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Taxonomic characterization, morphological variability, and geographic patterns of *Juniperus turbinata* Guss. in Algeria

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Abstract. A biometric study of cones, seeds, needles, and branchlets was conducted in 15 natural populations of *Juniperus turbinata* Guss. within its Algerian range. Each population was represented by 20-30 individuals. A total of 386 individuals were examined to evaluate inter- and intraspecific variation, and its geographic patterns, confirming the status of *J. turbinata* in Algerian populations. Maritime and mainland (Atlas Mountains) populations differed significantly. Cones in the seaside areas tended to be longer and more turbinate, with fewer seeds (mean 4.80) and leaves on the terminal 5-mm section of lateral branchlets (mean 27.87), compared to those from the Atlas, with 5.75 seeds and 29.00 leaves on average. The Aurès Mountain populations had more leaves than other scale-like junipers and other species of the Cupressaceae. Furthermore, maritime populations stood out for having the most turbinated cones among recorded *Juniperus phoenicea* s.l. populations. Costal populations were more related to those located on oriental Mediterranean shores, while Atlas Mountain populations seemed to be related to Moroccan Atlas ones. A negative gradient of leaf number from east to west was identified in the Atlas group, extending into Morocco. The distinct separation between the 2 geographic patterns supports the hypothesis of migration of *J. turbinata* along 2 routes and relaunches the proposal of possible varieties within the group.

Key words: Atlas Mountains, biometry, biogeography, *Juniperus turbinata*, Mediterranean, plant variation, principal component analysis

1. Introduction

Juniperus phoenicea sensu lato (s.l.) is a an aggregate species of Mediterranean evergreen shrubs or trees up to 8-12 m tall. Adult individuals have spherical to turbinated fleshy cones and scale-like leaves (Quézel & Santa 1962; Blanca *et al.* 2011; Adams 2014). *J. phoenicea* s.l. is an aggregation of taxa, of which *J. phoenicea* sensu stricto (s.s.) is confined to the eastern part of the Iberian Peninsula, south of France, and northwest Italy. In contrast, *J. turbinata* Guss. is spread out across the broader Mediterranean region (Amaral Franco 1986; Quézel & Médail 2003; Farjon 2005; El-Bana *et al.* 2010; Adams *et al.* 2013; Adams 2014; Salvà-Catarineu *et al.* 2021). Populations of *J. phoenicea* s.l. are made up of monoecious and dioecious individuals, and according to Mandin (2013), sexual plasticity in *J. phoenicea* can change from year to year, most likely due to the year's overall environmental conditions.

Since Linnaeus (1753) and Gussone (1844) first described *Juniperus phoenicea* L. and *J. turbinata*, respectively, the taxonomic status of the species aggregation in its Mediterranean range has undergone redefinitions, recombinations, and reevaluations. This complex has always been treated as a sympatric group, and comprises *J. phoenicea* subsp. *phoenicea* and *J. phoenicea* subsp. *turbinata* according to Adams (2014); however, *Juniperus canariensis* Guyot. has been treated as a variety within *J. turbinata* (Lebreton & Perez de Paz 2001).

The difference between the 2 taxa concerns primarily the phenology of pollen shedding, which happens in spring for *J. phoenicea* and in autumn for *J. turbinata* (Arista & Ortiz 1995). Mazur *et al.* (2003) found also a significant morphological distance between these 2 taxa, although earlier taxonomic achievements suggest that this is a distance between species rather than subspecies (Lebreton & Thivend 1981; Lebreton 1983; Lebreton & Rivera 1989). Genetic results converge in the same direction. After analysing DNA sequencing data (nrDNA and petN-psbM) of 19 *J. phoenicea* s.l. populations from its Mediterranean range, Adams *et al.* (2013) indicated an important difference in these DNA regions between the 2 taxa and classified *J. turbinata* at the species level. Furthermore, following a thorough review of available literature, Romo *et al.* (2019) reassessed the taxonomic status of *J. canariensis* at the species level due to significant morphological and genetic differences found among the 3 taxa.

Mazur *et al.* (2010, 2018) reported that intraspecific variation among *J. turbinata* populations is greater than that within *J. phoenicea* s.s., highlighting a high level of variation between European, Asian, and African populations. Using an Amplified Fragment Length Polymorphism (AFLP) marker, Sánchez-Gómez *et al.* (2018) evaluated the differentiation between *J. phoenicea* s.s., *J. turbinata*, and *J. canariensis*, finding that geographic patterns of variation are more pronounced among *J. turbinata* populations. This is most likely due to the extensive geographic range and the impact of climatic and geological alterations occurring since the Oligocene. This is consistent with the results obtained earlier by other authors, who also showed significant variation within the *J. turbinata* group, with a low level of variability in *J. phoenicea* s.s., stating that the range of *J. turbinata* is sufficiently large but fragmented and discontinuous (Quézel 1980; Browicz 1982; Boratyński *et al.* 2009). Several authors have analysed the essential oil chemical variability within the *J. turbinata* group around the Mediterranean (Adams *et al.* 2014; Rajčević *et al.* 2018) and in Algeria (Bekhechi *et al.* 2012). Three chemotypes were found, and several geographic patterns within the species were recorded. Adams (2013) mentioned a considerable variation in DNA sequencing within *J. turbinata*, with more divergent geographic patterns towards the Mediterranean edges. Considering the large geographic distance between western and eastern populations of *J. turbinata*, along with morphological, phytochemical, and genetic variation within the group, some geographic patterns of variation could be expected.

In Algeria, *J. turbinata* was classified in the flora of Quézel & Santa (1962) as *J. phoenicea* but Maire (1952) in the *Flora of North Africa* described several forms and varieties, so the existence of *J. phoenicea* s.s. was not excluded. Currently, this assumption is neglected, even though Pavon *et al.* (2021) mentioned that the existence of *J. phoenicea* s.s. is worth discovering based on field observations, especially when considering that a lot of taxonomic studies of *J. phoenicea* s.l. do not include the Algerian territory.

Therefore, the present study aims to provide a morphological characterization of *J. turbinata* within its Algerian range, which stands as one of the last remaining areas where taxonomic surveys of the species have not been exhaustive, providing a comprehensive understanding of its taxonomic position, morphological variability, and geographic patterns of variation.

2. Material and methods

2.1. Plant material

Plant material was collected from *J. turbinata* populations throughout its Algerian range, from west to east, and from the Mediterranean sandy coasts to the Saharan Atlas Mountains, passing through the Tell Atlas (Fig. 1). In total, 386 individuals from 15 natural populations were sampled, with 20-30 individuals representing each population (Table 1). Ten ripe cones and branchlets with needles were collected from the southern side of the shrub crowns (including the southwest and southeast).

2.2. Morphological measurements

For this study, the biometric measurement method employed by Mazur *et al.* (2003) and Marcysiak *et al.* (2007) was adopted (Table 2, Appendix 1). The measured features were: the percentage of specimens with 4 cone scale rows (CSR4), cone length (CL), cone width (CW), cone thickness (CT), cone scale number (CSN), seed number (SN), seed length (SL), seed width (SW), leaf number on the terminal 5-mm section of lateral branchlet (LN), and branchlet width (BW). For every feature, a mean of 5 measurements was calculated for each individual. A stereo microscope (Motic DM-143®) was used for the measurements. Additionally, several ratios were calculated: CL/CW, CL/CT, SL/SW, CT/SN, CT/SW, CL/CSN, and SN/CSN.

2.3. Data analyses

Normality tests were performed on the variables to assess the possibility of parametric statistical analyses. Therefore, the Shapiro-Wilk test was conducted within the variables of each population and among the variables of maritime and continental groups. The homoscedasticity of variances was verified using the Levene test. A logarithmic transformation towards normality was performed on the non-normally distributed data. After transformation, the variables that did not align with a Gaussian distribution were analysed, using non-parametric statistical tests (Dagnelie 1975).

Descriptive statistics (arithmetic mean, standard deviation, and variation coefficient) were counted for each population and for the continental and maritime

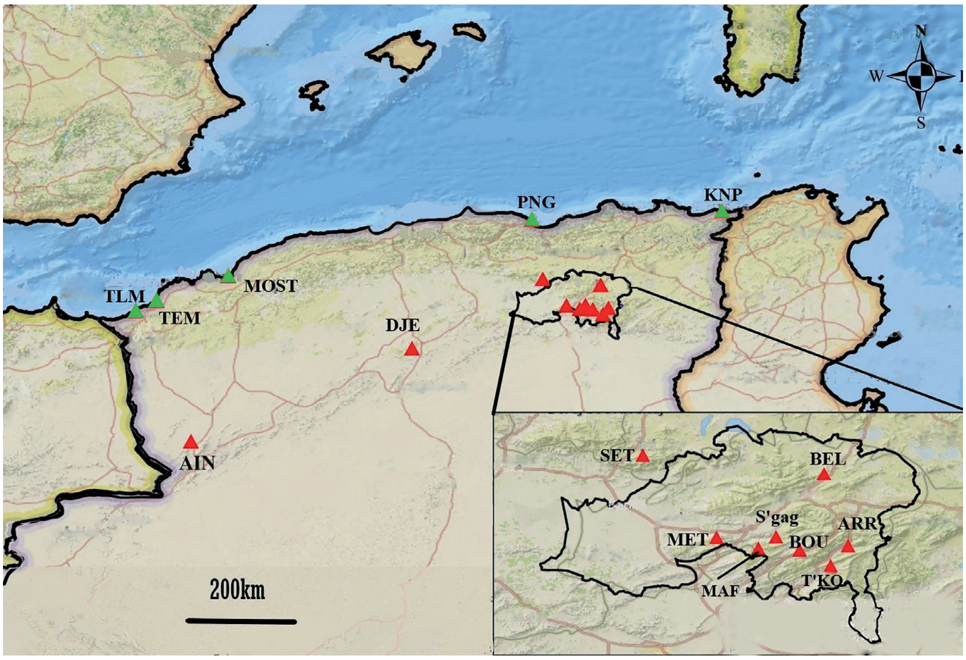

Fig. 1. Geographical distribution of the examined populations of *Juniperus turbinata* within its Algerian range – triangles in the Atlas Mountains (red) and maritime regions (green)

Table 1. Studied populations of *Juniperus turbinata* from Algeria

N	Acronym	Locality	Cluster	Number of individuals	Geographic coordinates	Bioclimatic zone	Altitude [m]
1	BEL	Belezma National Park	A	29	35.666'N 6.278'W	semiarid	1013
2	ARR	Aurès Mountains, Arris	A	30	35.275'N 6.408'W	semiarid	1293
3	T'KO	Aurès Mountains, T'kout	A	20	35.168'N 6.314'W	semiarid	1200
4	S'gag	Aurès Mountains, Beni Fedala, S'gag	A	20	35.323'N 6.018'W	semiarid	1080
5	MAF	Aurès Mountains, Mafaa	A	27	35.262'N 5.922'W	semiarid	1086
6	BOU	Aurès Mountains, Bouzina	A	25	35.253'N 6.146'W	semiarid	1410
7	MET	Batna, Ain Touta, Segana, Metlili	A	25	35.320'N 5.696'W	semiarid	1019
8	SET	Sètif, Djbel Boutaleb	A	27	35.766'N 5.296'W	semiarid	1243
9	DJE	Djelfa, Eastern Sen Elba	A	30	34.591'N 3.080'W	semiarid	1339
10	AIN	Ain Sefra, Haraza	A	23	33.017'N 0.667'W	semiarid	823
11	KNP	El Kala National Park	M	29	36.917'N 8.333'W	humid	10
12	PNG	Gouraya National Park	M	21	36.769'N 5.105'W	subhumid	10-100
13	TLM	Tlemcen, Trara Mountain, Honaine, forest El m'khaled	M	20	35.219'N 1.606'W	semiarid	110
14	TEM	Ain Temouchent, Ain Kihel	M	30	35.396'N 1.250'W	semiarid	65-74
15	MOST	Mostaganem, Estidia	M	30	35.817'N 0.037'W	semiarid	22

Explanations: A – Atlas Mountains, M – maritime (see Fig. 1). Bioclimatic zones based on ANAT (2004)

Table 2. Average values of morphological characters and results of their analysis using post hoc tests (Kruskal-Wallis and Tukey *T*-test), assessing how often the characters affect the variation between 15 populations of *Juniperus turbinata* at the significance level of $p \leq 0.05$. Population acronyms as in Table 1

Character	Acronym	AIN	ARR	BEL	BOU	DJE	KNP	MAF	MET	MOST	PNG	SET	S'gag	TEM	TLM	T'KO	Post hoc test
% of specimens with 4 cone scale rows	CSR4	92.1	80.0	93.8	93.6	93.3	96.6	76.3	70.4	93.3	95.1	84.4	90.0	93.3	92.0	93.0	37
Cone length [mm]	CL	9.71	9.94	9.30	8.29	9.02	10.63	9.13	8.79	10.50	9.02	10.46	9.39	9.59	9.02	8.46	50
Cone width [mm]	CW	9.31	9.73	9.30	8.73	8.44	9.78	9.13	9.47	9.66	8.15	10.33	9.30	8.09	8.50	8.77	47
Cone thickness [mm]	CT	8.87	9.26	8.66	8.34	7.94	9.22	8.66	9.08	9.05	7.71	9.88	8.74	7.55	7.91	8.31	47
Cone scale number	CSN	9.64	9.46	9.06	9.18	9.09	8.69	9.48	10.12	9.04	8.74	9.29	9.64	8.60	8.61	9.06	64
Seed number	SN	5.53	6.14	5.47	5.05	5.45	4.82	6.34	6.35	5.17	4.96	6.09	5.81	4.73	4.13	5.16	46
Seed length [mm]	SL	5.94	5.69	5.55	4.90	5.62	6.00	5.37	5.21	6.43	5.45	6.22	5.63	5.93	5.73	4.91	31
Seed width [mm]	SW	3.25	3.27	3.44	3.04	3.04	3.31	3.05	3.31	3.45	2.98	3.54	3.13	3.04	3.05	3.05	43
Leaf number on terminal 5-mm section of lateral branchlets	LN	25.58	30.46	28.72	30.45	26.25	26.12	29.27	30.95	29.55	28.02	29.26	29.26	28.03	27.54	29.97	45
Branchlet width [mm]	BW	0.87	0.82	0.87	0.84	0.88	0.77	0.87	0.85	0.85	0.73	0.86	0.85	0.78	0.78	0.89	36
Ratios	CL/CW	1.04	1.03	1.00	0.95	1.08	1.10	1.01	0.93	1.09	1.12	1.01	1.01	1.19	1.07	0.97	55
	CL/CT	1.10	1.08	1.08	1.00	1.14	1.19	1.06	0.97	1.18	1.19	1.06	1.08	1.27	1.15	1.02	62
	SL/SW	1.85	1.76	1.64	1.63	1.88	1.84	1.78	1.59	1.88	1.88	1.77	1.80	1.97	1.89	1.64	42
	CT/SN	1.67	1.59	1.66	1.80	1.55	2.03	1.43	1.49	1.83	1.64	1.68	1.57	1.72	2.06	1.70	40
	CT/SW	2.75	2.86	2.56	2.78	2.65	2.80	2.86	2.77	2.64	2.63	2.81	2.80	2.51	2.61	2.78	32
	CL/CSN	1.02	1.09	1.05	0.92	1.02	1.24	0.99	0.90	1.18	1.05	1.15	1.00	1.13	1.07	0.95	38
	SN/CSN	0.58	0.66	0.61	0.56	0.61	0.56	0.69	0.64	0.58	0.58	0.67	0.61	0.56	0.49	0.58	26

groups (Zar 2010). Spearman-Rank order and Pearson correlation coefficient among characters were verified to determine possible relations and to eliminate redundant ones (Dagnelie 1975). Analysis of variance (ANOVA) followed by post hoc tests (Tukey HSD and *t*-test) were conducted for normally distributed data, and the Kruskal–Wallis test was performed for non-normally distributed data to assess the significance of differences between features of different geographic regions. The independent samples *t*-test and Wilcoxon tests were performed (depending on the data distribution) to evaluate the difference between the maritime and Atlas Mountain groups (Zar 2010).

Principal component analysis (PCA) was conducted to reduce the dimensionality of the dataset, deduce potential geographic patterns of variability, and assess the impact of morphological characters on population variation and geographic patterns (Kassambara 2017a). Average values of the characteristics of maritime and Atlas Mountain populations were analysed using PCA along with reference data of *J. phoenicea* s.l. to deduce the taxonomic position of the Algerian populations (Mazur *et al.* 2016, 2018; Appendix 2). Hierarchical clustering on principal component analyses was conducted to summarize the results of discrimination between populations, identify population clustering groups, and delineate geographic patterns (Kassambara 2017b). Data analyses were performed with R 4.1.0 software.

3. Results

3.1. Variation and correlation

The Shapiro-Wilk test shows that only the percentage of specimens with 4 cone scale rows (CSR4) has a non-normal frequency distribution among all the tested populations. The frequency distribution of other characters varied between populations.

The ratio of seed number to cone scale number (SN/CSN) is the most heterogeneous variable, with variation coefficients higher than 27% in 6 populations. Seed number, with variation coefficients of 21-28%, was the most heterogeneous among the measured features. Almost all the other measured characters showed low to moderate variation coefficients. The features of cones (CL, CW, and CT) and cone shape (CL/CT) were the most homogenous (9-11%). The populations of S'gag, BEL, ARR, and AIN had the most homogenous variables, while the T'KO population had the most heterogeneous features. An average value of 17.37% was recorded for maritime populations, while for Atlas Mountain populations 16.88%. The average value of the entire Algerian group was 17.12%.

Most of the measured variables were correlated at $p < 0.01$ with some others (Table 3). The strongest positive correlation was found amid cone features (CL, CW, and CT): cone width to cone thickness and cone length ($r = 0.91$ and $r = 0.66$, respectively); cone length to cone thickness ($r = 0.63$); and seed length to cone length ($r = 0.68$). The same features were strongly correlated within the 2 groups, with significant improvement. Consequently, cone width (CW) was removed from the dimensional analyses because of its redundancy with cone thickness ($r = 0.91$, $p < 0.01$).

3.2. Intraspecific variation and morphological variability

Combining ANOVA and Kruskal-Wallis tests revealed that features of all 15 populations varied significantly at $p \leq 0.05$. Results of post hoc tests (the Tukey *T*-test and Kruskal-Wallis test) in Table 2 show that cone scale number (CSN) differed the most, followed by ratios describing the shape and length of cones (CL/CT, CL/CW, and CL, respectively). Populations of the maritime group differed from one another by an average of 5.2 (0-10) characters, and the Atlas Mountain populations by 5.7 (1-10). The 2 groups were distinguished from each other by an average count of 8.5 (1-14) characters. All populations differed in 7.1 characters on average (0-14) (Table 4). When the means of maritime and Atlas groups (Table 5) were compared, almost all features differed statistically at $p \leq 0.01$, except for SW.

The longest cones on average were recorded in populations KNP, MOST, and SET (10.63, 10.50, and 10.46 mm, respectively). Populations of the Aurès Mountains MAF, MET, S'gag, T'KO, BOU, and ARR have very high average values for leaf number (LN = 29.26-30.95; Table 2), while the most turbinated cones (average CL/CT = 1.27) were recorded in TEM, followed by PNG and TLM populations (1.19 and 1.15, respectively). Population SET had the thickest cones (average CT = 9.88) and the highest average seed length (SL = 6.22; Table 2). Maritime populations had longer cones, while in the Atlas Mountains, cones were wider and thicker, directly affecting their shape: in continental groups, they were more spherical (CL/CT = 1.06 ± 0.10), and in the seaside populations, they were more elongated (turbinated, 1.18 ± 0.13). Except for MOST, the number of seeds was lower within seaside populations (SN = 4.80 ± 1.30), compared to the mainland populations (SN = 5.75 ± 1.44). More leaves

Table 3. Coefficients of correlation among the 10 measured characters of *Juniperus turbinata*

	CSR4	CL	CW	CT	CSN	SN	SL	SW	LN
CSR4									
CL	0.018								
CW	0.110**	0.660**							
CT	0.162**	0.634**	0.913**						
CSN	0.504**	0.083**	0.155**	0.183**					
SN	0.245**	0.190**	0.405**	0.451**	0.248**				
SL	−0.013	0.688**	0.463**	0.420**	−0.053*	−0.017			
SW	−0.029	0.442**	0.521**	0.514**	0.026	0.023	0.405**		
LN	0.126**	−0.123**	0.027	0.035	0.067**	0.070**	−0.117**	0.022	
BW	0.034	0.007	0.064**	0.069**	0.082**	0.140**	0.003	0.069**	−0.063**

Explanations: character acronyms as in Table 2, * – significance level $p < 0.05$, ** – significance level $p < 0.01$)

Table 4. Number of characters differing significantly ($p \leq 0.05$) between *Juniperus turbinata* populations from the Algerian range, assessed using post hoc tests (Kruskal-Wallis and Tukey *T*-test). Shaded and darkly shaded cells indicate pairs differing in 6-9 and 10 or more characters, respectively

	AIN	ARR	BEL	BOU	DJE	KNP	MAF	MET	MOST	PNG	SET	S'gag	TEM	T'KO	TLM
AIN															
ARR	2														
BEL	3	4													
BOU	9	10	7												
DJE	4	8	6	8											
KNP	6	8	11	12	8										
MAF	6	3	4	8	7	12									
MET	8	6	8	7	10	11	3								
MOST	6	8	7	9	8	2	11	10							
PNG	8	10	7	9	2	6	9	13	7						
SET	3	1	8	9	9	10	7	9	5	13					
S'gag	1	1	2	4	2	9	1	3	8	7	5				
TEM	8	11	6	9	6	8	14	12	10	0	11	9			
T'KO	8	6	7	1	6	11	4	5	9	6	10	5	9		
TLM	7	10	10	10	3	5	10	13	9	2	10	7	3	8	

on the terminal 5-mm section of branchlets (LN) occurred within the continental group (LN = 29.00 vs. LN = 27.87; Table 5, Fig. 2).

3.3. Geographic patterns of variation

Principal component analysis (PCA) of the 15 populations showed that the first 2 principal components (PC1 and PC2) explained 72.72% of the total variation (Fig. 3A). The first component (PC1), which explained 46.31% of the variation, was highly positively correlated with seed and cone scale numbers (SN and CSN) and cone scale rows (CSR4), and negatively correlated with features describing the shape of cones and seeds (CL/CT and SL/SW) (Fig. 3B). The second component (PC2) was well correlated with features describing cones and

Table 5. Results of the analysis of morphological characters of cones, seeds, branchlets, and needles from the Algerian populations of *Juniperus turbinata* (maritime group vs. Atlas Mountain group)

	Maritime populations					Atlas Mountain populations					Significance:
Character	min	max	mean	SD	V	min	max	mean	SD	V	*p* of multivariate test*
CSR4 (%)	0	100	**94.1**			0	100	**95.9**			0.000
CL	6.73	13.55	**9.85**	1.26	12.80	6.06	12.55	**9.28**	1.16	12.46	0.000
CW	5.28	13.48	**8.90**	1.37	15.36	6.17	12.8	**9.26**	1.06	11.49	0.003
CT	5.05	12.11	**8.38**	1.36	16.22	5.74	12.6	**8.78**	1.06	12.11	0.000
CSN	6.00	12.00	**8.75**	1.24	14.14	6.00	15.0	**9.39**	1.64	17.45	0.000
SN	1.00	9.00	**4.80**	1.30	26.99	2.00	12.0	**5.75**	1.44	24.97	0.000
SL	3.30	8.55	**5.96**	0.75	12.62	3.10	8.06	**5.52**	0.75	13.52	0.000
SW	1.68	4.80	**3.19**	0.47	14.87	2.02	6.05	**3.22**	0.46	14.27	0.361
LN	16.00	40.0	**27.87**	4.01	14.41	18.0	42.0	**29.00**	4.01	13.84	0.001
BW	0.60	1.13	**0.79**	0.07	9.11	0.7	1.23	**0.86**	0.08	9.54	0.000
CL/CW	0.83	1.55	**1.12**	0.12	11.07	0.74	1.43	**1.00**	0.10	9.52	0.000
CL/CT	0.86	1.69	**1.19**	0.13	11.24	0.80	1.66	**1.06**	0.10	9.74	0.000
SL/SW	1.21	3.28	**1.88**	0.27	14.42	0.67	2.76	**1.74**	0.26	15.07	0.000
CT/SN	0.27	7.06	**1.85**	0.57	30.59	0.79	4.38	**1.61**	0.41	25.69	0.000
CT/SW	0.37	4.73	**2.64**	0.39	14.61	1.28	4.43	**2.76**	0.36	13.17	0.000
CL/CSN	0.69	1.92	**1.14**	0.19	16.32	0.48	1.64	**1.01**	0.19	19.23	0.000
SN/CSN	0.10	1.13	**0.55**	0.16	28.34	0.17	1.67	**0.62**	0.16	26.24	0.000

Explanations: V – variation coefficient, SD – standard deviation, * – Independent samples *t*-test for normally distributed data (Wilcoxon test for non-normal distributions), statistically significant at $p < 0.01$

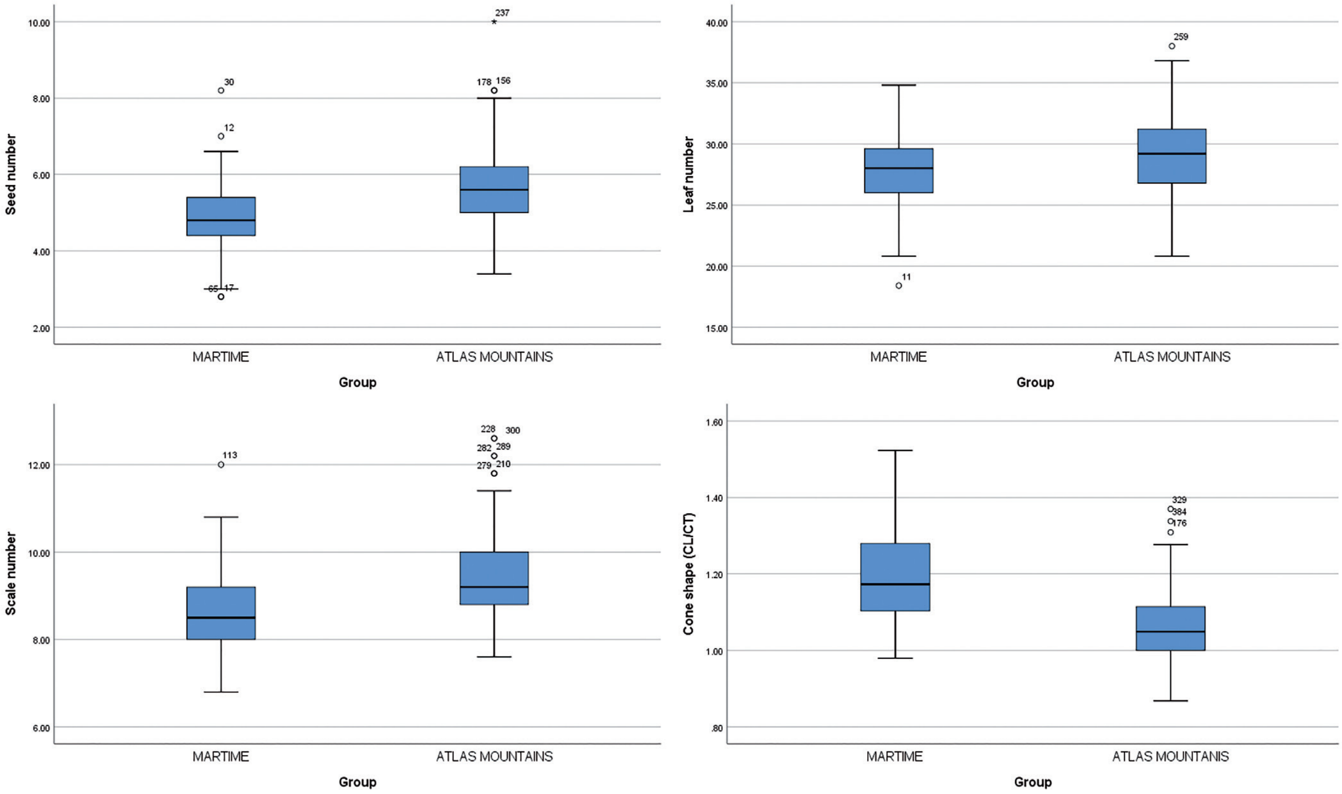

Fig. 2. Box-and-whiskers plot of features causing differentiation between maritime and Atlas Mountain populations of *Juniperus turbinata* from its Algerian range

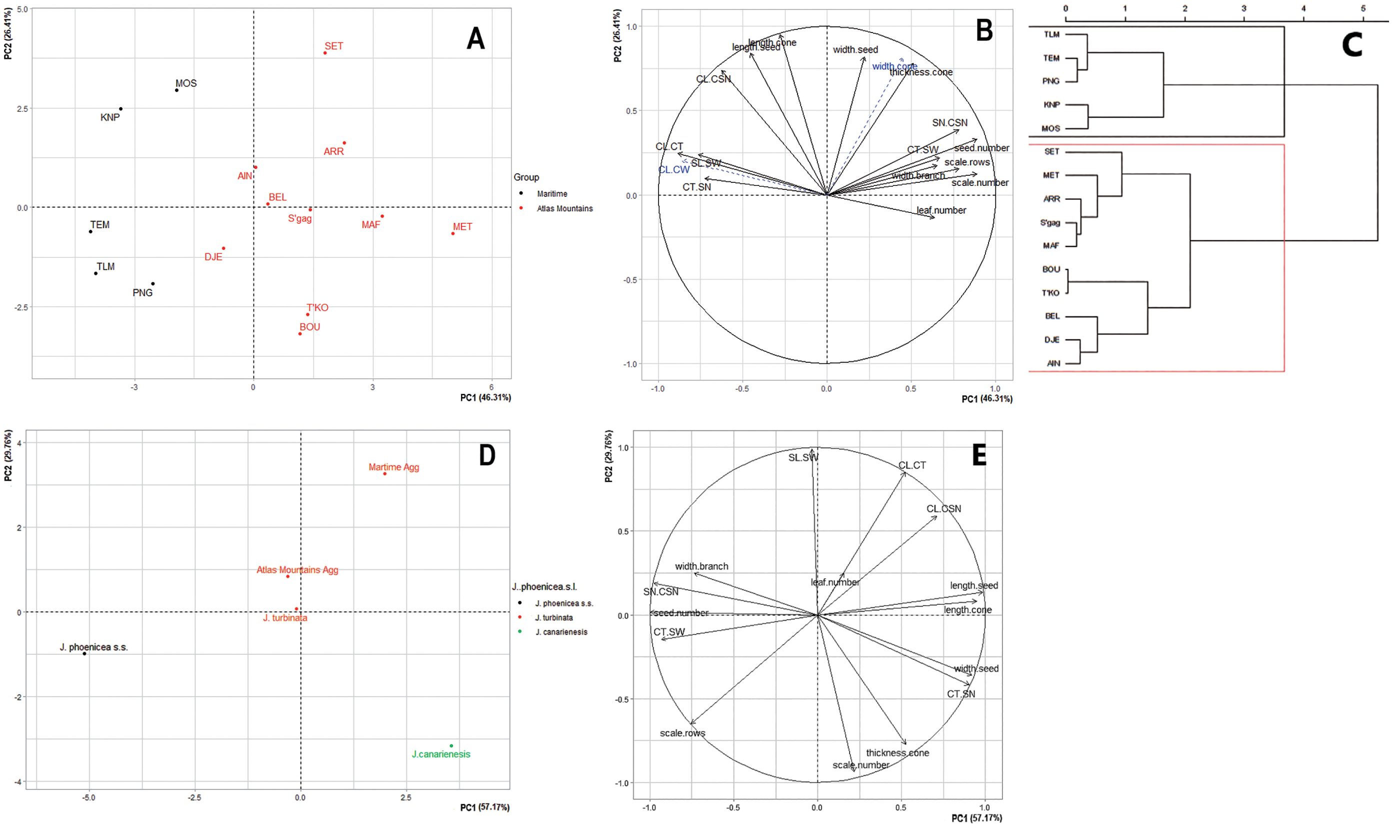

Fig. 3. Results of principal component analysis (PCA) based on cone, seed, branchlet, and needle characters; population and variable acronyms like in Tables 1 and 2. (A-C) PCA results for Algerian populations of *Juniperus turbinata* – maritime (black) and Atlas Mountains (red): (A) PCA factor map, (B) correlation circle, (C) hierarchical clustering analyses on PCA. (D-E) PCA results for Algerian geographic patterns of *J. turbinata* in the current study and published data of *J. phoenicea* s.l. (Mazur *et al.* 2016, 2018) presented in Appendix 2: (D) PCA factor map, (E) correlation circle, demonstrating the contributions of the analysed characters to variation within *J. phoenicea* s.l.

seeds (CL, SL, CW, and SW). The hierarchical clustering on principal component analyses of the 15 populations demonstrated the clear separation between the maritime and Atlas groups (Fig. 3C), which shows that all maritime populations were grouped in one cluster, and the Atlas populations were in another one.

Using PCA for comparison between the Algerian populations in this study and *J. phoenicea* s.l. investigated by Mazur *et al.* (2016, 2018) demonstrated that the first 2 components (PC1 and PC2) explained 86.93% of the total variation (Fig. 3D). PC1 explained 57.17% of the variation, with a highly positive correlation with seed features (SL and SW) and length of cones (CL), and a highly negative correlation with SN, SN/CSN, and CT/SW (Fig. 3E). The second axis (PC2), with a value of 29.76%, was highly positively correlated with features describing the shape of cones and seeds (CL/CT and SL/SW), and negatively correlated with CSN and CT.

4. Discussion

4.1. Variation and correlation characters

The variation coefficients for the Algerian populations resemble those reported by Mazur *et al.* (2018) for *J. phoenicea* s.s. and *J. turbinata* (17.4% and 17.8%, respectively). As in other studies conducted on conifer species and the family Cupressaceae, a strong correlation was found between cone and seed dimensions (Marcysiak *et al.* 2007; Douaihy *et al.* 2012; Boratyński *et al.* 2013; Sękiewicz *et al.* 2016).

4.2. Morphological variability

In the present study, the average values of cone features CL (9.47 mm) and CT (8.64 mm) are consistent with the general description of *J. phoenicea* s.l. (Mazur *et al.* 2003; Farjon 2005; Blanca *et al.* 2011; Adams 2014). However, our analysis of advanced descriptions shows that CL is similar to that of *J. turbinata* and CT is slightly smaller (Arista & Ortiz 1995; Mazur *et al.* 2016, 2018; Romo *et al.* 2019).

The mean value of SN (5.43) is similar to those of *J. turbinata* populations reported by Mazur *et al.* (2016) and Lebreton and Perez de Paz (2001), while *J. phoenicea* s.s. has 7-8. In this study, the clear difference in seed number (SN) between the coastline population (4.80 seeds) and the mainland population (5.75 seeds) was similarly reported by Lebreton & Perez de Paz (2001) on page 80, in the description of *J. turbinata.* However, the cited authors reported slightly more seeds per cone for the coastline populations SN (5), most likely due to the small number of sampled individuals. Notably, those authors reported 4 seeds per cone in the Oriental Mediterranean region (Crete and Cyprus) and 5 seeds per cone in the Occidental region (Atlas Mountains).

Leaf number on the terminal 5-mm section of lateral branchlets (LN) has been frequently employed as a diagnostic feature in the Cupressaceae, particularly for scale-like junipers (Mazur *et al.* 2004; Marcysiak *et al.* 2007; Douaihy *et al.* 2012; Sękiewicz *et al.* 2016; Mazur *et al.* 2018). The following average values were recorded: *Cupressus sempervirens* L. (LN = 22), *C. atlantica* Gaussen (LN = 24), *Juniperus excelsa* M. Bieb. (LN = 20-22), *J. thurifera* L. (LN = 20), *J. phoenicea* (LN = 26), and *J. turbinata* (LN = 24) (Mazur *et al.* 2004, 2018; Marcysiak *et al.* 2007; Douaihy *et al.* 2012; Sękiewicz *et al.* 2016). In our study, the average values of LN for Algerian populations ranged between 25.58 and 30.95, with a mean value of LN = 28.61. The coastline populations have an average value of LN = 27.87. This result is comparable to *J. canariensis*, which has an average value of LN = 27. Interestingly, Aurès Mountain populations (eastern Algerian Atlas) have an average of LN = 29-30, which is greater than for other *J. phoenicea* s.l. populations and for scale-like junipers and other studied species of the Cupressaceae. Western Algerian Atlas populations (AIN and DJE), with mean LN = 25.91, are more similar to those in the Moroccan part of the Atlas Mountains (Mazur *et al.* 2010; Sahib *et al.* 2022), which have fewer leaves (LN = 21-24). This validates the negative east-west gradient in leaf number among Atlas Mountain populations.

SL in this study reached an average of 5.67 mm. This result corresponds well with earlier *J. turbinata* data and is slightly higher than in *J. phoenicea* (Mazur *et al.* 2018), which confirms that the low number of seeds within *J. turbinata* is due to its longer seeds, as compared to *J. phoenicea*, which has more numerous but shorter seeds.

The ratio representing cone shape (CL/CT) in maritime populations notably exceeded that of other *J. phoenicea* s.l. populations, indicating that our analysis revealed the highest value for turbinate cones (1.18 ± 0.13). In comparison, *J. turbinata* exhibits a value of 1.06 ± 0.08, *J. phoenicea* s.s. has 0.96 ± 0.06, and *J. canariensis* records 0.98 ± 0.07 (Mazur *et al.* 2018).

The features causing the variation between the Algerian geographic patterns and the *J. phoenicea* s.l. populations are summarized in Fig. 3E. A strong relationship was demonstrated between the maritime group and the shape of cones and seeds (CL/CT, SL/SW), indicating that the maritime group features the most turbinated cones within *J. phoenicea* s.l. The Atlas Mountain populations have the highest mean leaf number. *J. phoenicea* s.s. differs from the other taxa of the group by having more seeds and scale rows and wider branchlets. *J. canariensis* differs by having the smallest seed number within the complex. However, its cones are the thickest, and its seeds are the largest (SL, SW).

4.3. Geographic patterns of variation

Fig. 3D summarizes the morphological comparison of the current study with the published data of Mazur *et al.* (2016, 2018) and the geographic patterns of variation. The PCA reveals that the Algerian populations aggregate with the *J. turbinata* group; furthermore, it confirms the segregation between the maritime and Atlas Mountain populations.

The phenotypic separation between maritime and Atlas populations aligns with phenolic compound chemotaxonomy reported by Lebreton & Perez de Paz (2001), who mentioned a similar distinction between the 2 groups due to prodelphinidin concentration. The cited authors proposed the names *J. turbinata* var. *occidentalis* for populations situated on the Mediterranean shores of northwest Africa and *J. turbinata* var. *montana* for Atlas Mountain populations. Results of volatile oil analyses converged in the same direction. Bekhechi *et al.* (2012) analysed 50 samples from *J. turbinata* in its Algerian range and found that almost all of the maritime specimens clustered in one group that differs by having a lower α-pinene content, as compared to the other cluster that contains almost all the Atlas Mountain samples. Adams *et al.* (2014) reported similar results. After analysing leaf essential oils for 16 populations of *J. turbinata* from its Mediterranean range, they found that the taxa had more of a mosaic geographic pattern than a continuous one and reported that the Algerian coastal populations were related to the populations of Italy, Greece, Sicily, Croatia, Turkey, and Madeira, which represent the Mediterranean pattern. However, the Algerian and the Moroccan Atlas form another cluster and are partly consistent with results of other authors, indicating that the Algerian coastal populations are related to central Mediterranean populations (Burban & Petit 2003; Terrab *et al.* 2008; Linares 2011; Sánchez-Gómez *et al.* 2018).

These findings corroborate those of Farjon (1998, 2005), who hypothesized that *J. turbinata* spread from Portugal to the Mediterranean coasts of North Africa, Corsica, and Crete. Mazur (2009) provided further information (Figs. 12 and 24), proposing that *J. turbinata* migrated from the Iberian Peninsula to Africa in along 2 routes. The first route of migration runs across Morocco and Algeria's Mediterranean coast on its way to Italy and Greece. The second route passes through Moroccan and Algerian parts of the Atlas Mountains on its way to the eastern Mediterranean area.

5. Conclusions

The results of the current study affirm the taxonomic position of *J. turbinata* within Algerian populations. The geographic patterns of variation, based on characters of cones, seeds, and needles, align well with chemotaxonomy. Morphological differences were identified between the maritime group and the Atlas Mountain group. These patterns are consistent with migratory directions proposed by several authors in the past, supporting the proposal for recognition of *Juniperus turbinata* var. *occidentalis* and *Juniperus turbinata* var. *montana*, with further accomplishments.

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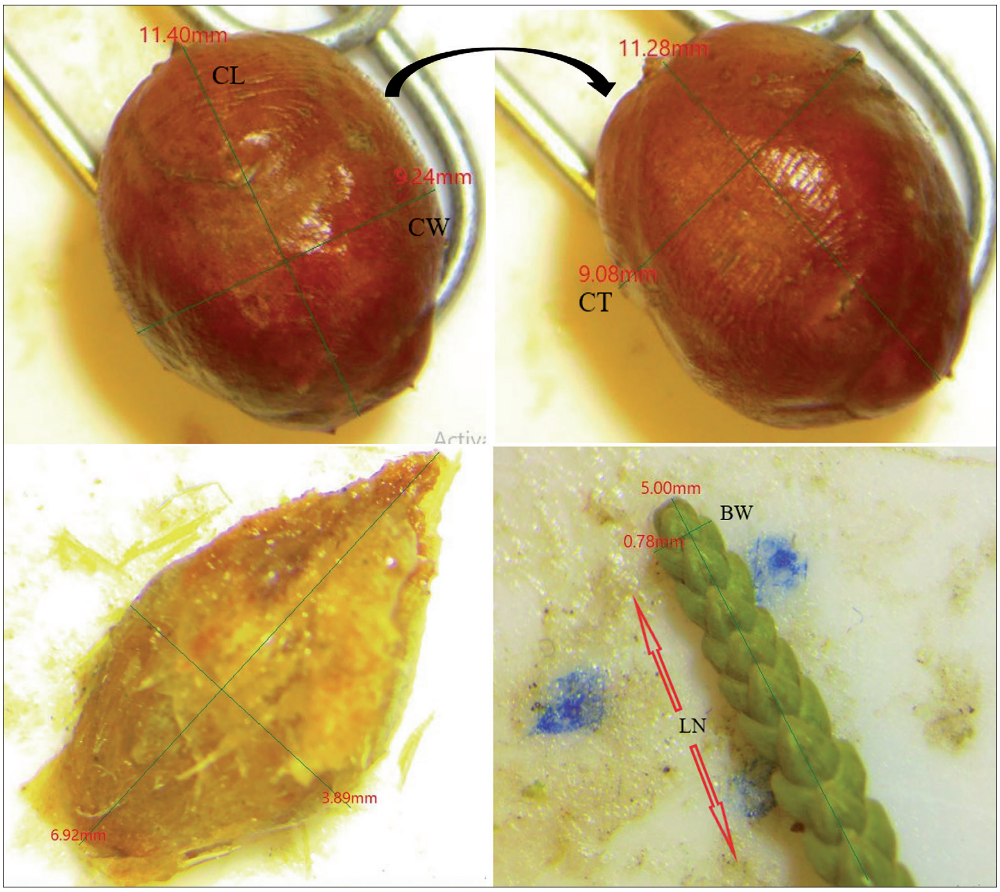
Appendices

Appendix 1. Measured characters of cones, seeds, branchlets, and needles of *Juniperus turbinata* from Algeria; for character descriptions, see Table 2 (CL and CW perpendicular, CT measured at a 90° angle)



Appendix 2. Average values of cone, seed, branchlet, and needle characters of *Juniperus phoenicea* s.l. * this study (Algeria), ** published data from the Mediterranean region (Mazur *et al.* 2016, 2018)

	CSR4	CL	CT	CSN	SN	SL	SW	LN	BW	CL/CT	SL/SW	CT/SN	CT/SW	CL/CSN	SN/CSN
Martime group*	4.12	9.85	8.35	8.75	4.80	5.95	3.19	27.87	0.79	1.18	1.87	1.74	2.62	1.13	0.55
Atlas group*	4.27	9.26	8.78	9.39	5.75	5.52	3.22	29.00	0.86	1.05	1.71	1.53	2.73	0.99	0.61
*J. phoenicea***	4.48	7.88	8.56	9.44	7.69	4.01	2.44	26.68	0.84	0.92	1.64	1.11	3.51	0.83	0.81
*J. turbinata***	4.32	9.85	9.62	9.15	5.79	5.34	3.10	24.26	0.81	1.02	1.72	1.66	3.10	1.08	0.63
*J. canarienesis***	4.30	10.09	10.32	10.26	4.10	6.10	4.04	27.16	0.76	0.98	1.51	2.52	2.55	0.98	0.40