In Roberti P. Adams (1939–2020) memoriam, peritus in re botanica qui monographias Juniperi (generis) edidit et opus systematicum in Juniperus phoenicea confecit, libenter dicata

Adam Boratyński*, Montserrat Salvà-Catarineu, Katarzyna Marcysiak, Małgorzata Mazur, Ángel Romo, Pietro Minissale, Kit Tan, Grzegorz Iszkuło, Radosław Witkowski, Andrzej Mazur

Biology and ecology of the *Juniperus phoenicea* – *J. turbinata* – *J. canariensis* complex I. Taxonomy, structure and distribution

Abstract: The *Juniperus phoenicea* complex consists of three taxa: *J. phoenicea* sensu stricto (s.s.), *J. turbinata*, and *J. canariensis*. A review of the literature on the biology of these taxa was conducted, focusing on taxonomy with paleo-data, structure, and geographical distribution to present current knowledge on these topics. Information on ecology, disease, utilization, and conservation will be presented in forthcoming parts of this monograph. Each of the three species included in the *J. phoenicea* complex is a monoecious or sometimes dioecious, evergreen gymnosperm with scale leaves when adult. The morphological differences between them are minor and mainly quantitative. This enables separation of taxa using a combination of traits. However, genetic features such as isozymes and nuclear microsatellites allow adequate differentiation from each other. *Juniperus phoenicea* s.s. occurs in the western part of the Mediterranean region, *J. turbinata* is circum-Mediterranean, while *J. canariensis* exists only on the Canary Islands, except Lanzarote and Fuerteventura, and on the Madeira archipelago. All species contain volatile oils which are used as traditional remedies for many various human and animal diseases, primarily in African and Asiatic countries. The published information for these topics is reviewed.

Keywords: Anatomy, biochemistry, geographical distribution, morphology, structure, taxonomy

Addresses: A. Boratyński, G. Iszkuło, Institute of Dendrology Polish Academy of Sciences, Kórnik, Poland; AB https://orcid.org/0000-0003-0678-4304, e-mail: borata@man.poznan.pl;
GI https://orcid.org/0000-0003-2067-729X, e-mail: iszkulo@man.poznan.pl;
M. Salvà-Catarineu, Department of Geography, Montalegre 6, Universitat de Barcelona, Spain, https://orcid.org/0000-0002-2815-1375, e-mail: salva@ub.edu.sp
K. Marcysiak, M. Mazur, Kazimierz Wielki University, Faculty of Biological Sciences, Bydgoszcz, Poland;
KM https://orcid.org/0000-0001-6162-6232, e-mail: marc@ukw.edu.pl
MM https://orcid.org/0000-0003-0043-3706, e-mail: mazur@ukw.edu.pl
Á. Romo, Botanical Institute of Spanish National Research Council, Barcelona, Spain; https://orcid.org/0000-0001-8135-8570, e-mail: angel.romo@gmail.com;
P. Minissale, Department of Biological, Geological and Environmental Sciences, University of Catania, Via A. Longo 19, 95125 Catania, Italy; https://orcid.org/0000-0002-4047-4169, e-mail: p.minissale@unict.it

K. Tan, Institute of Biology, University of Copenhagen, Denmark;
ⓘ https://orcid.org/0000-0001-8742-4612, e-mail: kitt@bio.ku.dk
R. Witkowski, A. Mazur, Department of Entomology and Forest Phytopathology,
University of Life Sciences, Poznań, Poland
RW ⓘ https://orcid.org/0000-0003-4630-765X, e-mail: radoslaw.witkowski@up.poznan.pl
AM ⓘ https://orcid.org/0000-0003-2877-8394, e-mail: andrzej.mazur@up.poznan.pl
* corresponding author

Taxonomy and origin

Palaeo-origin

The formation of the genus *Juniperus* L. and its divergence from other representatives of the family Cupressaceae took place in the Palaeocene, before c. 60 MA, as revealed using molecular analyses (Mao et al., 2019). *Juniperus phoenicea* L. diverged from the ancient junipers during the turn of Eocene to Oligocene, before 30–35 MA (Mao et al., 2010). It was speculated, that this species complex had originated from western and central Europe (Mao et al., 2010), despite there being very few fossils confirming this statement (Palamarev, 1989; Kvaček, 2002; Palamarev et al., 2005).

The representatives of the Cupressaceae and especially junipers evolved in arid environments (Willis & McElwain, 2002; Stockey et al., 2005; Postigo-Mijarra et al., 2009; Pound & Salzmann, 2017), and these environmental conditions make their macro-fossils very scarce and fragmentarily preserved. In addition, the pollen grains of different juniper species are similar and in palynological studies at generic level (Carrión, 2002; Carrión et al., 2001; Barrón et al., 2010), it is impossible to analyse any particular species migration, even in the Holocene, especially when several different species occur in the same region.

The regions of the Earth with dry environments expanded during the Oligocene, favouring plants with reduced water demands, and sclerophyllous formations in general (Axelrod, 1975; van Andel, 2002; Stockey et al., 2005). The Cupressaceae family evolved during that time, covering large areas in the northern hemisphere (Willis & McElwain, 2002). The geological and climatic events during the Neogene, surely influenced evolutionary processes in the Mediterranean region, and were a possible reason for further differentiation of the species which diverged earlier as *J. phoenicea* (Mao et al., 2010).

The juniper pollen in the Holocene sediments of Laguna de Vallesco in the island of Gran Canaria, concerns *J. canariensis* Guyot & Mathou in Guyot and/or *J. cedrus* Webb & Berthel., as there are no other species representing genus *Juniperus* (Rumeu et al., 2009a,b, 2011). Juniper species currently are extremely rare on Gran Canaria, but were dominant

trees before human colonization of the island (De Nascimento et al., 2016).

In south-eastern Sicily, along the gulf of Gela, the pollen diagrams obtained from core samples carried out at „Biviere di Gela" show a notable abundance of juniper pollen in the period 6900–6650 B.P. (Noti et al., 2009). Here, now with residual populations, only two species of juniper exist: *Juniperus macrocarpa* Sm. on the coastal dunes and *J. turbinata* Guss., from the coast up to 7–8 kilometers inland (Minissale & Sciandrello, 2013), which therefore in the past must have been the dominant species in terms of population size.

Taxonomy

Phoenician juniper - *Juniperus phoenicea* L. s.l. (*sensu lato*) represents the monophyletic section *Sabina* Spach of the monophyletic genus *Juniperus* L. (Farjon, 2005; Adams, 2014). This is the largest section within the genus including over 50 species and a number of lower rank taxa (Adams, 2014), divided into five different groups distinguished by plastid DNA (cpDNA) analysis. *Juniperus phoenicea* and *J. turbinata* form a separate group within the section (Mao et al., 2010).

Juniperus phoenicea was described by Linnaeus based on specimens collected in the vicinity of Montpellier in France (Linnaeus, 1753). At the same time, Linnaeus described *J. lycia*, also indicating France as the region of its occurrence ("Habitat in Gallia, Sibiria", Linnaeus, 1753), which is currently treated as a synonym of *J. phoenicea* (Farjon, 2005; Adams, 2014), or *J. turbinata* Guss. (POWO, 2023).

Phoenician juniper is variable, composed of several taxa of different rank (Farjon, 2005; Adams, 2014; Pavon et al., 2020; Boratyński & Boratyńska, 2021), occurring in the Mediterranean and Macaronesian regions, also entering the Saharo-Indian area (floristic regions after Takhtajan, 1986). The complex of *J. phoenicea* is distributed from the Arabian Peninsula (Browicz & Zieliński, 1982; Kerfoot & Lavranos, 1984) and Mount Sinai (Danin, 1983; El-Bana et al., 2010) in the east, along the coast of the Mediterranean Sea and on the Mediterranean islands, the Atlantic coast of north-west Africa and south-west Europe (Jalas & Suominen, 1973; Farjon & Filer, 2013), up to the Canary Islands and Madeira archipelagos

in the west (Mazur et al., 2016, 2018; Pavon et al., 2020; Salvà-Catarineu et al., 2021), covers a distance of about 6,500 km. These regions, during Oligocene, Miocene, Pliocene and Pleistocene underwent radical geological changes, with extinction of the Thetys Sea, formation of the Mediterranean Sea with its Messinian Salinity Crisis and Zanclean megaflood (Krijgsman et al., 1999; Goes et al., 2004; Ivanov et al., 2011; Fernández-Palacios et al., 2011; Pound & Salzmann, 2017; Garcia-Castellanos et al., 2020; Miller et al., 2020). The mentioned drastic changes resulted also in development of the Mediterranean-type climate (Jalut, et al., 1997, 2009; Zahos et al., 2001; Abrantes et al., 2012; Lionello, 2012; Lionello et al., 2012).

The geological and climatic changes could be a reason for periodic spatial isolation among local populations of *J. phoenicea* s.l. in particular regions, triggering processes leading to differences between them (Conord et al., 2012; Jiménez et al., 2017; Benítez-Benítez et al., 2018; Sánchez-Gómez et al., 2018). Currently observed diversity of *J. phoenicea* s.l. could additionally be deepened by complexity of the environmental conditions in different parts of the Mediterranean and Macaronesian regions (Zohary, 1973; Thompson, 2005, 2020; Fernández-Palacios et al., 2008; Otto et al., 2012). However, the morphological differences between the taxa are not very visible, despite the genetic differences. In case of *J. phoenicea* s.l., the results of studies on biochemical composition (Lebreton & Thivend, 1981; Lebreton & Rivera, 1989; Adams et al., 1996; Lebreton & Pérez de Paz, 2001; Adams et al., 2009), genetic structure (Meloni et al., 2006; Adams et al., 2002, 2010, 2013, 2014; Adams, 2014 and literature cited herein; Boratyński et al., 2009; Dzialuk et al., 2011; Jiménez et al., 2017; Sánchez-Gómez et al., 2018) and morphological (Lebreton & Rivera, 1989; Mazur et al., 2003, 2010, 2016, 2018) diversity and differentiation, allowed distinction between *J. phoenicea* s.s., *J. turbinata* and *J. canariensis*.

Juniperus turbinata Guss. was described in 1844 by Giovanni Gussone from Sicily (Ferrer-Gallego et al., 2017). It is treated most frequently as a subspecies of the Phoenician juniper, *J. phoenicea* subsp. *turbinata* (Guss.) Nyman (e.g. Amaral Franco, 1968, 1986), however, in many floras, chorological atlases and data bases it hasn't been distinguished up to the end of 20th century and even later (e.g. Coode & Cullen, 1965; Fennane et al., 1999; Achhal, 2002). In recent decades *J. turbinata* has been accepted at species rank (Adams, 2014; Mazur et al., 2016, 2018; Romo et al., 2019; Farjon, 2020; Salvà-Catarineu et al., 2021; POWO, 2023).

The Canarian specimens resembling *J. phoenicea*, described as *J. canariensis* Guyot (Guyot, 1942), were treated as a synonym of *J. phoenicea* (Amaral Franco,

1964, 1993; Hansen & Sunding, 1985, 1993). Afterward, this taxon was combined as *J. phoenicea* var. *canariensis* (Guyot) Gaussen (Gaussen, 1968; Adams et al., 2002), or as *J. turbinata* subsp. *canariensis* (Guyot in Mathou & Guyot) Rivas Mart., Wildpret & P. Pérez (Rivas-Martínez et al., 1993). The latter combination remains not validly published in accordance to the rules of the International Code of Nomenclature for algae, fungi and plants (Turland et al., 2018). Despite the name *J. turbinata* subsp. *canariensis* has been adopted in the literature concerning the Canary Islands (e.g. Otto et al., 2010, 2012), but sometimes not accepted and included into *J. phoenicea* subsp. *phoenicea* (Dobignard & Chatelain, 2010) or treated as a synonym of *J. phoenicea* (e.g. Farjon 2005, 2010) or *J. turbinata* (e.g. Adams, 2014).

The studies on the chemical and morphological variation of *J. phoenicea* complex (Lebreton & Thivend, 1981; Lebreton & Rivera, 1989), summarized by P. Lebreton and P.L. Pérez de Paz (2001), allow to distinguish two species, *J. phoenicea* L. and *J. turbinata* Guss. Within the latter, Lebreton and Pérez de Paz (2001) distinguished two subspecies, the typical *J. turbinata* subsp. *turbinata* and *J. turbinata* subsp. *canariensis* (Guyot) P. Lebreton & P. Pérez. *Juniperus turbinata* subsp. *turbinata* was divided into var. *orientalis* P.Lebreton & P.Pérez, var. *occidentalis* P.Lebreton & P.Pérez and chemovar. *montana* P.Lebreton & P.Pérez (Lebreton & Pérez de Paz, 2001). Adams et al. (2002), using random amplified polymorphic DNA analysis (RAPD), recognised four taxa within the complex of *J. phoenicea*: *J. phoenicea* var. *phoenicea*, *J. phoenicea* var. *canariensis*, *J. phoenicea* subsp. *eumediterranea* P.Lebreton & Thivend and *J. phoenicea* var. *turbinata*. Farjon (2005) distinguished only two taxa, namely *J. phoenicea* subsp. *phoenicea* and *J. phoenicea* subsp. *turbinata* (Guss.) Nyman. Later, Adams (2014) using molecular data recognised these two taxa at the species level: *J. phoenicea* s.s. and *J. turbinata*.

During the last decades, biochemical (Lebreton & Pérez de Paz, 2001), molecular (Adams et al., 2002; Boratyński et al., 2009; Dzialuk et al., 2011; Adams & Schwarzbach, 2013; Adams et al., 2013, 2014) and morphological studies (Mazur et al., 2010, 2016, 2018 and literature cited herein), support the specific level of *J. phoenicea* and *J. turbinata*. The molecular studies on the broad material covering almost the complete geographic range of the complex of *J. phoenicea* (Adams et al., 2013; Jiménez et al., 2017; Sánchez-Gómez et al., 2018), supported taxonomic rank of *J. phoenicea* and *J. turbinata*, but also indicated the separate position of *J. canariensis*. These results were confirmed in biometrical studies (Mazur et al. 2018), and finally three species, *J. phoenicea* s.s., *J. turbinata* Guss. and *J. canariensis* Guyot & Mathou were distinguished (Romo et al., 2019; Marcysiak, 2021; Mazur, 2021) and accepted (POWO, 2023).

Recently, Pavon et al. (2020) proposed the rank of subspecies for these three taxa due to differences in distinguishing them on herbarium materials and specimens in the field using morphological characteristics. However, considering the exact genetic differentiation found using isoenzymes (Boratyński et al., 2009), analyses of nrDNA and petN-PsbM cp region (Adams et al., 2010, 2013, 2014), amplified fragment length polymorphism (AFLP) (Sánchez-Gómez et al., 2018), genome size and chromosome number (Farhat et al., 2019, 2023), the status of species for *J. phoenicea* s.s., *J. turbinata* and *J. canariensis* should be conserved. The frequent cryptic species detected within several organisms when using molecular markers support this conception. The occurrence of the cryptic species has been detected also in another Mediterranean juniper, *J. oxycedrus* L. Within the latter taxon *J. deltoides* R.P.Adams was distinguished in the central and eastern Mediterranean region. It differs from *J. oxycedrus* L. s.s. mainly in terpene composition and random amplification of polymorphic DNA (RAPD), but only slightly in the leaf form (Adams, 2004; Adams et al., 2005). Morphological differences were found between these two species in the biometrical study on the cone and seed characteristics (Klimko et al., 2007; Vidaković et al., 2024), and also biochemical differences (Roma-Marzio et al., 2017).

Summarising, the taxa of the Phoenician juniper complex should rather be treated at species rank. We therefore consider it appropriate to maintain the status of separate species for *J. phoenicea* s.s., *J. turbinata* and *J. canariensis*, despite slight morphological differences and difficulties in classification of the herbarium specimens. Due to the relatively good recognition of their geographical ranges (see below), in determination should also be used origin of the specimens.

Among the three species, *J. turbinata* is a non-homogenous taxon. It contains three taxa of unclear position and without valid taxonomic description, treated lastly as varieties (Pavon et al., 2020). The populations occurring along the Atlantic coast of Europe and Africa are treated as 'var. *occidentalis*' (Lebreton & Perez de Paz, 2001). They slightly differ from other ones in the morphology of cones (Mazur et al., 2018) and in AFLP (Sánchez-Gómez et al., 2018), however, in broad geographic variation it is not clear and should be verified. The second, 'var. *orientalis*' (Lebreton & Perez de Paz, 2001) occurs in the eastern Mediterranean, and was believed to be distinguished from the previous one by the smaller number of seeds in cones (Pavon et al., 2020), this however, is not clear (Mazur et al., 2018) and also should be verified. The third is a 'chemovar. *montana*', distinguished from the Atlas and Aurès Mountains on the contents of prodelphinidin (Lebreton & Perez de Paz, 2001) and composition of the essential oils (e.g. Mansouri

et al., 2011; Bekhechi et al., 2012). The latter, however, are very variable and should be verified in a special study of a broader range of material.

The populations of the *J. phoenicea* complex indicate clear differences among *J. phoenicea*, *J. turbinata*, and *J. canariensis*. The study by Sánchez-Gómez et al. (2018) shows also differences between populations from the High Atlas, when compared to the Tell Atlas and Aurès Mountains populations, resembling differentiation of *Cedrus atlantica* (Endl.) Manetti ex Carrière (Terrab et al., 2008) and *J. thurifera* L. (Taib et al., 2020).

The key proposed below for the determination of three species within *J. phoenicea* complex has been prepared, supplemented and detailed in comparison to the key proposed by Romo et al. (2019) and Pavon et al. (2020), including data from Lebreton and Rivera (1989), Lebreton and Pérez de Paz (2001), Boratyński et al. (2009), and Mazur et al. (2010, 2016, 2018). Due to the quantitative nature of morphological features and a high level of variability as well as partial overlapping of their values between species, to determine correctly, several morphological features should be used.

Key

1   Cones (5)-6–9-(11) mm long, diameter (5.5)-7–11-(12) mm; diameter of cones usually greater than length; Cone with (2–3)-7–10-(13–16) seeds; Seed (2.5)-4-(5.5) mm long; pollination in early spring, usually in February-March; Leaves (scales) obtuse to subacute; Young twig straight (not flexible), with obtuse apex; Shrubs about 3 m tall, rarely higher; Most often on limestone (dolomite) slopes and/or cliffs; Western Mediterranean; Leaves do not contain prodelphinidin; high content of allele 1 Shdh 2 and allele 6 6-pgi 2 in the seeds.

Juniperus phoenicea

1* Cones (6)-8–12-(15) mm long, diameter (5)-7–11-(14) mm, diameter less than or equal to length; Cone usually with (2)-4–6-(11) seeds; Seed (3)-5–7-(9.5) mm long; Pollination in autumn, usually in October-November; Leaves (scales) acute to acuminate; Young twigs often elongated and flexible, with truncate apex; Polycormic trees up to 8–12 m tall, sometimes low dense shrubs (especially on coastal dunes); Most often on the substrates without calcium (sands and rocks along the coast) or in the basaltic rocks; Along the Mediterranean coast of Europe, Asia and Africa, and on the Atlantic coasts in southern Europe and northern Africa; inland Africa and Asia in the mountains, in the Canary Islands and Madeira; The leaves contain prodelphinidin;

Seeds without allele 1 Shdh 2 and allele 6 6-pgi 2 (broader be verified for Canarian specimens)

2

2 Cones with (3)-4–8-(9–12) seeds; Seed (3)-4-6-(7) mm long; Leaves (scales) without hard and thorny tips; Twig bark reddish; Around the Mediterranean Sea on maritime sands or rock in the mountains of Africa and Arabian Peninsula

J. turbinata

2* Cones with (1–2)-3–4-(5–6) seeds; Seed (3.5)-5–7.5-(9.5) mm long; Leaves (scales) with rather hard and prickly tips; Twig bark brown; Canary Islands and Madeira, on basaltic rock

J. canariensis

Synonyms

Due to several taxonomic combinations, there are many names, which refer to every of the three mentioned species. We present synonyms critically compiled from works of Farjon (2005), Adams (2014), Romo et al. (2019), Pavon et al. (2020) and POWO (2023).

J. phoenicea L. s.s.
Synonyms:
Cupressus tetragona Humb. & Bonpl. ex Carrière in Traité Gén. Conif., ed. 2: 33 (1867)
J. bacciformis Carrière in Traité Gén. Conif.: 56 (1855)
J. divaricata Carrière in Traité Gén. Conif., ed. 2: 51 (1867), pro syn.
J. formosa Carrière in Traité Gén. Conif., ed. 2: 51 (1867), pro syn.
J. langoldiana Gordon in Pinetum, Suppl.: 38 (1862)
J. lycia L. in Sp. Pl.: 1039 (1753), nom. utique rej. prop.
J. malacocarpa Carrière in Traité Gén. Conif., ed. 2: 50 (1867)
J. myosuros Sénécl. in Cat. Sénécl.: 35 (1854)
J. myurus Beissn. in Handb. Nadelholzk.: 117 (1891)
J. phoenicea var. *prostrata* Willk. in Suppl. Prodr. Fl. Hispan.: 4 (1893)
J. phoenicea var. *pyramidalis* Carrière in Traité Gén. Conif.: 51 (1855)
J. terminalis Salisb. in Prodr. Stirp. Chap. Allerton: 397 (1796), nom. superfl.
J. tetragona Moench in Methodus: 699 (1794), nom. superfl.
Sabina bacciformis (Carrière) Antoine in Cupress.-Gatt.: 69 (1857)
Sabina phoenicea (L.) Antoine in Cupress.-Gatt.: 42 (1857)

Sabinella phoenicea (L.) Nakai in Tyosen Sanrin Kaiho 165: 14 (1938)

Juniperus canariensis Guyot & Mathou in Guyot, Trav. Lab. Forest. Toulouse Tome 1. iii. Art. 20: 7 (1942)
Synonyms:
J. phoenicea subsp. *canariensis* (Guyot) Romo, Mazur, Salvà-Catarineu & Borat., Phytotaxa 406(1): 66 (2019).
   Comment: We disagree with the criteria employed by Pavon et al. (2020). They consider the nomenclatural combination: *J. phoenicea* subsp. *canariensis* (Guyot) Romo, Mazur, Salvà-Catarineu & Borat. as a '*nomen invalidum*' after the article 36 of the Code of Botanical Nomenclature (Turland et al., 2018). Well, although article 36.2 says: 'Since January 1, 1953, when in the same publication the same author simultaneously accepts two or more different names (called alternative names) based on the same type for the same taxon, none of them, being new, is validly published'. It also says that: 'This rule does not apply in cases where the same combination was used simultaneously in different ranks, both for infraspecific taxa and for genus subdivisions.' In the case proposed by us (Romo et al., 2019), it conforms to this exceptional rule.
J. phoenicea subsp. *canariensis* (Guyot) D.Pav., Véla & Médail, Ecol. Medit. 46: 93 (2020 publ. 2021), nomen superfluum
J. turbinata subsp. *canariensis* (Guyot & Mathou) Rivas Mart., Wildpret & P.Pérez in Itin. Geobot. 7: 511 (1993)
J. canariensis Knight [1850, Syn. Conif.: 13] (nomen nudum)

Juniperus turbinata Guss. in Fl. Sicul. Syn. 2(2): 634. (1883–1884)
Synonyms:
Cupressus devoniana Beissn. in Handb. Nadelholzk.: 116 (1891)
J. lycia L. in Sp. Pl.: 1039 (1753), nom. utique rej. prop.
J. oophora Kunze in Flora 29: 637 (1846)
J. phoenicea subsp. *eumediterranea* P.Lebreton & Thivend in Naturalia Monspel., Sér. Bot. 47: 8 (1981)
J. phoenicea var. *lobelii* Guss. in Pl. Rar.: 370 (1826)
J. phoenicea var. *lycia* (L.) St.-Lag. in A.Cariot, Étude Fl., éd. 8, 2: 762 (1889)
J. phoenicea var. *macrocarpa* St.-Lag. in A.Cariot, Étude Fl., éd. 8, 2: 762 (1889)
J. phoenicea var. *malacocarpa* Endl. in Syn. Conif.: 30 (1847)
J. phoenicea subsp. *turbinata* (Guss.) Nyman, Consp. Fl. Europ. 3: 676 (1881)
J. phoenicea var. *turbinata* (Guss.) Parl., in Candolle, Prodr. 16(2): 487 (1868)

J. phoenicea var. *turbinata* (Guss.) Parl., Fl. Ital. 4: 91 (1867)

J. phoenicea subsp. *turbinata* (Guss.) D.Pav., Véla & Médail in Ecol. Medit. 46: 93 (2020 publ. 2021)

J. phoenicea subsp. *turbinata* (Guss.) Arcangeli, Consp. Fl. Ital.: 637 (1882)

J. phoenicea f. *megalocarpa* Maire in Bull. Soc. Hist. Nat. Afrique N. 32: 224 (1941)

J. phoenicea f. *prostrata* Debreczy & I.Rácz in Stud. Bot. Hung. 29: 87 (1998 publ. 1999), nom. illeg.

J. phoenicea var. *sclerocarpa* Endl. in Syn. Conif.: 30 (1847)

J. phoenicea L. var. *galbulis mollibus* Ball in Journ. Linn. Soc. (Bot.), 16(94): 671 (1878)

Sabina lycia (L.) Antoine in Cupress.-Gatt.: 44 (1857)

J. lycia var. *tarraconensis* Sennen Diagn. Nouv.: 272 (1936)

Sabina turbinata (Guss.) Antoine, Cupress.-Gatt.: 41 (1857)

Among the synonyms listed, *J. lycia*, *J. terminalis* and *J. tetragona* (Adams, 2014; POWO, 2023), due to unknown or uncertain origin of the specimens on the basis of which they were described, may also be synonyms of *J. turbinata*. In any case, clarification of the synonymy of *J. phoenicea* s.l. requires special study.

The relations among populations of *J. turbinata* in the eastern part of the species geographic range require further studies, especially with inclusion of populations from Arabian Peninsula, which could elucidate their taxonomy. Additionally, in the south-easternmost regions of *J. turbinata* distribution in Saudi Arabia, they may co-occur with *J. procera* (Al-Yasi, 2019).

Hybrids

The specimens of hybrid origin with *J. phoenicea* were reported from Iberian Peninsula, from province of Castellon in Spain:
– *Juniperus ×palanciana* J.M.Aparicio & Uribe-Ech. was described as hybrid of *J. phoenicea* (s.s.) and *J. thurifera* (Aparicio Rojo & Uribe-Echebarría, 2006).
– *Juniperus ×herragudensis* J.M.Aparicio & Uribe-Ech. was described as a hybrid of *J. phoenicea* (s.s) and *J. sabina* L. (Aparicio Rojo & Uribe-Echebarría, 2008).

Geographical and altitudinal distribution

The three species of the *J. phoenicea* complex have only been properly distinguished during last decades. For that reason, the maps of distribution published before the end of the second millennium and even later concerned *J. phoenicea* s.l. are not reliable for distinguishing the distribution of the species of the complex (e.g. Amaral Franco, 1968; Jalas & Suominen, 1973; Browicz & Zieliński, 1982; Boratyński et al., 1992; Charco, 2001; Mazur et al. 2003; Debreczy & Racz, 2011; Caudullo & de Rigo, 2016; Dakhil et al., 2022; El-Barougy et al., 2023). Some maps, constructed on the GBIF data without verification, presented doubts in distribution in Turkey and Italy (eg. Wazen et al., 2020; Dakhil et al., 2022; El-Barougy et al., 2023). The geographic range descriptions indicated the West-Mediterranean geographic distribution of *J. phoenicea* s.s. starting from the end of 20th century (e.g. Amaral Franco, 1986, 1993; Arrigoni, 2006; Dobignard & Chatelain, 2010; Cabezudo, 2011; Dimopoulos et al., 2016; Bartolucci et al., 2018).

The maps of geographic ranges of *J. phoenicea* and *J. turbinata* (as *J. phoenicea* subsp. *phoenicea* and *J. phoenicea* subsp. *turbinata*) were published for the first time by Lebreton and Pérez de Paz (2001). These maps were repeated and supplemented by Adams et al. (2013), Mazur et al. (2016) and by Pavon et al. (2020). A schematic map of distribution of *J. turbinata* was published in Flora of Israel and adjacent areas (Danin & Fragman-Sapir, 2016). The maps of distribution of natural localities of *J. phoenicea*, *J. turbinata* and *J. canariensis* were published by Salvà Catarineu et al. (2021). The data used in the latter paper, after corrections and supplementations, are adopted here to present the distribution of the three taxa of *J. phoenicea* complex.

Juniperus phoenicea occurs in the western Mediterranean region (Fig. 1), with most of localities (retrieved from literature, herbaria, authors' field notes and also from GBIF), in the Iberian Peninsula and southern France, with restricted area of distribution in northwestern Italy (Bolòs & Vigo, 1984; Mazur et al., 2016). Occurrences of *J. phoenicea* were also reported from the Sierra Tramuntana in Mallorca (L. Sáez Gonyalons, after Pavon et al., 2020), from Monte Albo in Sardinia (G. Bacchetta, after Pavon et al., 2020) and from Cabo de Espichel in Portugal, where on the calcareous cliffs among *J. turbinata* were detected single specimens morphologically resembling *J. phoenicea* (Mazur et al., 2018: Fig. 1; Salvà-Catarineu et al., 2021: Fig. 1). Suggestion on the occurrence of *J. phoenicea* in the mountains of northern Africa (Pavon et al., 2020), needs verification.

In the core area of distribution in eastern Spain and southern France, *J. phoenicea* occurs inland, mainly on limestone rock or on the substrata developed from the calcium-containing soil bedrock. In the Iberian Peninsula, its frequent and in some places common occurrence was found in the eastern part of Central Iberian Mediterranean (Loidi, 2017), in the Betic and Valencian-Provençal provinces (biogeographic division of Iberian Peninsula after Rivas-Martínez et al.,
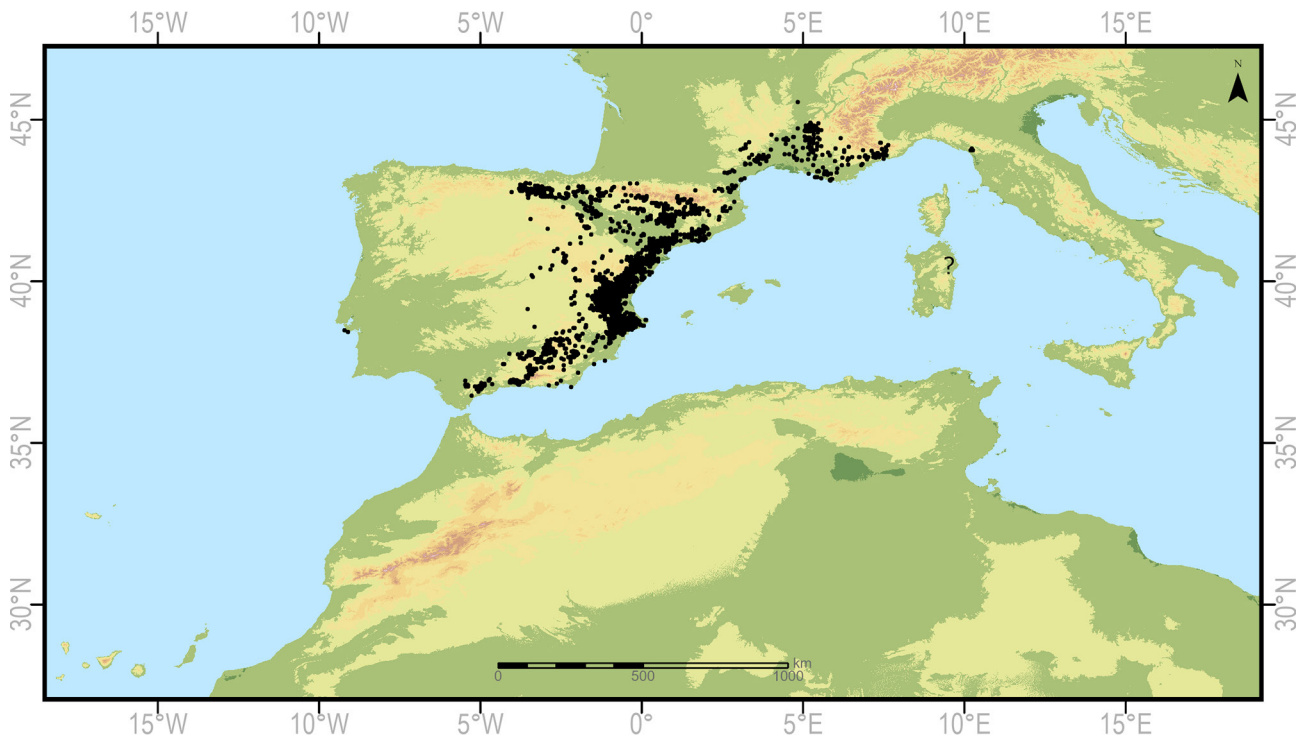
Fig. 1. Distribution of *Juniperus phoenicea* s.s. (after Salvà Catarineu et al., 2021: Fig. 1, supplemented)

2017). It grows locally also in the Murcia and Almeria Provinces (Salvà-Catarineu et al., 2021) and in Pyrenean Province, in the southern and eastern Pyrenees (Villar et al., 1997; Salvà Catarineu et al., 2021). In France, the species occurs in southeastern provinces of the country, mainly in the Prealpes and in the West and Maritime Alps, in Provence, Cévennes and Mount Ventoux and in Languedoc (Garraud, 2003; Tison et al., 2014). In Italy it was found in the Maritime Alps and in the Apuan Alps (Pignatti, 2017) and was reported from Monte Albo in Sardinia (Pinna et al., 2014), but lhe latter shall be verified.

Regions, where *J. phoenicea* occurs most frequently are recognized as refugial areas of the Tertiary floras. The distribution centres of *J. phoenicea* (Fig. 1) and localisation of particular refugia correspond well to each other (Médail & Diadema, 2009: Fig. 1). This might indicate the ancient occurrence of *J. phoenicea*, and a relic character of the species, which persisted within mountainous refugial areas due to local environmental conditions (Stewart et al., 2010; Nieto Feliner, 2011), which however, needs to be confirmed in palaeo remnants.

Juniperus phoenicea grows at elevations from 50–100 m to about 1,600–1,800 m (Fig. 2), with the highest number of localities between 400 and 1,200 m (Salvà-Catarineu et al., 2021). Its highest elevations were reported at 1,900 m and 1,970 m in the Sierra Nevada and Sierra Mágina (Spain), respectively.

The geographic range of *J. turbinata* covers the Mediterranean region and the mountains in northwestern Africa and western parts of the Arabian
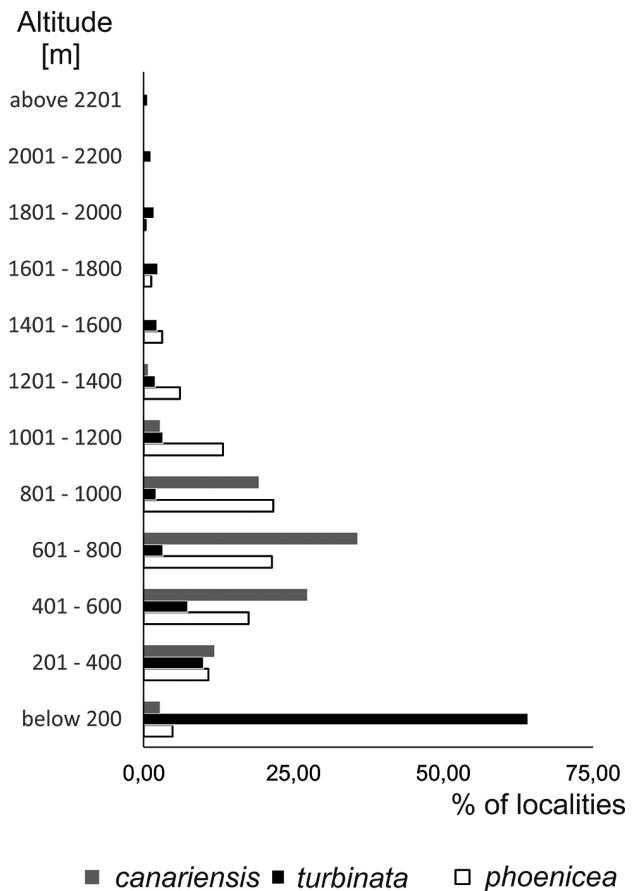

Fig. 2. Percentage of georeferenced localities of *Juniperus canariensis* (canariensis), *J. turbinata* (turbinata) and *J. phoenicea* s.s. (phoenicea) depending on elevation (after Salvà Catarineu et al., 2021: Fig. 2, supplemented)

Peninsula. The main centres of occurrence lie in the maritime regions of the central and eastern Mediterranean, and in the mountains of the High Atlas in Africa (Fig. 3). The occurrence of *J. turbinata* in Mediterranean countries has been described in detail by Pavon et al. (2020). In the western part of the European Mediterranean region, this species grows mostly along the shores, on maritime dunes or rocks, and as a rule does not cross an elevation of 100–200 m (Asensi et al., 2007; Salvà-Catarineu et al., 2021). *Juniperus turbinata* was also reported from the inland regions of the Iberian Peninsula. The most intriguing locality was recently described from the Extremadura (Vicente Orellana & Galán de Mera, 2019). The species has also relic localities in the southern Andalusian mountains, where it occurs on the sands of Pliocene Sea (Cabezudo et al., 2003; Pérez Latorre & Cabezudo, 2009; Cabezudo, 2011; Hidalgo et al., 2014; Pérez Latorre et al., 2014).

The absolute northern localities of *J. turbinata* were reported from latitude 44.2° in the Velebit mountains in Croatia (in sched., Steffan Fritz, GZU), and even 45.2° in the Krk islands (Nikolić, 2015). In Africa, the southernmost localities are south of Tizi n'Test in the High Atlas in Morocco, at about 30.8° (authors' field observations) and 30.7° in Jebel Siroua in the Anti Atlas Mountains (Quézel & Barbero, 1981), and even 29.8° at Aït-Adellah (Msanda et al., 2002). However, on the Arabian Peninsula, in the mountains along the Red Sea shores, it goes to latitude of 21° (Kerfoot & Lavranos, 1984; Chaudhary, 1999; Al Yasi, 2019). The latter is the southernmost locality of *J. turbinata* over its entire geographic range, and with the east longitude of about 40.35°, the easternmost one. More to

the south, the species was reported from vicinities of Abha, from latitude of about 18.5–19.0° (Samoylenko et al., 2008; Badahdah et al., 2015). This last would be the southernmost, and the easternmost locality of the species, crossing the east longitude of 42°, however, its origin shall be verified.

Along the shore of the Atlantic Ocean, *J. turbinata* occurs on coastal dunes and somewhat inland, colonizing the rocky hills above the cliffs, as for example on the Cabo de São Vincente in Portugal. On the Atlantic coastal dunes of the southern Europe, it attains as far to the north as about 40.8° at the vicinities of Quintas do Sul in Portugal (Sánchez-Gómez et al., 2018; Salvà-Catarineu et al., 2021), and to the south in Africa at about 31.5° at the environs de Essaouria in Morocco (Lebreton & Rivera, 1989; Salvà-Catarineu et al., 2021). The latter is also the westernmost locality of *J. turbinata* within its entire geographic range.

On the coasts of Mediterranean Europe, *J. turbinata* occurs on maritime sites from Iberian Peninsula to the Halkidiki Peninsula and easternmost locality at Agios Andreas near Kavala. On the continent, it colonised the sites close to the sea shore. Only in the southern Balkan Peninsula and in the larger islands it reaches higher elevations, but as a rule does not exceed 500–600 m, with the highest altitude at 920 m in Mount Ossa (Greece). Many of the European localities were described from the islands, even the very small, where *J. turbinata* grows both at sea shores and inland sites. It grows on the coasts of the west-Mediterranean large islands, as Corse and Sardinia (Paradis, 1993; Jeanmonod & Gamisans, 2013), but more frequently it colonizes the small islets around Sardinia (Bocchieri, 1992; Bocchieri & Giani, 1998).
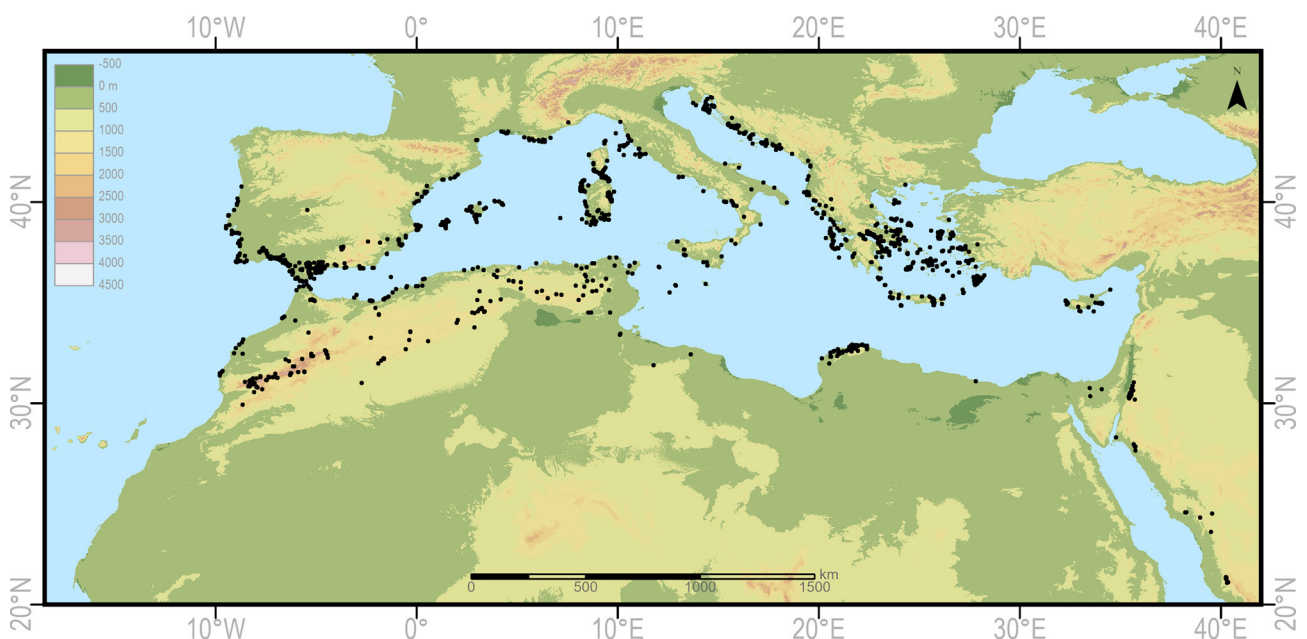

Fig. 3. Geographic distribution of *Juniperus turbinata* on the topographic background (after Salvà Catarineu et al., 2021: Fig. 1, supplemented)

As regards Sicily, the largest Mediterranean island, in many places where it has been reported in the past, *J. turbinata* has disappeared or is extremely rare (Minissale & Sciandrello, 2013), although the species was described from this island (Ferrer-Gallego et al., 2017). However, important populations have been discovered in recent years, especially in south-eastern Sicily on sandy soils a few kilometers from the sea (Minissale & Sciandrello, 2013). *Juniperus turbinata* is present also on the small islands of the Sicilian Channel, both on volcanic such as Pantelleria (Gianguzzi, 1999) and Linosa (Pietro Minissale personal observations) and on limestone such as Lampedusa (Bartolo et al., 1988), where in the past it was quite widespread. In the Maltese Islands it is very rare and probably introduced (Pavon et al., 2020), nevertheless, it is probable that in the past, although infrequent, it was present, as attested by the fossil pollen attributed to the genus *Juniperus* (Gambin et al., 2016) and woody macroremains (charcoals) ascribed to *J. phoenicea* s. l. (Fiorentino et al., 2013).

The localities of *J. turbinata* on the coast of the Mediterranean Sea from the Gibraltar on the west to the Scila-Haribda Straigts, and further along the Adriatic Sea up to the coast of northern Croatia, are few and scattered (Fig. 3). On the northern shores of the Mediterranen Sea, the species is more frequent on the small islets in the Adriatic Sea along the Croatian shore (Kovačić et al., 2001; Pandža, 2004; Pandža et al., 2011; Jasprica et al., 2018), but rather dispersed along the Albanian shores (Barina, 2017). More to the southeast, it occurs along the coast of Greece (Boratyński et al., 1992; Boratyński & Browicz, 1996; Kokmotos & Georgiadis, 2005) and on the islands on the Aegean Sea, the Dodecanese and Sporades (Boratyński et al., 1992; Christensen, 1997; Tsiourlis et al., 2016). It is mainly coastal, on dunes or on rocks, but also inland, as for example on Chios island or on the Marmaris Peninsula (Boratyński et al., 1987; Mazur et al., 2018). On the large islands, such as Evia, Crete and Rhodes, *J. turbinata* occurs along the sea-shore or only slightly inland (Boratyńska et al., 1985; Boratyński et al., 1988), but more frequently on small islets, as Gavdos and Chrysi islands south of Crete (Delipetrou et al., 2015). The localities of *J. turbinata* are also dispersed close to the seashores of Cyprus. It enters somewhat inland, but not far from the coasts, reaching an elevation of about 500–600 m (Anonym, 2009).

Up to now, *J. turbinata* has not been reported from the Mediterranean coasts between the Marmaris Peninsula and Cyprus. The latter island is the last centre of frequent occurrence of *J. turbinata* (orig. *J. phoenicea*) in the eastern Mediterranean basin (Meikle, 1977; Browicz & Zieliński, 1982). Further east the species is known from the Arabian Peninsula and Sinai Peninsula (Danin & Fragman-Sapir, 2016). In the mountainous regions of the Arabian Peninsula, *J. turbinata* is one of the important woody species, occurring from the biblical Edom on the north to the mountains along the Red Sea near Taif on the south (Chaudhary, 1999), at a latitude of about 21° N. More to the south, the species was reported from vicinities of Abha (see above). The data on the occurrence of *J. turbinata* (orig. *J. phoenicea*) in the vicinities of Palestinian Al Dawaimah in Israel (Ighbareyeh et al., 2022) seems doubtful or concern planted specimens (O. Fragman-Sapir, personal comm.).

In the Sinai Peninsula *J. turbinata* is confined to three dispersed and separate populations on Mts Yelleq, Halal and Maghra (e.g. El-Bana et al., 2010; Magdy et al., 2010; Farahat, 2020). The localities of *J. turbinata* on the Arabian and Sinai peninsulas have a relict character, possibly from the Last Glacial Period (Salvà-Catarineu et al., 2021: Fig. 6). The occurrence of the species in some places on the Arabian Peninsula has been reduced due to over-exploitation during the Bronze and Iron Ages, as the wood of juniper was used as a fuel in the copper and iron smelting in some regions of current Jordan and Saudi Arabia (Collenette, 1985; Engel & Frey, 1996). Similarly, a human activities caused the extinction of *J. turbinata* on the Negev during the late 6th and 5th millennia BC (Vardi et al., 2023).

The relict character has the locality of *J. turbinata* (orig. *J. phoenicea*) at Jebel Haggage in the Western Desert of Egypt (Long, 1955; Zohary, 1973: 507). The juniper was found there together with other thermophilic woody species, as *Olea europaea* L. var. *oleaster* (Hoffmanns. & Link) A.DC. (=*O. europaea* subsp. *europaea*) and *Ceratonia siliqua* L. (Zohary, 1973). The occurrence of *J. turbinata* between Nile delta and Cyrenaica was confirmed by Le Houérou (2004), without citing precise localities. The occurrence of *J. turbinata* (in the most cases reported as *J. phoenicea*) in Cyrenaica was reported several times (e.g. Brullo & Furnari, 1979, 1994; Sherif & El-Taife, 1986; El-Barasi et al., 2011; El-Barasi & Barrani, 2013; Elmahdy & Mohamed, 2016). The occurrence of *J. turbinata*, not *J. phoenicea* there was confirmed by Brullo and Guglielmo (2001). Further west, *J. turbinata* was reported from Tripolitania, but without precise locality (Sherif & El-Taife, 1986; Pavon et al., 2020: Fig. 2). The occurrence of the species in the Nafusa Mountains in western Tripolitania (Charco, 1999) is an extension and the easternmost position of the species populations from the Aurès Mountains.

In northwestern Africa, most of the stands of *J. turbinata* are in the High and Middle Atlas, and reach Anti Atlas in the south (Fig. 3). More to the east it grows on the coast of the Mediterranean Sea, and is scattered in the Tell Atlas, the Saharan Atlas and Aurès Mountains (Quézel & Médail, 2003). Inland of northwestern Africa, *J. turbinata* is a high mountain

species growing generally higher than 1,000–1,200 m (Sahib et al., 2022), frequently crossing an altitude of 2,000 m (Benabid, 2000; Charco, 2001) with maximum altitude of 2,410 m above sea level below Tizi n'Illisi along the road to Zouiat Ahanzal (Quézel & Barbero, 1981), and even 2,450 m (authors' personal observations).

The junipers rapidly colonize open areas, abandoned fields and pasture lands (Biondi, 1990; García et al., 2014; Cano-Ortiz et al., 2015; Garcia-Cervigon et al., 2017), and are called '(forest) foundation species' (Whitham et al., 2006). The rapid expansion of *J. turbinata* was described from Doñana National Park in SW Spain (García et al., 2014; Isla et al., 2022). On the other hand, the maritime occurrence of the species was strongly restricted in recent times due to summer resort and agriculture expansion (Mota et al., 1996; Salvà-Catarineu et al., 2021).

Juniperus canariensis occurs in the Canary Islands except Lanzarote and Fuerteventura, and on Madeira and Porto Santo (Fig. 4). The largest populations of the species are at present on El Hierro and La Gomera. On Gran Canaria, Tenerife and La Palma, *J. canariensis* distribution is strongly reduced, compared to the potential area of suitable habitats (Stierstorfer, 2005; von Gaisberg, 2005; Del Arco Aquilar & Rodríguez Delgado, 2006; Romo, 2018). The reduction of the area of distribution resulted from frequent utilization of its wood in the past and conversion of the juniper suitable sites into agricultural land. Only isolated individuals of *J. canariensis* occur scattered on Gran Canaria, where probably previously extensive populations of the species existed (González Artiles, 2007). On La Palma, the species is found in scattered localities to the windward in Mazo and Las Breñas and to the leeward in El Charco (Fernández-Palacios et al., 2008). In Tenerife, the well preserved woodland of *J. canariensis* grows in the Anaga massif (Afur

and Punta Anaga) at the northeastern part of the island, to the north in El Guincho, to the west in Montaña de Tejina, and in Ladera de Guímar and Arico to the southeast.

On El Hierro and on La Gomera are the most extensive woodlands dominated by *J. canariensis*, covering 1,142 and 2,820 ha, respectively (Del Arco Aquilar & Rodríguez Delgado, 2006). On El Hierro, in the Gulf area near Sabinosa, exists a humid forest of *J. canariensis*, and in Dehesa are the oldest individuals showing good regeneration. In the highest areas of El Crees and leeward of El Julan, the species at its highest altitude occurs in localities near the transition zone of *J. canariensis* and *Pinus canariensis* C.Sm. ex DC. forests (Montserrat Salvà-Catarineu & Ángel Romo personal observations). On La Gomera, the largest area of juniper forest is at the northern part of the island in the Hermigua highlands and in Tamargada-Vallehermoso-Epina (Montserrat Salvà-Catarineu & Ángel Romo personal observations). The woodlands of *J. canariensis* on Tenerife were exploited for fuel by native islanders (Tomé et al., 2022). Some populations of *J. canariensis* are currently protected and re-established thanks partly to the LIFE project (Otto et al., 2006). Similar action should also be provided for other islands.

Woodlands of *J. canariensis* can develop in flat areas with relatively deep soil, and in rocky areas with poor soil layers. In general, the oldest trees were found in steep areas difficult to access, this prevented them from being cut for timber. On the other hand, the Dehesa area (El Hierro) is an open area, with numerous juniper trees on relatively flat land.

Juniperus canariensis grows at different altitudes on windward and leeward slopes. To the windward, it is found between coastal scrub and laurel forest between 0 and 500 m, and to the leeward it grows between the coastal scrub and *Pinus canariensis* forest, between 300 and 900 m, however, it can reach 1100 m (Fig. 2). The highest locations are located on El Hierro. As a result of the different exposures we find a dry juniper forest on the leeward side and a humid juniper forest on the windward.

In the Madeira archipelago, scattered occurrences on Pico Branco and the island of Porto Santo were reported, but they have to be confirmed (Azevedo, 1914; Costa et al., 2004). These localities were from the coast and at 280 m on Roca de Novio.

Structure

Morphology

Growth form

Juniperus phoenicea s.l. is a single- or multi-stemmed, large shrub or small tree up to 8–12 m in height. Young specimens have conical crowns,
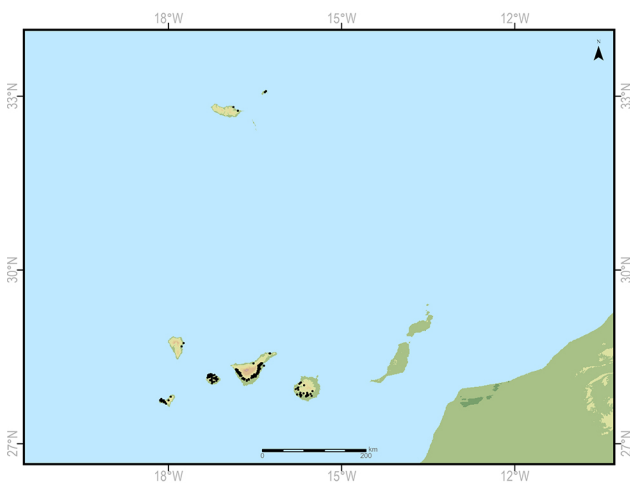
Fig. 4. Geographic distribution of *Juniperus canariensis* on the topographic background (after Salvà-Catarineu et al., 2021: Fig. 1, supplemented)

Fig. 5. *Juniperus phoenicea* habit: slopes below church Sant Cerni de Nagol, Sant Julià de Lòria, Andorra (a), rocky wall of Gorge de l'Ardèche, Pont du Saint-Esprit, France (b) stem cross section of dead individual fallen from the rocky wall of Gorge de l'Ardèche, Pont du Saint-Esprit, France with age determined by Jean Paul Mandin as c. 1200 years (c) (Photo by A. Boratyński 2010 (a) and 2017 (b and c)

which become rounded and irregular with age (Farjon, 2005; Adams, 2014). It is an evergreen acropetal branch-shedder (Orshan, 1989).

Typical *J. phoenicea* s.s. is a shrub up to 2 m or small tree 3–4 m tall, rarely attaining 6–8 m in height (Molero & Marfil, 2017). Old specimens on the cliffs have a spare habit, sometimes pendent on the rock walls (Mandin, 2005; Mathaux et al., 2016; Camarero & Ortega-Martínez, 2019). The age of the oldest *J. phoenicea* in Spain growing in such conditions was estimated at over 900 years (Camarero & Ortega-Martínez, 2019). The specimens growing on the rock walls of calcareous walls in Gorges du Verdon attain the age of 1,000 and more (Larson, 1999), and Gorge du Ardèche in France around 1,450 years (Fig. 5), and even more, depending on dating methodology (Mandin, 2005; Mathaux et al., 2016; Mathaux, 2017).

Juniperus turbinata is a shrub or tree to 10–12 m high, frequently with several trunks (Al-Ramamneh et al., 2012; Minissale & Sciandrello, 2013; Martinis et al., 2018; Pavon et al., 2020). The crowns of young specimens are conical (Fig. 6), however, sometimes the lowest branches grow and form several trunks around the main one, especially when not shaded by other trees (Fig. 6). The multi-stemmed form of specimens can also result from the injury to the main stem, which is frequent in the mountainous regions of the northern Africa (Charco, 1999, 2001; Boratyński & Boratyńska, 2021). The age of the oldest trees of *J. turbinata* in the relict locality of the species in the Sinai was determined as 430 years, with DBH to 24 cm and height to 7 m (Farahat, 2020) and even more than 600 years in the mountains of Jordan (Alananbeh et al., 2023). In less extreme environmental conditions, old trees of *J. turbinata* can become 200 years old (Martinis et al., 2018).

Juniperus canariensis is a tree c. 4–7 m tall (Fig. 7), rarely a dense shrub. It has one, sometimes 2–3 stems. The crowns of the young specimens are conical, but frequently become modified due to wind action, especially in exposed places (Otto et al., 2010, 2012; Romo & Salvà-Catarineu, 2013; Romo et al., 2014). Consequently, the old trees in such conditions have flag-shaped crowns and prostrate stems (Fig. 7). The age of the tree-like individual on
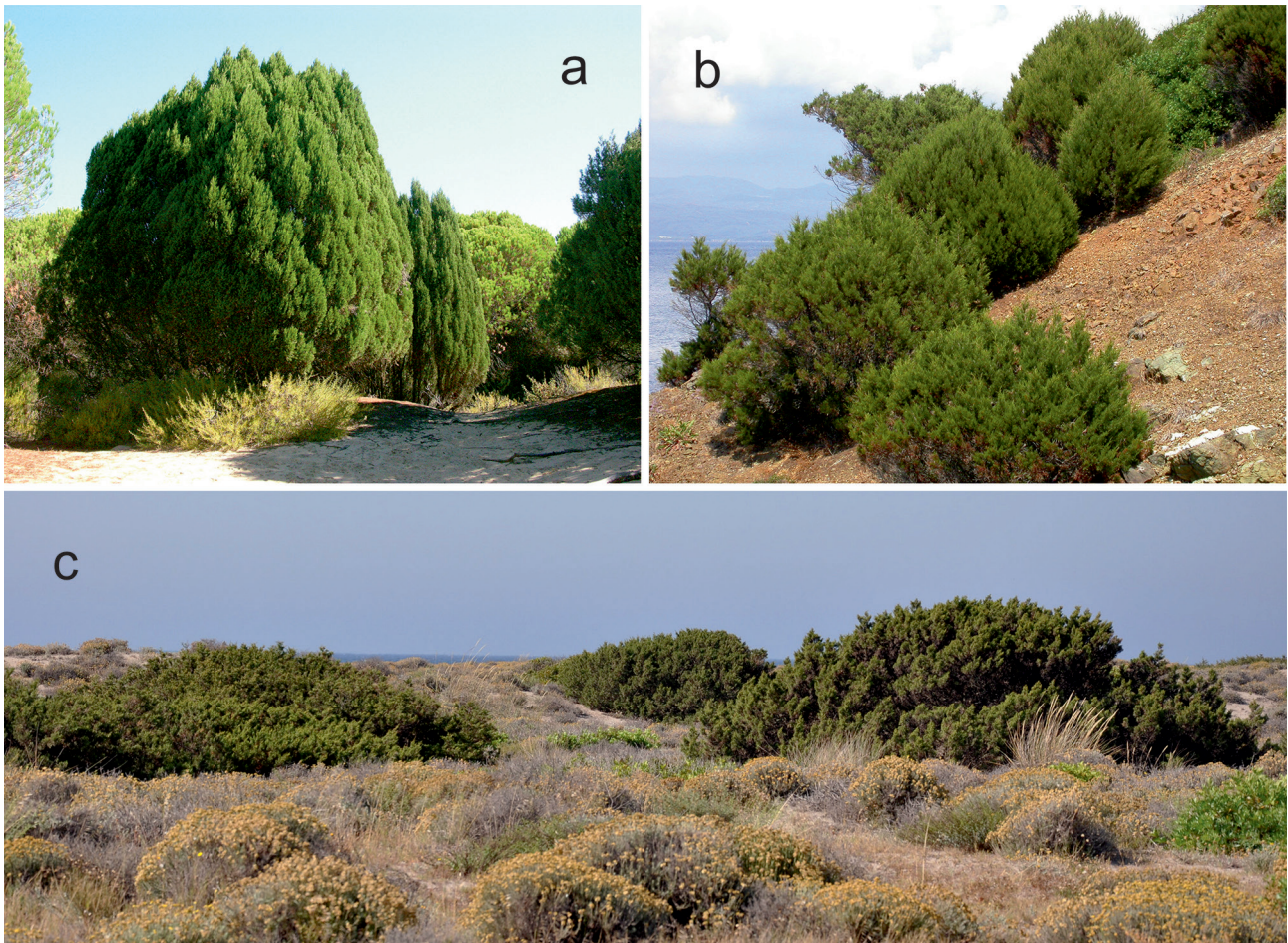

Fig. 6. *Juniperus turbinata* habit: conical crowns of specimens growing on the Punta Umbira, Cadiz, Spain (a) and on the slopes above the Gulf of Toroni Kassandras on Akros Agios Nicolaos, Kassandreia, Greece (b), prostrate individuals in Punta Entinas-Sabinar, Almeria, Spain (c) (Photo by A. Boratyński, 2008, 2004 and 2014, respectively)
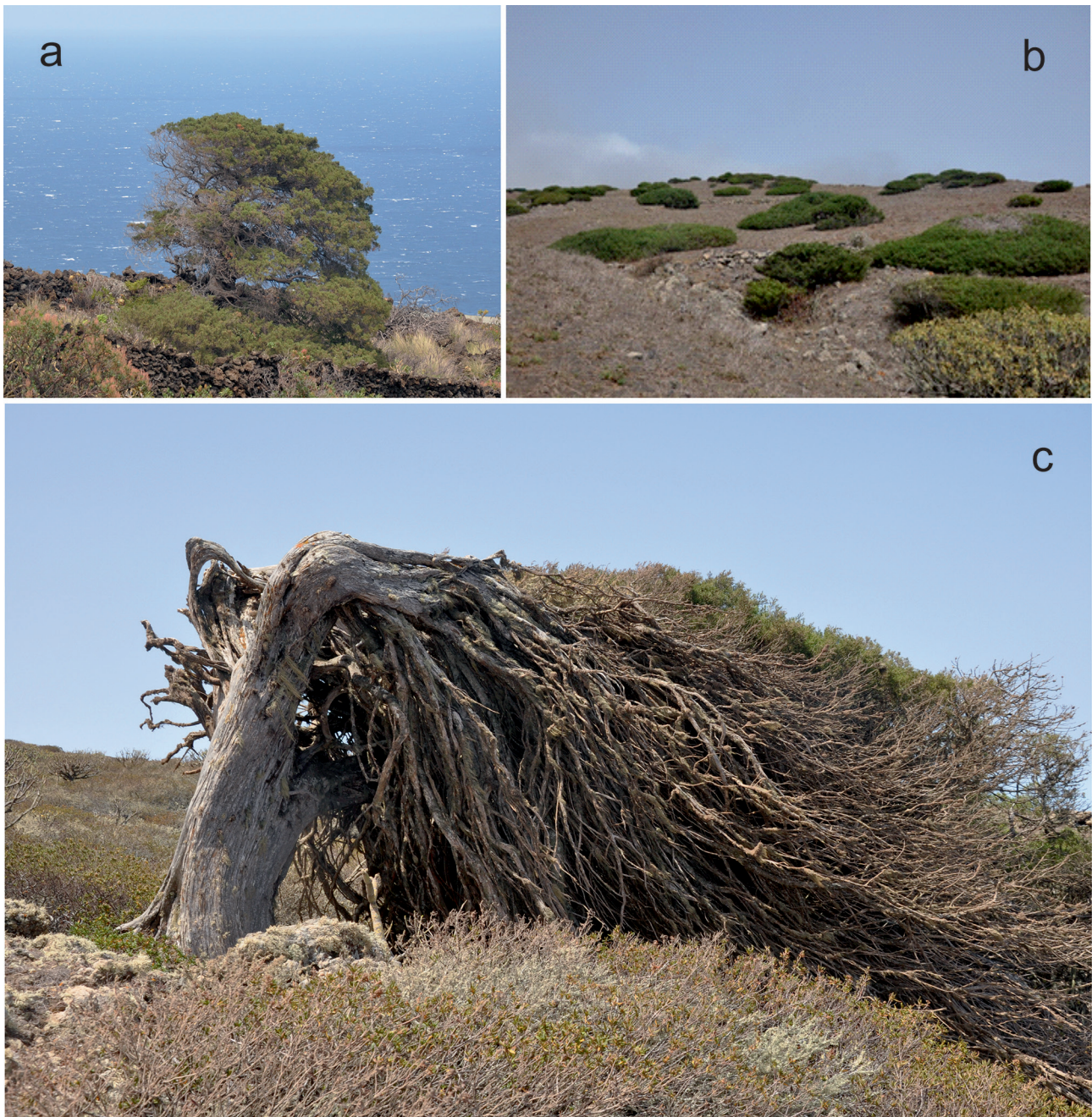
Fig. 7. *Juniperus canariensis* habit: broad crown of old specimen, Lodero, La Palma, Spain (a), prostrate young shrubs; every patch formed by one, two or more individuals (b), old tree with bent crown, Dehesa, El Hierro, Spain (c) (Photo by A. Boratyński, a – 2014, c – 2012)

El Hierro island was determined as c. 165–170 years (Montserrat Salvà-Catarineu and Ángel Romo personal observations).

Trunk

The trunk of *J. phoenicea* s.l. can reach up to 1 m in diameter at the base (Farjon, 2005). The bark on the trunk is greyish-brown, exfoliating in long, narrow strips (Farjon, 2005; Adams, 2014).

The stem of *J. phoenicea* s.s. is short and irregular in cross-section (Fig. 5b). Old specimen trunks frequently have only a small part of the stem living, with a prevalent dead section, without bark and cambium. Such trunks, however, can function even for centuries thanks to living narrow strip of cambium (Mandin, 2005; 2013; Mathaux, 2017). Consequently, the trunk cross-section is extremely irregular and for correct determination of the age, the section of the trunk is necessary. Despite, on the stem cross-section, there are frequent faults and/or partially missing yearly increments (=wedging rings), which are visible under the microscope only (Mathaux et al., 2016). This makes age estimations of *J. phoenicea* only approximate.

The stem of *J. turbinata* is more regular in cross-section than the stem of *J. phoenicea*, however, it is not circular as in conifers from the family Pinaceae. *Juniperus turbinata* normally has up to 4–5 stems, which form the specimens resembling rather 'large shrubs', not trees. In the extreme dry conditions of the mountains of Sinai, the stems are short, not exceeding 2 m (Farahat, 2020). The trunk diameter can attain 40 cm in the Cyrenaica (Ali & El Shatshat, 2015). The basal parts of trunks in the High Atlas can measure even 100–120 cm in circumference at ground level (authors' personal observations).

Juniperus canariensis is most frequently monocormic, with the stem very irregularly rounded in cross-section. In Anaga in Tenerife, the trunks of *J. canariensis* reach 25–28 cm DBH on average (Otto et al., 2010). In El Hierro, in places exposed to the wind, the trunks of old specimens are bent or even prostrate, dead for the most part and decorticated (Fig. 7).

Twigs and leaves

The twigs of *J. phoenicea* s.l. are terete, on young specimens upright, on older ones bent or even pendent. The leaf-bearing branchlets on the old specimens are short, bent or pendent and in tufts at the ends of main branches.

The young branchlets (last year's increment) of old specimens of *J. phoenicea* s.s are rather short, straight or only slightly bent, with obtuse apex and grey to brownish bark. The branchlets with leaves have an average diameter of 0.84 mm (Mazur et al., 2003, 2010, 2016, 2018). The lateral, one-year-old branchlets of *J. turbinata* are elongated and bent, reddish, truncate at apex, with an average diameter (with leaves) of 0.81 mm. Analogous branchlets of *J. canarinesis* are elongated and bent to pendent, brownish, with truncate apex and an average diameter of 0.76 mm (Mazur et al., 2018; Romo et al., 2019).

The leaves of one- or two-year-old seedlings, and leaves developed on heavily shaded twigs in the centres of tree crowns in the taxa of *J. phoenicea* complex are elongated, acicular and prickly, 5–14 mm long and 0.5–1 mm wide, usually ternate, sometimes decussate (Amaral Franco, 1964, 1968, 1984). The leaves of adult specimens are scale-like, rhombic and gibbous, appressed to the twigs, amphistomatic, decussate or in alternate whorls of three, with ovate to elongated glands on the protruding abaxial side with single resin cavity (Amaral Franco, 1964, 1968, 1984; Farjon, 2005). The leaf surface is smooth, light green and somewhat lustrous or greyish; the leaf margins are entire or only very slightly denticulate. The leaves on the vigorously growing, upright shoots are prickly and approximately two times longer than on the lateral branchlets of the last year (Farjon, 2005). The leaves are persistent, functioning for 3–4 years, then remain on the twigs as dead, dry and brown, sometimes for one or two years (as seen on herbarium material). The apical 5 mm part of the lateral branchlet is covered with 25–27 leaves (Mazur et al., 2018).

The leaves of typical *J. phoenicea* are gibbous and obtuse to subacute (Farjon, 2005), shorter than those of the other two species, on the main straight shoots around 2 mm in length (Romo et al., 2019). The leaves of *J. turbinata* are not so gibbous, acutish and more elongate than those of *J. phoenicea* s.s., on main shoots usually longer than 2 mm and attaining even 4 mm in length, acute to long acuminate (Romo et al., 2019) and prickly.

The leaves of *J. canariensis* are clearly acute with elongated, prickly apex (Rivas-Martínez et al., 1993); the leaves on the main shoots do not exceed 2 mm in length (Romo et al., 2019).

Root system

Juniperus phoenicea s.l., like other species of the genus *Juniperus* (Kutschera & Lichtenegger, 1997), has a long and wide-growing, but a shallow roots. *Juniperus phoenicea* s.s. growing in the rocky soils or in rock fissures, has roots penetrating fissures and crevices, where the humus or clay particles resulting from erosion are cumulated (Mandin, 2005; Mathaux et al., 2016). The specimens of *J. phoenicea* can survive in such rather harsh environments due to relatively high precipitation and symbiosis with mycorrhizal fungi (Sanguin et al., 2016). Despite these fragmentary data, the root system of *J. phoenicea* requires more particular studies.

Juniperus turbinata does not have a taproot on the dune system at Punta Umbria (Spain). It has shallow, horizontal roots, which are present mostly at a depth of 35–45 cm (Castillo et al., 2002; Baquedano & Castillo, 2007). The roots are prostrate on sandy grounds in Cyrenaica (Kabiel et al., 2016). Specimens of *J. turbinata* growing in the rock crevices of Dana nature reserve in Jordan, have long, deeply penetrating roots, reaching several meters below the tree (Danin & Fragman-Sapir, 2016). The branches of prostrate forms of *J. turbinata* are rooting, especially when covered with sand in maritime dunes (Debreczy & Rácz, 1999, also authors' personal observations from Sabaudia).

The root system of *J. canariensis* is also broad with horizontal roots dispersed shallowly (Salvà-Catarineu & Romo, personal observations).

Reproductive structures

Species from the *J. phoenicea* complex are wind-pollinated, usually monoecious, but in most populations functionally dioecious individuals can be found, characterized by a predominance of female or male strobili. The proportion of functionally female individuals in Spanish populations is 31–40%, and in

Fig. 8. Microstrobili (brown) and macrostrobili (green) of monoecious *Juniperus turbinata* tree, about 2-3 weeks after pollen shedding and pollination; Acate, Sicily, Italy (Photo by Pietro Minissale, 2010)

Moroccan populations it does not exceed 10%. For comparison, functionally male individuals produce less than 10 female cones per year, and females much more. In addition, the cones on functionally male specimens are smaller and contain fewer seeds than on monoecious or functionally female specimens (Jordano 1991, 1993; Pavón García et al., 2006), this topic, however, should be verified by further studies.

Microstrobili of specimens of *J. phoenicea* s.l. start to develop in late summer, shortly before macrostrobili. The microstrobili are ellipsoidal, to 4 mm long and 2 mm wide, yellowish-green or whitish-green, turning yellowish when mature, and are located at the ends of short shoots (Fig. 8). They are composed of 6–16 microsporophylls, decussate or less frequently ternate in alternate whorls. The shield-shaped, serrate microsporophylls produce 3 to 5 microsporangia, which are located close to the lower margin of the microsporophyll; spherical pollen grains are numerous (Lemoine Sébastian, 1967a; Arista et al., 1997; Farjon, 2005). After pollen shedding, the microstrobili became brownish and persist on the trees until the summer (Fig. 8).

The internal structure of macrostrobili is very variable compared to other species of the genus *Juniperus* (Lemoine Sébastian, 1967b). The most variable are the number of scale whorls, the number of ovules per seed scale, the decussate or ternate arrangement of scales, and the presence or absence of a distal ovule. As many as c. 30 different types scale arrangement and associated seeds have been found (Schulz et al., 2003). Some general patterns of the macrostrobilus structure have been described: (1) the basal fertile scales produce more ovules than the distal scale, (2) the symmetrical arrangement of the ovules around the cone axis, which may occur in several variants, e.g.: three ovules on the scale, including one in the middle; or there are only two ovules, while the

middle third has not developed or its development has stopped; there may also be only a middle ovule on the scale, (3) a single terminal ovule can be developed at the top of the cone axis (distal scale). The accidentally asymmetric arrangement of the ovules on the seed scales is a secondary phenomenon caused by the interruption of the development of the ovule after fertilization (Schulz et al., 2003). The ovules have a single integument, fused at the base with the nucellus (Lemoine Sébastian, 1967b; Schulz et al., 2003).

The macrostrobili (female cones) are greenish, sometime pinkish, 2 mm wide and 1.5 mm long (Fig. 8) composed of 4–9 bracts with 1–2–(3) ovules each (Arista et al., 1997). The particular study on the Phoenician juniper cones by Schulz et al. (2003) indicate that the cone is composed of 2–4 dimerous or trimerous whorls of fertile scales, sometimes with an additional ovule located distally to the uppermost scale, which prolongs the cone axis. Several infertile

Fig. 9. Three-year-old seedling of *J. canariensis*; Lodero, La Palma, Spain (Photo by A. Boratyński, 2014)

scales may be present below fertile ones. On average, 9 cone scales were found in the ripe cone of *J. phoenicea* and *J. turbinata* and 10 in *J. canariensis* (Mazur et al., 2010, 2016, 2018). Decussate scale arrangement prevailed in *J. turbinata* and *J. phoenicea* (88% and 75%, respectively), while ternate cones were more frequent in *J. canariensis* (56%) (Mazur et al., 2018).

Mature cones of *J. phoenicea* s.l. are spheroidal or ovoid, 5 to 15 mm in diameter, and their pulp is tender or fibrous. They are soft and juicy at first, becoming dry when mature (Lemoine-Sébastian, 1967b; Eliçin, 1977; Arista et al., 1997; Farjon, 2005; Mazur et al., 2018; Sahib et al., 2022). The average fresh weight of a single cone is 0.32 g, and the dry weight is 0.15 g (Jordano 1993). A single cone contains usually 3 to 9, relatively small, triangular or flattened seeds (Farjon, 2005; Jordano, 1993; Arista et al., 1997; Schulz et al., 2003, Mazur et al., 2018).

Juniperus phoenicea s.s. cones are brown, red or copper-red, spheroidal, often broader than long, 5–11 mm long and 5.5–12 mm in diameter, with 2–16 seeds, 2.5–5.5 mm long. Cones of the *J. turbinata* and *J. canariensis* are dark red to brown, ovoid to globose. *Juniperus turbinata* cones are 5.5–15 mm long and 5.5–15 mm in diameter, with 3–12 seeds, 3–7 mm long (Karagiannakidou, 1996; Mazur et al., 2010, 2016; Sahib et al., 2022). The cones of *J. canariensis* are 6.4–15 mm long, and contain 1–9 seeds, 3.5–9.5 mm long (Mazur et al., 2018).

Seedling

The seedlings of taxa of *J. phoenicea* complex have two cotyledons. The juvenile leaves in seedlings are in whorls of three, decurrent, epistomatic, pungent, with the acicular part 8–10 mm long and 1 mm wide (Farjon, 2005). Acicular leaves are retained in two to three year old seedlings (Fig. 9)

Anatomy

Developmental remarks

As far as we know, studies on juniper anatomy are limited, except for wood, concerning also species of *J. phoenicea* complex (Esau, 1977; Heynowicz, 2002; Evert & Eichhorn, 2006; Cebrat, 2007). A review was presented in a recent publication on *J. drupacea* Labill. (Boratyński et al., 2023).

Leaf anatomy

The leaf cross-section of *J. turbinata* (orig. *J. phoenicea*) was presented by Rossi et al. (2001: Fig. 4B1). The thick layer of epicuticular waxes form papillae on the outer walls of adaxial cuticle. The thick cuticle is composed of one layer irregular, thick-walled cells, below them 10 μm thick layer of hypodermis sclerenchymatic cells with thick walls and narrow lumen (Rotondi et al., 2003). The hypodermis layer of adaxial leaf surface is interrupted by stomata, which are confined in groves (Rossi et al., 2001). The stomata of abaxial epidermis are invisible, hidden in the pits, and covered with cuticular papillae. The palisade mesophyll, formed at the abaxial surface of the leaf, is plicate. The spongy mesophyll is composed of loosely arranged, irregular cells of different lumina and surrounded by intercellular air spaces, which fill about 30%. The vascular bundle is centrally located and surrounded with transfusion tissue. The centrally located resinous ducts are surrounded by mesophyll (Rossi et al., 2001). Similar data have not been presented for *J. phoenicea* nor for *J. canariensis*.

Stem

On the twig and/or stem cross-section of *J. phoenicea* s.l., the bark, wood and pith are easily distinguished. The brownish heartwood is clearly visible in the central part of stem, surrounded by lighter, yellowish sapwood. The bark of *J. turbinata* (orig. *J. phoenicea*) in Cyprus consists of groups of sieve cells and collapsed sieve cells, and sclerenchyma cells in phloem and in cortex. The fibres form tangential lines in phloem and are scattered or irregularly dispersed in cortex. The phellem cells are homogeneous, layered (Crivellaro & Schweingruber, 2013).

The pith shape in *J. turbinata* twig cross-section is polygonal. It consists of parenchyma, with some number of thick-walled parenchyma cells. The pits are present in transverse and longitudinal cell walls (Crivellaro & Schweingruber, 2013).

On Strofades Island (Greece), the yearly increment of *J. turbinata* stem during the first four decades of growth is 0.8–1.4 mm, in older specimens generally lower, down to 0.6–0.7 mm in individuals 70–80 years old (Martinis et al., 2018: Fig. 2). Individuals older than 120–130 years had rotten heartwood (Martinis et al., 2018).

Wood structure

The wood density of *J. phoenicea* s.l. in fresh state reaches 1.16 g/cm³, in dry state 0.80 g/cm³ (Engel & Frey, 1996). Wood does not contain resin canals, but the heartwood is resinous, which protects against insects and fungi (Danin, 1983), and colours the wood a reddish brown (Eliçin, 1977).

The wood of *J. phoenicea* s.s. from cliffs is hard and heavy, with density higher than 1g/cm³. The yearly increment includes tracheids with thin walls and large lights forming early wood. The late wood is composed of tracheids with thick walls and narrow lumen in the wood cross-section. The transition between early- and late-wood is abrupt (Mathaux et al., 2016).

The wood of *J. turbinata* (orig. *J. phoenicea*) from Cyprus in dry state has a density of 0.67 g/cm³ (Crivellaro & Schweingruber, 2013). The reddish-brown

heartwood of *J. turbinata* (orig. *J. phoenicea*), starts to develop in 13 year old specimens (Eliçin, 1977). The light, whitish-yellow sapwood is rather thin and encompass no more than last 10 increment rings (Eliçin, 1977). The boundaries of growth rings are somewhat sinuous, distinct due to thick-walled tracheids with relatively small lumen in late wood (Eliçin, 1977; Crivellaro & Schweingruber, 2013). The average thickness of yearly increment attains 1.01 mm in relatively young specimens (Eliçin, 1977). About 1,950–3,000 tracheids was observed on 1 mm^2 of wood cross-section in average. The tangential diameter of tracheids is 21.6 μm, the radial diameter 3.2 μm in average (Eliçin, 1977). The tangentially zonate axial parenchyma is dispersed in the wood (Crivellaro & Schweingruber, 2013). The tracheids have cupressoid, predominantly uniseriate, simple pits on the transverse and longitudinal (radial) cell walls; on the transverse wall 1–3 pits on average (Crivellaro & Schweingruber, 2013).

Rays in the wood of *J. turbinata* (orig. *J. phoenicea*) from Cyprus are exclusively uniseriate, with height up to 4 cells (Crivellaro & Schweingruber, 2013). In Turkey, the rays comprise in average of 3.36 parenchyma cells and are 79.9 μm high. The parenchyma cells of the rays are 28.6 μm long, and 16.3 μm broad (Eliçin, 1977).

The wood of *J. canariensis* (orig. *J. phoenicea* var. *canariensis* Guyot) is typical for junipers, with reddish heartwood and yellowish sapwood, without resin canals in transverse section and with clearly visible yearly increments (Palacios et al., 2014). The transition from early wood to late wood is abrupt, and the latter is very narrow, sometimes only one or two cells (Palacios et al., 2014). Axial parenchyma in the wood is sparse and diffuse, tangentially zonate and one cell wide (Palacios et al., 2014). Tracheids are rectangular, with spaces among cells, uniseriate pits on the tangential walls and uniseriate or rarely biseriate on radial walls. Pits are cupressoid in form. Walls have crassulae. Rays are uniseriate, homogenous, most frequently 2–3 celled, sporadically up to 19 cells high; the average height of rays is 62.1 μm, ranging between 12.5 and 352.9 μm. Tracheids are 2.6 mm long on average, but ranging between 1.0–7.0 mm, with longest found in locality of El Hierro. The average tracheid diameter is 27.6 μm, ranging between 16.5–48.0 μm, with the highest values detected in El Hierro (Palacios et al., 2014). The average diameter of pits on the tracheids is 13.5 μm, oscillating between 8.6 and 22.6 μm, with the broadest pits on tracheids from El Hierro (Palacios et al., 2014).

Biochemical data

The mineral and biochemical composition of different parts of species from the *J. phoenicea* complex

has been investigated in several areas, mainly due to the known composition of their essential oils (EOS) which are important in traditional medicine, veterinary use and cosmetics. Phytochemical analyses of leaves and cones of *J. turbinata* (orig. *J. phoenicea*) revealed carbohydrates, glycosides, flavonoids, sterols and triterpenes (Maamoun et al., 2016). The cones were also analysed for their nutritional value. The EOS most frequently were retrieved from leaves or cones, rarely from wood.

Leaf

The leaves of *J. turbinata* and *J. phoenicea* from Portugal contain a broad spectrum of phenolic compounds, the most common identified were psydrin, procyanidine and epicatechin (Tavares et al., 2012). The leaves of *J. turbinata* from the Middle Atlas in Morocco also contained oxygenated diterpenes (Barrero et al., 2004) and phenolic acids, flavonoid glycosides, and flavonoid aglycones (Dane et al., 2016). The leaves of *J. turbinata* (orig. *J. phoenicea*) from Algeria contained thirteen individual phenolic compounds, the most frequent 3-p-coumaroylquinic acid, quercetin- and myricetin-o-pentoside (Ghouti et al., 2018). Phenols detected in aerial parts of shrubby *J. turbinata* (orig. *J. phoenicea*) in Algeria include significant amounts of gallic acid, protocatechuic acid, p-hydroxybenzoic acid, catechin, p-coumaric acid, rutin, saidzein, luteolin, cinnamic acid, gesperidin and chrysin (Er Kemal et al., 2023).

The leaves of *J. turbinata* from Cyrenaica in Lybia contain seven phenols, twice more than cones, with the most frequent being catechin, quercetin and gallic acid (Hamad & Aisha, 2017). The methanol extract from *J. turbinata* leaves contains phenols, alkaloids, flavonoids, terpenoids, anthraquinones, and glycosides (Al-Mustafa et al., 2021). Additionally, myricitrin, quercetin, cosmosin and quercitrin were isolated (e.g. Abu-Darwish et al., 2014; Abu-Darwish & Ofir, 2014; Rajčević et al., 2018; Al Groshi et al., 2019).

The yield of EOS extracted from the leaves and/or aerial parts of *J. phoenicea* s.l. differs from population to population. The possible yield of EOS obtained from the leaves was 1.3–1.7% of the air-dried mass of raw material (e.g. Abu-Darwish et al., 2014; Harmouzi et al., 2016; Rajčević et al., 2018). The yield of EOS found in different regions varies from 0.41% in Portugal, and up to c. 2% in the Sinai mountains (Derwich et al., 2010, table II). To our knowledge, the composition of leaf EOS was frequently analysed in the populations of *J. turbinata*, but only rarely studied in *J. phoenicea* and *J. canariensis*. The most frequent constituent of the leaf EOS independently of species is α-pinene (Table 1).

The composition of *J. turbinata* leaf EOS revealed much variation, with a predominance of monoterpene hydrocarbons in most of the tested populations,

Table 1. Average percent content of the most frequent leaf EOS components in *Juniperus phoenicea*, *J. turbinata* and *J. canariensis* reported in references (Table S1)

EOS component	J. phoenicea	J. turbinata	J. canariensis
α-pinene	47.35	45.41	64.75
β-pinene	2.30	2.17	1.43
myrcene	3.60	4.09	2.78
α-terpineol	2.40	1.53	0.13
δ-cadinene	0.10	2.16	0.20
limonene	0.61	3.46	1.58
δ-3-carene	1.60	6.44	0.08
citronellol	0.55	1.39	0.03
ρ-cymene	–	1.35	0.30
caryophyllene oxide	0.85	1.66	0.68
γ-terpinene	0.20	1.33	0.35
β-phellandrene	5.40	8.30	2.75
elemol	1.50	1.59	0.15
γ-cadinene	0.15	1.91	0.93
α-terpinyl acetate	–	5.76	1.33
α-cadinol	0.15	1.82	0.80
germacrene D	0.45	1.00	–
β-elemene	0.03	1.00	–
α-phellandrene	0.75	–	0.28
iso-pulegol	0.85	–	–
linalool	1.15	0.52	0.36
β-caryophyllene	0.50	1.05	–

varying between 32.6% in Mediterranean Tunisia (Ennajar et al., 2011) to 89.5% in Atlantic Portugal (Cavaleiro et al., 2001), averaging 61.9%. The other main components of the leaf EOS are sesquiterpene hydrocarbons, which content varied between 1.1% in Portugal (Cavaleiro et al., 2001) and 37.1% in High Atlas in Morocco (Harmouzi, 2016), an average of c. 12%.

The EOS extracted from the leaves or aerial parts of particular populations of *J. turbinta* can contain more than 200 components, but most of them were found in only one or a few populations/specimens examined, and predominantly in trace quantities (less than 0.05%) (Venditti et al., 2018). The most frequent monoterpene dominant in almost all populations of *J. turbinata* was α-pinene. Other most frequently detected hydrocarbons are β-pinene, myrcene, camphene, α- and β-phellandrene, germacrene D, β-caryophyllene, limonene and caryophyllene oxide, also monoterpene alcohols, as α-terpineol, elemol, iso-pulegol and linalool. Out of 46 samples accessed from publications (Table S1), only α-pinene was found in all of them and β-pinene in 44.

The composition and content of EOS in the leaves/aerial parts of *J. turbinata* vary strongly between regions. The percentage of particular components were different, even in relatively not distant populations, and depending on the season of collection, the fresh *versus* dry plant material used in the analyses, the method of drying samples and method of distillation (e.g. Medini et al., 2009; Ennajar et al.,

2011; Bekhechi et al., 2012; Rajčević et al., 2018, and literature cited therein).

Juniperus turbinata (orig. *J. phoenicea*) from Jordan (Taif) leaf water extract consisted of monoterpene hydrocarbons (47.26%), with β-phellandrene (17.55%) as a main important component. The sesquiterpene hydrocarbons (26.87%), consisting mainly of α-humulene (20.95%). The oxygenated sesquiterpene and terpene represented 20.1% and 7.5%, respectively. Others, as alkane hydrocarbon, fatty acids, and hydrocinnamic acid were present at 1.7%, 0.1%, and 0.12% respectively (Al Masoudi et al., 2023).

The aerial parts of *J. phoenicea* s.s. in southern France contain glucosides, namely 3-oxo-α-ionol (junipeionoloside), 6-hydroxy-junipeionoloside, norterpenoid glucoside (roseoside) and a sesquiterpenoid glucoside (dihydrophaseic acid 4'-O-β-D-glucopyranoside) (Champavier et al., 1999). The EOS *J. phoenicea* (orig. *J. p.* var. *phoenicea*) extracted from fresh leaves sampled from El Peñon in Spain contained a high manoyl oxide (Adams et al. 2009), not found or rarely found in other taxa of *J. phoenicea* complex (Table S1).

The composition of EOS extracted from the fresh leaves of *J. canariensis* (orig. *J. phoenicea*) sampled from Madeira and from the Canary Island archipelago only slightly differed from the EOS of *J. phoenicea* and *J. turbinata* (Adams et al., 2009). The effect of sex of specimens and dioecy on the EOS composition remains uninvestigated and would be interesting for further studies.

Cone

The cones of *J. phoenicea* s.l. are composed of fibers, which share 44% of dry mass, but contain also up to 11.5% of fats and 4.4% of proteins and sugars. The nutritional content makes the cones an attractive food for birds (Jordano, 1993). Dependent on the region, the cones may also contain several mineral elements (Nasri et al., 2011), including heavy metals. Cones of *J. turbinata* (orig. *J. phoenicea*) in Jordan contain 168.07 or 190.11 ppm of Fe, 11.29 or 6.60 ppm of Mn, 40.71 or 13.72 of Zn and 31.51 or 71.86 ppm of Cu, in Dana nature reserve and Al-Hisha forest, respectively (Abu-Darwish & Ofir, 2014). Flavonoids, fatty acids, sterols and hydrocarbons were detected in cones of *J. turbinata* (orig. *J. phoenicea*) in Egypt (Abu-Darwish et al., 2014). The polymeric tannins composed of gallocatechin, known under the name of prodelphinidin, were reported from the species of *J. phoenicea* complex. The very high content of prodelphinidin in the *J. turbinata* cones was a reason for distinguishing chemovar. *montana* P.Lebreton & P.Pérez from the mountains of NW Africa (Lebreton & Pérez de Paz, 2001).

The EOS content in the cones of *J. turbinata* (orig. *J. phoenicea*) depends on the region of origin and can vary from 0.9 to 3.7% between population from Dana and Al-Hisha (Jordan, Arabian Peninsula), respectively (Abu-Darwish & Ofir, 2014). Independent of origin, *J. turbinata* cone EOS contain mainly monoterpenoids and sesquiterpenoids, with a high amount of α-pinene, camphene, δ-3-carene and trans-verbenol (Abu-Darwish et al., 2014). The very high amount of α-pinene in the cone EOS of *J. turbinata* (orig. *J. phoenicea*) was reported from Jordan (Abu-Darwish et al., 2014), and Tunisia (Ennajar et al., 2009). These results indicate that cones of *J. turbinata* in these two countries can be a good natural source of α-pinene for medicinal purposes.

El-Sawi et al. (2007) isolated diterpenes from the cones of *J. turbinata* (orig. *J. phoenicea*) from Sinai. They identified mainly sandaracopimaric acid and pimaric acid. In cones from Cyrenaica only traces of phenolic acids were found, mainly catechin (Hamad & Aisha, 2017). Scutellarin, isoscutellarin, shikimic acid and the new palmitoyl lactone were also noted (Aboul-Ela et al., 2005).

The cones of *J. turbinata* (orig. *J. phoenicea*) from Greece contained 22,1% of α-pinene, 13.2% of diterpene 4-epi-abietal and 7.4% of germacrene (Koutsaviti et al., 2017). The cones of *J. turbinata* (orig. *J. phoenicea*) from Turkey contained c. 2% of EOS, but mainly phenols and flavonoids, 32.64% and 13.53%, respectively (Öztürk et al., 2011). In Saudi Arabia, the extract of *J. turbinata* (orig. *J. phoenicea*) cones revealed β-sitosterol, stigmasterol, labdane 1–4 and pimarane diterpenoids among other constituents (Badahdah et al., 2015). In general, cone EOS of *J. turbinata* include α-pinene, δ-3-carene, myrcene, γ-cadinene and β-phellandrene (Table S2). Studies on cone EOS of *J. phoenicea* s.s. and *J. canariensis* are unknown.

Seeds

The oil content in seeds of *J. turbinata* (orig. *J. phoenicea*) from Tunisia ranges from 7.0 to 18.2% dry weight (Nasri et al., 2011). The oil composition is c. 86% of unsaturated fatty acids, mainly linolenic (33.0%) linoleic (28.3%) and oleic acids (12.8%). The palmitic (7.8%) and stearic (4.4%) fatty acids are present in relatively high amounts, and several others have been detected in small or trace quantities (Nasri et al., 2011). The seeds of *J. turbinata* contain 6.0 to 9.6% of protein, and in 1g of dry mass of seed was detected 168.8 to 228.1 mg of sugar (reduced to glucose). The 100 g of dry mass of seed contain also c. 65 mg of Na, 150–500 mg of K, 110 mg of Mg, 80–100 mg of Ca and smaller amounts of Cu, Zn, Fe and Mn (Nasri et al., 2011: Table 3).

Wood

The heartwood of *J. turbinata* (orig. *J. phoenicea*) is very durable and resistant to destruction by fungi (Lykidis et al., 2023). The essential oils contain several substances which make the wood resistant to insect and fungal attack. Sesquiterpene thujopsene and sesquiterpene alcohol cedrol were reported as major components of wood EOS (Runeberg, 1960; Adams, 1991).

Acknowledgements

Literature

Aboul-Ela M, El-Shaer N & El-Azim TA (2005) Chemical constituents and antihepatotoxic effect of *Juniperus phoenicea* berries - Part II. Natural Product Sciences 11: 240–247.

Abrantes F, Voelker AHL, Sierro FJ, Naughton N, Rodrigues T, Cacho I, Aritzegui D, Brayshaw D, Sicre M-A & Batista L (2012) Paleoclimate variability in the mediterranean region. In: The climate of the mediterranean region. From the past to the future (ed. by P Lionello) Elsevier, Amsterdam, pp. 1–86. doi:10.1016/B978-0-12-416042-2.00001-X.

Abu-Darwish MS & Ofir R (2014) Heavy metals content and essential oil yield of *Juniperus phoenicea* L. in different origins in Jordan. Environmental Engineering and Management Journal 13: 3009–3014. doi:10.30638/eemj.2014.339.

Abu-Darwish MS, Cabral C & Salgueiro L (2014) *Juniperus phoenicea* from Jordan. In: Medicinal and aromatic plants of the middle-east (ed. by Z Yaniv & N Dudai) pp. 241–251. doi:10.1007/978-94-017-9276-9_13.

Achhal A (2002) Cupressaceae: Checklist of vascular plants of N Morocco with identification keys, 1. (ed. by B Valdés, M Rejdali, A Achhal El Kadmiri, JL Jury & JM Montserrat) CSIC, Madrid, pp. 74–76.

Adams RP & Schwarzbach AE (2013) Phylogeny of *Juniperus* using nrDNA and four cpDNA regions. Phytologia 95: 179–187.

Adams RP (1991) Cedar wood oils – analyses and properties In: Essential oils and waxes (ed. by HF Linskens & JF Jackson) Springer, Berlin, pp. 159–173. doi:10.1007/978-3-642-84023-4_8.

Adams RP (2004) *Juniperus deltoides*, a new species, and nomenclatural notes on *Juniperus polycarpos* and *J. turcomanica* (Cupressaceae). Phytologia 86: 49–53.

Adams RP (2014) Junipers of the world: The genus *Juniperus*. 4th ed. Trafford, Bloomington.

Adams RP, Altarejos J, Arista M & Schwarzbach AE (2014) Geographic variation in *Juniperus phoenicea* var. *phoenicea* from throughout its range: analysis of nrDNA and the petN-PsbM cp region. Phytologia 96: 247–251.

Adams RP, Barrero AF & Lara A (1996) Comparison of the leaf essential oils of *Juniperus phoenicea*, *Juniperus phoenicea* subsp. *eu-mediterranea* Lebr. & Thiv. and *Juniperus phoenicea* var. *turbinata* (Guss.) Parl. Journal of Essential Oil Research 8: 367–371. doi:10.1080/10412905.1996.9700642.

Adams RP, Boratyński A, Arista M, Schwarzbach AE, Leschner H, Liber Z, Minissale P, Mataraci T & Manolis A (2013) Analysis of *Juniperus phoenicea* from throughout its range in the Mediterranean using DNA sequence data from nrDNA and petN-psbM: the case for the recognition of *J. turbinata* Guss. Phytologia 95: 202–209.

Adams RP, Morris JA, Padney RN & Schwarzbach AE (2005) Cryptic speciation between *Juniperus deltoides* and *Juniperus oxycedrus* (Cupressaceae) in the Mediterranean. Biochemical Systematics and Ecology 33: 771–787. doi:10.1016/j.bse.2005.01.001.

Adams RP, Padney N, Rezzi S & Casanova J (2002) Geographic variation in the random amplified polymorphic DNAs (RAPDs) of *Juniperus phoenicea*, *J. p.* var. *canariensis*, *J. p.* subsp. *eumediterranea* and *J. p.* var. *turbinata*. Biochemical Systematics and Ecology 30: 223–229. doi:10.1016/S0305-1978(01)00083-7.

Adams RP, Rumeu B, Nogales M & Fontinha S (2009) Geographic variation and systematics of *Juniperus phoenicea* L. from Madeira and the Canary islands: analyses of leaf volatile oils. Phytologia 91: 40–53.

Adams RP, Rumeu B, Nogales M & Fontinha S (2010) Geographic variation and systematics of *Juniperus phoenicea* L. from Madeira and the Canary islands: SNPS from nrDNA and petN-psbM. Phytologia 92: 59–67.

Alananbeh KM, Othman YA, Tahat MM, Al-Dakil H, Yahya AA, Ayasrah B, Al-Share T, Alkhatatbeh S, Al-Zoubi R, Alnaanah M, Sufian Malkawy S & Alananbeh MB (2023) Forest health assessment in four Jordanian reserves located in semi-arid environments. Forests 14: 918. doi:10.3390/f14050918

Al Groshi A, Jasim HA, Evans AR, Ismail FMD, Dempster NM, Nahar L & Sarker SD (2019) Growth inhibitory activity of biflavonoids and diterpenoids from the leaves of the Libyan *Juniperus phoenicea* against human cancer cells. Phytotherapy Research 33: 2075–2082. doi:10.1002/ptr.6397.

Al Masoudi LM, Alqurashi AS, Abu Zaid A & Hamdi H (2023) Characterization and biological studies of synthesized titanium dioxide nanoparticles from leaf extract of *Juniperus phoenicea* (L.) growing in Taif Region, Saudi Arabia. Processes 11: 272. doi:10.3390/pr11010272.

Ali M & El Shatshat S (2015) Ecological study of *Juniperus phoenicea* L. in EL-Gabal El-Akhdar area, Libya. European Journal of Experimental Biology 5: 71–76.

Al-Mustafa A, Al-Tawarah M, Al-Sheraideh MS & Al-Zahrany FA (2021) Phytochemical analysis, antioxidant and in vitro β-galactosidase inhibition activities of *Juniperus phoenicea* and *Calicotome villosa* methanolic extracts. BMC Chemistry 15: 55. doi:10.1186/s13065-021-00781-y.

Al-Ramamneh E, Dura S & Daradkeh N (2012) Propagation physiology of *Juniperus phoenicea* L. from Jordan using seeds and in vitro culture techniques: Baseline information for a conservation perspective. African Journal of Biotechnology 11: 7684–7692. doi:10.5897/AJB12.485.

Al-Yasi HM (2019) Genetic relationship among *Juniperus* spp. in Taif, Saudi Arabia, based on molecular marker (RAPD), SDS-PAGE profile and seed morphological taxonomy. Bioscience Research 16: 1776–1783.

Amaral Franco J, do (1964) *Juniperus* L. In: Flora Europaea 1 (ed. by TG Tutin, VH Heywood, NA Burges, DH Valentine, SM Walters & DA Webb) Cambridge University Press, Cambridge, pp. 38–39.

Amaral Franco J, do (1968) Distribuição de zimbros e pomóideas da Península Ibérica. Collectanea Botanica 7: 449–481.

Amaral Franco J, do (1986) *Juniperus* L. In: Flora Iberica 1. (ed. by S Castroviejo, M Laínz, G López González, P Montserrat, F Muñoz Garmendia, J Paiva & L Villar) Real Jardín Botánico CSIC, Madrid, pp. 181–188.

Amaral Franco J, do (1993) *Juniperus* L. In: Flora Europaea 1. 2nd ed. (ed. by TG Tutin, Vh Heywood, NA Burges, DH Valentine, SM Walters & DA Webb) Cambridge University Press, Cambridge, pp. 46–48.

Anonym (2009) Tree of the year 2009. Phoenician juniper (*Juniperus phoenicea* L.). Ministry of Agriculture, Natural Resources and Environment, Department of Forests, http://www.moa.gov.cy/moa.

Aparicio Rojo JM & Uribe-Echebarría PM (2006) *Juniperus × palancianus*, nuevo híbrido de la provincia de Castellón. Toll Negre 8: 5–8.

Aparicio Rojo JM & Uribe-Echebarría PM (2008) *Juniperus × herragudensis*, otro nuevo híbrido de la provincia de Castellón. Mainhardt 60: 83–85.

Arista M, Ortiz PL & Talavera S (1997) Reproductive isolation of two sympatric subspecies of *Juniperus phoenicea* (*Cupressaceae*) in southern Spain. P1ant Systematics and Evolution 208: 225–237. doi:10.1007/BF00985443.

Arrigoni PV (2006) Flora dell'isola di Sardegna 1. Società Botanica Italiana/Carlo Delfino, Sassari.

Asensi A, Díez-Carretas B & Quézel P (2007) Plant communities of *Juniperus turbinata* Guss. subsp. *turbinata* in the Mediterranean Region. A biogeographical, bioclimatical and syntaxonomical survey. Phytocoenologia 37: 599–623. doi:10.1127/0340-269X/2007/0037-0599.

Axelrod DI (1975) Evolution and biogeography of Madrean-Tethyan sclerophyll vegetation. Annals of the Missouri Botanical Garden 62: 280–334.

Azevedo de Menezes C (1914) Flora do Archipelago da Madeira. Junta Agricola da Madeira, Funchal.

Badahdah KO, Ahmed HM, Alamri FB & Abdel-Mogib M (2015) Total antioxidant capacity of labdane and pimarane diterpenoids of *Juniperus phoenicea* L. International Journal of Science and Engineering Applications 4: 287–293. doi:10.7753/IJSEA0405.1011.

Baquedano FJ & Castillo FJ (2007) Drought tolerance in the Mediterranean species *Quercus coccifera*, *Quercus ilex*, *Pinus halepensis*, and *Juniperus phoenicea*. Photosynthetica 45: 229–238. doi:10.1007/s1109 9-007-0037-x.

Barina Z (2017) Distribution atlas of vascular plants in Albania. Hungarian Natural History Museum, Budapest.

Barrero AF, Quilez del Moral JF, Herrador MM, Akssira M, Bennamara A, Akkad S & Aitigri M (2004) Oxygenated diterpenes and other constituents from Moroccan *Juniperus phoenicea* and *Juniperus thurifera* var. *africana*. Phytochemistry 65: 2507–2515. doi:10.1016/j.phytochem.2004.07.021.

Barrón E, Rivas-Carballo R, Postigo-Mijarra JM, Alcalde-Olivares C, Vieira M, Castro L, Pais J & Valle-Hernández M (2010) The Cenozoic vegetation of the Iberian Peninsula: a synthesis. Review of Palaeobotany and Palynology 162 (SI): 382–402. doi:10.1016/j.revpalbo.2009.11.007.

Bartolo G, Brullo S, Minissale P & Spampinato G (1988) Flora e vegetazione dell'Isola di Lampedusa. Bollettino Accademia Gioenia Scienze Naturali 21: 119–255.

Bartolucci F, Peruzzi L, Galasso G, Albano A, Alessandrini A, Ardenghi NMG, Astuti G, Bacchetta G, Ballelli S, Banfi E, Barberis G, Bernardo L, Bouvet D, Bovio M, Cecchi L, Di Pietro R, Domina G, Fascetti S, Fenu G, Festi F, Foggi B, Gallo L, Gottschlich G, Gubellini L, Iamonico D, Iberite M, Jiménez-Mejías P, Lattanzi E, Marchetti D, Martinetto E, Masin RR, Medagli P, Passalacqua NG, Peccenini S, Pennesi R, Pierini B, Poldini L, Prosser F, Raimondo FM, Roma-Marzio F, Rosati L, Santangelo A, Scoppola A, Scortegagna S, Selvaggi A, Selvi F, Soldano A, Stinca A, Wagensommer RP, Wilhalm T & Conti F (2018) An updated checklist of the vascular flora native to Italy. Plant Biosystems 152: 179–303. doi:10.1080/1126350 4.2017.1419996.

Bekhechi C, Bekkara FA, Consiglio D, Bighelli A & Tomi F (2012) Chemical variability of the essential oil of *Juniperus phoenicea* var. *turbinata* from Algeria. Chemistry & Biodiversity 9: 2742–2753. doi:10.1002/cbdv.201200028.

Benabid A (2000) Flore et écosystèmes du Maroc. Évaluation et préservation de la biodiversité. Ibis Press, Paris and Librairies et éditions Kalila Wa Dimna, Rabat.

Benítez-Benítez C, Escudero M, Rodríguez-Sánchez M, Martín-Bravo S & Jiménez-Mejías P (2018) Pliocene–Pleistocene ecological niche evolution shapes the phylogeography of a Mediterranean plant group. Molecular Ecology 27: 1696–1713. doi:10.1111/mec.14567.

Biondi E (1990) Population characteristics of *Juniperus oxycedrus* L. and their importance to vegetation dynamics. Giornale Botanico Italiano 124: 330–337. doi:10.1080/11263509009428153.

Bocchieri E & Giani L (1998) Flora of the Mortorio Archipelago (N. E. Sardinia). Flora Mediterranea 8: 49–83.

Bocchieri E (1992) Flora of the small islands of the archipelago of Maddalena (north-eastern Sardinia) and floristic contributions regarding some of

the main islands of the Archipelago. Flora Mediterranea 2: 33–64.

Bolòs O, de & Vigo J (1984) Flora del països Catalans 1. Barcino, Barcelona.

Boratyńska K, Boratyński A, Browicz K & Dolatowski J (1985) Trees and shrubs of Rodhos – a monographic study. Arboretum Kórnickie 30: 127–199.

Boratyński A & Boratyńska K (2021) Jałowce występujące w sposób naturalny w Europie i w regionie śródziemnomorskim – przegląd. Rocznik Polskiego Towarzystwa Dendrologicznego 69: 17–34.

Boratyński A & Browicz K (1996) Trees and shrubs of the Ionian Islands (Greece) – a preliminary list. Arboretum Kórnickie 41: 55–58.

Boratyński A, Browicz K & Zieliński J (1987) Woody flora of Chios. Arboretum Kórnickie 32: 37–91.

Boratyński A, Browicz K & Zieliński J (1988) Woody flora of Euboea (Evvoia). Arboretum Kórnickie 33: 13–74.

Boratyński A, Browicz K & Zieliński J (1992) Chorology of trees and shrubs in Greece. Institute of Dendrology of Polish Academy of Sciences, Kórnik.

Boratyński A, Lewandowski A, Boratyńska K, Montserrat JM & Romo A (2009) High level of genetic differentiation of *Juniperus phoenicea* (Cupressaceae) in the Mediterranean region: geographic implications. Plant Systematics and Evolution 277: 163–172. doi:10.1007/s00606-008-0122-z.

Boratyński A, Dönmez AA, Bou Dagher-Kharrat M, Romo Á, Tan K, Ok T, Iszkuło G, Sobierajska K & Marcysiak K (2023) Biology and ecology of *Juniperus drupacea* Labill. Dendrobiology 90: 1–29. doi:10.12657/denbio.090.001.

Browicz K & Zieliński J (1982) Chorology of trees and shrubs in South-West Asia and adjacent regions 1. Polish Academy of Science, Poznań – Kórnik

Brullo S & Furnari F (1979) Taxonomic and nomenclatural notes on the flora of Cyrenaica (Libya). Webbia 34: 155–174. doi:10.1080/00837792.1979.10670168.

Brullo S & Furnari F (1994) La vegetazione del Gebel el-Akhdar (Cirenaica settentrionale). Bollettino Accademia Gioenia Scienze Naturali 27: 197–412.

Brullo S & Guglielmo A (2001) Phytogeographic considerations on N Cyrenaica. Bocconea 13: 209–222.

Cabezudo B (2011) *Juniperus* L. In: Flora vascular de Andalucía Oriental 1 (ed. by G Blanca, B Cabezudo, M Cueto, C Fernández López & C Morales Torres) 2a edición corregida y aumentada. Granada, Universidades de Almería, Granada, Jaén y Málaga, pp. 87–90.

Cabezudo B, Pérez Latorre A, Navas D, Caballero G & Gavira O (2003) Aportaciones a la flora de Andalucía. II. Acta Botanica Malacitana 28: 254–257.

Camarero JJ & Ortega-Martínez M (2019) Sancho, the oldest known Iberian shrub. Dendrochronologia 53: 32–36. doi:10.1016/j.dendro.2018.11.003.

Cano-Ortiz A, Piñar Fuentes JC, Pinto-Gomes CJ, Musarella CM & Cano E (2015) Expansion of the *Juniperus* genus due to anthropic activity. In: Old-growth forests and coniferous forests. Ecology, Habitat and Conservation (ed. by R Weber) Nova Science Publishers, New York, pp. 55–65.

Carrión JS (2002) Patterns and process of Late Quaternary environmental change in a montane region of southwestern Europe. Quaternary Science Reviews 21: 2047–2066. doi:10.1016/S0277-3791(02)00010-0.

Carrión JS, Andrade A, Bennett KD, Navarro C & Munuera M (2001) Crossing forest thresholds: inertia and collapse in a Holocene sequence from south-central Spain. Holocene 11: 635–653. doi:10.1191/09596830195672.

Castillo JM, Rubio Casal AE, Luque CJ, Luque T & Figueroa ME (2002) Comparative field summer stress of three tree species co-occurring in Mediterranean coastal dunes. Photosynthetica 40: 49–56. doi:10.1023/A:1020133921204.

Caudullo G & de Rigo D (2016) *Juniperus phoenicea* in Europe: distribution, habitat, usage and threats. In: European atlas of forest tree species (ed. by J San Miguel Ayanz, D de Rigo, G Caudullo, T Houston Durrant & A Mauri) Publication Office of the European Union, Luxembourg, pp. e012f63+.

Cavaleiro C, Rezzi S, Salgueiro L, Bighelli A, Casanova J & da Cunha AP (2001) Infraspecific chemical variability of the leaf essential oil of *Juniperus phoenicea* var. *turbinata* from Portugal. Biochemical Systematics and Ecology 29: 1175–1183. doi:10.1016/S0305-1978(01)00041-2.

Cebrat J (2007) Atlas of plant anatomy. Wydawnictwo Uniwersytetu Przyrodniczego we Wrocławiu, Wrocław.

Champavier Y, Comte G, Vercauteren J, Allais DP & Chulia AJ (1999) Norterpenoid and sesquiterpenoid glucosides from *Juniperus phynicea* and *Galega officinalis*. Phytochemistry 50: 1219–1223. doi:10.1016/S0031-9422(98)00697-9.

Charco J (1999) El bosque mediterráneo en el Norte de Africa. Agencia Española de Cooperación Internacional, Madrid.

Charco J (2001) Guía de los árboles y arbustos del Norte de África. Agencia Española de Cooperación Internacional, Madrid.

Chaudhary S (1999) Flora of the Kingdom of Saudi Arabia 1. Ministry of Agriculture & Water, Riyadh.

Christensen KI (1997) *Juniperus* L. In: Flora Hellenica 1 (ed. by A Strid & K Tan) Koelz, Königstein, pp. 10–14.

Collenette S (1985) An illustrated guide to the flowers of Saudi Arabia. Scorpion Publishing Ltd., London.

Conord C, Gurevitch J & Fady B (2012) Large-scale longitudinal gradients of genetic diversity: a meta-analysis across six phyla in the Mediterranean basin. Ecology and Evolution 2: 2595–2609. doi:10.1002/ece3.350.

Coode MJE & Cullen J (1965) *Juniperus* L. In: Flora of Turkey 1 (ed. by PH Davis) Edinbourgh University Press, Edinbourgh, pp. 78–84.

Costa JC, Capelo J, Jardim R, Sequeira M, Espírito-Santo D, Lousã M, Fontinha S, Aguilar C & Rivas-Martínez S (2004) Catálogo sintaxonómico e florístico das comunidades vegetais da Madeira e do Porto Santo. Associação Lusitana de Fitossociologia. http://hdl.handle.net/10198/5335.

Crivellaro A & Schweingruber FH (2013) Atlas of wood, bark and pit anatomy of eastern Mediterranean trees and shrubs with a special focus on Cyprus. Springer, Heidelberg. doi:10.1007/978-3-642-37235-3.

Dakhil MA, El-Barougy RF, El-Keblawy A & Farahat EA (2022) Clay and climatic variability explain the global potential distribution of *Juniperus phoenicea* toward restoration planning. Scientific Reports 12: 13199. doi:10.1038/s41598-022-16046-0.

Dane Y, Mouhouche F, Canela-Garayoa R & Delpino-Rius A (2016) Phytochemical analysis of methanolic extracts of *Artemisia absinthium* L. (Asteraceae), *Juniperus phoenicea* L., and *Tetraclinis articulata* (Vahl) Mast, (Cupressaceae) and evaluation of their biological activity for stored grain protection. Arabian Journal for Science and Engineering 41: 2147–2158. doi:10.1007/s13369-015-1977-2.

Danin A (1983) Desert vegetation of Israel and Sinai. Cana, Jerusalem.

Danin A & Fragman-Sapir O (2016) Flora of Israel and adjacent areas. https://flora.org.il/en/plants/.

De Nascimento L, Nogué S, Criado C, Ravazzi C, Whittaker RJ, Willis KJ & Fernández-Palacios JM (2016) Reconstructing Holocene vegetation on the island of Gran Canaria before and after human colonization. The Holocene 26: 113–125. doi:10.1177/0959683615596836.

Debreczy Z & Rácz I (1999) The prostrate form of the Phoenician juniper: *Juniperus phoenicea* L. f. *prostrata*, f. nov. Studia Botanica Hungarica 29: 87–94.

Debreczy Z & Rácz I (2011) Conifers around the world: conifers of the temperate zones and adjacent regions. Dendropress, Budapest.

Del Arco Aguilar MJ & Rodríguez Delgado O (2006) El Hierro: Mapa de vegetación de Canarias (ed. by MJ Del Arco Aguilar) GRAFCAN, Santa Cruz de Tenerife, pp. 353–376.

Delipetrou P, Ghosn D, Kazakis G, Nyktas P, Remoundou E & Vogiatzakis IN (2015) Vegetation dynamics of coastal dunes with *Juniperus* spp. in Crete, Gavdos and Chrysi Islands (Greece). Ecologia Mediterranea 41: 45–60.

Derwich E, Benziane Z & Boukir A (2010) Chemical composition of leaf essential oil of *Juniperus phoenicea* and evaluation of its antibacterial activity. International Journal of Agriculture and Biology 12: 199–204.

Dimopoulos P, Raus T, Bergmeier E, Constantinidis T, Iatrou G, Kokkini S, Strid A & Tzanoudakis D (2016) Vascular plants of Greece: An annotated checklist. Supplement. Willdenowia 46: 301–347. doi:10.3372/wi.46.46303.

Dobignard A & Chatelain C (2010) Index synonymique de la Flore de l'Afrique du Nord 1, Éditions de Conservatoire et Jardin Botaniques de Genève, Geneve.

Dzialuk A, Mazur M, Boratyńska K, Montserrat JM, Romo A & Boratyński A (2011) Population genetic structure of *Juniperus phoenicea* (Cupressaceae) in the western Mediterranean Basin: gradient of diversity on a broad geographical scale. Annals of Forest Science 68: 1341–1350. doi:10.1007/s13595-011-0150-7.

El-Bana M, Shaltout K, Khalafallah A & Mosallam H (2010) Ecological status of the Mediterranean *Juniperus phoenicea* L. relicts in the desert mountains of North Sinai, Egypt. Flora 205: 171–178. doi:10.1016/j.flora.2009.04.004.

El-Barasi M & Barrani MW (2013) Threats to plant diversity in the North Eastern part of Libya (El-Jabal El-Akahdar and Marmarica Plateau). Journal of Environmental Science and Engineering A2: 41–58.

El-Barasi YM, Barrani MW, El-Amrouni AO & Mohamad NF (2011) Check list of flora and vegetation on south Elmarj zone: south El-Jabal El-Akhadar, Libya. Annals of Faculty Engineering Hunedoara 9: 141–146.

El-Barougy RF, Dakhil MA, Halmy MWA, Cadotte M, Dias S, Farahat EA, El-Keblawy A & Bersier LF (2023) Potential extinction risk of *Juniperus phoenicea* under global climate change: Towards conservation planning. Global Ecology and Conservation 46: e02541. doi:10.1016/j.gecco.2023.e02541.

Eliçin G (1977) Türkiye doğal ardiç (*Juniperus* L.) taksonlarının yayılışları ile önemli morfolojik ve anatomik özellikleri üzerinde araştırmalar. İstanbul Üniversitesi, Orman Fakültesi Yayınları, İstanbul, 2327/232.

Elmahdy SI & Mohamed MM (2016) Factors controlling the changes and spatial variability of *Juni-*

perus phoenicea in Jabal Al Akhdar, Libya, using remote sensing and GIS. Arab Journal of Geoscience 9: 478. doi:10.1007/s12517-016-2500-0.

El-Sawi SA, Motawae HM & Ali AM (2007) Chemical composition, cytotoxic activity and antimicrobial activity of essential oils of leaves and berries of *Juniperus phoenicea* L. grown in Egypt. African Journal of Traditional, Complementary and Alternative Medicines 4: 417–426. doi:10.4314/ajtcam.v4i4.31236.

Engel T & Frey W (1996) Fuel resources for copper smelting in antiquity in selected woodlands in the Edom highlands to the Wadi Arabah/Jordan. Flora 191: 29–39. doi:10.1016/S0367-2530(17)30687-4.

Ennajar M, Afloulous S, Romdhane M, Ibrahim H, Cazaux S, Abderraba M, Raies A & Bouajila J (2011) Influence of the process, season, and origin on volatile composition and antioxidant activity of *Juniperus phoenicea* L. leaves essential oils. Journal of Food Science 76: C224–C230. doi:10.1111/j.1750-3841.2010.01995.x.

Ennajar M, Bouajila J, Lebrihi A, Mathieu F, Abderrabba M, Raies A & Romdhane M (2009) Chemical composition and antimicrobial and antioxidant activities of essential oils and various extracts of *Juniperus phoenicea* L. (Cupressacees). Journal of Food Science 74: M364–M371. doi:10.1111/j.1750-3841.2009.01277.x.

Er Kemal M, Bakhiche B, Kemal M, Cheraif K, Kara Y, Bardaweel SK, Miguel MG, Yildiz O & Ghareeb MA (2023) Six Algerian plants: Phenolic profile, antioxidant, antimicrobial activities associated with different simulated gastrointestinal digestion phases and antiproliferative properties. Journal of Herbal Medicine 38: 100636. doi:10.1016/j.hermed.2023.100636.

Esau K (1977) Anatomy of seed plants. Wiley, New York/Santa Barbara.

Evert RF & Eichhorn SE (2006) Esau's plant anatomy. Meristems, Cells, and Tissues of the Plant Body: Their Structure, Function, and Development. 3rd ed. Wiley and Sons, Hoboken, New Jersey.

Farahat EA (2020) Age structure and static life tables of the endangered *Juniperus phoenicea* L. in North Sinai Mountains, Egypt: implication for conservation. Journal of Mountain Science 17: 2170–2178. doi:10.1007/s11629-020-6123-2.

Farhat P, Hidalgo O, Robert T, Siljak-Yakovlev S, Leitch IJ, Adams RP & Bou Dagher-Kharrat M (2019) Polyploidy in the Conifer Genus *Juniperus*: An unexpectedly high rate. Frontiers in Plant Science 10: 676. doi:10.3389/fpls.2019.00676.

Farhat P, Siljak-Yakovlev S, Takvorian N, Bou Dagher Kharrat M & Robert T (2023) Allopolyploidy: An underestimated driver in *Juniperus* evolution. Life 13: 1479. doi:10.3390/life13071479.

Farjon A & Filer D (2013) An atlas of the world's conifers. An analysis of their distribution, biogeography, diversity and conservation status. Brill Academic Publishers, Leiden, The Netherlands. doi:10.1163/9789004211810.

Farjon A (2005) A monograph of Cupressaceae and *Sciadopitys*. Royal Botanic Gardens, Kew.

Farjon A (2010) A handbook of the world's conifers. Brill, Leiden-Boston.

Farjon A (2020) *Juniperus turbinata* (amended version of 2020 assessment). The IUCN Red List of Threatened Species 2020: e.T16349692A179049709. doi:10.2305/IUCN.UK.2020-3.RLTS.T16349692A179049709.en.

Fennane M, Ibn Tattou M, Mathez J, Ouyahya A & E Oualidi J (1999) Flore pratique de Maroc. Travaux de l'Institut Scientifique, Série Botanique 36, Rabat.

Fernández-Palacios JM, de Nascimento L, Otto R, Delgado JD, García-del-Rey E, Arévalo JR & Whittaker RJ (2011) A reconstruction of Palaeo-Macaronesia, with particular reference to the long-term biogeography of the Atlantic island laurel forests. Journal of Biogeography 38: 226–246. doi:10.1111/j.1365-2699.2010.02427.x.

Fernández-Palacios JM, Otto R, Delgado JD, Arévalo JR, Naranjo A, González Artiles F, Morici C & Barone R (2008) Los bosques termófilos de Canarias. Proyecto IFE04/NAT/ES/000064. Excmo. Cabildo Insular de Tenerife.

Ferrer-Gallego P, Nazzaro R, Ferrando-Pardo I & Laguna E (2017) Typification of the Mediterranean endemic conifer *Juniperus turbinata* (Cupressaceae). Phytotaxa 302: 165–173. doi:10.11646/phytotaxa.302.2.6.

Fiorentino G, D'Oronzo C & Colaianni G (2013) Human-environmental interaction in Malta from the Neolithic to the Roman period: archaeobotanical analyses at Tas-Silg. Scienze dell'antichità 18: 169–184.

Gaisberg M von (2005) Die Vegetation der Fußstufe von El Hierro (Kanarische Inseln). Dissertationes Botanicae 395. Cramer, Berlin-Stuttgart.

Gambin B, Andrieu-Ponel V, Médail F, Marriner N, Peyron O, Montade V, Gambin T, Morhange C, Belkacem D & Djamali M (2016) 7300 years of vegetation history and climate for NW Malta: a Holocene perspective. Climate of the Past 12: 273–297. doi:10.5194/cp-12-273-2016, 2016.

García C, Moracho E, Díaz-Delgado R & Jordano P (2014) Long-term expansion of juniper populations in managed landscapes: patterns in space and time. Journal of Ecology 102: 1562–1571. doi:10.1111/1365-2745.12297.

Garcia-Castellanos D, Micallef A, Ferran Estrada F, Camerlenghi A, Ercillad G, Periáñez R & Abril JM (2020) The Zanclean megaflood of the Mediterranean – Searching for independent evidence. Earth-Science Reviews 201: 103061. doi:10.1016/j.earscirev.2019.103061.

Garcia-Cervigón AI, Velázquez E, Wiegand T, Escudero A & Olano JM (2017) Colonization in Mediterranean old-fields: the role of dispersal and plant-plant interactions. Journal of Vegetation Science 28: 627–638. doi:10.1111/jvs.12500.

Garraud L (2003) Flore de la Drôme. Atlas écologique et floristique. Conservatoire botanique national alpin de Gap-Charance.

Gaussen HM (1968) Les Gymnospermes actuelles et fossiles. Fascicule X, Les Cupressacées. Toulouse Faculté des Sciences. Travaux du Laboratoire Forestier de Toulouse. Tome II, Volume I, Partie II (2), Fascicule X, Chapitre XIII: 1–326.

Ghouti D, Rached W, Abdallah M, Pires TCSP, Calhelha RC, Alves MJ, Hamadi Abderrahmane L, Barros L & Ferreira ICRF (2018) Phenolic profile and in vitro bioactive potential of Saharan *Juniperus phoenicea* L. and *Cotula cinerea* (Del) growing in Algeria. Food and Function 9: 4664–4672. doi:10.1039/c8fo01392f.

Gianguzzi L (1999) Vegetazione e bioclimatologia dell'Isola di Pantelleria (Canale di Sicilia). Braun Blanquetia 22: 1–70.

Goes S, Giardini D, Jenny S, Hollenstein C, Kahle HG & Geiger A (2004) A recent tectonic reorganization in the south-central Mediterranean. Earth and Planetary Science Letters 226: 335–345. doi:10.1016/j.epsl.2004.07.038.

González Artiles FJ (2007) El bosque termófilo en Gran Canaria. Tesis doctoral, Unviersidad de Las Palmas de Gran Canaria. http://hdl.handle.net/10553/1977.

Guyot AP (1942) Contribution à l'étude de *Juniperus phoenicea* Lin. Thèses Pharmacie. Toulouse 93: 1–73.

Hamad MAH & Aisha MRA (2017) Separarion and identification the speciation of the phenolic compounds in fruits and leaves of some medicinal plants (*Juniperus phoenicea* and *Quercus coccifera*) growing at Al–Gabal Al–Akhder Region (LIBYA). Indian Journal of Pharmaceutical Education and Research 51Suppl: S299–S303. doi:10.5530/ijper.51.3s.34.

Hansen A & Sunding P (1985) Flora of Macaronesia. Checklist of Vascular Plants, 3rd revised ed. Sommerfeltia 1: 1–167. doi:10.2478/som-1985-0001.

Hansen A & Sunding P (1993) Flora of Macaronesia. Checklist of Vascular Plants, 4th revised ed. Sommerfeltia 17: 1–301. doi:10.2478/som-1993-0003.

Harmouzi A, Boughdad A, El Ammari Y & Abdelaziz Chaouch A (2016) Chemical composition and toxicity of Moroccan *Tetraclinis articulata* and *Juniperus phoenicea* essential oils against *Aphis citricola* Goot, 1912 (Homoptera, Aphididae). Research on Chemical Intermediates 42: 7185–7197. doi:10.1007/s11164-016-2528-5.

Heynowicz Z (2002) Anatomia i histologia roślin naczyniowych. Wydawnictwo Naukowe PWN, Warszawa.

Hidalgo N, Pérez AV & Cabezudo B (2014) Las poblaciones de *Juniperus turbinata* en el valle del río Guadalhorce (Málaga, España) como indicadoras de territorios relictos paleobiogeográficos. In: Biogeografía de sistemas litorales. Dinámica y Conservación (ed. by R Cámara Artigas, B Rodríguez Pérez & JL Muriel Gómez) Universidad de Sevilla, Sevilla, pp. 377–380.

Ighbareyeh JMH, Suliemieh AA-RA, Sheqwarah M, Cano-Ortiz A & Carmona E C (2022) Flora and phytosociological of plant in Al-Dawaimah of Palestine. Research Journal of Ecology and Environmental Sciences 2: 58–91. https://www.scipublications.com/journal/index.php/rjees/article/view/202.

Isla J, Jácome-Flores ME, Pareja D & Jordano P (2022) Drivers of individual-based, antagonistic interaction networks during plant range expansion. Journal of Ecology 110: 2190–2204. doi:10.1111/1365-2745.13942.

Ivanov D, Utescher T, Mosbrugger V, Syabryaj S, Djordjević-Milutinović D & Molchanoff S (2011) Miocene vegetation and climate dynamics in Eastern and Central Paratethys (Southeastern Europe). Palaeogeography Palaeoclimatology Palaeoecology 304: 262–275. doi:10.1016/j.palaeo.2010.07.006.

Jalas J & Suominen J (1973) Atlas florae Europaeae 2. The Committee for Mapping the Flora of Europe and Societas Biologica Fennica Vanamo, Helsinki.

Jalut G, Dedoubat JJ, Fontugne M & Otto T (2009) Holocene circum-Mediterranean vegetation changes: climate forcing and human impact. Quaternary International 200: 4–18. doi:10.1016/j.quaint.2008.03.012.

Jalut G, Esteban Amat A, Riera I Mora S, Fontugna M, Mook R, Bonnet L & Gauquelin T (1997) Holocene climatic changes in the western Mediterranean: installation of the Mediterranean climate. Comptes rendus de l'Académie des sciences. Série 2, Sciences de la terre et des planètes 325: 327–334. doi:10.1016/S1251-8050(97)81380-8.

Jasprica N, Dolina K & Milović M (2018) The flora and vegetation of the NE Mediterranean islet with centuries-long human influences. Acta Botanica Croatica 77: 126–134. doi:10.2478/botcro-2018-0007.

Jeanmonod D & Gamisans J (2013) Flora Corsica, 2nd ed. Bulletin de la Société Botanique du Centre Ouest, num. spéc. 39.

Jiménez JF, Sánchez-Gómez P, Cánovas JL, Hensen I & AouissatM (2017) Influence of natural habitat fragmentation on the genetic structure of Canarian populations of *Juniperus turbinata*. Silva Fennica 51: 1678. doi:10.14214/sf.1678.

Jordano P (1991) Gender variation and expression of monoecy in *Juniperus phoenicea* L. (Cupressaceae). Botanical Gazette 152: 476–485. doi:10.1086/337909.

Jordano P (1993) Geographical ecology and variation of plant-seed disperser interactions - Southern Spanish junipers and frugivorous thrushes. Vegetatio 107/108: 85–104. doi:10.1007/BF00052213.

Kabiel HF, Hegazy AK, Lovett-Doust L, Al-Rowaily SL & Al Borki AES (2016) Ecological assessment of populations of *Juniperus phoenicea* L. in the Al-Akhdar mountainous landscape of Libya. Arid Land Research and Management 30: 269–289. doi:10.1080/15324982.2015.1090499.

Karagiannakidou V (1996) Statistische untersuchungen der samen von *Juniperus*-arten in Griechenland. Mitteilungen der Deutschen Dendrologischen Geselschaft 82: 129–137.

Kerfoot O & Lavranos JJ (1984) Studies in the flora of Arabia X: *Juniperus phoenicea* L. and *J. excelsa* M.Bieb. Notes of the Royal Botanic Garden Edinbourgh 41: 483–489.

Klimko M, Boratyńska K, Montserrat JM, Didukh Ya, Romo A, Gómez D, Kluza-Wieloch M, Marcysiak K & Boratyński A (2007) Morphological variation of *Juniperus oxycedrus* subsp. *oxycedrus* (Cupressaceae) in the Mediterranean region. Flora 202: 133–147. doi:10.1016/j.flora.2006.03.006.

Kokmotos E & Georgiadis T (2005) The flora of Mountains Elikon, Xerovouni and Neraidolakkoma (Boeotia, Sterea Ellas, Greece). Flora Mediterranea 15: 403–451.

Koutsaviti A, Tzakou O, Maria Galati E, Certo G & Germanò MP (2017) Chemical composition of *Juniperus phoenicea* and *J. drupacea* essential oils and their biological effects in the choriallantoic membrane (CAM) assay. Natural Product Communications 12: 449–452. doi:10.1177/1934578x1701200336.

Kovačić S, Jasprica N & Ruščić M (2001) Floristic characteristics of Phoenician juniper macchia (ass. *Pistacio lentisci – Juniperetum phoeniceae* Trinajstić 1987) in central and southern Dalmatia (Croatia). Natura Croatica 10: 73–81.

Krijgsman W, Hilgen FJ, Raffi, I, Sierro FJ & Wilson DS (1999) Chronology, causes and progression of the Messinian salinity crisis. Nature 400: 652–655. doi:10.1038/23231.

Kutschera L & Lichtenegger E (1997) Bewurzelung von Pflanzen in verschiedenen Lebensräumen. Stapfia 49: 1–331.

Kvaček Z (2002) A new juniper from the Paleogene of Central Europe. Feddes Repertorium 113: 492–502. doi:10.1002/fedr.200290001.

Larson DW, Matthes U, Gerrath JA, Gerrath JM, Nekola JC, Walker GL, Porembski S, Charlton A & Larson NWK (1999) Ancient stunted trees on cliffs. Nature 398: 382–383. doi:10.1038/18800.

Le Houérou NH (2004) Plant diversity in Marmarica (Libya and Egypt): a catalogue of the vascular plants reported with their biology, distribution, frequency, usage, economic potential, habitat, and main ecological features, with an extensive bibliography. Candollea 59: 259–308.

Lebreton P & Pérez de Paz PL (2001) Définition du Genévrier de Phénicie (*Juniperus* aggr. *phoenicea*), reconsidéré à ses limites biogéographiques: Méditerranée orientale (Crète et Chypre) et Atlantique (Iles Canaries). Bulletin mensuel de la Société Linnéenne de Lyon 70: 73–92. doi:10.3406/linly.2001.11373.

Lebreton P & Rivera D (1989) Analyse du taxon *Juniperus phoenicea* L. sur des bases biochimiques et biométriques. Naturalia Monspeliensia, Serie botanique 53: 17–41.

Lebreton P & Thivend S (1981) Sur une sus-espéce du Genévrier de Phénicie *Juniperus phoenicea* L., définie á partir de critéres biochimiques. Naturalia Monspeliensia, Serie botanique 47: 1–12.

Lemoine Sébastian C (1967a) Appareil reproductour mâle des *Juniperus*. Travaux du Laboratoire Forestier de Toulouse 1: 1–35.

Lemoine-Sébastian C (1967b) L'inflorescence femelle des Junipereae: Ontogenèse, structure, phylogenèse. Travaux du laboratoire forestier de Toulouse 1: 1–455.

Linnaeus C (1753) Species plantarum. Laurenti Salvii, Holmiae.

Lionello P (2012) The climate of the Mediterranean region. From the past to the future. Elsevier, Amsterdam.

Lionello P, Abrantes F, Congedi L, Dulac F, Gacic M, Gomis D, Goodess C, Hoff H, Kutiel H, Luterbacher J, Planton S, Reale M, Schröder K, Struglia MV, Toreti A, Tsimplis M, Ulbrich U & Xoplaki E (2012) Introduction. In: Mediterranean climate – background information: The climate of the Mediterranean region. From the past to the future (ed. by P Lionello) Elsevier, Amsterdam.

Loidi J (2017) The vegetation of the Iberian Peninsula 1–2. Plant Vegetation 12–13. Springer.

Long GA (1955) The study of the natural vegetation as a basis for pasture improvement in the western desert of Egypt. Bulletin de L'Institut Desert d'Égipte 5: 18–45.

Lykidis Ch, Bak M & Mantanis GI (2023) Biological resistance of Phoenician juniper wood. Wood Material Science & Engineering. doi:10.1080/17480272.2023.2221657.

Maamoun MI, Motawae HM & El- Sawi S (2016) Phytochemical and biological investigation of *Juniperus phoenicea* L. Lambert Academic Publishing.

Magdy EB, Kamal S, Ahmed K & Hosni M (2010) Ecological status of the Mediterranean *Juniperus phoenicea* L. relicts in the Desert Mountains of North Sinai, Egypt. Flora 205: 171–178. doi:10.1016/j.flora.2009.04.004.

Mandin J-P (2005) Découverte de très vieux genévriers de Phénicie (*Juniperus phoenicea* L.) dans les gorges de l'Ardèche (France). Le Journal de Botanique 29: 53–62.

Mandin J-P (2013) Plasticité phénotypique de l'expression sexuelle de *Juniperus phoenicea* L. dans les gorges de l'Ardèche (France). Ecologia Mediterranea 31: 155–168.

Mansouri N, Satrani B, Ghanmi M, El Ghadraoui L & Aafi A (2011) Étude chimique et biologique des huiles essentielles de *Juniperus phoenicea* ssp. *lycia* et *Juniperus phoenicea* ssp. *turbinata* du Maroc. Biotechnologie, Agronomie, Société et Environnement 15: 415–424.

Mao K, Hao G, Liu J, Adams RP & Milne RI (2010) Diversification and biogeography of *Juniperus* (Cupressaceae): variable diversification rates and multiple intercontinental dispersals. New Phytologist 188: 254–272. doi:10.1111/j.1469-8137.2010.03351.x.

Mao K, Ruhsam M, Ma Y, Graham SW, Liu J, Thomas Ph, Milne RI & Hollingsworth PM (2019) A transcriptome-based resolution for a key taxonomic controversy in Cupressaceae. Annals of Botany 123: 153–167. doi:10.1093/aob/mcy152.

Marcysiak K (2021) Biometry in plant systematics of European and Mediterranean gymnosperms, a review. Plant and Fungal Systematics 66: 133–140. doi:10.35535/pfsyst-2021-0012.

Martinis A, Chaideftou E, Minotou C & Poirazidis K (2018) Ecological assessment of *Juniperus turbinata* Guss. forest on the Strofades Islands, Ionian Sea, Greece. Journal of Forest Science 64: 345–352. doi:10.17221/52/2018-JFS.

Mathaux C (2017) Vivre dans des conditions difficiles en falaise: potentialités et longévité du genévrier de Phénicie (*Juniperus phoenicea* L.). Thèse pour obtenir le grade de Docteur en Sciences de l'Environnement, Aix Marseille Université, École doctorale Sciences de l'Environnement (ED251).

Mathaux C, Mandin JP, Oberlin C, Edouard JL, Gauquelin T & Guibal F (2016) Ancient juniper trees growing on cliffs: toward a long Mediterranean tree-ring chronology. Dendrochronologia 37: 79–88. doi:10.1016/j.dendro.2015.12.005.

Mazur M (2021) Differentiation of Mediterranean species of *Juniperus* from the *Sabina* section as a result of their migrations. Plant and Fungal Systematics 66: 141–154. doi:10.35535/pfsyst-2021-0013.

Mazur M, Boratyńska K, Marcysiak K, Gómez D, Tomaszewski D, Didukh J & Boratyński A (2003) Morphological variability of *Juniperus phoenicea* (Cupressaceae) from three distant localities on Iberian Peninsula. Acta Societatis Botanicorum Poloniae 72: 71–78.

Mazur M, Klajbor K, Kielich M, Sowińska M, Romo A, Montserrat JM & Boratyński A (2010) Intra-specific differentiation of *Juniperus phoenicea* in the western Mediterranean region revealed in morphological multivariate analysis. Dendrobiology 63: 21–31.

Mazur M, Minissale P, Sciandrello S & Boratyński A (2016) Morphological and ecological comparison of populations of *Juniperus turbinata* Guss. and *J. phoenicea* L. from the Mediterranean region. Plant Biosystems 150: 313–322. doi:10.1080/11263504.2014.994579.

Mazur M, Zielińska M, Boratyńska K, Romo A, Salvà-Catarineu M, Marcysiak K & Boratyński A (2018) Taxonomic and geographic differentiation of *Juniperus phoenicea* agg. based on cone, seed, and needle characteristics. Systematics and Biodiversity 16: 469–482. doi:10.1080/14772000.2018.1439120.

Médail F & Diadema K (2009) Glacial refugia influence plant diversity patterns in the Mediterranean Basin. Journal of Biogeography 36: 1333–1345. doi:10.1111/j.1365-2699.2008.02051.x.

Medini H, Elaissi A, Farhat F, Larbi Khouja M, Chemlia R & Harzallah-Skhiric F (2009) Seasonal and geographical influences on the chemical composition of *Juniperus phoenicea* L. essential oil leaves from the Northern Tunisia. Chemistry & Biodiversity 6: 1378–1387. doi:10.1002/cbdv.200800202.

Meikle RD (1977) Flora of Cyprus 1. Te Bentham-Moxon Trust/Royal Botanic Gardens, Kew.

Meloni M, Perini D, Filigheddu R & Binelli G (2006). Genetic variation in five Mediterranean populations of *Juniperus phoenicea* as revealed by inter-simple sequence repeat (ISSR) markers. Annals of Botany 97: 299–304. doi:10.1093/aob/mcj024.

Miller KG, Browning JV, Schmelz WL, Kopp RE, Mountain GS & Wright JD (2020) Cenozoic sea-level and cryospheric evolution from deep-sea geochemical and continental margin records. Scince Advances 6: eaaz1346. doi:10.1126/sciadv.aaz1346.

Minissale P & Sciandrello S (2013) A relic wood of *Juniperus turbinata* Guss. (Cupressaceae) in Sicily: Structural and ecological features, conservation

perspectives, Plant Biosystems 147: 145–157. doi:10.1080/11263504.2012.743931.

Molero J & Marfil JM (2017) Betis and Southwest Andalucia. In: The vegetation of the Iberian Peninsula 2. (ed. by J Loidi) Springer, Cham, pp. 143–247.

Mota JF, Pelqas J, Castro H, Cabello J & Guirado JS (1996) Agricultural development vs biodiversity conservation: the Mediterranean semiarid vegetation in El Ejido (Almeria, southeastern Spain). Biodiversity and Conservation 5: 1597–1617. doi:10.1007/BF00052118.

Msanda F, El Aboudi A & Peltier JP (2002) Originalité de la flore et de la végétation de l'Anti-Atlas sud-occidental (Maroc). Feddes Repertorium 113(7–8): 603–615.

Nasri N, Tlili N, Elfalleh W, Cherif E, Ferchichi A, Khaldi A & Triki S (2011) Chemical compounds from Phoenician juniper berries (*Juniperus phoenicea*). Natural Product Research 25:18: 1733–1742. doi:10.1080/14786419.2010.523827

Nieto Feliner G (2011) Southern European glacial refugia: A tale of tales. Taxon 60: 365–372. doi:10.1002/tax.602007.

Nikolić T (2015 - continued) Flora Croatica database. On-line. Department of Botany, Faculty of Science, University of Zagreb. http://hirc.botanic.hr/fcd.

Noti R, van Leeuwen JFN, Colombaroli D, Vescovi E, Pasta S, La Mantia T & Tinner W (2009) Mid- and late-Holocene vegetation and fire history at Biviere di Gela, a coastal lake in southern Sicily, Italy. Vegetation History and Archaeobotany 18: 371–387. doi:10.1007/s00334-009-0211-0.

Orshan G (1989) Plant phenomorphological studies in Mediterranean type ecosystems. Kluwer, Dordrecht-Boston-London.

Otto R, Krüsi BO, Schaffner S, Meuwly P, Delgado JD, Arévalo JR & Fernández-Palacios JM (2006) Ecología, estructura y dinámica de las poblaciones de la sabina canaria *Juniperus turbinata* ssp. *canariensis*) en Tenerife y La Gomera. RIULL - Universidad de La Laguna. http://riull.ull.es/xmlui/handle/915/21272.

Otto R, Barone R, Delgado JD, Arévalo JR, Garzón-Machado V, Cabrera-Rodríguez F & Fernández-Palacios JM (2012) Diversity and distribution of the last remnants of endemic juniper woodlands on Tenerife, Canary Islands. Biodiversity and Conservation 21: 1811–1834. doi:10.1007/s10531-012-0278-2.

Otto R, Krüsi BO, Delgado JD, Fernández-Palacios JM, García-del-Rey E & Arévalo JR (2010) Regeneration niche of the Canarian juniper: the role of adults, shrubs and environmental conditions. Annals of Forest Science 67: 709. doi:10.1051/forest/2010034.

Öztürk M, Tümen İ, Uğur A, Aydoğmus-Öztürk F & Topçu G (2011) Evaluation of fruit extracts of six Turkish *Juniperus* species for their antioxidant, anticholinesterase and antimicrobial activities. Journal of the Science of Food and Agriculture 91: 867–876. doi:10.1002/jsfa.4258.

Palacios P de, Esteban LG, Fernández FG, García-Iruela A, Conde M & Román-Jordán E (2014) Comparative wood anatomy of *Juniperus* from Macaronesia. IAWA Journal 35: 186–198. doi:10.1163/22941932-00000059.

Palamarev E (1989) Paleobotanical evidences of the Tertiary history and origin of the Mediterranean sclerophyll dendroflora. Plant Systematics and Evolution 162: 93–107. doi:10.1007/BF00936912.

Palamarev E, Bozukov V, Uzunova K, Petkova A & Kitanov G (2005) Catalogue of the Cenozoic plants of Bulgaria (Eocene to Pliocene). Phytologia Balkanica 11: 215–364.

Pandža M (2004) Vegetation of Phoenician juniper macchia – *Pistacio lentisci-Juniperetum phoeniceae* Trinajstić 1987 (Oleo-Ceratonion) on the island of Murter and the small surrounding islands. Natura Croatica 13: 201–212.

Pandža M, Milović M, Krpina V & Tafra D (2011) Vascular flora of the Vrgada islets (Zadar archipelago, eastern Adriatic). Natura Croatica 20: 97–116.

Paradis G (1993) Les formations à *Juniperus phoenicea* et à *Juniperus oxycedrus* subsp. *macrocarpa* sur le littoral de la Corse. Colloques Phytosociologiques 20: 345–358.

Pavon D, Véla E & Médail F (2020) Are Mediterranean trees well known? "*Juniperus turbinata*" (Cupressaceae), a common but misunderstood taxon. Ecologia Mediterranea 46: 77–104. doi:10.3406/ecmed.2020.2110.

Pavón García J, De la Cruz Rot M, Rejos Ballesteros J & Bartolomé Esteban C (2006) Estrategía sexual de las poblaciones de sabina albar y sabina negral. Actas del 3º coloquio internacional sobre sabinares y enebrales, Soria, 24-26 mayo 2006. 1: 365–372.

Pérez Latorre AV & Cabezudo B (2009) Gimnospermas. In: Flora vascular de Andalucía Oriental 1 (ed. by G Blanca, B Cabezudo, M Cueto, C Fernández López & C Morales Torres) Consejería de Medio Ambiente, Junta de Andalucía, Sevilla, pp. 77–93.

Pérez Latorre AV, Casimiro-Soriguer Solanas F, García Sánchez J & Cabezudo B (2014) Flora y vegetación del Paraje Natural Desfiladero de los Gaitanes y su entorno (Málaga, España). Acta Botanica Malacitana 39: 129–177. doi:10.24310/abm.v39i1.2599.

Pignatti S (2017) Flora d'Italia, 1. 2nd ed. Edagricole, Milano.

Pinna MS, Grillo O, Mattana E, Cañadas EM & Bacchetta GL (2014) Inter- and intraspecific morphometric variability in *Juniperus* L. seeds (Cupressaceae). Systematics and Biodiversity 12: 211–223. doi:10.1080/14772000.2014.904827.

Postigo-Mijarra JM, Barrón E, Gómez Manzaneque F & Morla Juaristi C (2009) Floristic changes in the Iberian Peninsula and the Balearic Islands during the Cenozoic. Journal of Biogeography 36: 2025–2043. doi:10.1111/j.1365-2699.2009.02142.x.

Pound MJ & Salzmann U (2017) Heterogeneity in global vegetation and terrestrial climate change during the late Eocene to early Oligocene transition. Scientific Reports 7: 43386. doi:10.1038/srep43386.

POWO (2023) https://powo.science.kew.org/taxon/676800-1.

Quézel P & Barbero M (1981) Contribution a l'étude des formations pre-steppiques à Genévriers au Maroc. Boletim da sociedade Broteriana Ser. 2. 53: 1137–1160.

Quézel P & Médail F (2003) Écologie et biogéographie des forêts du basin méditerranéen. Elsevier, Paris

Rajčević NF, Labus MG, Dodoš TZ, Novaković JJ & Marin PD (2018) *Juniperus phoenicea* var. *turbinata* (Guss.) Parl. leaf essential oil variability in the Balkans. Chemistry and Biodiversity 15: e1800208. doi:10.1002/cbdv.201800208.

Rivas-Martínez S, Peñas Á, del Río S, Díaz TE & Rivas-Sáenz S (2017) Bioclimatology of the Iberian Peninsula and the Balearic Islands. In: The vegetation of the Iberian Peninsula 1 (ed. by J Loidi) Plant and Vegetation 12: 29–80. doi:10.1007/978-3-319-54784-8_2.

Rivas-Martínez S, Wildpret W & Pérez de Paz PL (1993) Datos sobre *Juniperus phoenicea* aggr. (Cupressaceae). Itinera Geobotanica 7: 509–512.

Roma-Marzio F, Najar B, Alessandri J, Pistelli L & Peruzzi L (2017) Taxonomy of prickly juniper (*Juniperus oxycedrus* group): A phytochemical-morphometric combined approach at the contact zone of two cryptospecies. Phytochemistry 141: 48–60. doi:10.1016/j.phytochem.2017.05.008.

Romo A (2018) Woody plants on an oceanic island: seed dispersal syndromes, life forms, life-history and chorology along an altitudinal gradient of the biosphere reserve of El Hierro, Canary Isles (Spain). In: Biologia i ekologia roślin drzewiastych (ed. by D Tomaszewski & AM Jagodziński) Materiały konferencyjne. Bogucki Wydawnictwo Naukowe, Poznań. pp 51–65.

Romo A, Mazur M, Salvà-Catarineu M & Boratyński A (2019) A re-evaluated taxon: Genetic values and morphological characters support the recognition of the Canary Island juniper of the *phoenicea* group at a specific level. Phytotaxa 406: 64–70. doi:10.11646/phytotaxa.406.1.3.

Romo AM & Salvà-Catarineu M (2013) Phytodiversity of the remnants of Canarian endemic juniper woodlands on El Hierro, Canary Islands. Ecologia Mediterranea 39: 191–199.

Romo AM, Boratyński A & Salvà-Catarineu M (2014) Diversidad funcional de los sabinares en una isla oceánica: El Hierro, Islas Canarias; Functional diversity of *Juniperus* woodlands on an Oceanic Island: El Hierro, Canary Isles. In: Biogeografía de Sistemas Litorales. Dinámica y Conservación (ed. by R Cámara, B Rodríguez & JE Muriel) Universidad de Sevilla, Sevilla, pp. 197–201.

Rossi F, Facini O, Rotondi A, Loreti S & Georgiadis T (2001) Optical properties of juniper and lentisk canopies in a coastal Mediterranean macchia shrubland. Trees 15: 462–471. doi:10.1007/s00468-001-0132-8.

Rotondi A, Rossi F, Asunis C & Cesaraccio C (2003) Leaf xeromorphic adaptations of some plants of a coastal Mediterranean macchia ecosystem. Journal of Medietarranen Ecology 4: 25–35.

Rumeu B, Elias RB, Padilla DP, Melo C & Nogales M (2011) Differential seed dispersal systems of endemic junipers in two oceanic Macaronesian archipelagos: the influence of biogeographic and biological characteristics. Plant Ecology 212: 911–921. doi:10.1007/s11258-010-9875-x.

Rumeu B, Nogales M, Elias RB, Padilla D, Resendes T, Rodriguez A, Valdés F & Dias E (2009a) Contrasting phenology and female cone characteristics of the two Macaronesian island endemic cedars (*Juniperus cedrus* and *J. brevifolia*). European Journal of Forest Research 128: 567–574. doi:10.1007/s10342-009-0304-4.

Rumeu B, Padilla D & Nogales M (2009b) The key role of a Ring Ouzel (*Turdus torquatus*) wintering population in seed dispersal of the endangered endemic *Juniperus cedrus* in an insular environment. Acta Ornithologica 44: 199–204.

Runeberg J (1960) The chemistry of the order Cupressales. 31. The heartwood constituents of *Juniperus phoenicea* L. Acta Chemica Scandinavica 14: 1995–1998. doi:10.3891/acta.chem.scand.14-1995.

Sahib N, Boumediene M, Abid M, Mihamou A, Serghini-Caid H, Elamrani A, Hano C & Addi M (2022) Phenotypic comparison of three populations of *Juniperus turbinata* Guss. in North-Eastern Morocco. Forests 13: 287. doi:10.3390/f13020287.

Salvà-Catarineu M, Romo A, Mazur M, Zielińska M, Minissale P, Dönmez AA, Boratyńska K & Boratyński A (2021) Past, present, and future geographic range of the relict Mediterranean and Macaronesian *Juniperus phoenicea* complex. Ecology and Evolution 11: 5075–5095. doi:10.1002/ece3.7395.

Samoylenko V, Dunbar DC, Gafur MA, Khan SI, Ross SA, Mossa JS, El-Feraly FS, Tekwani BL, Bosselaers J & Muhammad I (2008) Antiparasitic, nematicidal and antifouling constituents from *Juniperus* berries. Phytotherapy Research 22: 1570–1576. doi:10.1002/ptr.2460

Sánchez-Gómez P, Jiménez JF, Cánovas JL, Vera JB, Hensen I. & Aouissat M (2018) Genetic structure and phylogeography of *Juniperus phoenicea* complex throughout Mediterranean and Macaronesian regions: different stories in one. Annals of Forest Science 75: 75. doi:10.1007/s13595-018-0741-7.

Sanguin H, Mathaux C, Guibal F, Prin Y, Mandin J-P, Gauquelin T & Duponnois R (2016) Ecology of vertical life in harsh environments: The case of mycorrhizal symbiosis with secular cliff climbing trees (*Juniperus phoenicea* L.). Journal of Arid Environments 134: 132–135. doi:10.1016/j.jaridenv.2016.07.008.

Schulz C, Jagel A & Stutzel T (2003) Cone morphology in *Juniperus* in the light of cone evolution in Cupressaceae s.l. Flora 198: 161–177. doi:10.1078/0367-2530-00088.

Sherif AS & El-Taife A (1986) Flora of Lybia. Gymnosperms. Department of Botany, Faculty of Science Tripoli University (formerly Al-Fateh University), Tripoli.

Stewart JR, Lister AM, Barnes I & Dalén L (2010) Refugia revisited: individualistic responses of species in space and time. Proceedings of the Royal Society B 277: 661–671. doi:10.1098/rspb.2009.1272.

Stierstorfer C (2005) The vascular plant vegetation in the forest belt of El Hierro (Canary Islands). Dissertationes Botanicae 393. Cramer, Berlin-Stuttgart.

Stockey RA, Kvaček J, Hill RS, Rothwell GW & Kvaček Z (2005) The fossil record of Cupressaceae sensu lato. In: A monograph of Cupressaceae and *Sciadopitys* (ed. by A Farjon) Royal Botanic Gardens, Kew, pp. 54–68.

Taib A, Morsli A, Chojnacka A, Walas Ł, Sękiewicz K, Boratyński A, Romo À & Dering M (2020) Patterns of genetic diversity in North Africa: Moroccan-Algerian genetic split in *Juniperus thurifera* subsp. *africana*. Scientific Reports 10: 4810. doi:10.1038/s41598-020-61525-x.

Takhtajan A (1986) Floristic regions of the world. University of California Press, Berkeley.

Tavares L, McDougall GJ, Fortalezas S, Stewart D, Ferreira RB & Santos CN (2012) The neuroprotective potential of phenolic-enriched fractions from four *Juniperus* species found in Portugal. Food Chemistry 135: 562–570. doi:10.1016/j.foodchem.2012.05.023.

Terrab A, Hampe A, Lepais O, Talavera S, Vela E & Stuessy TF (2008) Phylogeography of North African Atlas cedar (*Cedrus atlantica*, Pinaceae): combined molecular and fossil data reveal a complex Quaternary history. American Journal of Botany 95: 1262–1269. doi:10.3732/ajb.0800010.

Thompson JD (2005) Plant evolution in the Mediterranean. Oxford University Press, Oxford.

Thompson JD (2020) Plant Evolution in the Mediterranean: Insights for conservation, 2nd ed. Oxford University Press, Oxford. doi:10.1093/oso/9780198835141.001.0001.

Tison JM, Jauzein P & Michaud H (2014) Flore de la France méditerranéenne continentale. Naturalia Publications, Turriers.

Tomé L, Jambrina-Enríquez M, Égüez N, Herrera-Herrera AV, Davara J, Marrero Salas E, Arnay de la Rosa M & Mallol C (2022) Fuel sources, natural vegetation and subsistence at a high-altitude aboriginal settlement in Tenerife, Canary Islands: Microcontextual geoarchaeological data from Roques de García Rockshelter. Archaeological and Anthropological Sciences 14:195. doi:10.1007/s12520-022-01661-9.

Tsiourlis G, Konstantinidis P & Xofis P (2016) Syntaxonomy and synecology of *Juniperus phoenicea* L. shrublands in Greece. Journal of Environmental Protection and Ecology 17: 182–190.

Turland NJ, Wiersema JH, Barrie FR, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Kusber W-H, Li D-Z, Marhold K, May TW, McNeill J., Monro AM, Prado J, Price MJ & Smith GF (2018) International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regnum Vegetabile 159. Glashütten: Koeltz Botanical Books. doi:10.12705/Code.2018.

Van Andel TH (2002) The climate and landscape of the Middle Part of the Weichselian Glaciation in Europe: The Stage 3 Project. Quaternary Research 57: 2–8. doi:10.1006/qres.2001.2294.

Vardi J, Yegorov D, Degen-Eisenberg D, Boaretto E, Langgut D, Avni Y & Caracuta V (2023) The utilization and extinction of Juniper trees from the Negev desert (Israel) - Data from a late 6th–5th millennia site of Har Harif. Journal of Arid Environments 210: 104906. doi:10.1016/j.jaridenv.2022.104906.

Venditti A, Maggi F, Quassinti L, Bramucci M, Lupidi G, Ornano L, Ballero M, Sanna C, Bruno M, Rosselli S & Bianco A (2018) Bioactive constituents of *Juniperus turbinata* Guss. from La Maddalena Archipelago. Chemistry & Biodiversity 15: e1800148. doi:10.1002/cbdv.201800148.

Vicente Orellana JA & Galán de Mera A (2019) *Juniperus turbinata* Guss. (Cupressaceae), novedad para la flora de Extremadura (España). Acta Botanica Malacitana 44: 79–81. doi:10.24310/abm.v44i0.5386.

Vidaković A, Šatović Z, Tumpa K, Idžojtić M, Barišić A & Poljak I (2024) Secondary sexual dimorphism and morphological diversity in two allopatric juniper species: *Juniperus oxycedrus* and *J. deltoids*. Acta Botanica Croatica 83: 14–25. doi:10.37427/botcro-2024-007.

Villar L, Sesé JA & Ferrández JV (1997) Atlas de la flora del Pirineo Aragonés, 1. Consejo de Protección de la Naturaleza de Aragón, Huesca.

Wazen N, Garavaglia V, Picard N, Besacier C & Fady B (2020) Distribution maps of twenty-four Mediterranean and European ecologically and economically important forest tree species compiled from historical data collections. Annals of Silvicultural Research 44: 95–101. https://journals-crea.4science.it/index.php/asr.

Whitham TG, Bailey JK, Schweitzer JA, Shuster SM, Bangert RK, LeRoy CJ, Lonsdorf EV, Allan GJ, DiFazio SP, Potts BM, Fischer DG, Gehring CA, Lindroth RL, Marks JC, Hart SC, Wimp GM & Wooley SC (2006) A framework for community and ecosystem genetics: From genes to ecosystems. Nature Reviews Genetics 7: 510–523. doi:10.1038/nrg1877.

Willis JK & McElwain JC (2002) The evolution of plants. Oxford University Press, Oxford, New York. doi:10.1093/aob/mcf232.

Zachos J, Pagani M, Sloan L, Thomas E & Billups K (2001) Trends, rhythms, and aberrations in global climate 65 Ma to present. Science (New York, N.Y.) 292: 686–693. doi:10.1126/science.1059412.

Zohary M (1973) Geobotanical foundations of the Middle East. Fischer–Swets and Zeitlinger, Stuttgart–Amsterdam.