moussa, a mountainous ridge known as southern column of Hercules at the Straits of Gibraltar.

2) *Ptilostemon rhiphaeus* (Pau & Font Quer) Greuter is distributed throughout the Western and Central Rif in N Morocco. Disjunct populations occur in the Djurdura Mts of N Algeria. The species colonizes screes and boulders in open montane forests. Beside the widespread and edaphically indifferent variety *rhiphaeus* with whitish pink flowers (*P. pseudo-hispanicus* (Arènes) Raynaud & Sauvage) a purple flowered variety (var. *tetauensis* (Font Quer) Greuter) occurs on limestone. It is restricted to the Western Rif between the cities of Tetouan and Chaouen.

3) *Ptilostemon dyricola* (Maire) Greuter is known from limestone areas in the Middle Atlas, the western High Atlas and the Anti-Atlas in Morocco. It occurs in open evergreen forests with *Quercus rotundifolia* Lam. and *Cedrus atlantica* Manetti.

4) *Ptilostemon leptophyllus* (Pau & Font Quer) Greuter, a strictly acidophilous taxon, is endemic to the Central and Eastern Rif. An outpost occurs in the Tazzeke Mts in the N Middle Atlas.

The first three taxa are members of *Ptilostemon* sect. *Fontqueria*. *P. leptophyllus*, on which the present contribution focuses, was separated by Greuter (1973) into the unispecific *P.* sect. *Leptophyllon*, which is characterized by nodding heads, pronounced tubercles at the basis of the appendix of the involucrel bracts and marginal achenes with a plumose pappus.

Ptilostemon leptophyllus was discovered by the Catalan botanist Pio Font y Quer when exploring the Rif Mts, shortly after the Spanish occupation of N Morocco in 1927. The species was first described as *Chamaepeuce leptophylla*. Information about its ecology and associated species is rare and restricted to herbarium labels and brief comments in floras and checklists. The only geobotanical study dealing with *P. leptophyllus* was performed by Quézel & al. (1988). Based upon five relevés from one locality in the upper Qued Nekor, these authors describe the *Ptilostemo leptophylli*-*Fontqueretum* pauii. This plant community is characterized by endemics of the surroundings of Jabal Azrou Akechar in the semiarid, subcontinental Eastern Rif Mts such as *Perralderia pauii* Font Quer (= *Fontquera pauii* (Font Quer) Maire), *Teucrium huotii* Emb. & Maire, *Acanthorrhinum ramosissimum* (Cass. & Durieu) Rothm. and S Ibero-Mauretanian taxa such as *Matthiola fruticulosa* (L.) Maire and *Moricandia suffruticosa* (Desf.) Cass. & Durieu. A species-poor variant with *Ptilostemon leptophyllus* is mentioned to be more widespread.

A more detailed study of plant communities of rocks and screes in the Central Rif Mts and of alluvial material in beds of intermittent rivers has shown that *Ptilostemon leptophyllus* and *Perralderia pauii* considerably differ in their ecology and distribution. The knowledge about *Perralderia pauii* is given by Deil (2005), whereas the present contribution summarizes the knowledge for *Ptilostemon leptophyllus*, including new data about its distribution, ecology and phytosociology.

Study area

The Central Rif is a mountain range between Jabal Tizirene and Oued Nekor (Fig. 1). It culminates in Jabal Tidiquin at 2448 m. Predominant bedrock are schist, grauwacke and sandstone from the Cretaceous period. The highest peaks are formed by quartzitic ridges. The coastal ranges east of Al Hoceima, called Bokkoya, are dominated by limestone from the Trias and Jura. Deeply incised valleys such as Oued Nekor drain the Rif Mts to the north and south. Most of the rivers are intermittent (“wadis” = “oueds”) and flow during the wet winter and spring. After heavy rainfall and thunderstorms, occasional floods can occur in early summer. The lower parts are semi-arid

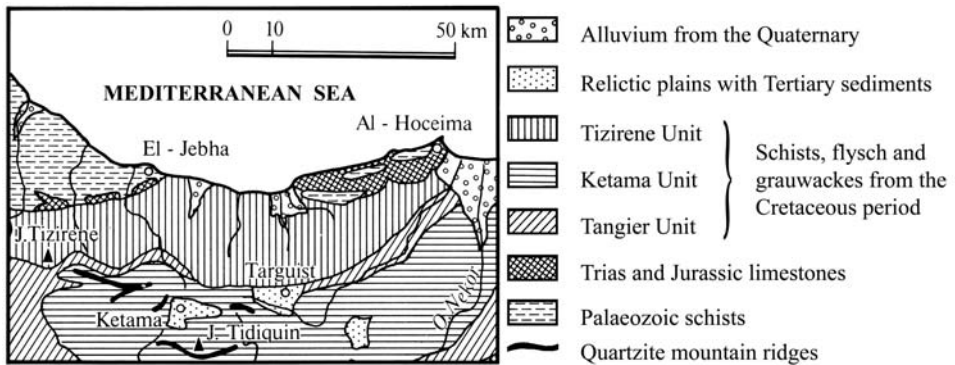


Fig. 1. Geological map of the Central Rif Mts (after Despois & Raynal 1967, modified).

with about 300 mm mean annual precipitation at Al Hoceima. The mid elevations are subhumid, the high elevations humid (Fig. 2). The bioclimatic zones range from the semi-arid infra- and thermo-Mediterranean to the oro-Mediterranean belt with dominating *Stipa tenacissima* L. and *Tetraclinis articulata* Mast. at the lower elevations, *Quercus rotundifolia*, *Juniperus oxycedrus* L., *J. phoenicea* L. and *Pinus halepensis* Mill. in the middle part and *Cedrus atlantica* in the montane-Mediterranean zone. Snow beds with *Teucrium afrum* subsp. *rhiphaeum* (Pau & Font Quer) Castrov. & Bayón and wind-exposed ridges with scattered elements of a thorn cushion belt (with *Bupleurum fruticosum* subsp. *spinosa* (Gouan) O. Bolòs & Vigo, *Cytisus balansae* (Boiss.) Ball and *Astragalus granatensis* Steud.) occur above the tree line (for more details see Emberger 1939 and Deil 1984). The southern and eastern areas around Taza and Msoun are shielded from the western and northern influx of humid air masses. They harbour remnants of steppe vegetation and some scattered *Pistacia atlantica* Desf. trees.

Material and methods

The distribution map for *Ptilostemon leptophyllus* (Fig. 2) is based upon own observations and the data provided by Greuter (1973), Fennane & Ibn Tattou (1998) and Devesa (2002).

Phytosociological data sampling was restricted to vascular plants. Sample points are documented in Fig. 2. The classification of the relevés follows Braun-Blanquet (1964). Plant nomenclature follows the recent checklist for N Morocco (Valdés & al. 2002), the nomenclature of plant communities the checklist published by Rivas-Martínez & al. (2002) for the Iberian Peninsula and Quézel & al. (1992) for N Morocco. The knowledge about the scree- and rock communities in the Rif Mts is too preliminary to establish a hierarchical system according to floristic similarity and to describe plant communities in a formal way according to the rules by Weber & al. (2000). The vegetation types are therefore treated as rankless communities.

Results

Distribution. – *Ptilostemon leptophyllus* occurs from Ketama and Targuist on the northern slope to Jabal Outka and Taineste at the southern slope of the main ridge (Fig. 2). A southern outpost is on Jabal Tazzecca south of Taza, and northeastern outliers are found in the Oued Rhis, close to Beni Abdallah. The area includes the ecoregions Central Rif, Targuist, Imzorène and Aknoul sensu Valdés & al. (2002). Most of the populations are located around Jabal Oursane, a mountain ridge of mid altitude south of Targuist. The type locality Tizi Ifri, the “cold pass” in local Berber language, is also situated there. The altitudinal range of *P. leptophyllus* extends from 30 m in the Oued Rhis and the upper Oued Nekor up to c. 1500 m; most populations grow between 1000 and 1300 m.

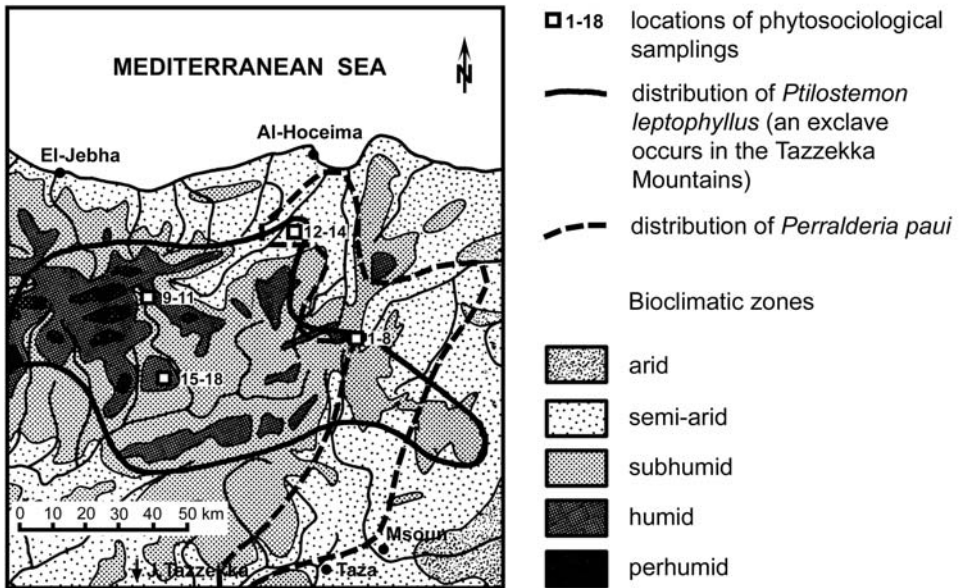


Fig. 2. Bioclimatic belts of the Central Rif Mts (adopted from Benabid 1984) and distribution of *Ptilostemon leptophyllus* and *Perralderia pau*.

Plant communities and associated species. – The only constant member of the communities with *Ptilostemon leptophyllus* is *Scrophularia canina* L. (Table 1). The other associated species change according to site conditions and region. The stands studied until now can be grouped into three vegetation types, according to floristic composition and ecology:

1) The *Ptilostemon leptophyllus*-*Antirrhinum tortuosum* community (Table 1, column 1-8) occurs in the Eastern Rif Mts around Tizi Ouzli and Jabal Azrou at mid elevations (1000 to 1200 m) (Fig. 2). Characteristic species are *Antirrhinum majus* subsp. *tortuosum* (Vent.) Rouy, *Teucrium maghrebinum* Greuter & Burdet and the N Moroccan endemic *Erucastrum rifanum* (Emb. & Maire) Gómez-Campo. The bioclimate is semi-arid with cold winters. An impoverished and ruderalized variant with *Bituminaria bituminosa* (L.) C. H. Stirt. (Table 1, column 9-11) was observed at the pass between Targuist and Beni Bounsar.

2) The *Echium canum*-*Rumex thyrsoides* community (Table 1, column 12-14) comprises the lowland populations in the semi-arid and winter-mild climate of the Oued Rhis, characterized by *Echium canum* Emb. & Maire, an Eastern Rif endemic, and by *Rumex thyrsoides* Desf. A constant associate is the Pegano-Salsoletea species *Launaea arborescens* (Batt.) Murb.

3) The *Convolvulus dryadum*-*Silene martyi* community (Table 1, column 15-18) is found in the Central Rif Mts between Beni Bounsar and Tahar Souk (Fig. 2). *Ptilostemon leptophyllus* is here associated with two other Rifean endemics, *Convolvulus dryadum* Maire and *Silene martyi* Emb. & Maire. Transgressive species of the neighbouring rockrose communities (Halimietalia, Cisto-Lavanduletea) such as *Teucrium afrum* subsp. *rhiphaeum*, *Nepa boivinii* Webb and *Origanum elongatum* (Bonnet) Emb. & Maire indicate the subhumid conditions of this area and an initial succession towards shrubland.

Ecology, life forms and vegetation dynamics. – *Ptilostemon leptophyllus* is a strictly acidophilous species. It occurs in a broad spectrum of climatic conditions (from semi-arid to humid climates) and vegetation zones (from the thermo-Mediterranean to the montane-Mediterranean belt). Steep slopes with massive schist bedrock and moderately moving micaschist screes are the preferred habitats. Vegetation cover is never closed, ranging from 15 to 60 %. On schistose slopes with shal-

Table 1. Scree communities with *Ptilostemon leptophyllus* – CS = character species; locality data and further relev details are given at the end of the table.

Relevé number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
Inclination in °	70	80	80	50	30	50	20	40	40	35	40	40	35	35	60	80	35	80	
Aspect	S	S	S	SW	S	SW	S	SW	S	SE	SE	SE	SE	SE	S	S	N	S	
Sampling area in sqm	25	25	25	25	25	25	25	25	50	30	50	30	30	30	30	30	30	30	
Total vegetation cover in %	20	15	20	30	20	30	30	20	15	30	15	30	40	40	50	50	60	40	
CS of <i>Ptilostemon leptophyllus</i>-community-group																			
<i>Ptilostemon leptophyllus</i>	.	+	1	2	3	2	2	1	2	3	3	2	1	1	2	2	2	+	
<i>Scrophularia canina</i> s.str.	1	1	.	1	1	1	1	+	+	+	+	.	
<i>Reseda lanceolata</i> subsp. <i>constricta</i>	1	+	+	+	
CS of <i>Ptilostemon leptophyllus</i>-<i>Antirrhinum tortuosum</i>-community																			
<i>Antirrhinum majus</i> subsp. <i>tortuosum</i>	2	1	1	+	.	1	1	1	
<i>Erucastrum rifanum</i>	1	.	+	+	1	1	1	+	+	
<i>Teucrium maghrebinum</i>	+	+	
SC of <i>Echium canum</i>-<i>Rumex thyrsoides</i>-community																			
<i>Echium canum</i>	1	2	1	
<i>Rumex thyrsoides</i>	2	1	+	
CS of <i>Convolvulus dryadum</i>-<i>Silene martyi</i>-community																			
<i>Convolvulus dryadum</i>	+	+	.	1	
<i>Silene martyi</i>	2	+	1	.	
<i>Anarrhinum pedatum</i>	1	1	.	1	
<i>Sanguisorba rupicola</i>	+	1	1	+	
<i>Cleome violacea</i>	1	1	+	1	
<i>Lotonotis bullonii</i>	1	+	.	.	
CS and constant companions of rock- and scree-communities																			
<i>Sedum sediforme</i>	.	.	+	+	+	+	+	+	
<i>Polygala rupestris</i>	+	+	+	
<i>Echinops spinosus</i>	1	1	1	1	2	2	
<i>Lactuca tenerrima</i>	1	+	+	
<i>Melica cupani</i>	1	+	+	.	.	.	+	1	1	.	
<i>Silene ibosii</i>	1	1	.	.	
<i>Telephium imperati</i>	1	1	+	
<i>Phagnalon saxatile</i>	1	.	2	
<i>Ononis hispida</i> s.str.	1	+	.	
<i>Biscutella baetica</i>	+	+	.	
<i>Galium viscosum</i>	1	+	.	
CS of <i>Perralderio</i>-<i>Halogetonum</i> and <i>Rosmarinetea</i>																			
<i>Anthyllis cytisoides</i>	1	2	2	2	+	2	1	
<i>Perralderia paui</i>	1	+	.	+	
<i>Teucrium huotti</i>	1	1	1	
<i>Erodium guttatum</i>	.	+	1	
<i>Matthiola fruticulosa</i>	+	+	
CS of <i>Pegano</i>-<i>Salsoleta</i> and <i>Lygeo</i>-<i>Stipetea</i>																			
<i>Launaea arborescens</i>	1	1	+	
<i>Senecio malacitanus</i>	+	+	
<i>Bituminaria bituminosa</i>	+	.	.	1	1	2	
<i>Dactylis glomerata</i> subsp. <i>hispanica</i>	1	.	1	1	
<i>Brachypodium retusum</i>	.	.	+	.	.	1	2	1	.	.	

continued next page

Continuation Table 1.

Relevé number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
CS of Halimietalia and Cisto-Lavanduletea																		
<i>Teucrium afrum</i> s.str.	+	2	+	2
<i>Lavandula stoechas</i>	2	1	+	+
<i>Nepa boivinii</i>	1	.	.	+	1
<i>Origanum elongatum</i>	1	1	2	+
Subnitrophilous annuals and ruderal perennials																		
<i>Arvena barbata</i> s.str.	2	.	.	.	2	2	2	1	1	1	1	2	1	.
<i>Carlina hispanica</i>	1	1	.	+	.	1	1	1	.	.	+	.	+	.	.	.	+	.
<i>Dittrichia viscosa</i>	+	.	.	1	.	.	.	1	+	+	+	1	+
<i>Sonchus tenerrimus</i>	.	+	+	+	+	.	.	+	.	.	.	+
<i>Misopates orontium</i>	2	1	1
<i>Paronychia argentea</i>	+	+	+
<i>Anacyclus clavatus</i>	1	+	.	1
<i>Bromus madritensis</i>	2	2	1	.
<i>Brachypodium distachyon</i>	+	1	.
<i>Paronychia capitata</i>	+	+	+	.	.
<i>Galactites tomentosa</i>	1	+
<i>Centranthus macrosiphon</i>	.	.	.	+	.	.	.	+
<i>Crucianella angustifolia</i>	+	1	.
<i>Rumex bucephalophorus</i>	+	.	+	.
<i>Trifolium angustifolium</i>	+	.	1	.
Initials of maquis vegetation																		
<i>Quercus rotundifolia</i>	.	.	.	+	.	.	.	+	+	.
<i>Juniperus oxycedrus</i>	+	.	+
<i>Pistacia lentiscus</i>	.	.	.	+	.	+	+

Further rare species:

in 1: *Colutea atlantica* +; in 2: *Phagnalon rupestre* +; in 4: *Quercus coccifera* +; in 5: *Putoria calabrica* +; in 6: *Piptatherum miliaceum* +; in 8: *Ononis speciosa* 1; in 12: *Atractylis cancellata* +; *Urospermum picroides* +; *Carthamus lanatus* +; in 13: *Eryngium ilicifolium* +; in 15: *Desmazeria rigida* 1; *Linum tenue* +; in 17: *Saxifraga globulifera* 1; *Muscari comosum* +; *Anthyllis vulneraria* subsp. *maura* 1; *Blackstonia perfoliata* +; *Jasione campestre* 1; in 18: *Jasione montana* subsp. *echinata* +.

Localities:

1-8: Ighzar Amekrane between Tizi Ousli and Tleta Ezlaf, Province Nador; rocky ridge of schists and quartzite (1-4), micascists, moderately moving (5-8); 1: relevé no. 276, 4.1986, 1100 m; 2: relevé no. 275, 4.1986, 1100 m; 3: relevé no. 277, 4.1986, 1000 m; 4: relevé no. 273, 4.1986, 1200 m; 5: relevé no. 270, 4.1986, 1200 m; 6: relevé no. 272, 4.1986, 1200 m; 7: relevé no. 274, 4.1986, 1200 m; 8: relevé no. 271, 4.1986, 1200 m.

9-11: massive rocky slope between Targuist and Beni Bousar, near Agni; Province Al-Hoceima; 9: relevé no. 506, 6.1987, 1200 m; 10: relevé no. 507, 6.1987, 1200 m; 11: relevé no. 508, 6.1987, 1200 m.

12-14: Oued Rhis near Tamesint, Province Al Hoceima; moderately moving schists; 12: relevé no. 531, 6.1987, 400 m; 13: relevé no. 530, 6.1987, 400 m; 14: relevé no. 532, 6.1987, 400 m.

15-18: between Tahar Souk and Beni Bousar, Province Taounate; schist slope, moderately moving; 15: relevé no. 603, 6.1987, 1200 m; 16: relevé no. 604, 6.1987, 1200 m; 17: relevé no. 609, 6.1987, 1200 m; 18: relevé no. 602, 6.1987, 1200 m.

low lithosoils and on moving screes, the communities with *P. leptophyllus* are permanent pioneer communities (pedoclimax). *P. leptophyllus* itself is an effective scree stabilizer. The stands are dominated by caespitose hemicryptophytes (*Ptilostemon leptophyllus*, *Erucastrum rifanum*, *Sanguisorba rupicola* (Boiss. & Reut.) Rivas Goday & Esteve, *Echinops spinosus* L., *Melica cupani* Guss.) and basally lignified subshrubs such as *Scrophularia canina* s.str., *Perralderia paui*, *Moricandia suffruticosa* and *Origanum elongatum*, and show some scattered shrubs of *Quercus rotundifolia*, *Juniperus oxycedrus*, *Pistacia lentiscus*, *Lavandula stoechas* L. and *Launaea arborescens*. A third stratum is formed by creeping or pulvinate perennials such as *Echium canum*, *Teucrium maghrebicum*, *T. huotii*, *Convolvulus dryadum* and *Lotononis bullonii* Emb. & Maire. In the spring phenophase, eye-catching annuals such as *Silene martyi*, *S. ibosii* Emb. & Maire and *Cleome violacea* L. make the rocks and screes very attractive.

Phytochorology. – *Ptilostemon leptophyllus* is one of the species that contribute to the Central and Eastern Rif Mts as a centre of endemism. Further examples are *Erucastrum rifanum*, *Echium canum*, *Convolvulus dryadum*, *Silene martyi*, *S. ibosii*, *Lotonotis bullonii* and *Perralderia paui*.

Conservation. – *Ptilostemon leptophyllus* is classified by Fennane & Ibn Tattou (1998) as rare. However, it does not seem particularly threatened, despite its stenochorous occurrence and its specific habitat requirements. Its habitats are not cultivable, and their spininess shelters the plants from being browsed. Yet the permanent, strong grazing pressure in Morocco will forestall the establishment of seedlings and a series of dry years might result in a serious reduction in number of the adults.

Discussion

Phytosociology of Ptilostemon leptophyllus. – The study of plant communities of rocks and screes in the Central Rif Mts and of alluvial material in the beds of intermittent rivers shows that *Ptilostemon leptophyllus* and *Perralderia paui* have a different ecology and distribution (Fig. 2). They co-occur only rarely. *Ptilostemon leptophyllus* has a clear preference for rock fissures and screes derived from schist, flysch and grauwacke. It ranges from the thermo- to the montane-mediterranean vegetation belt and from semi-arid to humid climatic conditions. *Perralderia paui* is more frequent on alluvial material, but also colonizes gypseous soils. Because it can tolerate drier conditions than *Ptilostemon leptophyllus*, it ranges from the infra- to the thermo-Mediterranean belt and from a semi-arid to an arid ombroclimate (Deil 2005). In the thermo-Mediterranean and subhumid bioclimate, both species can occur together, and it was in this environment that Quézel & al. (1988) first studied both species and described the *Ptilostemo-Fontqueretum*. According to the observations available now, this association must be regarded as a transition between the *Perralderia paui-Halogetonum alopecuroidis* Deil 2005 (Anarrhino-Astragaletalia armati, Rosmarinetea) and the *Ptilostemon* communities described here.

The syntaxonomic position of the *Ptilostemon leptophyllus* communities must remain open for now. They are linked to the *Thlaspietea rotundifolii* by aggregates such as *Scrophularia canina* s.l., but have only very few species (*Lactuca tenerrima* Pourr., *Biscutella baetica* Boiss. & Reut., *Galium viscosum* Vahl) in common with the alliances and orders known from Europe (Valachovic & al. 1997). Other taxa such as *Sanguisorba rupicola*, *Antirrhinum majus* s.l., *Cleome violacea*, *Polygala rupestris* Pourr., *Sedum sediforme* (Jacq.) Pau, *Phagnalon saxatile* Cass. and *Saxifraga globulifera* Desf. link the *Ptilostemon leptophyllus* communities to the *Asplenietea trichomanis*. There are, however, no close floristic and ecological relationships with other chasmophytic plant communities known from Morocco (Deil & Galán de Mera 1996) or the Iberian Peninsula (Rivas-Martínez & al. 2002). With more data available in the future a Rifean alliance within *Asplenietea trichomanis* might emerge, characterized by species such as *Silene martyi*, *S. ibosii*, *Ptilostemon leptophyllus*, *Convolvulus dryadum* and *Erucastrum riphannum*, restricted to the meso-Mediterranean zone of the Central Rif Mts. This syntaxon is replaced in the upper montane zone by communities with *Dianthus lusitanus* Brot., *Rumex scutatus* subsp. *induratus* (Boiss. &

Reut.) Malag., *Sedum brevifolium*, *Linaria tristis* Mill. and *Isatis djurjaedae* Cass. & Durieu (Diantho-Rumicion, Rumicetalia indurati).

Phytosociology of the genus Ptilostemon. – The stenochorous and stenoecious character of many *Ptilostemon* species makes them favourite candidates for diagnostic and even name-giving species in plant communities. This is apparent for *P. leptophyllus*. Most of its communities belong to the Thlaspietea rotundifolii, a class comprising the scree vegetation in the Western Palearctic, and to the Scrophulario caninae-Helichrysetea italici (screes in the Tyrrhenian area). Some other examples should be mentioned: *P. rhiphaeus* var. *rhiphaeus* stabilizes limestone boulders in the Western Rif Mts, while the variety *tetauensis* differentiates an open variant of kermes-oak maquis in the same area (Rusco hypophylli-Quercetum cocciferae ptilostemetosum tetauensis) (Benabid 1984). *P. niveus* (C. Presl) Greuter is a scree-stabilizer on limestone in the montane zone of Sicily (Senecioni-Ptilostemetum nivei) and S Apennines (Helichryso-Achnatheretum calamagrostis) (both associations in Linarion pedunculatae, Scrophulario-Helichrysetea italici) (Brullo 1984, Brullo & al. 1998, Angiolini & al. 2005), *P. afer* (Jacq.) Greuter colonizes similar habitats in the montane and oro-Mediterranean belts of the S Balkan Peninsula (Drypietalia spinosae, Thlaspietea rotundifolii) (Valachovic & al. 1997). It has a strong tendency to colonize secondary habitats such as roadside embankments. *P. casabonae* (L.) Greuter is a character species of the Ptilostemo casabonae-Euphorbion cupanii (Angiolini & al. 2005), a group of low shrub communities that occur in Sardinia and Corsica on riverbed gravel, screes and mining dumps. *P. chamaepeuce* (L.) Less. is listed by Dimopoulos & al. (1997) as character species of Onosmetalia frutescentis on the Peloponissos and of Petromaruletalia on Crete. The species is also name-giving to the Cirsietalia chamaepeucis, an order of basiphytic rock communities in the Aegean (Horvat & al. 1974). *P. strictus* (Ten.) Greuter occurs in thermophilous forest fringe communities (Ptilostemo strictae-Melampyretum italici, Geranion sanguinei) in the central Apennines (Biondi & al. 2001) and is widespread in thermophilous deciduous forests in the S Balkan.

Pioneer character of Ptilostemon. – Screes, rocky slopes and gravel beds of periodical to intermittent rivers are the primary habitats for most of the *Ptilostemon* species. Through its adaptation to moving substrates and its ability to recolonize open spaces, the genus is pre-adapted to man-made physical disturbance. An increasing density of the *P. leptophyllus* populations due to clearing of forests and maquis, shifting cultivation on schistose slopes and road construction can be concluded from the occurrence of the species on such man-made habitats in the Rif Mts. A pioneer and to some extent ruderal character is also recorded for *P. chamaepeuce*. This species colonizes abandoned quarries in Lebanon (Khater & al. 2003) and walls of ruins on Crete (Brandes 2002). Less viable populations seem to exist at the southern fringes of the distribution in Israel, where *P. chamaepeuce* figures on the Red List (Sapir & al. 2003). A recent apophytisation can also be observed in *P. casabonae*. This species shifted in Sardinia from gravel beds and screes as its primary sites to mining dumps as secondary habitat. It tolerates moderate concentrations of sulphides and heavy metals (Angiolini & al. 2005).

The observation of Greuter (1973), that most of the *Ptilostemon* species form stable and viable populations within their area of distribution and that, although they are often able to colonize man-made habitats, they do not show any tendency of expansion beyond their area, is confirmed by this study about *P. leptophyllus*. Greuter (1973) assumed that – in spite of anemochory – long-distance dispersal is rare because the achenes of *Ptilostemon* are heavy. Another factor might be seed predation by insect larvae, living in thistle heads. This is well known from other genera of the *Cardueae* (Zwölfer 1987, 1994), but has not yet been studied in *Ptilostemon*.

Endemism rate and habitat. – In comparison with the zonal vegetation, the chasmophyte communities have a higher rate of endemism and more stenochorous species. This results in floristically well defined associations of local or regional distribution. Examples are rock communities in Greece (Dimopoulos & al. 1997, Bergmeier 2002) and Morocco (see this contribution and Deil 1994, Deil & Galán de Mera 1996, Deil & Hammoumi 1997, Médail & Quézel 1999). The rocky environment (cliffs and screes) often harbours taxa with primitive characters. It seems to act as an

evolutionary trap (Snogerup 1971, Deil 1999). Several factors may favour speciation, relic occurrence and stenochory in the rock environment: (1) The populations are small and isolated, therefore genetic drift and founder effects are strong. (2) The special adaptations that are necessary to survive in rock fissures or on moving substrate reduce the capacity for adaptive radiation into other habitats. (3) The extreme conditions of the habitat enable a high spatial persistence through geological times. Climatic changes, which initiate large scale migrations of forest species, can be easily buffered by chasmophytes; they may shift from southern to northern exposure of the same cliff to compensate a strong increase in temperature and a decline in precipitation.

The genus *Ptilostemon* seems to be a suitable taxon to study these phenomena in more detail.

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