JSE Journal of Systematics and Evolution

doi: 10.1111/jse.12478

Research Article

Out of the Middle East: New phylogenetic insights in the genus *Tamarix* (Tamaricaceae)

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Received 7 August 2018; Accepted 19 December 2018; Article first published online 31 December 2018

Abstract *Tamarix* is one of the taxonomically most complex genera among the angiosperms, and there is little consensus regarding its infrageneric classification. Here we present the most complete phylogenetic reconstruction of the genus to date. This includes a DNA phylogenetic tree based on nuclear ribosomal ITS, and a plastid DNA phylogeny based on three intergenic spacers (*trnS-trnG, ndhF-rpl32*, and *trnQ-rps16*). In total, both nuclear and plastid phylogenetic analyses include more than 70 samples of 39 species from 27 countries, which represent close to 60% of the diversity of the genus. Two complementary trees, based only on one plastid marker, are also included. The first, based on *trnS-trnG*, is used to increase the number of species related to *T. amplexicaulis*. The second, based on *ndhF-rpl32,* is used to investigate the separation between *T. tetrandra* and *T. parviflora*. The incongruence between the available infrageneric classifications and the molecular results is confirmed. A reticulate evolution is inferred from the trees, showing characters such as vaginate leaves appearing at different stages along the evolutionary history of the genus. The presence of *T. canariensis* outside the Canary Islands is cast into doubt, and all such records from NW Africa and Europe are here considered to belong to *T. gallica.* The results also suggest independence of *T. karelinii* from *T. hispida,* and *T. parviflora* from *T. tetrandra.* Relationships between a number of species are still not resolved, and additional studies will be needed to further refine the complex taxonomy of *Tamarix.*

Key words: halophytes, ITS, ptDNA, systematics, taxonomy.

1 Introduction

Tamarix L. (Tamaricaceae Link) species are native to Africa and Eurasia, inhabiting mainly desert, sub-desert or arid zones, but are also found in freshwater riparian habitats in temperate and subtropical regions (Qaiser, 1981; Zohary, 1987). The genus is widespread in the Mediterranean, Irano-Turanian and Indian regions, where the highest number of species, and the two main diversity centres (East Mediterranean and Indo-Turanian, *sensu* Baum, 1978), are found (Baum, 1978, 1990; Villar et al., 2014a). From those two centres, *Tamarix* has reached the Eurasian parts of the Circumboreal Region, as well as the Indochinese, Eastern Asiatic, Saharo-Arabian, Sudano-Zambezian, Karoo-Namib and Macaronesian regions (names according to Takhtajan, 1986) (Baum, 1978; for a more detailed phytogeographical division of Africa and Southwest Asia, see White & Leonard, 1991).

In addition, some species (e.g., *T. aphylla* (L.) Karst., *T. ramosissima* Ledeb.) have been naturalized in Oceania (Csurhes, 2008) and America, where they were introduced as ornamentals in the 19th century (Prince & Sons, 1837; Warner Harper, 1903). In the last decades, many studies have dealt with the invasive potential of *Tamarix,* particularly in North America, where it is considered as the second worst plant invasion in the USA (Baum, 1967; Di Tomaso, 1998; Stromberg, 1998; Gaskin & Schaal, 2003; Villar et al., 2014a).

Tamarix comprises tall shrubs and trees up to 5–6 m in height, although some species such as *T. aphylla* may reach heights close to 20 m under favourable conditions. The leaves are deciduous, marcescent, or perennial, showing diverse shapes that fit into three categories: (i) vaginate, surrounding the twigs all along the limb, or pseudo-vaginate, with a visible scar along the contact of both leaf sides; (ii) amplexicaul, deltoid shaped, thick and broader than long, embracing more than half the twig or even clasping or scale-like, or triangular lanceolate, only the lower half amplexicaul; and (iii) scale-like, lanceolate, with a slightly decurrent narrow base or wide auriculate base, usually not embracing more than half of the twig. Intermediate forms can also be found. The inflorescences are formed as pedunculate racemes that are solitary, fasciculate, in simple panicles or in compound panicles. Raceme arrangements may vary at different flowering periods over the year (Baum, 1978; Yang & Gaskin, 2007). Bracts range from 0.5 to 8 mm long, usually one per flower, and have different shapes. The sepals and petals, 4–5 (9), show diverse shapes and the latter can be persistent or deciduous after anthesis. The stamens, 4–5 (10), 8–10 (15), can be equal in number, double, or unrelated to the number of petals and

sepals. The insertion of the staminal filaments on the nectariferous disc has been widely used as a diagnostic character (Baum, 1978). They can be inserted truncately or progressively above the disc lobes, or between the lobes. The gynoecium is usually formed of three carpels, sometimes four, exceptionally five or more. The fruits are dry capsules, dehiscent by 3 (4) valves. The seeds are oval shaped, 0.5–1.5 mm long, with an apical pappus formed of simple hollow hairs, with excavations at the base.

Several authors have made notable contributions to the knowledge of *Tamarix*. Prior to the 20th century, well-known botanists and naturalists such as Pallas (1789), Poiret (1789), Loureiro (1790), Bieberstein (1808), Willdenow (1816), Desvaux (1824), Ehrenberg (1827), Candolle (1828), Ledebour (1829, 1843), Bunge (1833, 1851), Webb & Berthelot (1840), Walpers (1843), Boissier (1849, 1856, 1867), and Niedenzu (1895) added new species to the genus, or dealt with its taxonomic classification in different geographic areas.

During the 20th century, the number of taxa continued to increase, particularly on account of local treatments (Freyn, 1903; Pau, 1906, 1922; Maire, 1931; Sennen, 1932; Sennen & Mauricio, 1934; Maire, 1935, 1938). Afterwards, Gorschkova (1949) made a remarkable contribution on the Central-Asian species, translated into English by Shinners (1957). Baum (1966) published the last comprehensive monograph of the genus, later re-edited and published with minor modifications (Baum, 1978). That monograph included almost every *Tamarix* name published so far, with specific and intraspecific ranks, accepting 54 species arranged in three sections and nine series. This work is still a key reference for the genus *Tamarix* worldwide, and has been the basis for most local and regional treatments of *Tamarix* (Pignatti, 1982; De Martis et al., 1984, 1986; Cirujano, 1993; Venturella et al., 2007; Salazar & Quesada, 2011).

Despite the numerous taxonomic revisions carried out in the last two centuries, *Tamarix* has been always considered a particularly difficult angiosperm genus for taxonomic classification (Bunge, 1852; Baum, 1978). Many groups of species are separated by small phenotypic differences, some only seasonally apparent, and therefore accurate identification is very difficult (Villar et al., 2012, 2014b, 2015a). Because of this, some species distributions have been erroneously expanded (Villar et al., 2012; Villar & Alonso, 2016). Variation in morphology within proposed species has resulted in a highly unresolved taxonomy, with a large number of synonyms and name combinations between more than 200 taxa, at different ranks, described to date (Villar et al., 2014a, 2015b; Villar & Alonso, 2017). Therefore, the number of species varies from 54 accepted by Baum (1966, 1978) to "about 90" suggested by Zohary (1987) or Yang & Gaskin (2007). Of course, Baum (1966) could not check the validity of the species (13 at least) that were described after the publication of his monograph (Baum, 1968; Liu, 1979; Qaiser, 1981; Zhang & Liu, 1988; Çakan & Zieliński, 2004; Villar et al., 2015a). Inside the above mentioned ranks, a reasonable estimation would be around 70 to 75 species.

In the 21st century, molecular techniques have been used to clarify the taxonomy of *Tamarix*. However, most of these efforts focused on the genetic characterization of invasive species out of their native range, as well as on the identification of hybrid individuals (Gaskin & Schaal, 2003; Gaskin & Shafroth, 2005; Gaskin & Kazmer, 2009; Mayonde et al., 2015). Moreover, plastid phylogenetic data were also used to identify a new species of *Tamarix* (Villar et al., 2015a). Some of the aforementioned works already showed that the series and sections proposed by Baum (1978) do not correspond to natural groups (Gaskin & Schaal, 2003; Villar et al., 2015a). Recent regional phylogenetic approaches have been conducted for: (i) Iran (Arianmanesh et al., 2016), with unreliable results due to mixing nuclear and plastid sequences from different specimens, usage of incorrectly identified GenBank specimens and other key mistakes; and (ii) China (Sun et al., 2016), with interesting results that are coincident with ours in certain groups.

In the present study, we analyze taxa from all previously described sections of *Tamarix* using nuclear and plastid DNA markers, with special focus on the Mediterranean region, but including representatives from Central and East Asia, and the Cape region of Africa. This represents the most complete molecular phylogenetic study of *Tamarix* conducted so far. The main aims of our study are to: (i) establish a phylogeny of *Tamarix* in order to evaluate the correctness and utility of current classification, (ii) detect the weakest points in the taxonomy of the genus, as a tool to point out possible future research lines, (iii) assess the value of the morphological characters used in classification and systematics of *Tamarix*.

2 Material and Methods

2.1 Taxon sampling

A total of 39 species of *Tamarix,* plus three outgroup Tamaricaceae, were sampled, representing most of the higher taxonomic units above the species level that have been proposed in the Tamaricaceae to date. Our samples also represent most of the geographical range of the family (Table 1; Fig. 1), including 27 countries. We sampled plant material from field specimens collected by the authors or collaborators, as well as from fragments provided by different herbaria (ABH, G, K, MO, P, TURP, VAL and W; Herbarium codes according to Thiers, 2018 continuously updated). Removal of fragments was properly marked on the herbarium sheets by the respective curators. Newly collected field specimens were deposited at ABH, MO and NPARL (USDA ARS, MT, USA; Gaskin accessions) (Table 1).

To assure their taxonomic identity, no specimens were included in this study without previous direct morphological examination by the authors. Many studies dealing with the taxonomy of *Tamarix* were consulted (Linnaeus, 1753; Pallas, 1789; Poiret, 1789; Loureiro, 1790; Willdenow, 1816; Desvaux, 1824; Ehrenberg, 1827; Candolle, 1828; Ledebour, 1829; Ledebour, 1843; Boissier, 1849; Bunge, 1851, 1852; Boissier, 1867; Niedenzu, 1895; Gorschkova, 1949; Baum, 1966, 1968, 1978; Qaiser, 1981; Zohary, 1987; Cirujano, 1993; Zieliński, 1994; Yang & Gaskin, 2007; Salazar & Quesada, 2011; Villar et al., 2012; Samadi et al., 2013; Villar et al., 2014a, 2014b, 2014c, 2014d, 2015a, 2015b), including original descriptions, treatments in local floras, and taxonomic papers. Herbarium materials from ABH, BCMEX, BM, G, HUAL, JAEN, K, MA, MO, MPU, P, PR, PRC VAL and W were examined (over 2500 specimens), with special attention to type specimens. Outgroup specimens included *Reaumuria alternifolia* (Labill.) Britten, *Myricaria*

Table 1 Material used for molecular analyses

Label on figures	Taxon	Country and location	Collectors and identification number	GenBank reference *trnS-trnG*	GenBank reference *trnQ-rps16*	GenBank reference *ndhF-rpl32*	GenBank reference ITS
Myricaria bracteata	*Myricaria bracteata* Royle	Kazakhstan, 25 km West of Almaty	Gaskin 1148. NPARL	KP244372	KP244398	KP244424	MH626260
Myrtama elegans	*Myrtama elegans* (Royle) Ovcz. & Kinzik.	China, Karakorum mountains, Yacheng Xian	B. Bartholomew et al. MO5799414	KP244373	KP244399	KP244425	MH626261
Reaumuria alternifolia	*Reaumuria alternifolia* (Labill.) Britten	Iran, Golestan, road from Shahrud to Gorgan	Gaskin 919. NPARL	KP244371	KP244397	KP244423	MH626262
Tamarix africana T13Mo	*Tamarix africana* Poir.	Morocco, Debdou	J.L. Villar et al. ABH54205	KP244378	KP244404	KP244430	MH626263
T. africana T17CRO	*Tamarix africana* Poir.	Croatia, Pakostane, Vransko-Jezero	J.L. Villar & E. Martínez. ABH57846	MH626121	MH626169	MH626214	MH626264
T. africana T1Ge	*Tamarix africana* Poir.	Spain, Girona, Port de la Selva	M.B. Crespo & E. Camuñas. ABH55078	MH626122	MH626170	MH626215	MH626265
T. africana T2To	*Tamarix africana* Poir.	Spain, Toledo, Laguna grande de Villacañas	A. Juan. ABH55362	MH626123	MH626171	MH626216	MH626266
T. africana T2V	*Tamarix africana* Poir.	Spain, Valencia, Villargordo del Cabriel	J.L. Villar et al. ABH55366	KP244379	KP244405	KP244431	MH626267
T. africana T30CD	*Tamarix africana* Poir.	Italy, Sardinia, Estintino	J.L. Villar et al. ABH54439	MH626124	MH626172	MH626217	MH626268
T. amplexicaulis T24AG	*Tamarix amplexicaulis* Ehrenb.	Algeria, Biskra	M.A. Alonso et al. ABH70685	MH626125	MH626173	MH626218	MH626269
T. amplexicaulis T25AG	*Tamarix amplexicaulis* Ehrenb.	Algeria, Biskra	M.A. Alonso et al. ABH70686	MH626126	MH626174	MH626219	MH626270
T. amplexicaulis T26AG	*Tamarix amplexicaulis* Ehrenb.	Algeria, Biskra	M.A. Alonso et al. ABH70687	MH626127	MH626175	MH626220	MH626271
T. amplexicaulis T27AG	*Tamarix amplexicaulis* Ehrenb.	Algeria, Biskra	M.A. Alonso et al. ABH70688	MH626128	MH626176	MH626221	MH626272
T. androssowii W08-98	*Tamarix androssowii* Litv.	Armenia, Kotayk, Asat river valley, 9 km Southwest of Garni	T. Voskanyan et al. W2008-05598	MH626129	MH626177	MH626222	MH626273
T. androssowii JG871	*Tamarix androssowii* Litv.	Iran, between Dameqan and Semnan	J. Gaskin. MO5568887	MH626130	MH626178	MH626223	–
T. aphylla TA1Mo	*Tamarix aphylla* (L.) H. Karst	Morocco, between Nador and Al-Hoceima	J.L. Villar et al. ABH54280	KP244374	KP244400	KP244426	MH626274
T. aphylla TACD	*Tamarix aphylla* (L.) H. Karst	Italy, Sardinia, Is Arutas	J.L. Villar et al. ABH54422	KP244375	KP244401	KP244427	MH626275
T. arabica P359	*Tamarix arabica* Bunge	Yemen	T. Monod. P05113359	–	–	–	MH626276
T. arabica P360	*Tamarix arabica* Bunge	Yemen	T. Monod. P05113360	–	–	–	MH626277
T. arborea W06-39	*Tamarix arborea* (Sieber ex Ehrenb.) Bunge	Egypt, Wadi el Gedid-Dakhla, 6 km East of Tendida	J. Walter. W2006-12039	MH626131	MH626179	MH626224	MH626278

Continued

Table 1 Continued

Label on figures	Taxon	Country and location	Collectors and identification number	GenBank reference *trnS-trnG*	GenBank reference *trnQ-rps16*	GenBank reference *ndhF-rpl32*	GenBank reference ITS
T. arborea W06-41	*Tamarix arborea* (Sieber ex Ehrenb.) Bunge	Egypt, Wadi el Gedid-Dakhla, Sheik Muftah	J. Walter. W2006-12041	–	–	–	MH626279
T. arceuthoides JG825	*Tamarix arceuthoides* Bunge	Iran, between Teheran and Qom	J. Gaskin. MO5568891	MH626132	MH626180	MH626225	MH626280
T. arceuthoides JG846	*Tamarix arceuthoides* Bunge	Iran, North of Evaniki, road to Absurd	J. Gaskin. MO5568908	–	–	–	MH626281
T. aucheriana JG850	*Tamarix aucheriana* (Decne. ex Walp.) B.R. Baum	Iran, 25 km East of Garnar, road to Semnan	J. Gaskin. MO5568836	MH626133	–	–	MH626331
T. austromongolica JG10163	*Tamarix austromongolica* Nakai	China, cultivated at Turpan Botanical Garden	J. Gaskin 10163. NPARL	MH626134	MH626181	MH626226	MH626282
T. boveana T18Mo	*Tamarix boveana* Bunge	Morocco, Barrage Mohamed	J.L. Villar et al. ABH54183	KP244388	KP244414	KP244440	MH626283
T. boveana T2Gr	*Tamarix boveana* Bunge	Spain, Granada, Salado del Margen	J.L. Villar et al. ABH55339	MH626135	MH626182	MH626227	MH626284
T. boveana T7AG	*Tamarix boveana* Bunge	Algeria, Oran, La Macta	A. Juan et al. ABH56326	KP244387	KP244413	KP244439	MH626285
T. boveana Tb2Eb	*Tamarix boveana* Bunge	Spain, Zaragoza, Chiprana	J.L. Villar et al. ABH54330	KP244389	KP244415	KP244441	MH626286
T. canariensis Gara	*Tamarix canariensis* Willd.	Spain, Canary Islands, Tenerife, Garachico	M. Martínez & M.B. Crespo. ABH53701	MH626136	MH626183	MH626228	–
T. canariensis Gui	*Tamarix canariensis* Willd.	Spain, Canary Islands, Tenerife, Güímar	M. Martínez & M.B. Crespo. ABH53707	MH626137	MH626184	MH626229	–
T. canariensis TGC1	*Tamarix canariensis* Willd.	Spain, Canary Islands, Gran Canaria, Fuente de la Guirrera	J.L. Villar & E. Martínez. ABH69605	MH626138	MH626185	MH626230	MH626287
T. canariensis TGC8	*Tamarix canariensis* Willd.	Spain, Canary Islands, Gran Canaria, Dunas de Maspalomas	J.L. Villar & E. Martínez. ABH69599	MH626139	MH626186	MH626231	MH626288
T. chinensis JG202	*Tamarix chinensis* Lour.	South Korea	J.F. Gaskin 202. NPARL	MH626140	MH626187	MH626232	MH626289
T. dalmatica T1ALB	*Tamarix dalmatica* B.R. Baum	Albania, prox. Sarande	J.L. Villar & E. Martínez. ABH57830	KP244380	KP244406	KP244432	MH626290
T. dalmatica T6MNE	*Tamarix dalmatica* B.R. Baum	Montenegro, prox. Kotor	J.L. Villar & E. Martínez. ABH57844	KP244381	KP244407	KP244433	MH626291
T. elongata JG10176	*Tamarix elongata* Ledeb.	China, cultivated at Turpan Botanical Garden	J.F. Gaskin 10176, NPARL	MH626141	MH626188	MH626233	MH626292
T. gallica T23Ken	*Tamarix gallica* L.	Morocco, Kenitra	J.L. Villar et al. ABH69587	MH626142	MH626189	MH626234	MH626293
T. gallica T2Fr	*Tamarix gallica* L.	France, Saints Maries de la Mer	J.L. Villar & E. Martínez. ABH57865	KP244395	KP244421	KP244447	MH626294
T. gallica TC1Eb	*Tamarix gallica* L.	Spain, Tarragona, Delta del Ebro	J.L. Villar et al. ABH54331	KP244396	KP244422	KP244448	MH626295

Continued

Table 1 Continued

Label on figures	Taxon	Country and location	Collectors and identification number	GenBank reference *trnS-trnG*	GenBank reference *trnQ-rps16*	GenBank reference *ndhF-rpl32*	GenBank reference ITS
T. gansuensis JG10171	*Tamarix gansuensis* H.Z. Zhang ex P.Y. Zhang & M.T. Liu	China, cultivated at Turpan Botanical Garden	J.F. Gaskin 10171. NPARL	MH626143	MH626190	MH626235	–
T. gracilis JG10173	*Tamarix gracilis* Willd.	China, cultivated at Turpan Botanical Garden	J.F. Gaskin 10173, NPARL	MH626144	MH626191	MH626236	MH626296
T. hampeana T2MNE	*Tamarix hampeana* Boiss. & Heldr.	Montenegro, Ulcinj, Sveti Nikola	J.L. Villar & E. Martínez. ABH57893	MH626145	MH626192	MH626237	MH626297
T. hampeana T3MNE	*Tamarix hampeana* Boiss. & Heldr.	Montenegro, Ulcinj, Sveti Nikola	J.L. Villar & E. Martínez. ABH57891	KP244392	KP244418	KP244444	MH626298
T. hampeana T6GRE	*Tamarix hampeana* Boiss. & Heldr.	Greece, Epirus, Igoumenitsa	J.L. Villar & E. Martínez. ABH59025	KP244390	KP244416	KP244442	MH626299
T. hampeana T72GRE	*Tamarix hampeana* Boiss. & Heldr.	Greece, Neo Thornio, Camping Venezuela	J.L. Villar & E. Martínez. ABH59877	KP244391	KP244417	KP244443	MH626300
T. hispida Ivl	*Tamarix hispida* Willd.	Kazakhstan, Zhezkazgan	V. Ivlev. MO s.n.	MH626146	MH626193	MH626238	MH626301
T. hispida JG10164	*Tamarix hispida* Willd.	China, cultivated at Turpan Botanical Garden	J.F. Gaskin 10164. NPARL	MH626147	MH626194	MH626239	MH626302
T. hohenackeri JG828	*Tamarix hohenackeri* Bunge	Iran, Road from Rahst to Teheran, near Gangeh	J.F. Gaskin. MO5568893	MH626148	MH626195	MH626240	–
T. hohenackeri W08-42	*Tamarix hohenackeri* Bunge	Georgia, Lekistskali gorge	N. Lachashvili. W2008-21042	MH626149	MH626196	MH626241	–
T. indica W67-10	*Tamarix indica* Willd.	Pakistan, 15 km South of Sehwan	K.H. Rechinger. W1967-1110	MH626150	MH626197	MH626242	MH626303
T. karelinii JG10161	*Tamarix karelinii* Bunge	China, cultivated at Turpan Botanical Garden	J.F. Gaskin 10161. NPARL	MH626151	MH626198	MH626243	MH626304
T. karelinii JG144	*Tamarix karelinii* Bunge	China, Xinjiang, Funkang	J.F. Gaskin 144. NPARL	MH626152	MH626199	MH626244	–
T. kermanensis W83-21	*Tamarix kermanensis* B.R. Baum	Iran, East of Bam	J. Leonard. W1983-09221	MH626153	MH626200	MH626245	MH626305
T. komarovii JG1059	*Tamarix komarovii* Gorschk.	Turkmenistan, East of Kum Dag	J.F. Gaskin 1059, NPARL	MH626154	–	–	–
T. laxa G-russ	*Tamarix laxa* Willd.	Russia, Kalmykia, Sadovoe	Russanovitch. G s.n.	–	–	–	MH626306
T. leptostachya Ivl	*Tamarix leptostachya* Bunge	Kazakhstan, Zhezkazgan	V. Ivlev. MO s.n.	–	–	–	MH626307
T. leptostachya JG1158	*Tamarix leptostachya* Bunge	China, cultivated at Turpan Botanical Garden	J.F. Gaskin 1158. NPARL	–	–	–	MH626308
T. leptostachya JG10177	*Tamarix leptostachya* Bunge	China, cultivated at Turpan Botanical Garden	J.F. Gaskin 10177. NPARL	MH626155	MH626201	MH626246	MH626309
T. macrocarpa W07-67	*Tamarix macrocarpa* Ehrenb. ex Bunge	Egypt, Dakhleh Oasis, between Sheik Wally and Mut	J. Walter. W2007-14067	MH626156	MH626202	MH626247	MH626310
T. minoa NT	*Tamarix minoa* J.L. Villar et al.	Greece, Crete, Georgioupoli	N.J. Turland. & P. Bareka. MO6207620	KP244384	KP244410	KP244436	MH626311

Continued

Table 1 Continued

Label on figures	Taxon	Country and location	Collectors and identification number	GenBank reference *trnS-trnG*	GenBank reference *trnQ-rps16*	GenBank reference *ndhF-rpl32*	GenBank reference ITS
T. minoa T2CR	*Tamarix minoa* J.L. Villar et al.	Greece, Crete, Georgioupoli	M.A. Alonso et al. ABH54194	KP244382	KP244408	KP244434	MH626312
T. minoa T4CR	*Tamarix minoa* J.L. Villar et al.	Greece, Crete, Georgioupoli	M.A. Alonso et al. ABH54195	KP244383	KP244409	KP244435	MH626313
T. nilotica TCR14	*Tamarix nilotica* (Ehrenb.) Bunge	Greece, Crete, Paleochora	J.L. Villar & A. Vicente. ABH54320	MH626157	MH626203	MH626248	MH626314
T. nilotica TCR5	*Tamarix nilotica* (Ehrenb.) Bunge	Greece, Crete, Kalo Nero	J.L. Villar & A. Vicente. ABH54317	MH626158	MH626204	MH626249	MH626315
T. nilotica W07-05	*Tamarix nilotica* (Ehrenb.) Bunge	Egypt, Sinai, Dahab, Wadi Qnai	J. Walter. W2007-25805	MH626159	MH626205	MH626250	–
T. nilotica W07-26	*Tamarix nilotica* (Ehrenb.) Bunge	Egypt, Sinai, Dahab, Wadi Qnai	J. Walter. W2007-25726	MH626160	MH626206	MH626251	–
T. octandra Ivl	*Tamarix octandra* Bunge	Kazakhstan, near Zhezkazgan Botanical Garden	V. Ivlev. MO s.n.	MH626161	MH626207	MH626252	MH626316
T. octandra JG189	*Tamarix octandra* Bunge	Russia, Kalmykia, road to Elista	A.K. Skvorstov. MO04992086	–	–	–	MH626317
T. octandra MO-07	*Tamarix octandra* Bunge	Russia, Kalmykia, between Elista and Astrakhan	V. Sagalaev & I. Rusanovich. MO05044107	MH626162	MH626208	MH626253	–
T. parviflora T8CR	*Tamarix parviflora* DC.	Greece, Crete, Aposelemis	M.A. Alonso et al. ABH54197	KP244393	KP244419	KP244445	MH626318
T. parviflora TCR10	*Tamarix parviflora* DC.	Greece, Crete, prox. Dermatos	J.L. Villar & A. Vicente. ABH54321	KP244394	KP244420	KP244446	MH626319
T. pycnocarpa JG1100	*Tamarix pycnocarpa* DC.	Turkmenistan, Turkmenbashi	J. F. Gaskin 1100. NPARL	MH626163	–	–	–
T. ramosissima W09-43	*Tamarix ramosissima* Ledeb.	Argentina, San Juan, Termas de Talacasto	J. Chiapella & E. Vitek. W2009-19143	MH626164	MH626209	MH626254	MH626320
T. senegalensis K242	*Tamarix senegalensis* DC.	Senegal, Mekhe	F.N. Hepper. K-DNA-38242	–	–	–	MH626321
T. senegalensis P240	*Tamarix senegalensis* DC.	Mauritania, Aftout	P.J. Lebrun. P05113240	MH626165	MH626210	MH626255	MH626322
T. smyrnensis JG4690	*Tamarix smyrnensis* Bunge	Turkey, Kutahya, Abide	H. Çakan. MO s.n.	MH626166	MH626211	MH626256	MH626323
T. smyrnensis JG4691	*Tamarix smyrnensis* Bunge	Turkey, Adana, Seyhan	H. Çakan. MO s.n.	–	–	–	MH626324
T. smyrnensis W03-43	*Tamarix smyrnensis* Bunge	Armenia, Yeghenazdor, 4 Km Southeast of Areni	E. Vitek et al. W2003-14043	MH626167	MH626212	MH626257	MH626325
T. taklamakanensis JG10172	*Tamarix taklamakanensis* M.-T. Liu	China, cultivated at Turpan Botanical Garden	J.F. Gaskin 10172. NPARL	MH626168	MH626213	MH626258	MH626326
T. tetragyna W07-28	*Tamarix tetragyna* Ehrenb.	Egypt, Sinai, Dahab, Wadi Qnai	J. Walter. W2007-25728	KP244385	KP244411	KP244437	MH626327

Continued

Table 1 Continued

Label on figures	Taxon	Country and location	Collectors and identification number	GenBank reference *trnS-trnG*	GenBank reference *trnQ-rps16*	GenBank reference *ndhF-rpl32*	GenBank reference ITS
T. tetragyna W07-48	*Tamarix tetragyna* Ehrenb.	Egypt, Dakhleh Oasis, South of el Qasr	J. Walter. W2007-14048	KP244386	KP244412	KP244438	MH626328
T. tetrandra G-Beli	*Tamarix tetrandra* Pall. ex M. Bieb.	Ukraine, Crimea, Sudak	Belianina & Schatko. G s.n.	–	–	MH626259	–
T. usneoides T1NMB	*Tamarix usneoides* E. Mey.	Namibia, Swakopmund	M. Martínez. ABH58684	KP244376	KP244402	KP244428	MH626329
T. usneoides TSA7	*Tamarix usneoides* E. Mey.	South Africa, between Lainsburg and Beaufort	M. Martínez. ABH58683	KP244377	KP244403	KP244429	MH626330

Herbaria: ABH, University of Alicante, Spain; G, Conservatory and Botanic gardens of Geneva, Switzerland; K, Royal Botanic Gardens, Kew, United Kingdom; MO, Missouri Botanical Garden, St. Louis, USA; NPARL, USDA ARS Northern Plains Agricultural Research Laboratory, Sidney, MT, USA; P, Herbarium of the National museum of Natural History, Paris, France; W, Natural History Museum of Viena, Austria.

bracteata Royle and *Myrtama elegans* (Royle) Ovcz. & Linzik., all of which belong to Tamaricaceae.

2.2 DNA extraction, amplification and sequencing

Total genomic DNA was extracted from silica-gel-dried or herbarium material using the modified method of 2x CTAB protocol (Doyle & Doyle, 1987) and purified using Ultraclean® PCR Clean-Up Kit (MOBIO, Carlsbad, CA, USA) minicolumns, according to the manufacturer's protocol.

Three plastid intergenic spacer regions were amplified for 68 *Tamarix* specimens using published primers: *trnQ*$^{(UUG)}$*-5'rps16* (Shaw et al., 2007), *trnS-trnG* (Hamilton, 1999), and *ndhF-rpl32* (Shaw et al., 2007). The nuclear ITS (Internal Transcribed Spacer) region was amplified for 69 *Tamarix* specimens using the primers ITS4 and ITS5 (White et al., 1990). Due to amplification problems, the samples used for plastid and nuclear DNA are not always identical. In addition, two complementary trees, based on single plastid regions, were created to gain insight into two specific topics that could not be resolved in the main phylogenetic trees due to amplification problems with some samples. The first tree, based on *trnS-trnG*, included 14 *Tamarix* specimens, increasing the number of individuals belonging to the group of species showing broadly amplexicaul leaves and double the number of stamens than sepals. Single specimens of the species *T. aucheriana* (Decne. ex Walp.) B.R. Baum, *T. pycnocarpa* DC. and *T. komarovii* Gorschk. were successfully sequenced for this plastid region. The second tree, based on *ndhF-rpl32,* included 11 *Tamarix* specimens and aimed to clarify the relationship between *T. parviflora* DC. and *T. tetrandra* Pall. ex M. Bieb., whose taxonomic identities have been considered either as synonyms or independent taxa, (e.g., Baum, 1978; Zieliński, 1994; Dimopoulos et al., 2013; Villar et al., 2014b). Other than *T. tetrandra* and *T. parviflora, T. aphylla* and *T. africana* Poir. would represent external groups as reflected in the large ptDNA phylogeny, plus some morphologically similar tetramerous species (*T. androssowii* Litv. and *T. octandra* Bunge), as well as the tetra-pentamerous species *T. hampeana* Boiss. & Heldr., whose distribution is to some extent sympatric with *T. parviflora.*

For all DNA regions, PCR amplifications were performed in a reaction volume of 25 μL, containing 22.5 μL ABGene 1.1x Master Mix, 2.5 mmol/L $MgCl_2$ (Thermo Scientific Waltham, MA, USA), 0.5 μL of bovine serum albumin (BSA), 0.5 μL of each primer (10 pmol/μl) and 1 μl of template DNA. The PCR programme used for all three plastid regions included an initial denaturation at 94 °C (2'), followed by 35 cycles of 94 °C (1'15''), 55 °C (1'30''), and 72 °C (2'), with a final elongation at 72 °C (10'). The profile used for ITS was an initial denaturation of 94 °C (2') followed by 30 cycles of 94 °C (1'), 53 °C (1') and 72 °C (1'), with a final elongation at 72 °C (5'). PCR products were purified using Ultraclean® PCR Clean-Up Kit (MOBIO, Carlsbad, CA, USA) mini-columns, following the manufacturer's instructions. Both strands were sequenced with the same primers for each region, and for all samples, at the Macrogen Europe Laboratory (www.macrogen.com) or at the USDA NPARL (Sidney MT, USA).

2.3 Phylogenetic analyses

Some specimens that had clear double signals in multiple key positions pointing to a possible hybrid origin were removed from the nDNA sequence matrix.

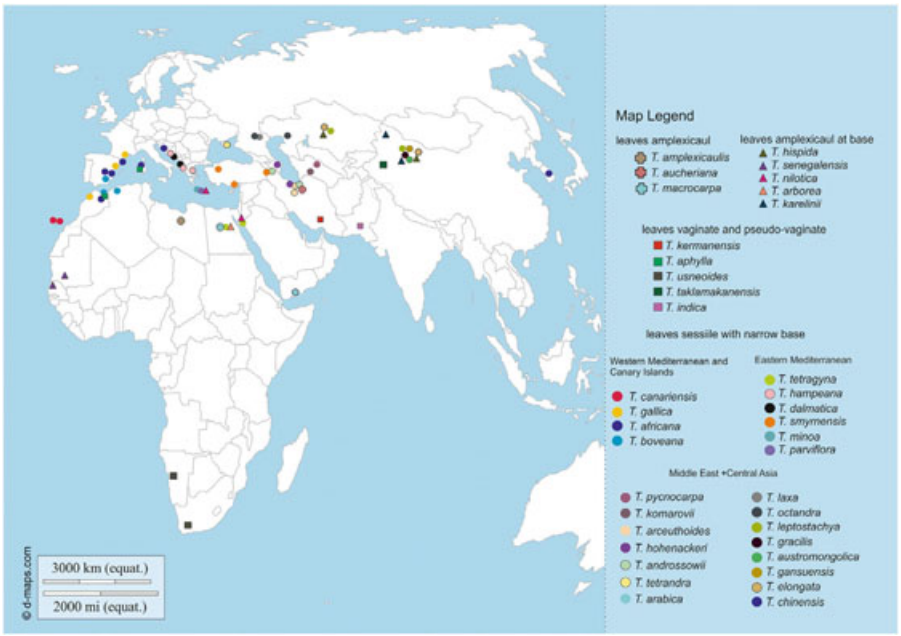

Fig. 1. Map of the locations of the material used in molecular analyses.

Sequencher 4.1 (Gene Codes Corp., Ann Arbor, MI, USA) was used to assemble the complementary strands. Each matrix was aligned using ClustalW, conducted in MEGA 7 (Kumar et al., 2016). Minor manual corrections were made for the final alignments. Maximum parsimony analyses (MP) and Bayesian analyses were performed on the combined plastid and nuclear matrices, as well as on the smaller single ptDNA region matrices. In the case of the large nDNA and ptDNA matrices, parsimony analyses were conducted in PAUP v.4.0b10 (Swofford, 2002), using heuristic search options. Searches included 1000 random addition replicates and tree-bisection-reconnection (TBR) branch swapping, with MULTREES in effect (keeping multiple most-parsimonious trees). All characters were treated as having equal weight. The shortest trees held in the heuristic search were used as initial trees for a final heuristic analysis, with the previously mentioned options. In order to reduce the number of trees retained, a second heuristic search was conducted on the trees stored in PAUP memory, keeping the same analysis parameters. MP support was assessed by 5000 bootstrap replicates, TBR branch swapping, simple addition sequence and with MULTREES in effect, keeping 10 trees per replicate (Salamin et al., 2003). In all MP analyses, gaps were treated as missing, thus avoiding long-branch attraction artefacts that were especially notable in the ptDNA phylogeny.

In the case of the two complementary plastid phylogenies, the MP analyses were also carried out in PAUP v.4.0b10 (Swofford, 2002), using Branch and Bound search options. Searches included 1000 random addition replicates with MULTREES in effect. All characters were treated as having equal weight. MP support was assessed using 1000 bootstrap replicates and the same settings as described for the main trees.

For the MP analyses, the consistency index (CI) and retention index (RI) were calculated excluding uninformative characters. Clades showing bootstrap (BS) values between 50–74% were considered as weakly supported, 75–89%: moderately supported, and 90–100%: strongly supported.

Bayesian Inference (BI) analyses were carried out using MrBayes v.3.2.5 (Ronquist et al., 2012). The most accurate evolutionary models required for Bayesian estimation were selected for every plastid and nuclear DNA matrix. In the case of the plastid combined matrix, models were selected individually for each of the three regions included. Model selection was undertaken using AICc (Akaike Information Criterion) (Posada & Crandall, 1998, Posada & Buckley, 2004), in JMODELTEST 2.1.5 (Darriba et al., 2012). Model parameters were included in MrBayes presets before running each of the analyses. In the case of the combined plastid DNA matrix, different model parameters were included for the matrix fragments corresponding to each ptDNA region. Default settings were used for MrBayes and two simultaneous independent analyses, each with four Markov Chain Monte Carlo (MCMC) were run for 10×10^6 generations and sampled every 1000 generations. The paired runs were checked for convergence and effective sample sizes in MrBayes output and Tracer 1.7.1 (Rambaut & Drummond, 2014). The first 25% of the trees were excluded ("burn-in") and the remaining trees were used to compile a posterior probability (PP) distribution using a 50% majority-rule consensus. Clades between 0.7 and 0.85 PP were considered weakly supported, 0.86–0.95 PP moderately supported and 0.96–1.0 PP strongly supported.

A single gap coding approach (Simmons & Ochotorena, 2000) was tested for both MP and Bayesian analyses. A presence-absence matrix was added to the alignments with FastGap 1.2 (Borchsenius, 2009). The partitions were then treated as "gaps" in PAUP and "restriction sites" in MrBayes. However, the results displayed (not shown) were nearly identical.

2.4 Topological incongruence

Topological incongruence between ptDNA and nDNA datasets was checked by two methods: ILD and visually. ILD has long been disregarded as an appropriate tool (Yoder et al., 2001; Pirie, 2015), but some authors have used it recently in *Tamarix* phylogenetic studies (Sun et al., 2016), so we performed ILD for comparison with their conclusions. ILD tests were performed in PAUP v. 4.0b10 (Swofford, 2002) using heuristic search options. Searches included 100 random addition replicates and tree-bisection-reconnection (TBR) branch swapping, with MULTREES in effect, keeping 10 trees per replicate. The sum of tree lengths for the original partition was 3002. Trees resulting from both datasets were also visually compared and a number of strongly supported incongruencies were found. Therefore, independent phylogenetic analyses were performed for ITS and combined plastid datasets.

3 Results

The ILD test comparing nuclear and plastid datasets indicates significant incongruence ($p = 0.01$). This result is similar to Gaskin & Schaal (2003) but differs with regard to the results obtained by Sun et al. (2016). Strong incongruence between ptDNA and nDNA branching in several clades, plus known existence of hybridization (Gaskin & Schaal, 2003; Gaskin & Kazmer, 2009; Mayonde et al., 2015), suggests that we do not concatenate the datasets (Pirie, 2015). Despite incongruence, *Tamarix* is robustly monophyletic in all trees, and the previously proposed (Baum, 1978) sections and series (based on morphology) are shown to be polyphyletic. Indeed, key identification morphological features such as floral part size and shape, insertion of the staminal filaments on the nectariferous disc, raceme size, bract size and shape and even leaf shape appear scattered across the phylogenetic trees (Figs. 2, 3). Detailed alignment and sequence information for the analysed regions and tree statistics from the phylogenetic analyses are described in Table 2.

3.1 nDNA phylogeny

MP and Bayesian analyses produced trees with similar topologies (Fig. 2). The *Tamarix* accessions are arranged in three strongly supported clades (A, B and C) and a moderately to weakly supported clade (D). The phylogenetic relationships within those cades are not fully resolved, and their phylogenetic positions appear to be collapsed or weakly supported by MP or BI.

Clade A includes two vaginate-leaved species, *T. aphylla* and *T. usneoides* E. Mey., which are strongly supported (BS 100/PP 1.00). Clade B groups the species *T. minoa* J.L. Villar et al. and *T. dalmatica* B.R. Baum (BS 100/PP 1.00), although their phylogenetic relationships appear collapsed. Similarly, Clade C is strongly supported (BS 98/PP 1.00), including *T. canariensis* Willd. and *T. africana.* These species do not form two independent clades, since *T. canariensis* appears totally embedded among *T. africana* accessions. The remaining *Tamarix* species are grouped in Clade D (BS 81/PP 0.83), whose basal phylogenetic relationships appear mostly unresolved. The species *T. hispida* Willd. forms a clade (BS 93/PP 0.99; subgroup D1) and the position of *T. karelinii* Bunge is not resolved (D2). The subgroup D3 comprises all of the accessions of *T. amplexicaulis* Ehrenb. (BS 64/PP 0.98), plus *T. macrocarpa* Ehrenb. ex Bunge (BS 84/PP 0.99) and *T. aucheriana* (BS 61/PP 0.96) as successive sister branches. The largest subgroup D4 is strongly supported by BS (PP 0.97), but not by MP (BS 52). Most of the internal phylogenetic relationships also appear unresolved. The most strongly supported cluster by both phylogenetic analyses corresponds to the *T. boveana* Bunge - *T. gallica* L. - *T. tetragyna* Ehrenb. clade (BS 98/PP 1.00), but their phylogenetic positions are collapsed. Another moderately to strongly supported clade (BS 89/PP 1.00) includes all of the studied accessions of *T. smyrnesis* Bunge as a clear monophyletic group (BS 87/PP 1.00), together with *T. chinensis* Lour., *T. austromongolica* Nakai, *T. ramossisima* and *T. taklamakanensis* M.T. Liu, whose phylogenetic position appears unresolved.

The Bayesian analysis gives strong support to a large clade (PP 0.99), where the accessions of *T. arceuthoides* Bunge, *T. nilotica* (Ehrenb.) Bunge and *T. senegalensis* DC. group in separate clades, whereas the accessions of *T. arborea* (Sieber ex Ehrenb.) Bunge appear related to *T. indica* Willd. (BS 90/PP 1.00) or to *T. senegalensis* and *T. arabica* Bunge (PP 0.87). The species *T. leptostachya* Bunge groups in a weakly to strongly supported clade (BS 67/PP 0.97). The species *T. androssowii*, *T. hampeana,* and *T. parviflora* group in another clade (BS 55/PP 0.98). The phylogenetic relationships between *T. hampeana* and *T. parviflora* are unresolved (BS 70/PP 1.00), whereas *T. androssowii* remains as an external sister group. Finally, the species *T. elongata* Ledeb., *T. gracilis* Willd., *T. octandra,* and *T. laxa* Willd. cluster together (BS 58/PP 0.95), although their phylogenetic relationships are not resolved.

3.2 ptDNA phylogeny

Bayesian and MP analyses display similar topologies (Fig. 3). In this case, the *Tamarix* accessions are arranged in five strongly supported clades (1, 2, 3, 4 and 5).

Clade 1 includes *T. aphylla* and *T. usneoides*, both strongly supported as independent branches (BS 99/PP 1.00). This clade is equivalent to nDNA Clade A. In addition, Clade 1 is sister to the remaining *Tamarix* specimens, all of which form a strongly supported clade (BS 98/PP 0.99). Within that large clade, Clade 2 includes only the *T. dalmatica* accessions (BS 100/PP 1.00), giving strong support to its independence to any other analysed species, which appear grouped (BS 99/PP 1.00). Clades 3 and 4 are sister groups. Clade 3 includes all *T. africana* accessions as a strongly supported group (BS 100/PP 1.00).

Clade 4 includes all of the remaining *Tamarix* species (BS 96/PP 1.00), whose basal phylogenetic relationships appear unresolved, though several inner clades show strong support. *Tamarix hispida* and *T. karelinii* group together in subclade 4a (BS 65/PP 0.88), in which *T. karelinii* accessions form a strongly supported clade (BS 98/PP 1.00), and the accessions of *T. hispida* are sister branches. Subclade 4b groups the accessions belonging to *T. austromongolica, T. chinensis, T. hohenackeri* Bunge, and *T. ramosissima* (BS 96/PP 1.00); their relationships are not resolved. Subclade 4c gives strong support (BS 97/PP 1.00) to *T. canariensis* accessions, as is the case for *T. octandra* in subclade 4d (BS 95/PP 1.00). Finally, subclade 4e (BS 93/PP 1.00) clusters three groups: the first includes *T. macrocarpa* and two of the four studied accessions

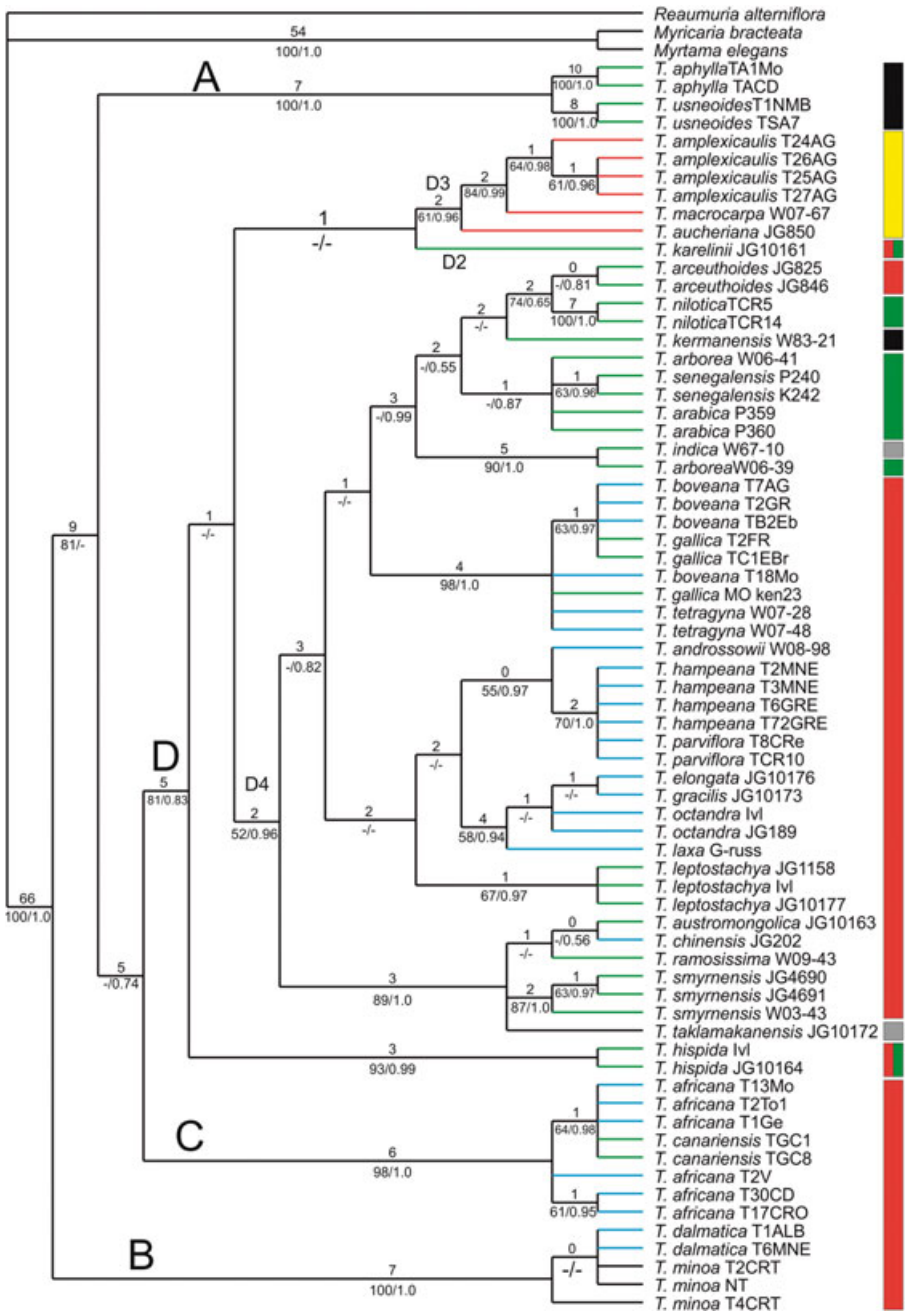

Fig. 2. One of the 10 most parsimonious trees obtained from the second MP heuristic search, based on the ITS matrix. Branch length is given above branches. Maximum parsimony bootstrap support (BS) and Bayesian posterior probability (PP) are shown below branches (BS/PP). Coloured branch tips refer to Baum's sections (1978): green terminal branches, *Tamarix* section *Tamarix*; blue terminal branches, *T.* section *Oligadenia*; red terminal branches, *T.* section *Polyadenia*; black terminal branches, no section assigned. Vertical bars refer to leaf shape: red vertical bar, sessile with narrow base; green vertical bar, triangular-lanceolate with amplexicaul base; yellow vertical bar, fully amplexicaul; grey vertical bar, pseudo-vaginate; black vertical bar, vaginate.

of *T. amplexicaulis* (BS 99/PP 1.00); the second is composed of *T. minoa* and *T. indica* (BS 100/PP 1.00), whose phylogenetic relations are not resolved; and finally, *T. gansuensis* H.Z. Zhang ex P.Y. Zhang & M.T. Liu appears as an independent branch. The phylogenetic relationships among these three groups are collapsed.

Despite its inclusion within Clade 4, the large and strongly supported Clade 5 (BS 90/PP 1.00) is noted given the considerable number of accessions included in it. Within Clade 5, the phylogenetic relationships among the groups and branches are not resolved. A clade with moderate to strong support contains *T. hampeana* and *T. gracilis* (BS 86/PP 1.00),

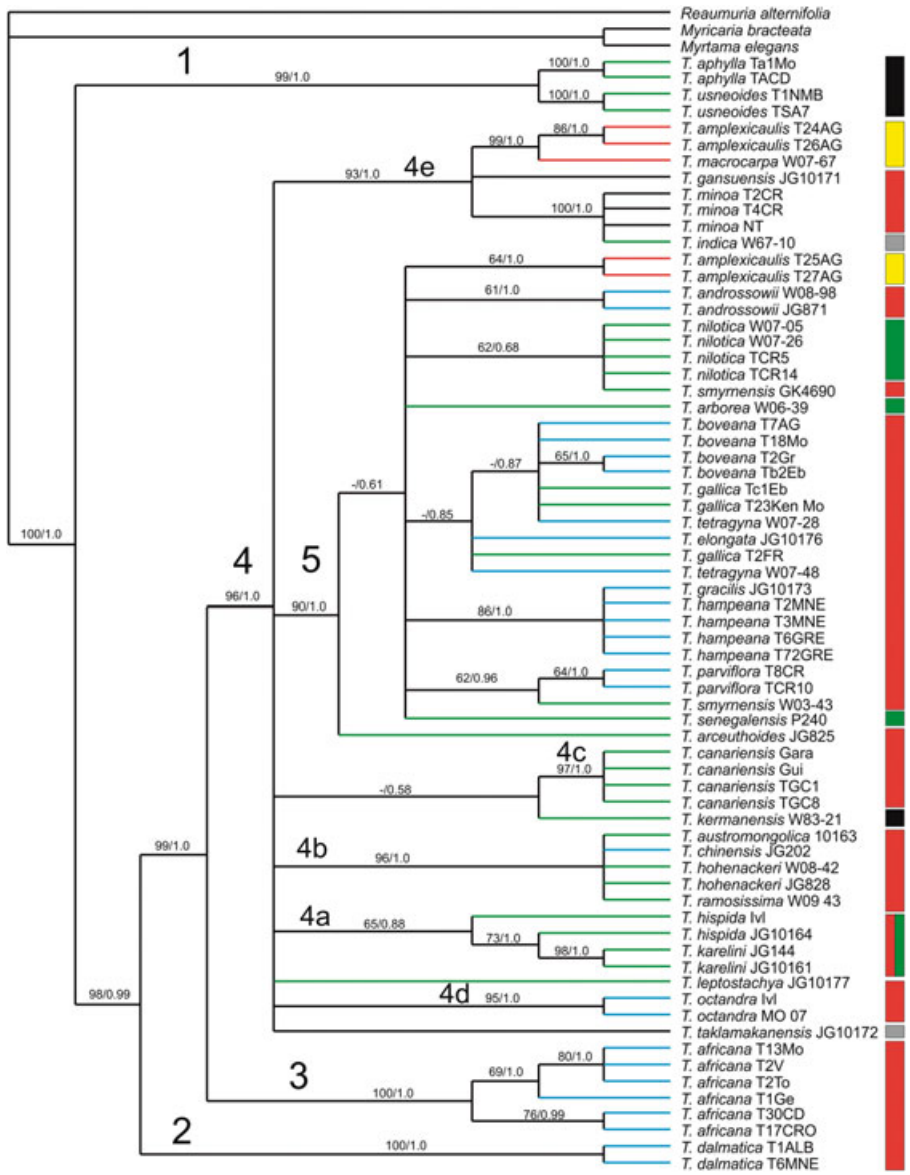

Fig. 3. Strict consensus tree obtained from the 10 MP trees obtained from the second heuristic search, based on the combined plastid matrix. Maximum parsimony bootstrap support (BS) and Bayesian posterior probability (PP) are shown above branches (BS/PP). Coloured branch tips refer to Baum's sections (1978): green terminal branches, *Tamarix* section *Tamarix*; blue terminal branches, *T.* section *Oligadenia*; red terminal branches, *T.* section *Polyadenia*; black terminal branches, no section assigned. Vertical bars refer to leaf shape: red vertical bar, sessile with narrow base; green vertical bar, triangular-lanceolate with amplexicaul base; yellow vertical bar, fully amplexicaul; grey vertical bar, pseudo-vaginate; black vertical bar, vaginate.

whose relationships are not resolved. Three more clades showing strong PP support for their phylogenetic independence are those formed by *T. androssowii* (BS 61/PP 1.00); *T. parviflora* (BS 64/PP 1.00), which are clustered alongside a *T. smyrnensis* accession (BS 62/PP 0.96); and finally, two of the four studied accessions of *T. amplexicaulis* (BS 64/PP 1.00). All of the accessions of *T. nilotica* and one of the two *T. smyrnensis* accessions group in a weakly supported clade (BS 62/PP 0.68). The single accessions of *T. arceuthoides, T. senegalensis,* and *T. arborea* appear as independent branches, respectively. Finally, the largest group in clade 5 is only weakly supported by PP (0.85), and includes all *T. boveana, T. elongata, T. gallica,* and *T. tetragyna.* It is remarkable that none of these species form independent clades, and that their relationships are not resolved.

3.3 Complementary ptDNA phylogenies

The tree shown in Fig. 4, expands the group of species characterized by wide amplexicaul leaves and twice the number of stamens as sepals, through the addition of *T. aucheriana, T. komarovii* and *T. pycnocarpa.* All three added species group in a clade with *T. amplexicaulis* and *T. macrocarpa* (BS 73/PP 0.97). Moreover, inside this clade, *T. aucheriana, T. pycnocarpa, T. komarowii,* and *T. macrocarpa*

Table 2 Phylogenetic analyses and tree data

		ITS	*trnQ-rps16*	*ndhF-rpl32*	*trnS-trnG*	*trnQ-rps16* + *ndhF-rpl32* + *trnS-trnG*	*trnS-trnG* (Fig.3)	*ndhF-rpl32* (Fig. 4)
Parsimony analyses	Number of accessions (Taxa)	72 (36)	71 (36)	71 (36)	71 (36)	71 (36)	16 (10)	13 (8)
	Aligned characters	705	1142	926	998	3066	990	923
	Parsimony informative characters (%)	162 (22.9%)	91 (8%)	108 (11.7%)	97 (9.7%)	296 (9.6%)	48 (4.85%)	33 (3.6%)
	Trees retained (after second heuristic search)	7971 (10)	820	750	800	7530 (10)	3	19
	CI	0.7990	0.905	0.912	0.896	0.8969	0.9689	0.965
	RI	0.8977	0.914	0.919	0.896	0.9103	0.9231	0.7917
	Tree lengths	423	232	375	251	864	193	286
Bayesian inference analyses	Model of Molecular Evolution	TIM2+G	TVM+G	GTR+G	TIM1+G	model for each region	TPM1uf+G	GTR+G

CI, Consistency inde; RI, Retention index.

are clustered together (BS 62/PP 0.96) and *T. aucheriana* and *T. pycnocarpa* form a monophyletic group (BS 62/PP 0.99). As in Fig. 3, the same two *T. amplexicaulis* samples behave similarly in this tree and group in a strongly supported clade (BS 98/PP 1.00) alongside *T. gallica* samples.

The tree shown in Fig. 5 includes the unique sequence obtained from *T. tetrandra.* Once *T. aphylla* (BS 100/PP 0.85) and *T. africana* (BS 72/PP 0.78) show their separation in outer branches, the remaining *Tamarix* accessions, including *T. parviflora* and *T. tetrandra,* group in a moderately supported clade (BS 86/PP 0.92). *Tamarix tetrandra* appears as a sister branch to the remaining accessions, although this separation is weakly supported (BS not supported/PP 0.70). However, *T. parviflora* accessions form an independent clade with strong

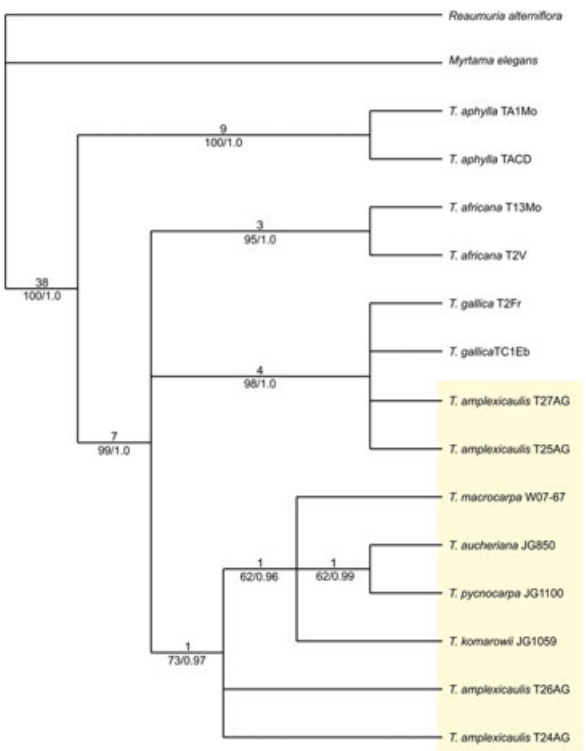

Fig. 4. One of the three most parsimonious trees obtained from the MP heuristic search, based on the *trnS-trnG* plastid region. Amplexicaully leaved species are included inside the yellow rectangle. Branch length is shown above branches. Maximum parsimony bootstrap support (BS) and Bayesian posterior probability (PP) are shown below branches (BS/PP).

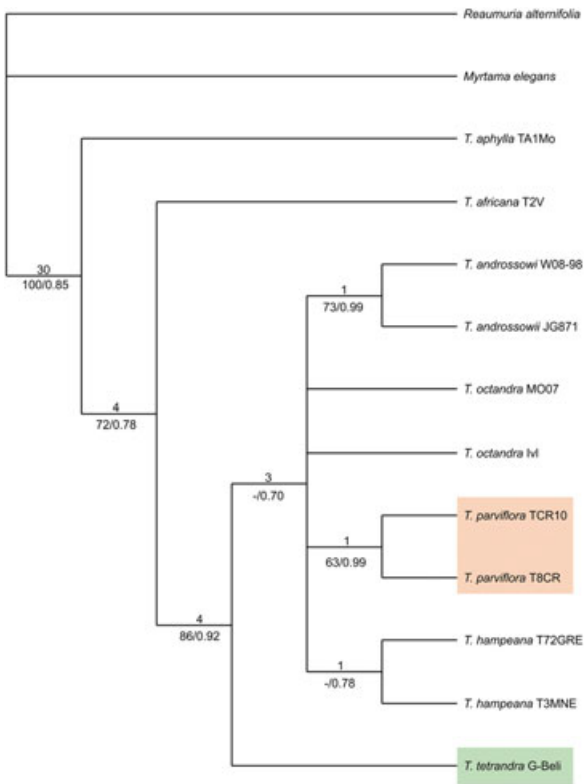

Fig. 5. One of the 19 most parsimonious trees obtained from the MP heuristic search, based on the *ndhF-rpl32* plastid region, focusing on the differentiation between *Tamarix tetrandra* (green rectangle) and *T. parviflora* (light orange square). Branch length is given above branches. Maximum parsimony bootstrap support (BS) and Bayesian posterior probability (PP) are shown below branches (BS/PP).

PP support (0.99), although weakly supported by MP (BS 63). Therefore, *T. parviflora* and *T. tetrandra* do not cluster together.

4 Discussion

This work represents the most complete molecular phylogenetic study of the genus *Tamarix* so far, based on a combination of nuclear and plastid DNA sequences obtained from species and accessions sampled across the entire geographic range of the genus. The monophyly of *Tamarix* within Tamaricaceae is clear and strongly supported for both nuclear and plastid data, as previously reported by Gaskin & Schaal (2003), Villar et al. (2015a) and Sun et al. (2016) based on partial molecular phylogenies.

Neither older infrageneric *Tamarix* arrangements (Bunge, 1852; Niedenzu, 1895; Gorschkova, 1949), nor the most recent taxonomical classification of sections and series (Baum, 1978), have proven to be natural according to the nuclear and plastid data presented here (Figs. 2, 3). Incongruence between molecular studies and the sections and series recognised by Baum (1978) had been previously highlighted (Gaskin & Schaal, 2003; Villar et al., 2015a; Sun et al., 2016). There are also many examples in which those sections and series remained open to discussion from a morphological point of view. Inside *Tamarix* L. section *Tamarix* B.R. Baum, *Tamarix* series *Gallicae* B.R. Baum and *Tamarix* series *Leptostachyae* B.R. Baum, mainly differentiated by the presence or absence of papillae, species whose synonymy is currently under question (Samadi et al., 2013; Villar et al., 2014c, 2015b) are now separated (*T. arceuthoides* and *T. korolkowi* Regel & Schmalah. from *T. karakalensis* Freyn and *T. aralensis* Bunge). Moreover, this character variation can change within a single plant within a year. Inside *Tamarix* L. section *Oligadenia* (Ehernb.) Endl. *sensu* Baum (1978) there are also species placements open to discussion. For instance, it is remarkable in section *Oligadenia* that *T. chinensis* is separated from morphologically similar relatives, *T. ramosissima* and *T. smyrnensis,* which were placed in section *Tamarix.* It is also worth mentioning the inclusion of *T. africana* into series *Anisandrae* Bunge *sensu* Baum (1978), among mainly tetramerous species such as *T. boveana, T. tetragyna* and *T. elongata.* The species included in *Tamarix* L. section *Polyadenia* (Ehrenb.) B.R Baum also need a thorough revision. Moreover, *Tamarix* L. series *Arabicae* B.R. Baum would seem unnecessary. It is based on stamen number greater than 10 for *T. aucheriana* and *T. pycnocarpa.* However, our study of type material would point to these species having 10 stamens and higher numbers just being sporadic. Moreover, the Identity of these taxa in relation to *T. passerinoides* Delile is currently under question, and will be discussed below. Therefore, considering these morphological and molecular phylogenetic conflicts, we have opted to avoiding the use of infrageneric groups in further discussion.

Our phylogenetic data reveal many examples in which morphological features do not always correspond to clades and even closely-related groups. Among others, the sections that are characterised by vaginate leaves, or even quite similar species such as *T. canariensis* or *T. gallica* do not group together, as we will explain later in detail. Indeed, no infrageneric taxa were previously included in some large taxonomic works dealing with *Tamarix* (cf. Qaiser, 1981; Yang & Gaskin, 2007). Some of the key morphological features that are used to identify sections and species (e.g., vaginate or amplexicaul leaves, tetramery versus pentamery, stamen number, etc.) appear in *Tamarix* at different stages of its evolution, or are just transferred to different clades via hybridization events. This hypothesis is supported by, for example, the clear separation of *T. kermanensis* B.R. Baum from *T. aphylla* and *T. usneoides,* as well as the phylogenetic distance between species that have twice the number of stamens than sepals, such as *T. octandra* and the external "amplexicaules" group.

In addition, incongruence has been observed between gene trees in most of the phylogenetic studies that investigated multiple markers (e.g., Doyle et al., 2003). Gene tree incongruence is mainly caused by evolutionary processes such as hybridization or ILS (incomplete lineage sorting). Several studies have investigated both processes as a major cause of gene tree incongruence and non-monophyly in Mediterranean plants (Blanco-Pastor et al., 2012). Although detailed analyses are necessary, Whitfield & Lockhart (2007) suggested that when different molecular markers indicate that the same branches are short or have low support, this could be used as an indication of rapid radiation. This might have been caused by reticulate evolution via introgression processes that may still happen through hybridization. Current hybridization processes in *Tamarix* have frequently been reported (Gaskin & Schaal, 2003; Gaskin & Kazmer, 2009), even between extremely different species (Gaskin & Shafroth, 2005; Samadi et al., 2013; Mayonde et al., 2015). These findings are supported by incongruencies found between nDNA and ptDNA phylogenies. Some of the incongruent positions of certain species in this study might also be explained by this process.

Due to the differences between the plastid and nuclear trees, the lack of a strong correspondence between some key morphological features and the phylogenetic groups and the likely importance of hybridization processes we have discussed, the position of the different species based on either morphological or biogeographical features. Therefore, we have used one or another approach depending on the clustering of each group of species into the different phylogenetic trees.

4.1 Vaginate-leaved species

As previously confirmed by Gaskin & Schaal (2003), both ptDNA and nDNA phylogenies show a strong relationship between *T. aphylla* and *T. usneoides,* which are placed in external clades. This is expected due to similarities in their morphology, e.g., vaginate leaves, five petals, sepals and stamens, and similar flower size (Baum, 1978). In fact, *T. kermanensis* B.R. Baum is morphologically the closest species to *T. aphylla*, as pointed out in its description (Baum, 1968). Although *T. kermanensis* shares these morphological features, it is not placed phylogenetically close to *T. aphylla* and *T. usneoides* in either the nDNA or ptDNA analyses, so series Vaginantes (*sensu* Baum) is not monophyletic. Therefore, although being a clearly distinguishable morphological feature, vaginate leaves cannot be considered as a character good enough to describe an infrageneric taxon. Samadi et al. (2013) experienced some difficulties in the morphological identification of *T. kermanensis*, as they reported morphological variability based on two studied accessions, which also showed different chromosome counts (triploid and tetraploid). It would useful to study the phylogenetic relationships of *T. aphylla* and *T. usneoides* with the other fully vaginate-leaved species *T. dioica.* The latter is mainly distributed in Iran, Afghanistan, Pakistan and India (Baum, 1978; Qaiser, 1981) and is the only dioecious species alongside *T. usneoides. T. usneoides* can behave as both monoecious or dioecious and monoecious specimens have sometimes been treated as a different species (e.g., *Tamarix angolensis* Nied. (Baum, 1978)).

4.2 The amplexicaully-leaved and duplicated stamens group

According to our results, we find a monophyletic group of species characterized by broad amplexicaul leaves and twice the number of stamens as sepals, though some species can show a few less (*T. macrocarpa*) or more stamens (*T. pycnocarpa*) (Baum, 1978). The studied species also show a similar phylogenetic pattern based on plastid data, with the exception of two samples of *T. amplexicaulis* (Figs. 3, 4). These two accessions are in a different clade in the ptDNA phylogeny (see Clade 5, Fig. 3), and appear more closely related to other species of the genus that have very different leaf and androecium characters (e.g., *T. nilotica*, *T. gallica*, *T. hampeana*, among others). This unexpected placement is also observed in other *Tamarix* groups. However, in this case, these specimens group together with strong support, and do not show evidence of introgression with any other particular species.

The morphological separation between *T. pycnocarpa* and *T. aucheriana* is quite doubtful, as the morphological differences reported by Baum (1978) regarding the androecium, sepal and petal features might be considered as phenotypic variation. Recently, Samadi et al. (2013) suggested them to be conspecific, with *T. pycnocarpa* the priority name. This taxonomic suggestion is supported by our morphological observations of type materials as well as our phylogenetic plastid results (Fig. 4). Other authors (Gorschkova, 1949; Assadi, 1989; Zieliński, 1994) even regarded *T. aucheriana, T. pycnocarpa* and *T. macrocarpa* as synonyms of *T. passerinoides* (not included in our study). These taxonomic hypotheses reflect a broad morphological interpretation of this group. However, local treatments have never dealt with the full geographic range of this group that extends at least from Pakistan to the Middle East and from the southeastern Mediterranean, through the Sahara, to Morocco and Mauritania (Baum, 1978; Qaiser, 1981; Zohary, 1987). Therefore, new nuclear and plastid molecular data, along with morphological data, should be analysed for the aforementioned taxa, plus some suggested synonyms (*Tamarix balansae* J.Gay ex Munby, *Tamarix pauciovulata* J.Gay ex Munby and their numerous varieties). In addition, the presence of hybrid specimens has been reported within this group, (*T. pycnocarpa* x *T. androssowii* by Samadi et al. (2013))

and Gorschkova (1949) wrote about the possible hybrid origin of the species *T. komarovii* from *T. passerinoides* and *T. ramosissima.*

4.3 Mediterranean *Tamarix* species and related groups

We find a strong relationship between the Eastern Mediterranean species *T. dalmatica* and *T. minoa* in the nDNA phylogeny (Clade B, Fig. 2), both forming monophyletic groups. These species show a general resemblance when observed in the wild, as they are trees of the same height and their racemes are similar in colour and size. Moreover, both species show a tendency to produce tetramerous and pentamerous flowers intermixed (Baum, 1978; Villar et al., 2012, 2015a). However, *T. dalmatica* is generally tetramerous, sometimes developing some pentamerous flowers (Villar et al., 2012), whereas *T. minoa* is primarily pentamerous and sometimes develops tetramerous flowers (Villar et al., 2015a). Conversely, the ptDNA phylogeny splits both species into distinct, strongly supported clades. Hence, *T. dalmatica* is a monophyletic group with an external phylogenetic position (Clade 2, Fig. 3) similar to the nuclear phylogeny. However, *T. minoa* appears as an independent monophyletic group together with the unexpected species *T. indica* inside subclade 4e (Fig. 3). This topological incongruence between biparental (nuclear) and uniparental (plastid) genomes has often been considered evidence of plastid capture via interspecific hybridization (see examples in Albadalejo et al., 2005; Kim et al., 2008, Soltis & Soltis, 2009; Cires et al., 2013). Our current phylogenetic evidence suggests that *T. minoa* might have a hybrid origin, with *T. dalmatica*, as a likely paternal contributor, supported also by independent evidence from geography and morphology. According to the plastid DNA, the close relationships with *T. indica* would suggest this taxon as the likely maternal donor. However, this aspect must be confirmed by further DNA studies, since this unexpected relationship is not supported by geographical or morphological data. According to our own observations, *T. indica* is characterised by pseudo-vaginate leaves that are strongly amplexicaul with coherent margins along most of their length. Nevertheless, Baum (1966, 1978) reported a higher plasticity in leaf shape. According to Samadi et al. (2013), a critical revision is needed for *T. indica* and its close relatives, some of them described by Qaiser (1981), such as *T. pakistanica* Qaiser. If closely related species described by Qaiser (1981) are considered as synonyms of *T. indica* (Samadi et al., 2013), the natural distribution of *T. indica* would extend from India, Bangladesh, Sri-Lanka, Pakistan and Afghanistan (Baum, 1966, 1978) to Southwestern Iran (Samadi et al., 2013).

A monophyletic group composed of the three Mediterranean species (*T. boveana*, *T. gallica* and *T. tetragyna*) is clearly recognized by both the nuclear and plastid data, although the Asian *T. elongata* is also included based on the plastid analysis (see Fig. 3). *Tamarix boveana*, *T. tetragyna* and also *T. elongata* share long and wide racemes, long oblong bracts, large tetramerous flowers, and stamens that are generally equal in number to sepals (see Ehrenberg, 1827; Bunge, 1852; Baum, 1978). These features are also shared with *T. brachystachys* Bunge and *T. meyeri* Boiss. (sometimes considered as a variety or as a synonym of *T. tetragyna*) (Villar et al., 2015b), which were not included in this study. *Tamarix boveana* is widely distributed across the Southwestern Mediterranean Basin, especially in Algeria and Morocco, and is also present in the Iberian Peninsula and Tunisia (Baum, 1978; Villar et al., 2012). On the other hand, *T. tetragyna* is widespread in the southeastern Mediterranean basin, especially in Egypt (Ehrenberg, 1827; Bunge, 1852; Baum, 1978), so both species show vicariance in the western and eastern Mediterranean. The distribution of *T. elongata* extends from the eastern shores of the Caspian Sea to the northeast, reaching Mongolia (Gorschkova, 1949; Baum, 1978). Conversely, the type species of the genus, *T. gallica*, is well characterised by small racemes with small pentamerous flowers. The natural distribution of *T. gallica* is restricted to western Mediterranean countries and the southern coast of Great Britain. The unexpected phylogenetic relationship between *T. gallica* and the other three mentioned species is not resolved according to our present DNA data, although their identification is clearly supported by independent morphological and geographical data. The lack of phylogenetic resolution supports the use of other types of molecular markers or techniques which might clarify their genetic relationships and their taxonomic identification, as has been reported recently for other taxonomically difficult genera (e.g., Duminil et al., 2012; Prebble et al., 2012; Andrés-Sánchez et al., 2015).

In the case of *T. parviflora*, this species has been considered as a possible synonym of *T. tetrandra* (Zieliński, 1994; Dimopoulos et al., 2013), although they were also commonly treated as distinct taxa (Baum, 1966, 1978; Qaiser, 1981; Zohary, 1987; Cirujano, 1993; Salazar & Quesada, 2011; Villar et al., 2014b; Villar & Alonso, 2017). However, their well-separated phylogenetic position based on our plastid phylogeny supports their taxonomic independence. According to our observations, there are certain morphological features that can be used to segregate both species. Petals tend to be longer and wider in *T. tetrandra* (up to 2.75×1.25 mm), when compared with those of *T. parviflora* (up to 2.5×1.1 mm). Sepals have the same tendency, extending up to 1.5×1.2 mm in *T. tetrandra* and up to 1.25×0.9 mm in *T. parviflora.* Therefore, according to the data shown here, these two taxa might be considered taxonomically independent, supporting the interpretation of Baum (1966, 1978), among others.

In addition, the phylogenetic position of *T. parviflora* within the genus is somehow different based on nuclear and plastid phylogenies. In the nuclear phylogeny, this taxon clusters together with the Mediterranean species *T. hampeana*, which is widely distributed along the northwestern Mediterranean coast, from Montenegro in the west to Turkey in the east (Baum, 1978; Villar et al., 2015a). These two species appear as a sister clade to *T. androssowii*, the latter being distributed in central Asia with its westernmost localities in the Caucasus (Baum, 1978). This close relationship is not recovered by plastid data (Fig. 3). Conversely, *T. parviflora* and *T. hampeana* appear in different clades and are related to other species in the ptDNA phylogeny. On one hand, the phylogenetic identity of *T. parviflora* is strongly supported by PP in a clade that includes one of the *T. smyrnensis* accessions as an external branch. The placement of *T. smyrnensis* is discussed below, alongside morphologically similar species (*T. ramosissima, T. hohenackeri, T. chinensis* and *T. austromongolica*). On the other hand, *T. hampeana* groups together with *T. gracilis* (Fig. 3), whose known distribution extends from Russian shores of the Caspian Sea to Northern China and Mongolia,

with a westernmost locality in central Anatolia (Baum, 1978; Yang & Gaskin, 2007). Certain morphological features, as defined in Baum (1978) or Yang & Gaskin (2007) for *T. gracilis*, such as long pedicels and variability in number of petals and sepals, connect it to the concept of *T. hampeana* (Villar et al., 2014b, 2015a). Hence, a close relationship between *T. gracilis* and *T. hampeana* would seem natural.

The morphological relationships between *T. arabica*, *T. arborea* and *T. nilotica* remain unclear. These three species are notably similar in morphology, and also similar to the Atlantic African species, *T. senegalensis*. In fact, Baum (1966, 1978) suggested a close relationship between *T. arabica* and *T. senegalensis.* According to our observations, all of these species share small racemes (usually less than 5 cm long × 5 mm wide) with pentamerous flowers and leaves with their lower half amplexicaul or subamplexicaul (also see Candolle, 1828; Bunge, 1852; Zohary, 1987). Other than this, the taxonomic treatment of this group is still unclear. The type collection of *T. arborea* is quite heterogeneous, and some specimens are found to have a morphotype closer to *T. nilotica* (Bunge, 1852; Villar et al., 2015b). The main morphological feature to distinguish between both species is the staminal disc, with the stamens inserted between the lobes in *T. nilotica* and above them in *T. arborea* (Baum, 1978). However, as can be deduced by the reported existence of heterogeneous collections from certain localities (Bunge, 1852; Villar et al., 2015b), it seems clear that there has been introgression and that intermediate forms exist between the morphotypes represented by *T. arborea* and *T. nilotica* in the southeastern Mediterranean. The morphology of *T. nilotica* is more stable in the populations recently reported from some Greek islands (cf. Dimopoulos et al., 2013; Villar et al., 2014b). Moreover, Zohary (1987) included *T. arabica* and *T. arborea* in the synonymy of *T. nilotica* and other authors such as Marlin et al. (2017) have accepted the later three species as synonyms of *T. senegalensis.* Our phylogenetic results support the existence of these complex relationships. Although nuclear data groups them in an unresolved clade, together with other *Tamarix* species (e.g., *T. arceuthoides*, *T. indica*), only the accessions of *T. senegalensis* and *T. nilotica* form monophyletic groups. Despite the scarce number of sequenced accessions, *T. nilotica*, *T. senegalensis* and *T. arborea* correspond to independent monophyletic branches, and similar to nuclear data, none of their phylogenetic relationships is fully resolved. Our nuclear and plastid phylogenetic data unfortunately do not provide clear resolution about the relationships among them.

The case of *T. canariensis* and *T. gallica*

The phylogenetic separation between *T. canariensis* and *T. gallica,* as shown in both ptDNA and nDNA phylogenies, is a remarkable result. These two species have been commonly reported to be morphologically very similar to one another, with a widely overlapping distribution (Baum, 1966, 1968, 1978; Pignatti, 1982; Cirujano, 1993; Salazar & Quesada, 2011). Indeed, *T. canariensis* had either been treated as a variety of *T. gallica*, or not been included into the list of species by different *Tamarix* monographers back in the 19th century (Bunge, 1852; Niedenzu, 1895). The main morphological differences listed by Baum (1966, 1978) were: (i) a glabrous inflorescence rachis in *T. gallica* compared with the usually papillate rachis in *T. canariensis*; (ii) bracts narrowly triangular, acuminate, not exceeding the calyx vs. bracts linear-triangular, long acuminate to subulate, almost equalling to somewhat exceeding the calyx; (iii) entire sepals vs. sepals densely denticulate; and (iv) petals elliptic to elliptic-ovate, 1.5–1.75 mm long, vs. petals obovate, 1.25–1.5 mm long. Nevertheless, these species character states have been found to be rather variably mixed on a large number of European and North African specimens that we studied. In fact, we have observed all degrees of variation within single specimens throughout the flowering period in the Iberian Peninsula. In the first bloom (early May in the southeast of the Iberian Peninsula), specimens show a morphology closer to that assumed to represent *T. gallica,* with a glabrous rachis, triangular bracts not exceeding the calyx and sepals with entire or subentire margins. However, they can produce several secondary blooms until October, and those late racemes show a morphology similar to *T. canariensis*, with a strongly papillate rachis, triangular-linear subulate bracts, frequently exceeding the calyx, and denticulate margined sepals. A number of vouchers from individuals collected at different times and reflecting this seasonal morphological plasticity are kept at ABH. In light of these facts, the above mentioned differences are not useful enough to separate *T. canariensis* and *T. gallica.* In advance of deeper molecular and morphological studies to deal with this taxonomically complicated issue, our results initially suggest that *T. canariensis* is probably restricted to the Canary Islands, whereas *T. gallica* shows a wider geographical distribution along the Mediterranean and Atlantic territories, including samples corresponding to "*T. canariensis* auct.". In fact, more Mediterranean and Atlantic accessions of *T. gallica* were initially added to the nuclear and plastid phylogenies, and these specimens always clustered together (data not shown). Recently, Terzoli et al. (2014) stated that no genetic differences were found between the Italian *T. canariensis* and *T. gallica,* and considering our assumptions, they would have only analysed *T. gallica* samples. This would mean that all European and North African records of *T. canariensis* might belong to *T. gallica,* including a large number of synonyms usually assigned to *T. canariensis* (Baum, 1966, 1978). This approach has already been used in the Euro + Med treatment of Tamaricaceae (Villar & Alonso, 2017). In addition, and similarly to *T. minoa*, the different phylogenetic relationships of *T. canariensis* accessions within the genus might be due to a hybrid origin, with *T. africana* samples as the likely paternal donor. However, the results shown in the plastid tree prevent us from identifying any possible maternal donor for *T. canariensis*. More detailed studies are required, because the studied *T. canariensis* materials (from the Canary Islands) show no clear morphological differences with the widespread *T. gallica.* If no distinguishing morphological features are found, we would have to deal with the concept of cryptic species (Bickford et al., 2007), which would add another degree of complication to an already difficult genus.

4.4 Asian species

According to our plastid data, *T. hispida* and *T. karelinii* are a monophyletic group and the accessions of *T. karelinii* form a strongly supported clade. However, their positions based on the nuclear data were not resolved. In fact, *T. karelinii* has

been considered a variety of *T. hispida* (Baum, 1966, 1978; Villar et al., 2015b), as both species share several morphological features such as lanceolate leaves with a broadly auriculate sub-amplexicaul base, pentamerous flowers with deep purple petals (2 × 1 mm) and medium to long and thin racemes (up to 15 cm × 5 mm). However, they differ in the dense hairy indumentum found in *T. hispida*, which is not present in *T. karelinii,* although the latter can show some sparse hairs or papillae (Baum, 1978; Yang & Gaskin, 2007). Both share a central Asian distribution, from Iran in the southwest to Mongolia in the northeast, and *T. karelinii* has been also reported from Pakistan (Schiman-Czeika, 1964; Baum, 1978; Qaiser, 1981; Yang & Gaskin, 2007). The combined results of both nDNA and ptDNA phylogenies are mostly congruent with Sun et al. (2016), and provide some support to those authors who interpreted *T. karelinii* as independent from *T. hispida* (Schiman-Czeika, 1964; Qaiser, 1981, Yang & Gaskin, 2007). Nevertheless, a close relationship between these two species is here confirmed, and the existing intermediate forms reported by Baum (1966, 1978) point to the existence of introgression between the two species.

Tamarix leptostachya is an independent clade or branch for both phylogenies. From a morphological point of view, this taxon is characterised by long and thin racemes (up to 15 cm and 3–4 mm, respectively) and generally herbaceous bracts, with a distribution from the northwestof Iran to Mongolia, China and the north of India (see Baum, 1978; Qaiser, 1981; Yang & Gaskin, 2007). Nonetheless, the collapsed phylogenetic position does not provide any clues about the evolutionary relationships with other *Tamarix* species.

The clade of *T. arceuthoides* shows weak support in the nDNA phylogeny, and its relationships with other species remains unresolved in both the nDNA and ptDNA phylogenies. This species is mainly characterised by its sessile, narrow-based leaves (sometimes slightly auriculate), small pentamerous flowered racemes (usually less than 5 cm × 5 mm) and its staminal filaments inserted between the disc lobes (cf. Bunge, 1852; Gorschkova, 1949; Baum, 1966, 1978; Yang & Gaskin, 2007). It is widely distributed in central Asia, similar to *T. karelinii*, though reaching at least to Iraq in the west and Pakistan in the southeast (Baum, 1978; Qaiser, 1981). However, species showing strong morphological similarities with *T. arceuthoides*, such as *T. korolkowi, T. aralensis* or *T. karakalensis*, were not included in this study. Recently, the three latter species were treated as part of a broad concept of *T. arceuthoides* by Samadi et al. (2013).

Tamarix octandra is characterised by long and wide racemes (up to 12 × 1.4 cm), long and oblong bracts (4–6 (9) mm), large tetramerous flowers (petals 4–6 mm long), and its status as the only tetramerous species with twice the number of stamens assepals (Bunge, 1852; Gorschkova, 1949; Baum, 1966, 1978; Zieliński, 1993). Its distribution is restricted to the Caucasus and nearby areas between the Black and Caspian Seas, with known localities in Iran, Azerbaijan, Armenia Turkey and Russia, and a westernmost collection in Crimea (Gorschkova, 1949; Schiman-Czeika, 1964; Baum, 1966, 1978; Zieliński, 1993). This species forms a strongly supported clade in the ptDNA phylogeny, and its nDNA and plastid phylogenetic relationships are not resolved in relation to most of the other *Tamarix* species.

Finally, some species with morphological similarity to *T. androssowii* (see comments on *T. hampeana* and *T. parviflora*), such as *T. polystachya* Ledeb., *T. litwinowii* Gorschk. and *T. laxa* are needed for better clarification of the "small-flowered tetramerous species" growing in the Middle East and central Asia. Only a single specimen of *T. laxa* was included in the nDNA phylogeny but it does not group together with *T. androssowii*. Moreover, Samadi et al. (2013) suggested that the species *T. szowitsiana* Bunge may be an autopolyploid of *T. androssowii*. Further studies will be needed to resolve the relationships among these species, and to test whether the proposed hypothesis of Samadi et al. (2013) would be confirmed.

4.5 Asian and Mediterranean species with petals persistent after anthesis

The following group of species includes the sessile-leaved taxa with five stamens inserted between the nectariferous disc lobes, and petals persistent after anthesis: *T. austromongolica, T. chinensis, T. hohenackeri, T. ramosissima* and *T. smyrnensis*; the latter being distributed in the northeastern Mediterranean region, from the Greek and Turkish coasts to the east through the Anatolian Peninsula. In the nDNA phylogeny, they form a clade, that includes *T. taklamakanensis*, whose morphology is notably different (Yang & Gaskin, 2007). Close relations between this group of species were already pointed out by Bunge (1852), who placed them into *Tamarix* L. series *Xeropetalae* Bunge. All the studied specimens of *T. smyrnensis* are resolved in a small clade sister to the other species. However, the phylogenetic relationships are not resolved within this particular group. Similarly, most of the other species of this group, *T. austromongolica, T. chinensis, T. hohenackeri* and *T. ramosissima*, cluster together in the ptDNA phylogeny, in accordance with Sun et al. (2016), but *T. smyrnensis* is placed outside the group. In general, this monophyletic group is nearly coincident between the morphological and phylogenetic data, except for *T. smyrnensis*. Nevertheless, the morphological differences among the group studied here are rather complex. Although Baum (1966, 1978) placed *T. chinensis* and *T. ramosissima* in different sections (*T.* sect. *Tamarix* and *T.* sect. *Oligadenia*, respectively), their morphological distinction has been highly problematic, especially in North America, where their hybrids have been widely reported (Gaskin & Schaal, 2003; Gaskin & Kazmer, 2009). Moreover, the natural distributions of this group of species form a continuous geographical area, from the Mediterranean coasts of Greece and Turkey towards the Middle East and the Caucasus, to the Pacific coast of Asia and north to its Central Steppes (see Gorschkova, 1949; Baum, 1978; Yang & Gaskin, 2007). The morphological limits within the species of this group may therefore be quite diffuse (Baum, 1978; Yang & Gaskin, 2007). In addition, the phylogenetic position of *T. hohenackeri* should be further studied, as samples of this species were excluded from our nDNA phylogeny because they showed clear double signals in the key nucleotide positions in which *T. smyrnensis* shows differences with *T. austromongolica, T. ramosissima* and *T. chinensis*. This result might be interpreted as a possible hybrid origin of *T. hohenackeri.* In addition, the different phylogenetic positions of the two specimens of *T. smyrnensis* in the plastid phylogeny should be studied in detail. One of the *T. smyrnensis* specimens groups into a weakly supported clade alongside *T. nilotica* accessions, while the other specimen

groups in a clade as a sister branch to *T. parviflora.* More samples of *T. smyrnensis* from other geographical areas should be included in the ptDNA phylogeny to check if that species would show the observed tendency, or conversely would reveal a close relationship to morphologically related taxa.

Finally, we can conclude that there are still many issues to be clarified in the phylogenetic and taxonomic relations inside *Tamarix.* We hope our study helps resolve some issues and also highlight some species groups in need of further investigation. Hopefully, with modern molecular high-throughput approaches to DNA sequencing, we will be able to solve some of those problems, but in such a complicated genus, a precise morphological characterization of the studied specimens will also be essential to robustly interpret taxonomic hypotheses.

Acknowledgements

We warmly thank the curators and personnel of all the herbaria mentioned in the text. This study would not have been possible without the dedicated work done at these institutions. A special mention to Kim Mann for her help during the molecular work conducted in Sidney MT. The FPU programme (Mo de Educación, Spain), the I+D+I project CGL2008-05056 (Mo de Educación y Ciencia, Spanish Government), the project OAPN 354-2011 (Mo de Agricultura, Alimentación y Medio Ambiente, Spanish Government) and complementary supporting funds ACIE10-01, ACIE11-05, ACIE13-08 and ACIE17-01 (University of Alicante, Spain) funded this research.

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