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The section *Atlanticae* of the genus *Luzula* (Juncaceae)

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Abstract
The section *Atlanticae* of the genus *Luzula* (Juncaceae).- *Luzula atlantica* Braun-Blanq. and *Luzula tibestica* (Quézel) Zarhan ex Romo & Boratyński are the only representatives of the section *Atlanticae* Kirschner of the genus *Luzula*. *Luzula atlantica* is an endemic plant from the High Atlas Mountains and *Luzula tibestica* is endemic to the Tibesti massif. Both taxa are studied from a nomenclatural, morphological, chorological and biogeographical point of view. These taxa, owing to their low dispersion capacity, have probably diversified in situ.

Key words: Atlas Mountains; Juncaceae; *Luzula*; oromediterranean taxon; Tchad; Tibesti massif.

Resumen
La sección *Atlanticae* del género *Luzula* (Juncaceae).- *Luzula atlantica* Braun-Blanq. y *Luzula tibestica* (Quézel) Zarhan ex Romo & Boratyński son los únicos representantes de la sección *Atlanticae* Kirschner del género *Luzula*. *Luzula atlantica* es un endemismo del Alto Atlas y *Luzula tibestica* es una planta endémica del macizo de Tibesti. Ambos taxones son estudiados desde el punto de vista morfológico, nomenclatural, corológico y biogeográfico. Estos taxones, por su baja tasa de dispersión, se han diversificado probablemente *in situ*.

Palabras clave: Chad; Juncaceae; *Luzula*; macizo de Tibesti; montañas del Atlas; taxon oromediterráneo.

INTRODUCTION

The presence of closely-related vascular plant taxa in isolated mountainous zones has drawn the attention of the biogeographers (Quézel, 1978, 1981, 2002; Quézel & Médail, 2003) and has become a challenge when facing theories of long distance dispersion and/or vicariance. In the case of *Luzula* DC., for Mediterranean Maghreb region, it is represented by five taxa, each one inhabiting distinct mountainous zones (Maire, 1957). Only one is found in the Saharo-Arabian region, and five are present in Sub-Saharan Africa (Klopper *et al*., 2006).

This type of present distribution causes us to reconsider the role of the Saharo-Arabian region, and its possible function as a great barrier for long-distance dispersal on the one hand, and on the other, the protagonism of the great massifs that dot the Saharo-Arabian region from the highlands of Ethiopia, the Nuba Mountains, Jbel Marra, Tibesti Massif, Ain and Hoggar Massif across to the Atlas range, in vicariance processes. To what point have these massifs served as migratory routes in both directions in past ages and other climatic scenarios for the ancestors of some representatives of the present flora? Do taxa exist at present in these massifs and ranges which demonstrate

the hypothesis of vicariance as opposed to long distance dispersal? What can the study of the *Atlanticae* section of the genus *Luzula* contribute to this end?

The section *Atlanticae* of the genus *Luzula* was described by Kirschner & Kaplan (2001*a, b*), and until now only included one taxon: *Luzula atlantica* Braun-Blanq. This section exhibits a number of characters very unusual in the genus *Luzula*, such as: globose, smooth and shining seeds; reduced style; and membranous tepals with a brown, mucronate midrib. It is one of the seven sections recognized in this genus. *Luzula atlantica* is morphologically intermediate between species of sections *Anthelaea* and *Diprophyllatae* (Kirschner *et al*., 2002). Nonetheless this reality does not correspond with molecular data (Drábková & Vlcek, 2010).

MATERIAL AND METHODS

The herbarium material of MPU (Montpellier), P (Paris), and AIX (Aix en Provence) has been revised, and the literature references of these taxa under study have been consulted. The type specimens of *Luzula atlantica* and *L. atlantica subsp. tibestica* Quézel have been examined. Also the morphology, chorology and distribution of the taxa within the section have been studied. The paleo-biogeografical and paleo-ecological data have been analysed in order to evaluate the adaptive radiation of these taxa.

RESULTS AND DISCUSSION

Taxonomy

A revision of the herbarium material and the literature has led us to recognize a second taxon: *Luzula tibestica* (Quézel) Zahran ex Romo & Boratyński, which should be included in the section *Atlanticae*. *Luzula atlantica* was described by Braun-Blanquet (1928). Quézel (1958) described a new taxon from the Tibesti Mountains, and it was subordinated to *L. atlantica* as subspecies.

Luzula atlantica Braun-Blanq., Vierteljahrsschr. Naturf. Ges. Zürich 73: 347 (1928)

Ind. Loc.: "Im *Quercetum ilicis* subalpinum und auf Lichtungen zwischen 1500 und 2000 m im Tälchen oberhalb Zerekten"

Lectotype (here designated): Dr. R. Maire - Iter Maroccanum Undecimum / In Atlantis ditione Glaoua: in / rupestribus arenaceis quercetorum supra / Zerekten, 1500-2000 m / die 8 aprilis 1926 (MPU-Maire 002402).

L. spadicea sensu Litard. & Maire in Mém. Soc. Sci. Nat. Maroc 6: 21 (1924); *non* DC.

L. graeca sensu Jahand. in Mém. Soc. Sci. Nat. Maroc 3(1): 111 (1923); *non* Kunth

Luzula atlantica was first reported by Jahandiez (1923) and published under the name of *L. graeca*. A year later Litardière & Maire (1924) referred it to *Luzula spadicea*. Four years later it was described as a new taxon from the High Atlas Mountains by Braun Blanquet (1928). Two years later Litardière & Maire (1930) published an amplified description.

It is a diploid $2n = 12$, as reported by Galland (1988). After Galland (1988) it is close to *L. alpinopilosa* (Chaix) Breistr.

This taxon displays a number of morphological peculiarities that justified the creation of the section *Atlanticae* Kirschner within this genus (Kirschner & Kaplan, 2001*a*) and the designation of *L. atlantica* as type of the section and its unique representative. These authors consider it to be an isolated and clearly-differentiated taxon within the genus.

It is a very localized endemic plant, found growing at middle altitudes in the High Atlas, between 1500 and 2800 m (Maire, 1957). *Luzula atlantica* is cited from the following localities of the High Atlas: au-dessus Zerekten, 1500-2000 m; Reraya, au-dessus d'Arround, 2200 m; Sidi Chamarouch, 2400 m; Ourika, 2880m [all these localities after Jahandiez & Maire (1931)]; Adrar Tizerag à Oukaïmeden (Fennane & Ibn Tattou,1998); between Aït-Barka and Zerekten, Aït Barka forêt de Touzzane, Tizi'n Test northern slopes (Barbero *et al*., 1981); and Oukaïmeden (Dobignard & Jordan, 1987). Emberger & Maire (1941) mentioned a doubtful record from the Anti Atlas (Jbel Kest) stating that it had no flowers or fruits. The same Anti Atlas record is mentioned as being uncertain by Fennane & Ibn Tattou (1998).

It is an important floristic element of the North-African *Balanseo-Quercion* alliance (Barbero *et al*., 1981) and its presence in the field led to the assignation of a plant community under the name *Luzulo atlanticae-Quercetum rotundifoliae* (Barbero et al., 1981). Within it, typical elements can be recognized such

as: *Anarrhinum pedatum* Desf., *Conopodium glaberrimum* (Desf.) Engstrand, *Bupleurum montanum* Coss. & Durieu, *Genista tournefortii* Spach subsp. *jahandiezii* (Batt.) Talavera & P. E. Gibbs, *Luzula atlantica*, *Narcissus watieri* Maire, *Ptilostemon dyricola* (Maire) Greuter and *Origanum elongatum* (Bonnet) Emb. & Maire (Barbero *et al*., 1992).

The following herbarium material has been revised: Morocco: Grand Atlas, Reraya, au dessus de Sidi Chamarouch, au pied des grans rochers porphyriques sur la rive droite du torrent, 2380 m, 23.07.1823, *R. de Litardière s. n.* (MPU-Maire); In Atlantis Majoris Valle Reraya, Sidi-Chamarouch, 2400-2500 m, in fissuris rupium porphyr., 21.07.1924, *R. Maire s. n.* (R. Maire - Iter Maroccanum Octavum) (MPU-Maire 002401).

Luzula tibestica (Quézel) Zahran ex Romo & Boratyński, *comb. & stat. nov.*

Basionym: *L. atlantica* subsp. *tibestica* Quézel in Mém. Inst. Rech. Sahar. 4: 121 (1958)

Ind. Loc.: Emi Koussi: Lappiaz volcanique du flanc NW du cratère Kohor, où elle est localisée dans les suitements au fond de gorges obscures en compagnie de *Cystopteris fragilis*.

Lectotype (here designated): Mission Botanique / de l'Institut de Recherches Sahariennes / de l'Université d'Alger / au Borkou et au Tibesti / Emi Koussi / Lappiaz du flanc NW / 3100 m / Sept.-Novembre 1956 Dr. P. Quézel (AIX 000009). Of the eight individuals that make up the sheet, the one in the upper left-hand corner has been chosen as the type.

Zahran (2010: 36) proposed this combination, but since it lacked an indication of the basionym, it is not considered to be a valid proposition.

This taxon from the Tibesti mountains can be recognised by a series of characters that separate it from *L. atlantica*. Its basal leaves can be up to 8 mm wide, and their length is shorter (8-10 cm) than in *L. atlantica*. Of note are its few-flowered glomerules (2-4 flowered as opposed to 2-7 flowered); its external sepals which have a longer, black arista, as opposed to reddish-brown; its capsule which is smaller (*c.* 1.5 × 1.2 and not 2 × 1.15) mm and its seeds, which are also smaller (0.6-0.7 × *c*. 0.6, and not 0.8-1 × 0.8 mm), see Table 1.

This taxon manifests a notable geographical isolation, since it is to be found at more than 2400 km from the High Atlas populations. Moreover, the combined morphological characteristics, summarised in Table 1, clearly segregate both taxa. As a result of its geographic isolation and its different morphological characteristics, the specific status seems more adequate.

This plant is only known from the summit area (Emi Koussi, 3415 m) of the highest range in the Tchad and Sahara (Ozenda, 1991). The peaks of the Emi Koussi mountains harbour a relictual mountain (orophile) flora (Quézel, 1957) and, in the case of the taxon under study, this is represented by a scarce number of individuals. Quézel (1957) in two weeks of detailed exploration was only able to locate a dozen plants.

Luzula tibestica has been reported from Libya (Base de données des plantes d'Afrique, version 3.3.4), but neither literature references nor herbarium material from this country have been found.

Luzula tibestica grows on culminal lappiaz in the Tibesti Mountains, between 2800 and 3400 m, where it is found in a plant community dominated by *Helichrysum monodianum* Quézel and *Dichrocephala tibestica* Quézel and containing a lot of endemics such as: *Nepeta tibestica* Maire, *Festuca tibestica* Miré & Quézel, *Helictotrichon tibesticum* (Miré & Quézel) Holub, *Agrostis tibestica* Miré & Quézel, *Spergularia tibestica* Quézel & Monnier and *Bromus tibesticus* Maire (Quézel, 1965). In this plant community, *Luzula tibestica* and *Campanula filicaulis* Durieu var. *tibestica* Quézel are assumed to be representants of the Atlas Mountain lineages (Quézel, 1965), which represent a minority when compared to the oroafrican lineage, clearly more dominant.

The following herbarium material has been revised: Tchad: Mission Botanique de l'Institut de Recherches Sahariennes de l'Université d'Alger, au Borkou et au Tibesti, Emi Koussi, Lappiaz du flanc NW, 3100 m, Sept.-Novembre 1956, *P. Quézel s. n.* (AIX 000009); Mission Botanique de l'Institut de Recherches Sahariennes de l'Université d'Alger, au Borkou et au Tibesti, Sugzugan, 3100 m, Sept.-Novembre 1958, *P. Quézel s. n.* (AIX 000010).

Biogeographical insights

The close relationship between Atlas and Tibesti taxa was considered to be evidence of a continuous flora present in the mountains of North (Atlas Tibes-

Table 1. Comparison of morphological characters for the two taxa.

Taxon	Leaf length (cm)	Leaf width (mm)	Arista of sepals	Capsule (mm)	Seeds (mm)
L. atlantica	10-13	8-9.5	reddish-brown	2 × 1.15	0.8-1 × 0.8
L. tibestica	8-10	7.1-7.9	black	1.5 × 1.2	0.6-0.7 × 0.6

ti) and Central Africa (Axelrod, 1975; Quézel, 1978; Sunding, 1979). Many elements of this hypothetical continuous flora disappeared from several areas of North Africa after major climatic changes during the late Tertiary and the Quaternary (Axelrod, 1975; Quézel, 1978).

The isolated Saharan mountains (Hoggar, Aïr and Tibesti) have given rise to relictual populations of plants originating from the northwest, south and southeast (Lehouérou, 1997). This high degree of isolation, as in the case of Tibesti, has favoured the speciation process. These events probably go back to arid periods towards the end of the Miocene (Griffin, 2002) and more concretely to the Messinian Salinity Crisis (Krijgsman *et al*., 1999). At present the Tibesti is a refuge for mountain-specific flora (Anthelme *et al*., 2008).

Paleological data have provided more detailed accounts of paleoclimate, paleogeography (Schuster *et al.*, 2006) and vegetational changes in northern Africa (Menocal, 2004; Kröpelin *et al.*, 2008; Watrin *et al*., 2009) from the late Miocene to our days.

The existence of a Trans-saharan route via Hoggar and Tibesti to Jebel Marra and the Ethiopian highlands for the migration of plants has been pointed out by Wickens (1976) and Quézel (1958; 2002). This route seems to be the pathway employed by the taxa of the rand flora, and it highlights the radiation process of some genera, such as *Olea* L.*,* *Myrtus* L. and *Asparagus* L., in order to explain the vicariance process in plants.

This previous hypothesis has been ratified by Quézel & Martínez (1958). They have satisfactory demonstrated the extension of the Mediterranean flora into the Sahara during the Pleistocene, which would explain the survival of taxa with strong Mediterranean affinities in the higher elevations of the Saharan mountains. After Zarhan (2010), some of the characteristic species of this arid mountain vegetation in the Tibesti region are: *Agrostis tibestica, Festuca tibestica, Helictotrichon tibesticum* and *Luzula tibestica*, among others. Some such species for the Jebel Marra: *Silene lynesii* Norman, *Phagnalon scalarum* Schweinf. ex Blatt. subsp. *scalarum* and *Phagnalon scalarum* subp. *meridionales* Quézel, after Wickens (1976).

The Saharan mountains host vegetation with a high level of endemism (Quézel, 1965). Many of them, as opposed to taxa from the lowlands with a paleotropical affinity, have a clear oromediterranean or high mountain Mediterranean character and are remnants of a relictic flora.

Examining patterns of geographic distribution, endemism and morphology, this section of the genus *Luzula* is relict in origin, and derived from mountain relatives present during the Tertiary, since a mountain flora was present from the Atlas to the Tibesti Mountains in the late Miocene (Axelrod, 1975; Quézel, 1978; Sunding, 1979).

The genus *Luzula* originated about 55 Mya ago (Bremer, 2002). *Luzula atlantica* emerged as a terminal taxon related to the section *Alpinae* derived from a total of seven missing haplotypes. These results may confirm their placement into a separate taxonomic group (Drábková & Vlcek, 2010). This being the case, it is assumed that the extant taxa are relicts of the larger distribution tertiary flora that became partly fragmented or even extinct following the aridification episodes that took place from the end of the Miocene onwards. This, together with the low dispersal capacity of the taxa of this section, would support the hypothesis of and adaptative diversification in situ from a common ancestor (from among the mountain ranges near Tibesti and the Atlas chain), which would have colonized the Tibesti massif in the wake of the intense volcanic activity in the Tibesti Volcanic Province at the end of the Pliocene (Permenter & Oppenheimer, 2007). This ancestor would probably be close to the present *Luzula atlantica* of the Atlas, a mountains region in which it would have evolved after the last glacial episodes (Hughes *et al*., 2006). This ancestor would

have not persisted in the other massifs situated between the Atlas and the Ethiopian highlands: Hoggar, Aïn, Jbel Marra, Mount Mubo, and if in one of these it had established itself, at a posterior date it would have become extinct.

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