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# Insights on a rare species, *Geum atlanticum*, new data to differentiate from *Geum sylvaticum*

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**Abstract.** *Geum atlanticum* is a species described from North Africa and later found in Southern Iberian Peninsula. However, according to Flora iberica taxonomic treatment, it has been considered synonymous with *G. sylvaticum*, a species mainly distributed by Southeast of France, Iberian Peninsula, and North of Africa, sharing part of the distribution range and habitat. In this work, herbarium specimens of both *G. atlanticum* and *G. sylvaticum* were revised to evaluate morphological differences. Furthermore, the nuclear ribosomal ITS spacer was sequenced to study phylogenetic relationships among *G. atlanticum* and Iberian *Geum* species. The morphological study indicated clear differences with *G. sylvaticum*, and the phylogenetic analysis suggests that *G. atlanticum* was sister to *G. sylvaticum*. However, it shared several mutations with other Iberian *Geum* species. The number of populations is relatively low in the Iberian Peninsula, so its conservation status and its further inclusion in lists of threatened plants have been evaluated in this work.

**Keywords:** Conservation; Ibero African species; Rosaceae; taxonomy; western Mediterranean plants.

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## Introduction

*Geum* is a world-wide distributed genus belonging to family Rosaceae. This genus includes approximately 56 species (Gajewski, 1959), although depending on the author, the number has changed over time (see explanation below). Of them, seven are distributed throughout the Iberian Peninsula (Lainz, 1998). Its taxonomy has been subject of debate since introgression and allopolyploidization seems to be extensive in the tribe *Colurieae*. In fact, several classifications traditionally have included species belonging to *Geum* in other genera or alternatively, several genera were synonymized as *Geum* (Scheutz, 1870; Greene, 1899; Bolle, 1933; Hara, 1935; Yuzepchuk, 1941). Its phylogeny suggests that introgression and polyploidization have been a major role in the evolution of *Geum* and other closely related genera, pointing out that the classic circumscription of *Geum* is not supported (Smedmark & Eriksson, 2002).

As commented before, seven *Geum* species are located in the Iberian Peninsula, belonging to three subgenera (Lainz, 1998); i) *G. rivale* L., *G. sylvaticum* Pourr. *G. pyrenaicum* Mill., *G. urbanum* L., and *G. hispidum* Fr. Included in subgenus *Geum* L., which shows its widest distribution in Europe, North America and Asia, ii) *G. montanum* L. included in subgenus *Oreogeum* Ser., typical from the mountains of Europe and iii) *G. heterocarpum* Boiss. included in subgenus *Orthostylus* (C.A. Mey.) F. Bolle, whose species are mainly located in the Mediterranean Region (Lainz, 1998). These species are well defined morphologically. Even several of them are considered as sister species in the phylogenetic study of Smedmark & Eriksson (2002).

However, as a result of our botanical explorations made in the Southeast Iberian Peninsula (mainly in Albacete province), we detected several populations of deviant *G. sylvaticum*, with longer habit and achenia, which inhabited near “typical” populations of the same species. These individuals showed several morphological traits that belong to *G. atlanticum* Desf., a species described from North Africa (Tlemcen, Algeria) (Desfontaines, 1798). After that, Font Quer (1928) proposed a new combination, *G. sylvaticum* var. *atlanticum* Font Quer & Pau. A few years later, Lindberg (1932) proposed that this variety was an endemic taxon from North, being followed by Quézel (1980) in the “Flore de l’Afrique du Nord”, suggesting that *G. sylvaticum* var. *atlanticum* was exclusively located across the mountains of Algeria and Morocco, whereas *G. sylvaticum* s. str. would be distributed in the Iberian Peninsula and South of France. Interestingly, Quézel & Santa (1962) did not mention *G. atlanticum* in their work regarding Algerian flora, even as a synonym of *G. sylvaticum*. However, Cuatrecasas collected and reviewed accessions previously collected by Font Quer in Andalusia and Pau in Mongó mountain (Valencia) in the early twentieth century, which are the first identifications of *G. atlanticum* in the Iberian Peninsula, belonging to two herbarium accessions (MA55959, MA55990). Cuatrecasas proposed two new varieties for *G. atlanticum*; *G. atlanticum* var. *cabrillense* Cuatrec. *nomen nudum* (BC 20006), from Sierra de la Cabrilla (Jaén) and var. *rosulatum* Cuatrec. *nomen nudum* (BC91935), from Sierra del Pinar, in Grazalema (Cádiz).

More recently, several authors (Lainz, 1995, 1998; Ibn Tattou, 1999; Romo, 2002) considered populations of

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*G. atlanticum* from Iberian Peninsula and Northern Africa as a synonym of *G. sylvaticum* without further explanation or suggesting that this issue is not completely solved. Lainz (1995, 1998) pointed out that some accessions cited as *G. atlanticum* showed morphological traits deviant from the typical *G. sylvaticum*. However, this author, arguing that cariology and chorology studies were inconclusive, suggested that this morphological variability alone was not enough evidence to separate these two taxa.

In this work, we have performed a morphological and molecular analysis to elucidate the taxonomic status of *G. atlanticum*, focusing on the available material in order to i) explore their morphological and genetic differentiation from *G. sylvaticum*, and ii) to assess the conservation status of *G. atlanticum* according to IUCN criteria (IUCN, 2012).

## Material and Methods

### Morphological and chorological analysis

The morphological study was based on the material collected and deposited in BC, MNHN (P), MUB, MA, GDA, SALA, MPU, VAL and ANVL herbaria (Thiers, continuously updated). A portion of the accessions has been revised through digital images of preserved plants from some of the mentioned herbaria or digital platforms as GBIF, JSTOR or ANTHOS (GBIF, 2019; Anthos, 2020; MNHN, Chagnoux, 2020a; MNHN, Chagnoux, 2020b). Furthermore, morphological data of the newly located *G. atlanticum* populations from Southeastern Iberian Peninsula

(mainly Albacete) were obtained from direct examination of living plants from Alcaraz and Segura range mountains. Herbarium specimens belonging to *G. sylvaticum* and *G. atlanticum* (including those described as *G. sylvaticum* var. *atlanticum*) are listed in Appendix 1 and quantitative and qualitative morphological traits studied are listed in Table 1. To evaluate differences in morphometric traits between the two taxa we conducted a T-test after checking the homogeneity of variance and normality of data with a Levene's test and a Shapiro-Wilk's test, respectively. All analyses were performed with SPSS v.24, IBM Corp., 2016.

A distribution map of *G. atlanticum* has been performed using the locations indicated in the labels of the accessions reviewed and the newly collected material (Figure 1). Additionally, information relative to locations of *G. atlanticum* has been added (Muñoz Medina, 1951; Barbero *et al.*, 1981; González Bueno, 1988; Valdés *et al.*, 2006; Mateos & Valdés, 2009; Romo, 2009; Chamboleyron, 2012).

### Molecular analysis

For this work, the ITS (ITS1-5,8S-ITS2) region of nuclear ribosomal DNA from two individuals of *G. atlanticum*, *G. sylvaticum* and *G. hyspidum* was sequenced, which were complemented by previously published sequences (downloaded from GenBank) belonging to seven species of *Geum* and two sequences of *Rubus ulmifolius* Schott as outgroup taxon to root the tree. The taxa studied are listed in Table 2, with GenBank accession numbers and voucher details.

Table 1. Main morphological traits studied for *Geum atlanticum* Desf. and *Geum sylvaticum* Pourr. Morphometric variables are listed in the upper rows, whereas variables not included in the morphometric analysis are listed in the lower ones. For the morphometric variables, ranges of variables are listed in the first line, whereas mean and standard error (in parenthesis) obtained from the T-test are listed in the second. Asterisk indicate statistical significance ( $P < 0.01$ ); ns, non-significant.

Morphological trait	<i>G. atlanticum</i>	<i>G. sylvaticum</i>
Upper leaf length (*)	Up to 6(8) cm 4.06 ( $\pm$ 0.43)	Up to 3(4) cm 2.73 ( $\pm$ 0.14)
Sepal length (ns)	9-11 mm 10.25 ( $\pm$ 0.10)	9-11 mm 10.11 ( $\pm$ 0.17)
Sepal width (ns)	4-5 mm 4.69 ( $\pm$ 0.09)	4-5 mm 4.61 ( $\pm$ 0.13)
Petal length (ns)	8-10(11) mm 10.33 ( $\pm$ 0.12)	8-10(11) mm 10.19 ( $\pm$ 0.11)
Petal width (ns)	8-10(11) mm 10.59 ( $\pm$ 0.20)	8-10(11) mm 10.13 ( $\pm$ 0.38)
Achene length (seminiferous part only) (ns)	5-8 mm 5.89 ( $\pm$ 0.23)	4.5-6 mm 5.31 ( $\pm$ 0.14)
Achene width (seminiferous part only) (ns)	2-3 mm 2.68 ( $\pm$ 0.08)	2-2.8(3) mm 2.63 ( $\pm$ 0.10)
Achene beak length (*)	6-11 mm 8.26 ( $\pm$ 0.44)	5-8 mm 6.73 ( $\pm$ 0.31)
Achene size (seminiferous part and beak) (*)	12-17 mm 13.39 ( $\pm$ 0.31)	Up to 12 mm 11.43 ( $\pm$ 0.14)
Habit	Up to 70 cm, foliose	Up to 50 cm, scarcely foliose
N. achenia per flower	(33)40-58	15-25(30)
Achene indumentum	Seminiferous part with hirsute hairs up to 1.7 mm, and short hairs. Glandular short hairs up to the middle of the beak	Seminiferous part with short hairs up to 0.7 mm, rarely glandular. Short hairs in the basal part of the beak
Presence of carpophore	No	Yes

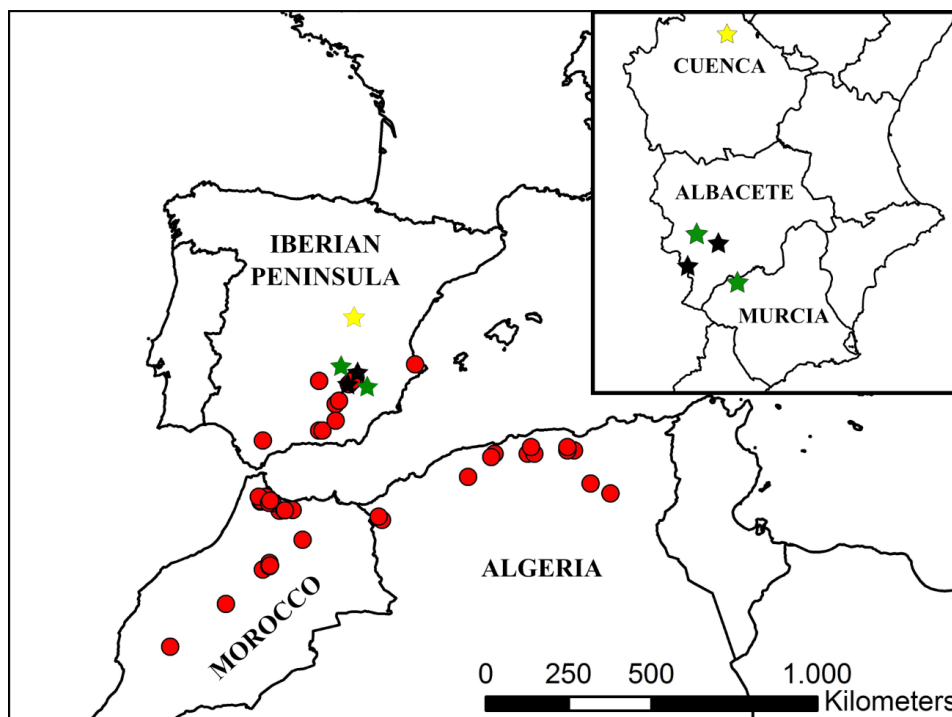


Figure 1. Distribution map of *Geum atlanticum*. Red circles show the known populations. Colored stars represent locations of individual sampled by authors for phylogenetic analysis. Black stars. *G. atlanticum*; green stars. *G. sylvaticum*; yellow star. *G. hispidum*.

### DNA extraction, PCR amplification and sequencing

Total DNA was extracted using the cetyltrimethyl ammonium bromide method (Doyle & Doyle, 1987) with slight modifications and stored frozen at  $-20^{\circ}\text{C}$  until amplification. The internal transcribed spacer region (ITS1-5.8S-ITS2) of nuclear ribosomal DNA was amplified with the primer pair 17S and 26S (Sun *et al.*, 1994). The PCR reactions were carried out in an Eppendorf Mastercycler thermocycler using the following program: an initial cycle of  $94^{\circ}\text{C}$  for 5 min, 35 cycles of  $94^{\circ}\text{C}$  for 30 s,  $52^{\circ}\text{C}$  for 45 s,  $72^{\circ}\text{C}$  for 1 min, and a final extension step of  $72^{\circ}\text{C}$  for 8 min to complete the PCR. The reactions were conducted in a final volume of 50  $\mu\text{l}$  using approximately 40 ng of DNA, 0.4  $\mu\text{M}$  of direct and reverse primers, 5  $\mu\text{l}$  of polymerase buffer (provided by the supplier of the enzyme), 0.2 mM of each of dNTPs, 2 mM of  $\text{MgCl}_2$  and 2 U of Taq polymerase (Biotools). Finally, 2  $\mu\text{l}$  of each amplification product were visualized on 1.5% agarose gels, and successful amplifications were cleaned using the GenElute PCR Clean-Up kit (SIGMA). Same primers were used in the sequencing reactions with the Big Dye sequencing kit and the products were separated in an automatic ABI 3700 sequencer following standard protocols. For each DNA sample, both strands were sequenced. Maximum likelihood (ML) and Bayesian inference (BI) analyses were performed with 17 nrITS sequences.

Sequences were checked for inaccurate base identification using Chromas Lite v2.01 (Technelysium Pty Ltd.). Consensus sequences of ITS were aligned using ClustalX (Thompson *et al.*, 1997). BioEdit (Hall, 1999) was used to make minor alignment adjustments. A Bayesian and Maximum Likelihood (ML) analysis were performed. Both analyses were carried out under GTR + G + I model of evolution according to JModeltest 2 (Guindon & Gascuel, 2003; Darriba *et al.*, 2012). MrBayes, v. 3.2 (Ronquist *et al.*, 2012) was used to perform Bayesian analyses. Two simultaneous runs were initiated by starting from random trees. To ensure that the two runs converged onto a stationary distribution, analyses were run until the average standard deviation of the split frequencies was 0.01. Convergence was evaluated using the potential scale reduction factor (PSRF), and 1,000,000 generations were run by sampling every 100th generation at the following settings: Nst = 6, rates = invgamma. Burnin (the number of starting generations ruled out from further analyses) was set at 200,000 generations after visually inspecting the likelihood values in Excel. A 50% majority-rule consensus tree was constructed using the “sumt” command of MrBayes. ML phylogenetic trees were conducted with 1,000 bootstrap replicates by the rapid Bootstrap analysis in v.1.5b1 of RAxMLGUI (Silvestro & Michalak, 2012). The best-scoring ML trees were chosen as the final trees and bootstrap values were added to nodes. Trees were edited with Figtree, v.1.4 (Rambaut, 2012).

Table 2. Origin of the material included in the molecular analyses, and GenBank accession numbers. Asterisks indicate the accessions used to generate ITS sequence data in the present study.

Species/accessions	Origin of sequence	Genbank accession nr.
<i>Geum aleppicum</i> _1	Zhang et al. (2017)	KX645654
<i>Geum aleppicum</i> _2	Zhang et al. (2017)	KX645653
<i>Geum atlanticum</i> _1	*Albacete. Cabezallera Sánchez-Gómez, Jiménez & Cánovas 30SWH6565	MT809031
<i>Geum atlanticum</i> _2	*Albacete, Calar de la Sima Sánchez-Gómez, Jiménez & Cánovas 30SWH4645	MT809032
<i>Geum geniculatum</i>	Smedmark & Eriksson (2002)	AJ302348
<i>Geum heterocarpum</i>	Smedmark & Eriksson (2002)	AJ302349
<i>Geum hispidum</i> _1	*Cuenca, Serranía de Cuenca. El Maillo 30TWK9261. Jiménez & Cánovas	MT809033
<i>Geum hispidum</i> _2	*Cuenca, Serranía de Cuenca. El Maillo 30TWK9261. Jiménez & Cánovas	MT809034
<i>Geum montanum</i>	Smedmark & Eriksson (2002)	AJ302350
<i>Geum rivale</i>	Smedmark & Eriksson (2002)	AJ302352
<i>Geum speciosum</i>	Smedmark & Eriksson (2002)	AJ302354
<i>Geum sylvaticum</i> _1	*Albacete, Sierra de Alcaraz, Peñascosa 30SWH5373. Sánchez-Gómez, Jiménez & Cánovas	MT809035
<i>Geum sylvaticum</i> _2	*Murcia, Moratalla, Paredones de La Muela, 30SWH9134. López & Carrión	MT809036
<i>Geum urbanum</i> _1	Smedmark & Eriksson (2002)	AJ302337
<i>Geum urbanum</i> _2	Eriksson et al. (1998)	U90802
<i>Rubus ulmifolius</i> _1	Sochor et al. (2015)	KM037609
<i>Rubus ulmifolius</i> _2	Sochor et al. (2015)	KM037602

## Results

### Morphological results

According to the morphological examination of herbarium accessions and fresh material from Southeastern Iberian Peninsula (mainly Albacete populations), we have observed clear distinctive patterns among *G. sylvaticum* and the fresh material plus several herbarium accessions from Spain and North Africa. These features are listed in Table 1. Most of the morphometric variables studied showed no significant differences between *G. sylvaticum* and *G. atlanticum*. Only total length of achene (seminiferous part plus beak), length of beak, and stem's leaves showed significant differences (Table 1). *G. atlanticum* achenia are longer than that of *G. sylvaticum* (up to 17 mm vs. 12 mm respectively) and with long patent hairs on the base of the achene. Moreover, the number of achenia per flower is higher in *G. atlanticum* (>40 per flower) than in *G. sylvaticum*. Moreover, the habit from the *G. atlanticum* morphological type usually shows longer stems with longer leaves than *G. sylvaticum*. Another remarkable difference is the absence of carpophore in *G. atlanticum* (Figure 2).

### Molecular Results

The two ITS1-5.8S-ITS2 sequences generated here for *G. atlanticum* from fresh material of two Albacete populations were identical and different from those corresponding to the rest of *Geum* species. We have observed that *G. sylvaticum* sequences (from Albacete) show several mutations compared to *G. atlanticum*, and

these mutations are shared between *G. atlanticum* and *G. hispidum* (from Serranía de Cuenca range mountain). Pairwise comparisons of percentage sequence divergence for the ITS region among all species used in the molecular analyses are summarized in Table 3. Sequence divergence between the species of *Rubus* and *Geum* ranged between 10.91% (*R. ulmifolius* vs. *G. atlanticum*) and 13.51% (*R. ulmifolius* vs. *G. speciosum* Albov). Sequence divergence among the *Geum* species ranged between 0.15% (*G. atlanticum* vs. *G. hispidum*) and 6.25% (*G. speciosum* vs. *G. heterocarpum*). Sequence divergence among *G. atlanticum* and *G. sylvaticum* is 1.04%.

The final sequence alignment of the 15 ingroups and two outgroup taxa was 719 bp long. Of these, 605 sites were constant, 25 were variable but parsimony uninformative, and 89 were parsimoniously informative. Both the ML and Bayesian inference searches resulted in trees with a similar topology. Therefore, the Bayesian posterior probability (PP) and ML bootstrap values (Bs) are provided in the same tree for all the analyses (Figure 3). The phylogenetic tree shows *G. heterocarpum* as basal species and *G. speciosum* as sister species (Bs = 100%, PP = 100%). This species is related to a clade with low bootstrap support (Bs = 72%) but high Bayesian support (PP = 100%), in which *G. montanum* and *G. rivale* are located a sister species, related to *G. aleppicum* Jacq. and *G. geniculatum* Michx. in a subclade with low Bs and PP support, whereas in other subclade are located *G. hispidum* and *G. urbanum*, as sister species of a subclade which includes *G. atlanticum* and *G. sylvaticum*. These subclades also show low support, suggesting the difficulty of elucidating the phylogenetic relationships in *Geum*.

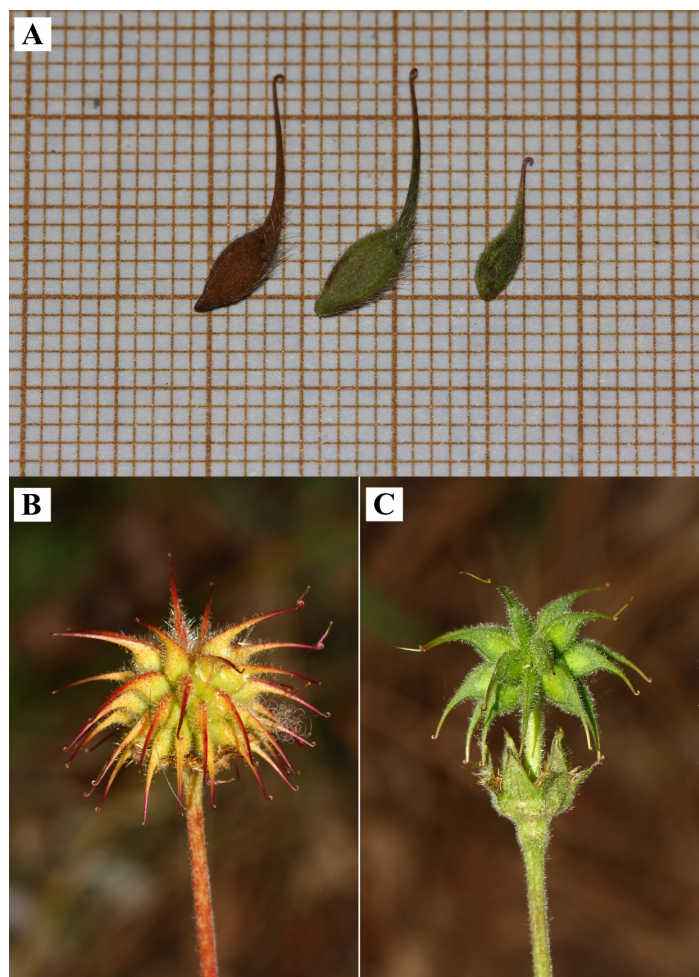


Figure 2. Main differences between *Geum atlanticum* and *G. sylvaticum*. A, Achenia. Left and central achenia belong to *Geum atlanticum*. Right achenium belongs to *G. sylvaticum*; B, *G. atlanticum* in fruiting; C, *G. sylvaticum* in fruiting with carpophore.

Table 3. Pairwise comparisons of sequence divergence (in percentages) of the entire ITS1-5.8S-ITS2 region among the species of *Geum* and *Rubus ulmifolius*. Identical sequences of *Rubus ulmifolius*, *G. urbanum*, *G. atlanticum*, *G. hispidum* and *G. sylvaticum* have been eliminated from the analysis.

	<i>R.u.</i>	<i>G.a.1</i>	<i>G.a.2</i>	<i>G.u.</i>	<i>G.g.</i>	<i>G.r.</i>	<i>G.m.</i>	<i>G.s.</i>	<i>G.h.</i>	<i>G.at.</i>	<i>G.hi.</i>	<i>G.sy.</i>
<i>R. ulmifolius</i>	0.00											
<i>G. aleppicum_1</i>	11.74	0.00										
<i>G. aleppicum_2</i>	11.89	0.77	0.00									
<i>G. urbanum</i>	12.40	0.99	0.50	0.00								
<i>G. geniculatum</i>	12.56	0.17	0.99	1.16	0.00							
<i>G. rivale</i>	12.38	1.48	1.32	1.15	1.65	0.00						
<i>G. montanum</i>	12.24	1.02	0.85	0.68	1.19	1.36	0.00					
<i>G. speciosum</i>	13.51	4.46	4.95	4.46	4.62	4.61	4.92	0.00				
<i>G. heterocarpum</i>	12.69	5.12	5.28	5.12	5.28	5.60	4.92	6.25	0.00			
<i>G. atlanticum</i>	10.91	0.79	0.47	0.17	0.99	0.99	0.68	4.46	4.96	0.00		
<i>G. hispidum</i>	11.03	0.79	0.63	0.16	0.99	0.99	0.68	4.28	4.94	0.15	0.00	
<i>G. sylvaticum</i>	11.61	1.57	1.73	1.65	1.81	2.14	1.69	4.77	5.76	1.04	1.34	0.00

### Distribution and habitat of *G. atlanticum*

According to the available data from studied herbarium accessions as well as bibliographic references with locations of *G. atlanticum* (Muñoz Medina, 1951; Barbero

*et al.*, 1981; González Bueno, 1988; Valdés *et al.*, 2006; Mateos & Valdés, 2009; Romo, 2009; Chambouleyron, 2012) (Figure 1), this taxon should be considered an Ibero-African species, present in North Africa and the South and Southeast of the Iberian Peninsula. In North Africa,

it is distributed for humid mountains from Morocco (Rif, Middle Atlas and rarer in High Atlas) and Algeria (Tell Atlas, from Tlemcen, Blida, Djurdjura, to the mountains of Babor and Constantine, and Saharan Atlas in Bellezma and Aurès mountains). In Northern Africa, it inhabits mesophyllous forests of conifers as *Cedrus atlantica* (Endl.) Manetti ex Carrière, *Abies spp.* and *Quercus spp.* at 1000–2400 m asl, in several types of soils. In the Iberian Peninsula, including the newly located populations, it is distributed along the Baetic mountains; Grazalema, Sierra Nevada, Baza mountains and the Subbaetic ranges of Cazorla, Segura and Alcaraz. Moreover, there is a narrow

and isolated population in the South of Valencia province (Montgó mountain) and at least another in Sierra Morena (Despeñaperros), where it is very rare.

In the Iberian Peninsula, *G. atlanticum*, as well as in Northern Africa, occurs in mesophyllous forests. However, it accompanies other species, for example, *Pinus pinaster* Aiton, *P. nigra* subsp. *salzmannii* (Dunal) Franco, *Quercus rotundifolia* Lam., *Q. faginea* Lam. and *Taxus baccata* L., always within the meso-supramediterranean (oromediterranean) belt, in subhumid or humid ombrotype, on limestone or siliceous soils. It flowers from May to July and fruit formation takes place from June to August.

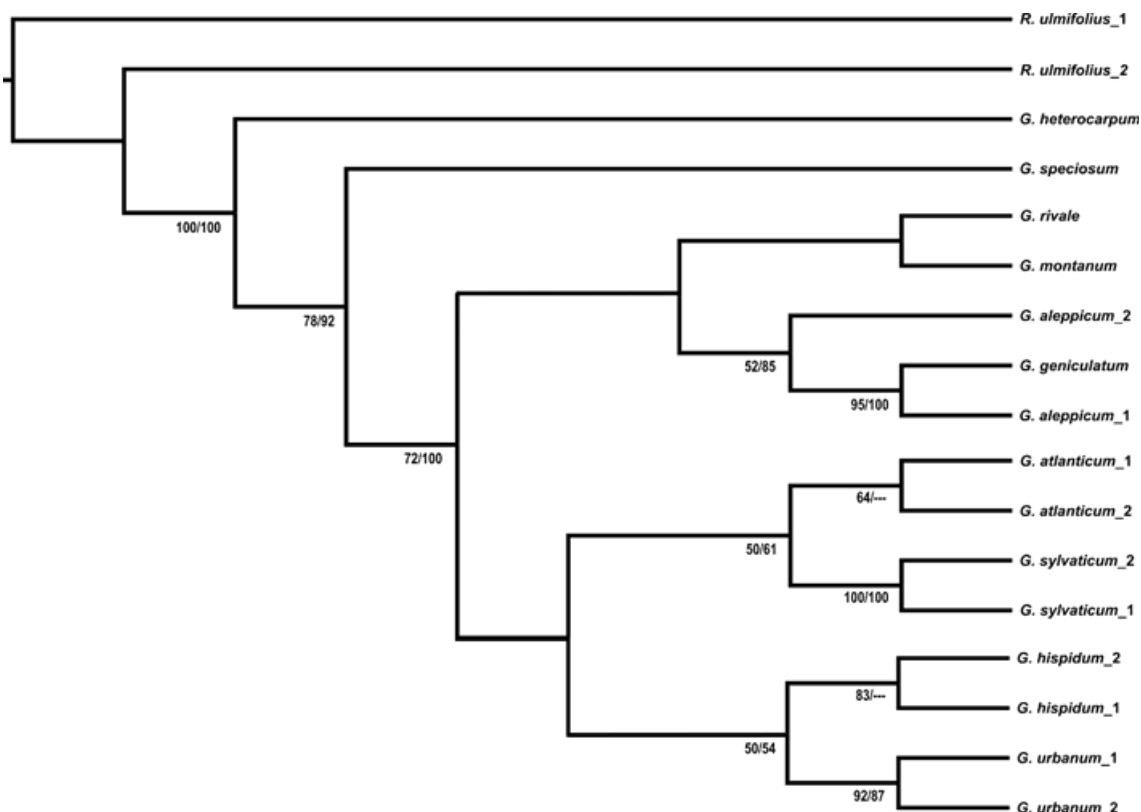


Figure 3. Maximum likelihood phylogenetic tree inferred for a sampling of select species of *Geum*. Bootstrap values (BS) followed by Bayesian posterior probabilities (PP) above 50% are given below the branches. The tree was rooted with *Rubus ulmifolius* as outgroup.

## Discussion

As commented before, *G. atlanticum* was described by Desfontaines from the mountains near Tlemcen, in Algeria (Desfontaines, 1798). However, several years later, Pau and Font Quer synonymized populations from North Africa as a variety of *G. sylvaticum* (*G. sylvaticum* var. *atlanticum*), with individuals from Morocco sharing an exsiccatae of this taxon with several herbaria. Individuals with such morphological features were located in the Iberian Peninsula, being named as the former variety, although Lindberg (1932) and Quézel (1980) suggested that this taxon was endemic from North Africa. Later, Láinz (1995) attempted to clarify the taxonomic status for these individuals with the search of fresh material in the previously cited populations to obtain chromosome numbers that shed light. Unfortunately, he could not obtain enough material to perform a satisfactory analysis

and suggested to maintain all the Iberian accessions as *G. sylvaticum*, although pointing out that more studies were needed to clarify the taxonomic status of *G. atlanticum* (Láinz, 1998).

In this work, we have sampled new individuals and populations with the morphological traits typical of *G. atlanticum*, as the number of achenia per flower, the size and indumentum of achenia, and the absence of carpophore, which are unique morphological traits that are fixed and consistent in every individual analyzed, and are absent in *G. sylvaticum*. Moreover, the phylogenetic study shows that *G. atlanticum* is closely related to *G. sylvaticum*, as expected, but it shares several mutations with *G. hispidum* and *G. urbanum*. Indeed, in the ML tree, it is located in an intermediate position between *G. sylvaticum* and the pair *G. hispidum*-*G. urbanum*. These circumstances point out that *G. atlanticum* should not be considered as

a synonym of *G. sylvaticum*, but a different species, as suggested by Desfontaines. Its distribution area would cover the North of Africa and the South and Southeast of the Iberian Peninsula, while *G. sylvaticum* would be restricted to the Iberian Peninsula and South of France. *G. atlanticum* distribution range seems to coincide with other mesophyllous and orophyllous Iberoafrikan species, which probably migrated between Africa and Europe through Baetic-Rifean belt (Blanca, 1990; Lavergne *et al.*, 2013; Sánchez-Robles *et al.*, 2014). Its ecology is quite similar in every population. However, in North Africa, it inhabits at a higher altitude, probably due to the lower latitude of these populations.

Although no morphological differences have been observed between African and Iberian individuals studied, some studies seem necessary to clarify the taxonomic status and phylogenetic position of this taxon. Taking into account the importance of introgression and polyploidization in the evolution of *Geum* genus (Gajewski 1958; Smedmark & Eriksson 2002), new chromosome counts, cytogenetic studies and new phylogenetic studies using more nuclear and plastid regions in which more populations were sampled (including several from North Africa), are needed. Also, a phylogeographic study in which the highest possible number of populations from the Iberian Peninsula and North Africa were involved could help to establish hypotheses about the origin and evolution of populations of this taxon.

### Implication in Conservation

According to available data, *G. atlanticum* is widely distributed in the most humid mountains of North Africa. Although overgrazing and environmental degradation in the most suitable habitats (Thomas, 2013; Benabid *et al.*, 2015) might have had a great impact on the survival of populations in recent times. However, a significant number of populations are located in National Parks in both Morocco and Algeria, which suggests that these populations would be free of anthropogenic threats. On the contrary, taking into account that recently located populations are narrow and their number of individuals are scarce (less than one hundred individuals per population), *G. atlanticum* seems to be a rare species in the South of the Iberian Peninsula, although it has probably gone undetected. However, most of the populations are located in protected territories under European level (Natura 2000 Network), or Regional Parks of Andalusia, Castilla-La Mancha, and Valencia.

The number of known populations suggests that *G. atlanticum* is not threatened at a global level. Nevertheless, according to IUCN criteria (IUCN, 2012), *G. atlanticum* should be considered as Data Deficient (DD). An extensive sampling of historical localities might help to elucidate its conservation status. Due to the scarcity of populations in the Iberian Peninsula is feasible that *G. atlanticum* was protected in several Autonomous Communities from Spain where it would probably be threatened at the regional level. Further population studies are needed to address its threat level and to perform adequate conservation policies.

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**Appendix 1.** Specimens of *G. sylvaticum* and *G. atlanticum* studied in morphological analysis.

***Geum sylvaticum***

**SPAIN. Albacete:** Gontar, Puente Honda, 1849 m, *Blanco* MNHN P02519627; Albacete, in grasslands on limestones, Sierra de Alcaraz, 1000/2000 m, 25/VI/1891, *Porta & Rigo* MNHN P02519619, MNHN P03133345; Alcaraz, Puerto de los Crucecillos, 30SWH56, pine grove, 1400 m, 02/VI/1978, *F. Alcaraz* MUB 3052; Mesones, 30SWH5660, pine forest in shade, 10/V/1979, *M. Honrubia & J.M. Egea* MUB 320; Sierra de Almansa, 30SXJ7411, kermes oak, 18/V/1985, *C. Obon*, MUB 23465; Letur, Calar de los Tornajos, 15/V/1988, *P. Sánchez Gómez*, MUB 25488; Paterna del Madera, Endrinales, under hazel trees, 21/VII/1992, *S. Ríos & A. Robledo*, MUB 35046; Yeste, ravine under Morciguillos bridge towards Los Prados, rushes and hydromorphic grassland, 04/V/2005, *J.F. Jiménez*, MUB 100794; Molinicos, Los Gallineros, 30SWH5465, grassland under thorny bushes, 14/VI/2012, *J.F. Jiménez, D. López, J.L. Cánovas & P. Sánchez Gómez*, MUB 113406, MUB 113407, MUB 113414; Peñascosa, Sierra de Alcaraz, 30SWH5373, grasslands on dolomitic soils, 1460 m, 12/VI/2013, *P. Sánchez Gómez, J.F. Jiménez & J.L. Cánovas*, MUB 113755; Yeste, near ravine of de Puntal de Collado Tornero, 30SWH4645, pine undergrowth, 1240 m, 22/VI/2016, *P. Sánchez Gómez, J.F. Jiménez & J.L. Cánovas*, MUB 114211. **Avila:** pine forest, Hoyoquasero, 21/VII/1863, *E. Bourgeau*, MNHN P02519631. **Barcelona:** Tibidabo, Rabassada ravine, V/VI/1919/1920, MNHN P02519598. **Castellon:** Sierra de Espadan, grasslands in shady locations on Triassic limestones, 1200 m, VI/1891, *E. Reverchon*, MNHN P03133356; Peñagolosa, 08/VI/1891, *C. Pau*, MNHN P04202647; entre Vistabella y Penyagolosa, oak forest glade, 1300 m, 01/VII/1946, *Font Quer & Rivas Goday*, GDA 38123; towards Fredes by road from Embalse de Uldecona, undergrowth of *Viola/Quercetum valentinae* forest, 600 m, 04/IV/1980, *O. Socorro & A. Tarrega*, GDA 11989. **Ciudad Real:** Venta de Cárdenas, IV/1944, GDA 38120. **Granada:** Sierra de Alfacar, Puerta de la Inquisicion, 27/IV/1852, *Joh. Lange*, MNHN P02519601; Sierra Alfacar, 2/VII/1873, *M. Winkler*, MNHN P02519632 bis; Sierra Alfacar, 9/VII/1876, *M. Winkler*, MNHN P02519633; Regnum Granatense, Sierra de Alfacar, shady grassland on limestone soil, 1300 m, 01/VII/1879, *Huter, Porta, Rigo*, MPU 1217012; *ibidem*, MNHN P02519595; Dehesa de Alfacar, 1909, *J.L. Diez Tortosa*, GDA 38121; Sierra de Alfacar, 15/V/1949, *J. Muñoz Medina*, GDA 38118; *ibidem*, VI/1949, *J. Muñoz Medina*, GDAC 6153, GDA 38124; between Alazores and Zafarraya, V/1964, *Laza*, GDA 38117; Cázulas, 16/V/1965, GDA 38116; Sierra Elvira, V/1968, *J. Varo*, GDAC 1470; Sierra Nevada, oak forest of Güejar/Sierra, 05/VI/1970, *C. Morales*, GDAC 1469; Fuente de la Teja, 07/V/1977, *F. Valle*, GDAC 6349; Huéscar, Sierra Sagra, Camino de las Santas, irrigation ditch border, 1200 m, 26/V/1978, *A.N. Negrillo*, GDA 12286; Huéscar, Sierra Sagra, Collado

Moril, irrigation ditch border, 03/VI/1978, *A.N. Negrillo*, GDA 12287; Huéscar, Sierra Sagra, near V. de la Cabeza chapel, irrigation ditch border, 03/V/1979, *A.N. Negrillo*, GDA 12288; Sierra de la Yedra, oak forest undergrowth, 23/IV/1981, *J. Guirado*, GDAC 15649; Sierra de Parapanda, oak forest in front of farmerhouse of Jorvas, 30SVG1932, 1100 m, 20/V/1982, *Aroza, Negrillo & Molero*, GDA 16034; Monachil, Sierra Nevada, near San Jerónimo, in Monachil river basin, in *Pinus sylvestris* forest, 1600 m, 28/VI/1982, *J. Molero Mesa & P. Pérez Raya*, GDA 18030; Iznalloz, Sierra del Rayo, near Cortijo de los Calderones, 30SVG4542, subhumid ombrotype holm oak forest, 1170 m, 03/VI/1989, *J. Gutierrez & F.J. García*, GDAC 37076; Sierra de Huétor, Las Mimbres, humid places under holm oaks, 1300 m, 17/V/2003, *M. Lerme, det. C. Morales*, GDA 47689; Sierra de Huétor, Barranco del Chorrillo, Cortijo del Chorrillo, 30SVG5827, near river, on limestones, 1150 m, 21/V/2004, *C. Morales, C. Quesada, M.T. Vicioso & L. Baena*, GDA 48677; Alfaguara, Fuente de la Teja, GDAC 42455). **Huesca:** shrubs at the base of the mountain Peña de Oroël, near Jaca. ad alt. c. 3000', VI/1850, *Willkomm.*, MNHN P02519629; San Juan de la Peña, 21/IV/1972, *G. G. Aymonin & M. Keraudren/Aymonin*, MNHN P04176292; Puerto de Monrepos road from Lanave towards Arguis, 1250 m, 05/VI/1975, *B. de Retz*, MNHN P04198901. **Jaén:** Sierra de Segura, 18/V/1850, *E. Bourgeau*, MNHN P02519600, MNHN P02519644, MNHN P03133362; Sierra de Cazorla, between Vadillo de Castril and the source of Guadalquivir river, 1200 m, 7/VI/1978, *B. de Retz*, MNHN P04198900; Garganta de los ladrones, 30SVG3566, 700 m, 15/V/1986, *Abel Ruiz, det. García Rojo & C. Fernández*, GDA26797; *ibidem*, MUB 46737; Siles, Río Madera, *Rubus canescens* community, 14/IV/1988, *S. Ríos*, MUB 18829; Siles, wet grasslands, 05/V/1988, *S. Ríos*, MUB 18812; Siles, Río Madera, wet grasslands, V/1988, *S. Ríos*, MUB 31539; Siles, Yelmo, Fuente Avellanar, undergrowth of deciduous forest, 06/V/1988, *S. Ríos*, MUB 18827, MUB 18830; Siles, Acebeas, *Daphno-Aceretum* forests, 06/VIII/1988, *S. Ríos*, MUB 18828; Sierra de Cazorla, source of Guadalquivir river, 14/V/1994, SALA 60397; Sierra de Cazorla, source of Guadalquivir river, 14/V/1994, VAL 96884; Collado de los Jardines, Parque Natural de Despeñaperros, next to nemoral plants, on acid soils, 11/IV/1997, *J.A. Algarra*, GDAC 42576; Sierra de Segura, Fuente Jordana, 30SWH3235, grassland under pine forest, 1350 m, 24/IV/2002, *J.F. Jiménez*, MUB104378). **Leon:** Monte San Isidro near Leon, 1/V/1864, *E. Bourgeau*, MNHN P02519630). **Madrid:** Bois de l'Escorial, 18/V/1854, *E. Bourgeau*, MNHN P02519603, MNHN P03133346, MNHN P03133348; near Escorial, Madrid), 15/V/1973, *Torre Pando*, MNHN P02519632). **Málaga:** Sierra de la Nieve, La Nava, 04/VI/1934, *Cuatrecasas, det. Rivas Goday & F. Bellot*, GDA 38115; crests of Sierra Almijara, plains of Sedella, subalpine meadow, 1600 m, 24/IV/1987, *A. Charpin*, MNHN P06787191). **Murcia:** Moratalla, Rincón del Agua, 30SWH9427, holm oaks undergrowth, 1000 m, 14/V/1983, *C. Selma*, MUB 28626; Sierra Espuña, 30SXG2993, shady habitats, 01/

VI/1985, *A. Robledo Miras*, MUB 9947; Sierra Espuña, Barranco de Leiva, 30SXG2993, scree at the base of shady rocky cliff, 950 m, 01/VI/1985, *A. Robledo Miras*, MUB 15321; Moratalla, Sierra de la Muela, 19/V/1988, *P. Sánchez Gómez*, MUB 25383; Moratalla, Rincón de los Huertos, grassland, 17/V/1998, *J.A. Jiménez & P. Sánchez Gómez*, MUB 104377; Sierra Espuña, 30SXG2294, grassland, 25/V/1998, *J.A. Jiménez*, MUB 104376; Moratalla, 30SWH8333, wet soils, 13/V/1998, *Rams, Reales & Zamora*, MUB 104375; Moratalla, rocky cliffs of La Muela, 30SWH9134, grasslands, 1350 m, 27/VI/2003, *J.A. López, J.M.R. & M. A. Carrión*, MUB 104374). **Soria:** Robleda, VII/1953, *Herb. Humbert*, MNHN P04202646). **Tarragona:** Priorat, coll de la Teiseta, booster antenna, shady holm oak forest, 13/VI/1980, *J. Molero*, GDA 50958). **Teruel:** Valacloche, V/1893, *E. Reverchon*, MNHN P04198938; Sierra del Pinar d'Albarracin, shady locations and grasslands in Triassic substrates, 1500 m, VI/1894, *E. Reverchon*, MNHN P02519616; Prov. de Teruel, 1894, *E. Reverchon*, MNHN P02519617). **Valencia:** Surars de Pinet, V/1975, *G. Mateo*, GDAC 16334).

**PORTUGAL.** Summit of Cintra Mountain, V/1840, *Steudel*, MNHN P02519596; Coimbra, 1878, MNHN P02519640; Mosquites près Caxarias, pine forests, IV/V/1879, *J. Daveau*, MNHN P02519615, MNHN P02519637, MNHN P02519641; Lusitania, Coimbrae, 1880, *A. Moller*, MNHN P02519614, MNHN P03133347, MNHN P03133349; Venda do Pinheiro, VI/1881, *Torres/Veddas*, MNHN P02519612; Coimbre, 1886, *Herb. M.A. de Coincy*, MNHN P02519613; Catanhede, Tocha, Cabo Mondego, 25/V/1972, *G.G. Aymonin & M. Keraudren/Aymonin*, MNHN P04274005).

### *Geum atlanticum*

**SPAIN. Albacete:** Bogarra, Cabezallera, 30SWH6565, pine forest undergrowth, 1140 m, 14/VI/2012, *J.F. Jiménez, D. López, J.L. Cánovas & P. Sánchez Gómez*, MUB 114216; Yeste, next to the ravine of Puntal de Collado Tornero, 30SWH4645, sotobosque de pinar, 1240 m, 22/VI/2016, *P. Sánchez Gómez, J.F. Jiménez & J.L. Cánovas*, MUB 114215; Yeste, Calar de la Sima, next to Los Corralizos, 30SWH4644, shrubs, 1500, 28/VI/2016, *P. Sánchez Gómez, J.F. Jiménez & J.L. Cánovas*, MUB 114214; Riópar, Calar del Mundo, 30SWH5358, grassland under mixed forest of *Pinus* and *Quercus faginea*, 1445 m, 09/VII/2016, *J.L. Cánovas & P. Sánchez Gómez*, MUB 114213; Riópar, Calar del Mundo, 30SWH5358, grassland on stony soils in doline, 1410 m, 09/VII/2016, *J.L. Cánovas & P. Sánchez Gómez*, MUB 114212). **Alicante:** Between Mongo and Denia at the base of rocky cliffs, 03/V/1901, *det. Cuatrecasas, 01/V/1938*), MA 00055959, MA 00055959 bis). **Cádiz:** Grazalema, Sierra del Pinar, forest, 1400 m, 01/VII/1925, *P. Font Quer*, BC 91935, BC 91935a). **Granada:** Sierra Nevada, subalpine zone at San Geronimo, VII/1851, *E. Bourgeau*, MNHN P02519621; Sierra de Baza, Barranco del Serval, 30SVG03, nemoral environment in semi/deciduous forest, 07/VI/1985, *J. Torres, G. Blanca & C. Morales*, GDAC 2964; Monachil,

Sierra Nevada, between La Cortijuela and Collado del Tejo. 30SVG5803, pine forest undergrowth, 1750 m, 18/VI/2016, *J. Fuentes*, GDA 64315). **Jaén:** Sierra Morena, Barranco de Valdeflores, in Despeñaperros, acid soil, 800 m, forests, 08/VI/1924, *Font Quer*, MA 55990; Peal de Becerro, Sierra de la Cabrilla, Barranco del Guadalentín, *Pinus nigra* forest, 1500 m, 12/VII/1926, *Cuatrecasas*, BC 20206, BC 20206a; Sierra de Cazorla, 20/VI/1978, *J. Varo, O. Socorro, J. A. Gil, G. Blanca & F. Valle*, GDAC 5419; Siles, Las Acebeas, wet grasslands, VIII/1987, *S. Ríos*, MUB 31540; Siles, Fresnedillas, wet grasslands, 01/VII/1988, *S. Ríos*, MUB 31541).

**MOROCCO.** Middle Atlas, Aïn Leuh, forest on limestones, 13/V/1924, *det. Cuatrecasas, (01/V/1938)*, MA 00055995; Djebel Tazekka, south of Taza, VI/1925, *H. Humbert*, MNHN P03302670; Iguermalez mountain, species flowering, also in fruiting near Imasinen, Atlante rhiphaeo), cedar forests, 1700 m, VI/1927, *Font Quer*, GDA 38119; *ibidem*, BC 20201; cedar forests Iguermalez mountain, species flowering, also in fruiting near Imasinen, Atlante rhiphaeo, 01/V/1938, *det. Cuatrecasas, 01/V/1938*), MA 00055992; cedar forest, Iguermalez mountain, species flowering, also in fruiting near Imasinen, Atlante rhiphaeo, *det. Cuatrecasas*, MA 00055993; between Ifrane and Azrou, Middle Atlas), V/1938, *G. et L'H.*, MNHN P02799749, MNHN P02799750; cedar forest above 2000 m, near Aïn/Kaala, Middle Atlas, 11/VII/1938, *L. Faurel, det. R. Maire*, MNHN P04151884; Bab-Rouida, 27/VI/1950, *J. Muñoz Medina*, GDA 38122.

**ALGERIA.** Tell Atlas, above Blida, *Herb. Dr. Miergues*, MNHN P03362565; cedar forest at Teniet al Haad, Algiers province, 23/VII/1852, *E. Cosson*, MNHN P03362558; Djibril Cheliah, Monts Aurès, Constantine province, 11/VI/1853, *E. Cosson*, MNHN P03362520, MNHN P03362550; northern slope of Djurdjura mountains, territory of Beni-bou, Dra-el-Mizan, Argiels province, 23/24/VI/1854, *E. Cosson*, MNHN P03362523, MNHN P03362554; *ibidem*, MPU 1217010; northern slope of Djebel Tamgout, Djurdjura mountains, Dra-el-Mizan, Argiels province, 03/VII/1854, *E. Cosson*, MNHN P03362519, MNHN P03362555; grasslands at the summit of Gharrouban mountain, south of Lalla/Maghmia, west of Oran province, 23/V/1856, *E. Bourgeau*, MNHN P03362521, MNHN P03362524, MNHN P03362556, MNHN P03362557; *ibidem*, MPU 1217018; surroundings of Fort Napoleon, Kabylia), 07/VI/1859, *G.-L. Durango*, ANVL 01798; Djebel Tabor, Little Kabylia, Constantine province, 21/VII/1861, *E. Cosson*, MNHN P03362548; forests between Sebdu and Aïn-Ghoraba, 13/VI/1874, *A. Warrion*, MNHN P03362549; Adgbar Amellal, Eastern Chabet-el-Akra, Constantine province, 01/VII/1880, *E. Cosson*, MNHN P03362551; north slope of Djebel Babor, Constantine province, 23/VI/1880, *E. Cosson*, MNHN P03362552; cedar forest near Teniet/el/Had, 17/V/1888, *leg. [...] Herb. Cosson*, MNHN P03362560; [...] Atlas, Argiels province, 11/V/18[...], *J. Lefebvre*, MNHN P03362553; Tell Atlas, Chrea, 27/V/1914, MNHN P03302669; [...] under cedar forest at Chrea above 1500 m, Tell Atlas, Blida province, 05/

VII/1930, *L. Faurel*, MNHN P04151879; Chrea, 1100 m, 11/VII/1931, *Gombault*, MNHN P03362559; Aïn-Ghoraba, near Terny, 30/VI/1933, *det. Cuatrecasas*, (01/V/1938), MA 00055991; Aïn-Ghoraba, near Terny, grasslands and shrubs, 1300 m, 30/VI/1933, *A. Faure*, MPU 104792, MPU 104793; wet places [...] Chelia Forest House, Aures mountain, 24/V/1935, *L. Faurel*, MNHN P04151880; under cedars above Tizi-Bou-el-

Ma mountain pass, 1700 m, Djurdjura, 10/VII/1935, *L. Faurel*, MNHN P04151881; cedar forest, Bordjem mountain, northwest of Batna, Sandy soil, 1900 m, 12/VI/1938, *R. Maire*, MNHN P03362716; *ibidem*, MPU 104791; Kefrida, Little Kabylie, 09/IV/1955, *H. Guillet*, MNHN P04166240; O. Gha-Rouban, *Pomel*, MPU 104796; La Chiffa, MPU 1217013; Illegible, MNHN P03362522.