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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

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

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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

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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 Valleseco 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 Tethys 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.,

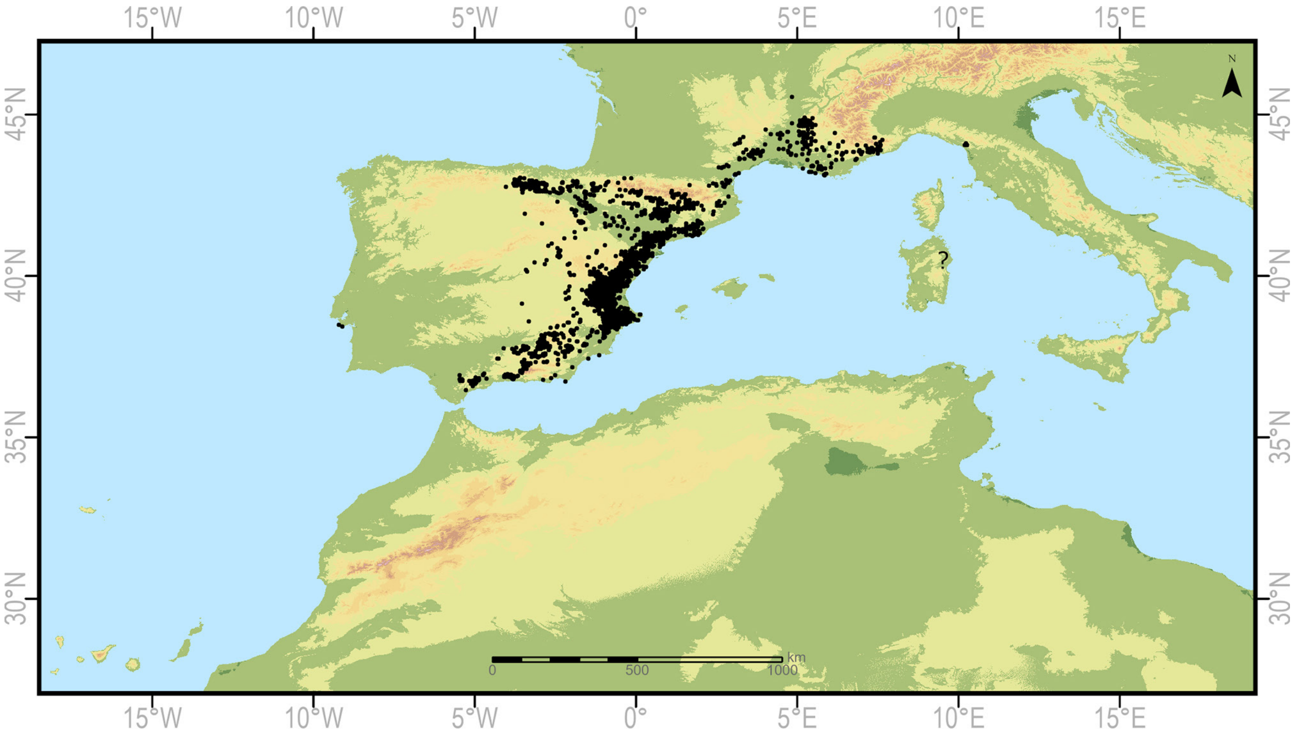

Fig. 1. Distribution of *Juniperus phoenicea* s.s. (after Salvà Catarineu et al., 2021: Fig. 1, supplemented)

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

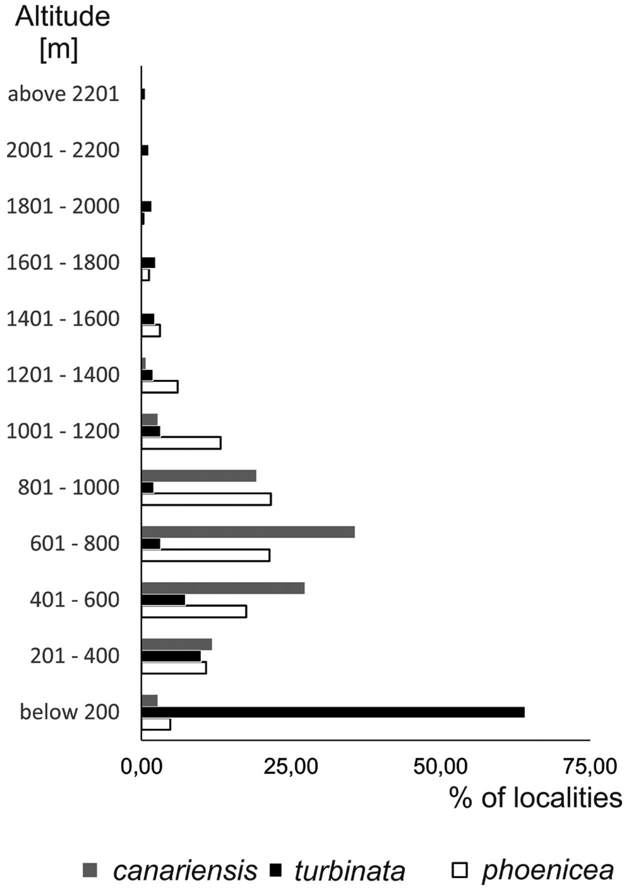

Fig. 2. Percentage of georeferenced localities of *Juniperus canariensis* (canariensis), *J. turbinata* (turbinata) and *J. phoenicea* s.s. (phoenicea) depending on elevation (after Salvà Catarineu et al., 2021: Fig. 2, supplemented)

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).

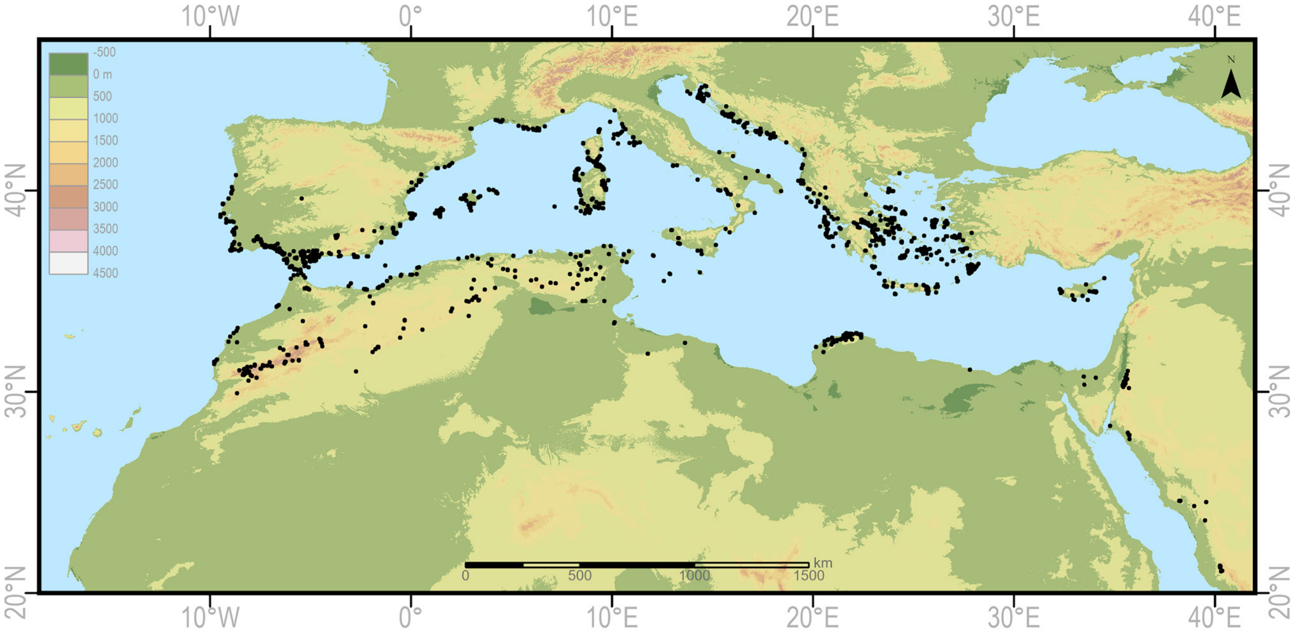

Fig. 3. Geographic distribution of *Juniperus turbinata* on the topographic background (after Salvà Catarineu et al., 2021: Fig. 1, supplemented)

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.

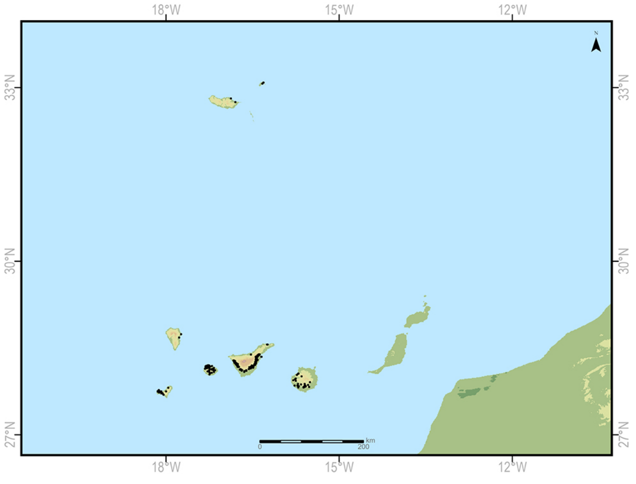

Fig. 4. Geographic distribution of *Juniperus canariensis* on the topographic background (after Salvà-Catarineu et al., 2021: Fig. 1, supplemented)

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. 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

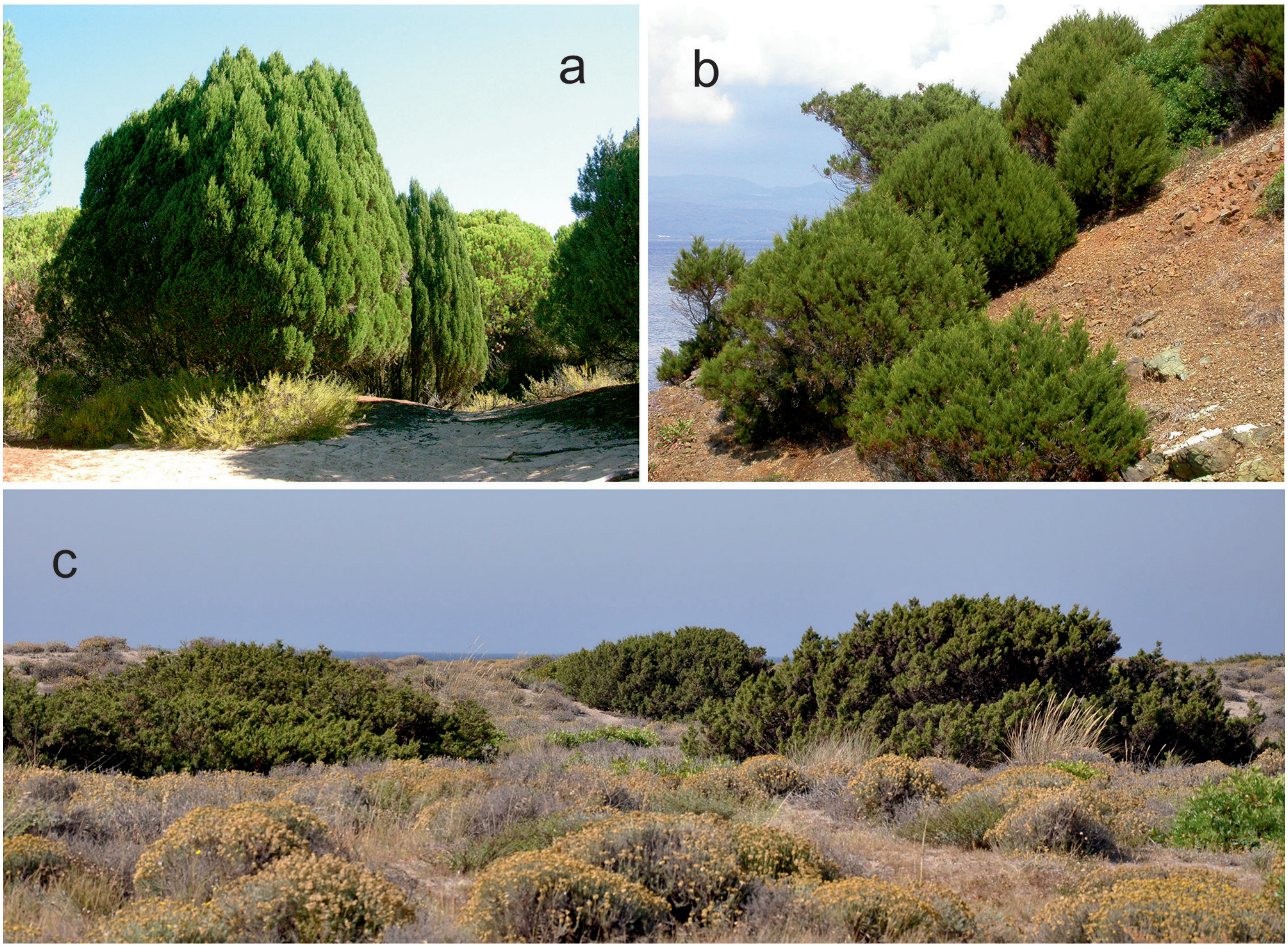

Fig. 6. *Juniperus turbinata* habit: conical crowns of specimens growing on the Punta Umbira, Cadiz, Spain (a) and on the slopes above the Gulf of Toroni Kassandras on Akros Agios Nicolaos, Kassandreia, Greece (b), prostrate individuals in Punta Entinas-Sabinar, Almeria, Spain (c) (Photo by A. Boratyński, 2008, 2004 and 2014, respectively)

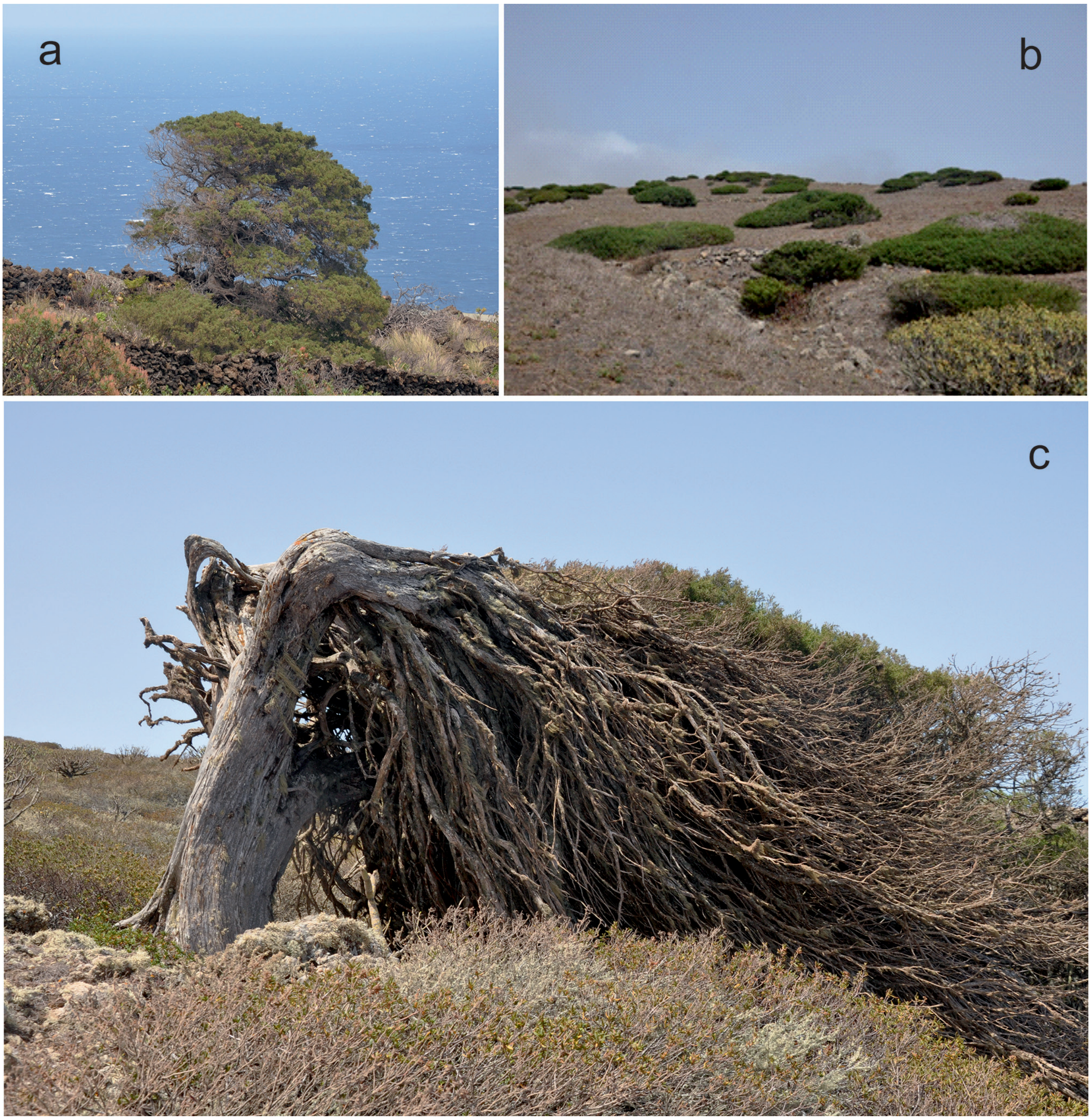

Fig. 7. *Juniperus canariensis* habit: broad crown of old specimen, Lodero, La Palma, Spain (a), prostrate young shrubs; every patch formed by one, two or more individuals (b), old tree with bent crown, Dehesa, El Hierro, Spain (c) (Photo by A. Boratyński, a – 2014, c – 2012)

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/cm^3, in dry state 0.80 g/cm^3 (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/cm^3. 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/cm^3 (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, nortерpenoid 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).

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