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

Pedro Sánchez-Gómez1, José Luis Cánovas2, & Juan F. Jiménez2

Received: 27 February 2020 / Accepted: 24 September 2020 / Published online: 12 April 2021

**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.

**How to cite:** Sánchez-Gómez, P., Cánovas, J.L. & Jiménez, J.F. 2021. Insights on a rare species, *Geum atlanticum*, new data to differentiate from *Geum sylvaticum*. Mediterr. Bot. 42, e68011. https://dx.doi.org/10.5209/mbot.68011

**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
**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; Chambouleyron, 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 | *G. atlanticum* | *G. sylvaticum* |
|---------------------|----------------|----------------|
| Upper leaf length (*) | Up to 6(8) cm | Up to 3(4) cm |
| Sepal length (ns) | 4.06 (± 0.43) | 2.73 (± 0.14) |
| Sepal width (ns) | 10.25 (± 0.10) | 10.11 (± 0.17) |
| Petal length (ns) | 4.69 (± 0.09) | 4.61 (± 0.13) |
| Petal width (ns) | 8-10(11) mm | 8-10(11) mm |
| Achene length (seminiferous part only) (ns) | 5-8 mm | 5.31 (± 0.14) |
| Achene width (seminiferous part only) (ns) | 2.3 mm | 2.3 (± 0.10) |
| Achene beak length (*) | 6-11 mm | 5-8 mm |
| Achene size (seminiferous part and beak) (*) | 12-17 mm | 11.43 (± 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. | Short hairs in the basal part of the beak |
| Presence of carpophore | No | Yes |
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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°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°C for 5 min, 35 cycles of 94°C for 30 s, 52°C for 45 s, 72°C for 1 min, and a final extension step of 72°C for 8 min to complete the PCR. The reactions were conducted in a final volume of 50 μl using approximately 40 ng of DNA, 0.4 μM of direct and reverse primers, 5 μl of polymerase buffer (provided by the supplier of the enzyme), 0.2 mM of each of dNTPs, 2 mM of MgCl₂, and 2 U of Taq polymerase (Biotools). Finally, 2 μl 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 & Michalák, 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. |
|--------------------|-------------------------------------------------------------------------------------|-----------------------|
| Geum aleppicum_1   | Zhang et al. (2017)                                                                  | KX645654              |
| Geum aleppicum_2   | Zhang et al. (2017)                                                                  | KX645653              |
| Geum atlanticum_1  | *Albacete. Cabezallera Sánchez-Gómez, Jiménez & Cánovas 30SWH6565                   | MT809031              |
| Geum atlanticum_2  | *Albacete, Calar de la Siva Sánchez-Gómez, Jiménez & Cánovas 30SWH4645              | MT809032              |
| Geum geniculatum   | Smedmark & Eriksson (2002)                                                           | AJ302348              |
| Geum heterocarpum  | Smedmark & Eriksson (2002)                                                           | AJ302349              |
| Geum hispidum_1    | *Cuenca, Serranía de Cuenca. El Maillo 30TWK9261. Jiménez & Cánovas                 | MT809033              |
| Geum hispidum_2    | *Cuenca, Serranía de Cuenca. El Maillo 30TWK9261. Jiménez & Cánovas                 | MT809034              |
| Geum montanum      | Smedmark & Eriksson (2002)                                                           | AJ302350              |
| Geum rivale        | Smedmark & Eriksson (2002)                                                           | AJ302352              |
| Geum speciosum     | Smedmark & Eriksson (2002)                                                           | AJ302354              |
| Geum sylvaticum_1  | *Albacete, Sierra de Alcaraz, Peñascosa 30SWH5373. Sánchez-Gómez, Jiménez & Cánovas| MT809035              |
| Geum sylvaticum_2  | *Murcia, Moratalla, Paredones de La Muela, 30SWH9134. López & Carrión               | MT809036              |
| Geum urbanum_1     | Smedmark & Eriksson (2002)                                                           | AJ302337              |
| Geum urbanum_2     | Eriksson et al. (1998)                                                               | U90802                |
| Rubus ulmifolius_1 | Sochor et al. (2015)                                                                 | KM037609              |
| Rubus ulmifolius_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 *Geum 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.

|                  | R.u. | G.a.1 | G.a.2 | G.u. | G.g. | G.r. | G.m. | G.s. | G.h. | G.at. | G.hi. | G.sy. |
|------------------|------|-------|-------|------|------|------|------|------|------|-------|-------|-------|
| R. ulmifolius    | 0.00 |       |       |      |      |      |      |      |      |       |       |       |
| G. aleppicum_1   | 11.74| 0.00  |       |      |      |      |      |      |      |       |       |       |
| G. aleppicum_2   | 11.89| 0.77  | 0.00  |      |      |      |      |      |      |       |       |       |
| G. urbanum       | 12.40| 0.99  | 0.50  | 0.00 |      |      |      |      |      |       |       |       |
| G. geniculatum   | 12.56| 0.17  | 0.99  | 1.16 | 0.00 |      |      |      |      |       |       |       |
| G. rivale        | 12.38| 1.48  | 1.32  | 1.15 | 1.65 | 0.00 |      |      |      |       |       |       |
| G. montanum      | 12.24| 1.02  | 0.85  | 0.68 | 1.19 | 1.36 | 0.00 |      |      |       |       |       |
| G. speciosum     | 13.51| 4.46  | 4.95  | 4.46 | 4.62 | 4.61 | 4.92 | 0.00 |      |       |       |       |
| G. heterocarpum  | 12.69| 5.12  | 5.28  | 5.12 | 5.28 | 5.60 | 4.92 | 6.25 | 0.00 |       |       |       |
| G. atlanticum    | 10.91| 0.79  | 0.47  | 0.17 | 0.99 | 0.99 | 0.68 | 4.46 | 4.96 | 0.00  |       |       |
| G. hispidum      | 11.03| 0.79  | 0.63  | 0.16 | 0.99 | 0.99 | 0.68 | 4.28 | 4.94 | 0.15  | 0.00  |       |
| G. sylvaticum    | 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 mesophylous 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 mesophylous 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, Laínz (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 (Laínz, 1998).

In this work, we have sampled new individuals and populations with the morphological traits typical of G. atlanticum, as the number of achene 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 mesophyous and orophyous Iberoafrican 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 polyploidyization 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.

**Acknowledgments**

This work has been partially carried out within a collaboration agreement between the University of Murcia and GEACAM. We thank Carlos Aedo for providing us with information and solving some doubts about accessions deposited in the MA herbarium. Additional thanks to two anonymous reviewers for their valuable comments on the different versions of the manuscript.

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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 Crueceillos, 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, 30SX7411, kermes oak, 1170 m, 03/VI/1989, *J. Gutierrez & F.J. Garcia*, GDAC 37076; Sierra de Huétor, Las Mimbres, humid places under holm oaks, 1300 m, 17/V/2003, *M. Lemne, det. C. Morales*, GDA 47689; Sierra de Huétor, Barranco del Chorrillo, Cortijo del Chorrillo, 30SVG5827, near river, in 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 Oroel, near Jaca. ad alt. c. 3000', 01/VI/1850, GDA 11989; *J.F. Jiménez, P. Sánchez Gómez*, 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. Garcia Rojo & C. Fernández*, GDAC 26797; *J.F. Jiménez, P. Sánchez Gómez*, MUB 46737; Siles, Rio Madera, Rubus canescens community, 14/IV/1988, S. Rios, MUB 18829; Siles, wet grasslands, 05/V/1988, S. Rios, MUB 18812; Siles, Rio Madera, wet grasslands, V/1988, S. Rios, MUB 31539; Siles, Yelmo, Fuente Avellanar, undergrowth of deciduous forest, 06/V/1988, S. Rios, MUB 18827, MUB 18830; Siles, Acébeas, Daphno-Acetum forests, 06/VIII/1988, S. Rios, MUB 18828; Sierra de Cazorla, source of Guadalquivir river, 14/V/1994, *S. Rios, det. J.A. Algarra*, SALA 60397; Sierra de Cazorla, source of Guadalquivir river, 14/V/1994, *A.N. Negrillo*, VAL 96884; Collado de los Jardines, Parque Natural de Despeñaperros, next to river, 1350 m, 01/VII/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, *A. Charpin*, MNHN P06787191). **Murcia:** Moratalla, Rincón del Agua, 30SWH9427, holm oaks undergrowth, 1000 m, 14/V/1983, *C. Selma*, MUB 28626; Sierra Espuña, 30XG2993, 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, 30SWH1344, grasslands, 1350 m, 27/V/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/V/1980, J. Molero, GDA 50958). Teruel: Valacleche, V/1893, E. Reverchon, MNHN P04198938; Sierra del Pinar d’Albarracin, shady locations and grasslands in Triassic substrates, 1500 m, V/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; Mosqites près Caxarias, pine forests, IV/V/1879, J. Daveau, MNHN P02519615, MNHN P02519637, MNHN P02519661; Lusitania, Coimbrae, IV/V/1879, MNHN P02519613; Catanhede, MNHN P03133347, MNHN P03133349; Venda do Pinheiro, VI/1881, Torres/Veddas, MNHN P02519612; Coimbre, 1886, Herb. M.A. de Coïnchy, MNHN P02519613; Catanhedea, Tocha, Cabo Mondego, 25/V/1972, G.G. Aymonin & M. Keraudren/Aymonin, MNHN P04274005).

Geum atlanticum

SPAIN. Albacete: Bogarza, 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; Riápier, 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; Riápier, 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, memorial 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. Vallee, GDAC 5419; Siles, Las Acebas, wet grasslands, VIII/1987, S. Rios, MUB 31540; Siles, Frenedillas, wet grasslands, 01/VII/1988, S. Rios, MUB 31541).

MOROCCO. Middle Atlas, Ain 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; Iguermelaz mountain, species flowering, also in fruiting near Imasinen, Atlanne rhiphaeo), cedar forests, 1700 m, VI/1927, Font Quer, GDA 38119; ibidem, BC 20201; cedar forests Iguermelaz mountain, species flowering, also in fruiting near Imasinen, Atlanne rhiphaeo, 01/VII/1938, det. Cuatrecasas, 01/V/1938), MA 00055992; cedar forest, Iguermelaz mountain, species flowering, also in fruiting near Imasinen, Atlanne rhiphaeo, det. Cuatrecasas, 01/V/1938), MA 00055993; between Ifrane and Azrou, Middle Atlas, V/1938, G. et L.H., MNHN P02799749, MNHN P02799750; cedar forest above 2000 m, near Ain/Kaala, Middle Atlas, 11/VII/1938, L. Faurel, det. R. Maire, MNHN P04151884; Bab-Roudia, 27/VI/1950, J. Muitoz Medina, GDA 38122).

ALGERIA. Tell Atlas, above Blida, Herb. Dr. Mierguez, MNHN P03362565; cedar forest at Teniet el Haad, Algiers province, 23/VII/1852, E. Cosson, MNHN P03362558; Djibril Cheliah, Monts Aurés, Constantine province, 11/VII/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 Djebl Tamgout, Djurdjura mountains, Dra-el-Mizan, Argiels province, 03/VII/1854, E. Cosson, MNHN P03362519, MNHN P03362555; grasslands at the summit of Gharrourban 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; Djebl Tababor, Little Kabylia, Constantine province, 21/VII/1861, E. Cosson, MNHN P03362548; forests between Sebdou and Ain-Ghoraba, 13/VI/1874, A. Worrian, MNHN P03362549; Adgar Amellal, Eastern Chabet-el-Akra, Constantine province, 01/VII/1880, E. Cosson, MNHN P03362551; north slope of Djebl Babor, Constantine province, 23/V/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[…] E. Cosson, 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.