Universitat d'Alacant
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El género Tamarix en el Mediterráneo Occidental y áreas adyacentes: aspectos taxonómicos, filogenéticos y nomenclaturales

José Luis Villar García

TESIS DOCTORAL

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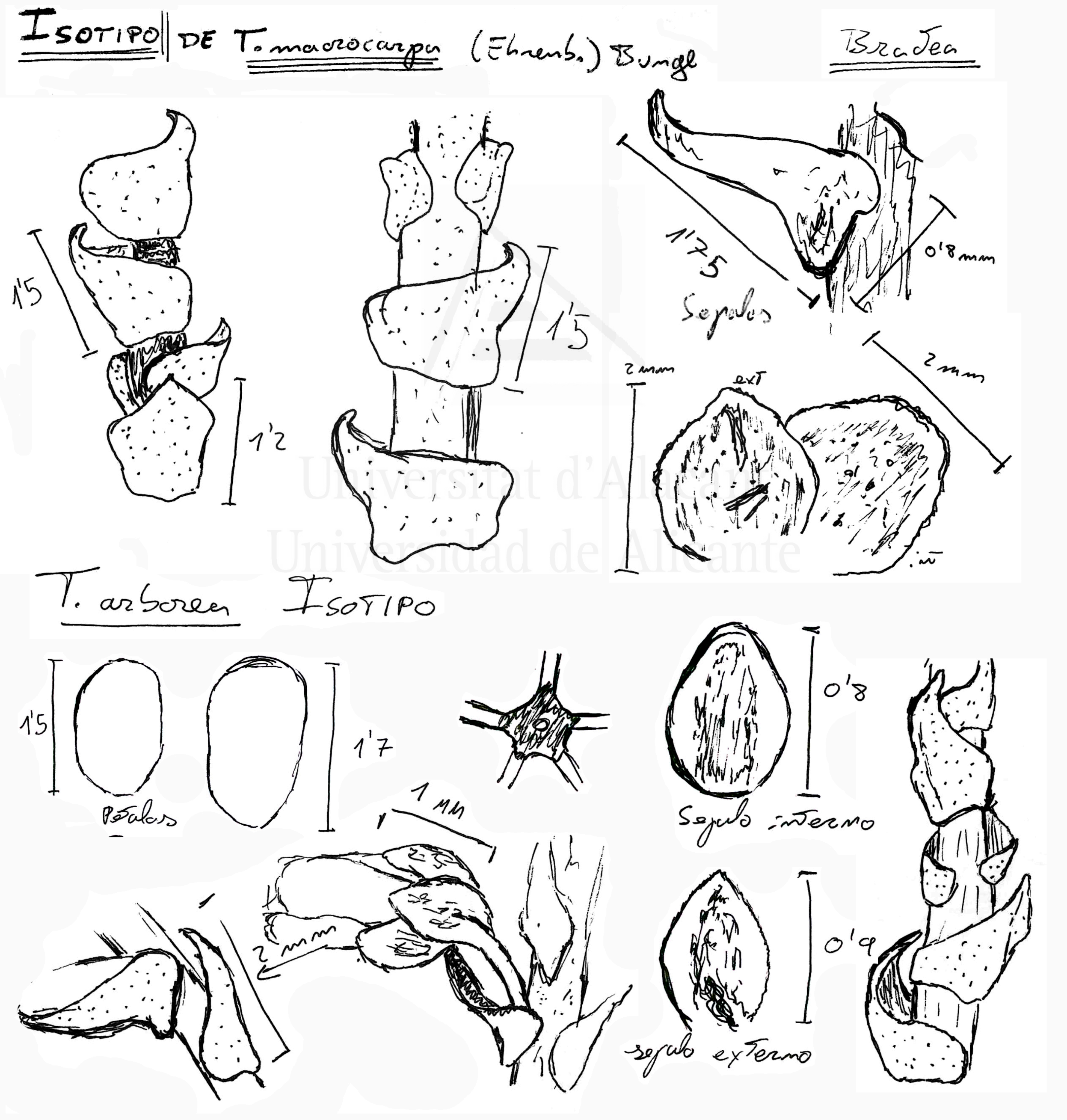

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José Luis Villar García

Tesis presentada para aspirar al grado de
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MENCIÓN DE DOCTOR INTERNACIONAL

Doctorado en Biodiversidad: Conservación y gestión de las especies y sus hábitat

Dirigida por:
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Justificación y objetivos

El género *Tamarix* L., es conocido por su complejidad taxonómica y nomenclatural. Tal complejidad atiende a diferentes motivos, que pasan, por un lado por la escasez de caracteres vegetativos útiles a nivel específico y por otro, por la elevada plasticidad morfológica de los caracteres reproductivos, favorecida por la gran cantidad de flores que se producen en las inflorescencias. La existencia en ciertas especies, de una o varias floraciones secundarias, que presentan características morfológicas diferentes a las primarias, también contribuye a la citada complejidad. Esto ha derivado en una disparidad de criterios en cuanto a la organización taxonómica del género, existiendo casos en los que se han aceptado especies que incluyen una gran diversidad fenotípica (*T. africana* Poir.), así como a casos donde se han descrito numerosas especies de morfología muy similar (*T. arceuthoides* Bunge*, T. karakalensis* Freyn*, T. askabadensis* Freyn*, T. aralensis* Bunge) (Baum 1978, Samadi & al. 2013, Villar & al. 2014b).

El género *Tamarix*, se distribuye ámpliamente por las regiones Irano-Turaniana, Indica y Mediterránea, alcanzando la Macaronesia al oeste, la costa pacífica de Asia al este y, con menor diversidad, el suroeste de África (Baum 1978).

Como objetivo principal de este trabajo se planteó la tarea de clarificar la taxonomía de las especies del género *Tamarix* del Mediterráneo Occidental. Sin embargo, ha sido inevitable ampliar el área de estudio a las especies de otras zonas geográficas para poder tener una visión más amplia del género, así como para poder estudiar de manera crítica los numerosos táxones, que han sido citados en el área de estudio y son originarios del Mediterráneo Oriental u otras regiones más alejadas.

La presente Tesis Doctoral aborda, por tanto, el estudio del género *Tamarix* desde una perspectiva amplia. Hasta la actualidad no se han publicado trabajos que traten de manera integrada la taxonomía del género desde el punto de vista morfológico y filogenético. Diferentes trabajos taxonómicos han tratado el género con mayor o menor profundidad, especialmente desde el siglo XVIII. Sin embargo, desde finales de los años 60 del siglo XX muy pocos trabajos han tratado críticamente los datos existentes hasta entonces, limitándose principalmente a la descripción de nuevos táxones en Asia, o bien a la extensión, con mayor o menor acierto, de las áreas de distribución en Europa de táxones previamente descritos. Se ha realizado un gran esfuerzo en contrastar la bibliografía previa con el estudio de numeroso material de herbario. A las nuevas recolecciones realizadas en la Península Ibérica, Islas Canarias, noroeste de África y los países europeos bañados por el Mediterráneo, hay que sumar el material estudiado en diferentes herbarios europeos y americanos (ABH,

BCMEX, BM, G, HUAL, JAEN, K, MA, MO, MPU, P, PR, PRC VAL y W) (acrónimos según Thiers, 2008+) con importantes colecciones de *Tamarix*, prestando especial atención a los pliegos de material tipo.

Los estudios filogenéticos previos a esta Tesis Doctoral se han centrado en la caracterización genética de especies invasoras en América y no han profundizado demasiado en la taxonomía del género (Gaskin & Schaal 2003, Gaskin & Shafroth 2005, Gaskin & Kazmer 2009, Mayonde & al. 2015, Villar & al. 2015). Así pues, se han realizado estudios basados en la obtención y comparación de secuencias correspondientes a tres espaciadores génicos del ADN plastidial (*trnS-trnG, trnQ-rps16* y *ndhF-rpl32*), así como a un espaciador génico de ADN nuclear (Internal Transcribed Spacer, ITS).

La combinación de estas técnicas ha permitido la resolución de ciertos aspectos taxonómicos, filogenéticos y nomenclaturales en *Tamarix*, lo que ha dado lugar a las ocho publicaciones (la última de ellas aún inédita) que se presentan como capítulos de esta Tesis Doctoral. Del mismo modo se han abierto nuevas posibles vías de investigación en el campo de la taxonomía y la filogenia del género.

El trabajo realizado tiene como fin conocer las diferentes unidades taxonómicas que presenta el género en la zona de estudio. Este es un paso clave, no solo para las áreas de conocimiento de la botánica y la ecología vegetal, sino también desde el punto de vista de la conservación, que no podrá dirigir sus esfuerzos con precisión mientras la taxonomía no proporcione los criterios adecuados.

Objetivos

- Realizar estudios taxonómicos de las especies del género *Tamarix,* con mayor énfasis en aquellas que se distribuyen en el Mediterráneo Occidental.
- Estudiar la mayor cantidad posible de pliegos de *Tamarix,* con especial atención a los tipos nomenclaturales y recolecciones antiguas.
- Trabajar sobre la precisión de los tipos nomenclaturales en aquellos casos en los que pudiera resultar necesario.
- Establecer las relaciones filogenéticas del mayor número de táxones posible, mediante el uso de herramientas moleculares.
- Proveer de una base sólida de conocimiento sobre la que se puedan emprender nuevas investigaciones sobre el género *Tamarix*.
- Proporcionar unos criterios taxonómicos que puedan servir de referencia para la gestión de la biodiversidad.

Esta Tesis Doctoral se ha presentado en el formato de compendio de publicaciones y se ha dividido en tres secciones que vienen marcadas por los objetivos propuestos, por el contenido de los artículos incluidos en cada una de ellas, así como por la metodología utilizada para la obtención de los resultados de cada una de ellas. Así pues: la sección I (artículos 1, 2 y 3) incluye trabajos que tratan aspectos nomenclaturales y de tipificación; la sección II (artículos 4, 5 y 6) incluye trabajos taxonómicos, basados en el estudio morfológico y bibliográfico; y por último, la sección III (artículos 7 y 8) incluye trabajos taxonómicos que incluyen herramientas moleculares. A continuación se enumeran los artículos incluidos en la Tesis Doctoral.

Sección I

Artículo 1: Villar J. L., Juan A., Alonso M. A. & Crespo M. B. 2014.Type specimens of *Tamarix* (Tamaricaceae) described by Josef Franz Freyn in 1903. *Phytotaxa* 172 (3): 289-292.

Artículo 2: Villar J. L., Alonso M. A., Juan A. & Crespo M. B. 2015. Remarks on typification of nineteen names in *Tamarix* L. (*Tamaricaceae*). *Nordic Journal of Botany* 33: 591-600.

Artículo 3: Villar J. L., Alonso M. A., Juan A., Gaskin J. F. & Crespo M. B. 2014. Proposal to conserve the name *Tamarix ramosissima* against *T. pentandra* (*Tamaricaceae*). *Taxon* 63 (5): 1140-1141.

Sección II

Artículo 4: Villar J. L., Alonso M. A., Juan A. & Crespo M. B. 2012. Does *Tamarix dalmatica* (Tamaricaceae) occur in Spain? *Anales del Jardín Botánico de Madrid* 69 (2): 253-258.

Artículo 5: Villar J. L., Juan A. & Alonso M. A. 2014. *Tamarix hohenackeri* Bunge, a new record for the flora of Mexico. *Acta Botánica Mexicana* 106: 117-128.

Artículo 6: Villar J. L., Alonso M. A., Vicente A., Juan A. & Crespo M. B. 2014. The genus *Tamarix* (*Tamaricaceae*) in Crete (Greece). *Willdenowia* 44: 321-326.

Sección III

Artículo 7: Villar J. L., Turland N., Juan A., Gaskin J. F., Alonso M. A. & Crespo M. B. 2015. *Tamarix minoa* (*Tamaricaceae*), a new species from the island of Crete (Greece) based on morphological and plastid molecular sequence data. *Willdenowia* 45 (2): 161-172.

Artículo 8 (no publicado): Villar J. L., Juan A., Alonso M. A., Gaskin J. F. & Crespo M. B. 2015. Preliminary phylogeny of the genus *Tamarix* (Tamaricaceae), with a focus on the Mediterranean taxa.

Para alcanzar los objetivos propuestos en la presente Tesis Doctoral, se ha estudiado el género *Tamarix* en profundidad. A continuación se presenta una síntesis general con numerosa información recopilada sobre el género, incluyendo aspectos morfológicos, filogenéticos y de distribución, así como un recorrido comentado sobre el contexto histórico.

El género *Tamarix,* pertenece a la familia *Tamaricaceae* Link., que forma uno de los clados basales de las Caryophylales Berchtold & J. Presl., junto a *Frankeniaceae* Desv.*, Plumbaginaceae* Juss. y *Polygonaceae* Juss*.* (APG III 2009). Dentro de *Tamaricaceae* se reconocen cuatro géneros: *Myricaria* Desv., *Myrtama* Ovcz. & Kinzik., *Reaumuria* L. y *Tamarix* (Yang & Gaskin 2007, Villar & al. 2015). Así mismo*,* los géneros *Hololachna* Ehrenb. y *Trichaurus* Arn. se consideran, respectivamente, sinónimos de *Reaumuria* y *Tamarix* (Baum 1978, Yang & Gaskin 2007)*.*

Aspectos morfológicos

Árboles o arbustos en su mayoría caducifolios o marcescentes (*T. gallica* L.*, T. africana, T. boveana* Bunge), aunque también hay especies perennifolias (*T. aphylla* (L.) Karst.*, T. usneoides* E. Mey.). Sin embargo, todavía existe un vacío de conocimiento a este respecto, y se desconoce el comportamiento de muchas especies, sobre todo en regiones con inviernos benignos. En este sentido, recientemente hemos conocido que los ejemplares de *T. canariensis* Willd., que crecen en las Islas Canarias, se comportan como perennifolios (Reyes-Betancourt com. pers.).

Los ***tallos*** leñosos pueden presentar distintas coloraciones, desde gris claro a tonalidades rojizas o casi negras. Esta coloración ha sido en ocasiones utilizada como carácter diagnóstico (Baum 1978, Cirujano 1993). Las ***hojas*** presentan glándulas secretoras de sal (figura 1), que pueden ser más o menos abundantes, dependiendo de la especie y del hábitat. Las hojas, a su vez, presentan diversas formas: vaginadas, que abrazan el tallo en casi toda la longitud del limbo foliar, con la zona de contacto fusionada (eg. *T. aphylla, T. dioica* Roxb. ex Roth.) o no (*T. indica* Willd.); amplexicaules, deltoides, más anchas que largas y engrosadas, abrazando más de la mitad del tallo o llegando a envainarlo casi totalmente (eg. *T. pycnocarpa* DC.*, T. macrocarpa* Ehrenb. ex Bunge*, T. amplexicaulis* Ehrenb.), o bien triangular lanceoladas, amplexicaules solo en su tercio o mitad basal (eg. *T. nilotica* (Ehrenb.) Bunge*, T. mascatensis* Bunge*, T. arborea* (Sieber ex Ehrenb.) Bunge); escuamiformes, ovado-lanceoladas, con base estrecha decurrente (eg. *T. boveana*) o más ancha, auriculada, sin llegar a envainar la mitad del diámetro del tallo (eg. *T. africana*). Es habitual encontrar formas intermedias entre las anteriormente descritas.

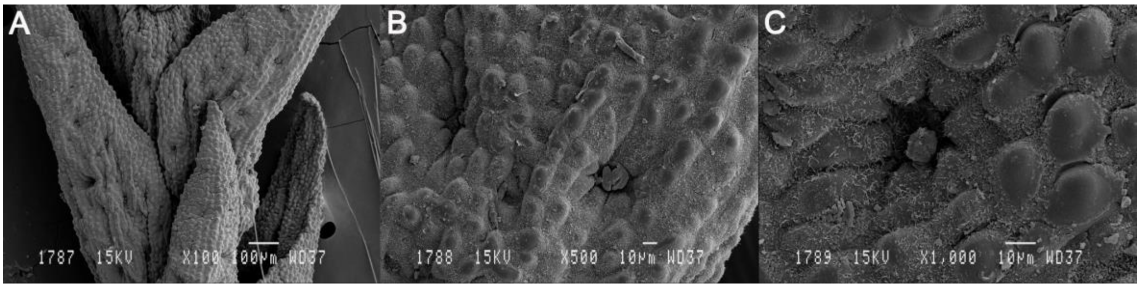

Figura 1. Detalle de las glándulas de *T. gallica* (ABH 37958) a 100 (A), 500 (B) y 1000 (C) aumentos.

Las ***inflorescencias*** se presentan en forma de racimos pedunculados con tamaños muy variables, que van desde los apenas 2 cm (eg. *T. smyrnensis* Bunge*, T. polystachya* Ledeb.) de los más cortos, hasta más de 15 cm (eg. *T. ericoides* Rottler*, T. hampeana* Boiss. & Heldr.). También la anchura de los racimos varía entre especies, aunque suele ser más estable que la longitud, sirviendo en muchos casos como carácter diagnóstico, y pudiendo variar entre 3 y 15 mm. Los racimos se organizan de distintas formas: **solitarios**, disponiéndose sobre ramas del año anterior, pudiendo intercalarse con ramillas verdes con hojas (eg. *T. tetragyna* Ehrenb.*, T. africana, T. boveana, T. octandra* Bunge); **fasciculados**, con varios racimos naciendo de un mismo punto (eg. *T. hohenackeri* Bunge y ocasionalmente *T. gallica* o *T. parviflora* DC.) o **formando panículas**, agrupados en ramas terminales generalmente del propio año (*T. parviflora, T. africana*), que se pueden dividir formando panículas compuestas (*T. nilotica, T. gallica, T. smyrnensis*). Muchas especies pueden presentar varias floraciones a lo largo del año, mostrando inflorescencias de distinto tipo en diferentes periodos. En nuestro territorio por ejemplo, *T. gallica* suele producir panículas simples en la primera floración primaveral, mientras que produce panículas compuestas en floraciones posteriores, al final del verano.

Los ***pedúnculos*** de los racimos suelen estar cubiertos de brácteas escariosas cuando los racimos son solitarios (*T. africana, T. boveana*), y desnudos o con pocas brácteas cuando las inflorescencias son más o menos paniculadas (*T. smyrnensis, T. canariensis*). Del mismo modo, los racimos solitarios suelen ser de mayor tamaño que aquellos que forman panículas.

Las ***brácteas***, normalmente una por flor, presentan diversos tamaños y formas, y su longitud relativa con respecto al cáliz se usa como carácter diagnóstico. Hay casos en los que superan al cáliz (*T. boveana, T. elongata* Ledeb.*, T. octandra*), mientras que en otros no llegan a superar el pedicelo (*T. polystachya*), si bien puede existir una gran variabilidad a este respecto (*T. hampeana*). En algunas especies se pueden encontrar, de manera ocasional, brácteas adicionales, dispuestas sobre el propio pedicelo (*T. rosea* Bunge*, T. hampeana, T. boveana, T. hohenackeri*), que en ciertos casos (*T. rosea*) han sido utilizadas como carácter diagnóstico (Baum 1978).

Los ***sépalos*** 4-5 (9), presentan diversos tamaños y formas. Desde triangular-lanceolados y agudos, como en las formas típicas de *T. smyrnensis*, a ovados anchos, casi redondeados como en *T. pycnocarpa.* También se pueden encontrar diferencias entre los sépalos externos e internos. Por lo general, las especies tetrámeras, presentan sépalos externos más grandes y más agudos que los internos (*T. boveana*), mientras que en las especies pentámeras suele haber menos diferencias, si bien en ocasiones los externos son menores (*T. pycnocarpa*). El margen de los sépalos puede variar de liso a dentado, serrado, etc., carácter que también se ha utilizado como diagnóstico (Baum 1978).

Los ***pétalos*** 4-5 (9), muestran diversos colores, tamaños y formas, siendo estos dos últimos caracteres ampliamente utilizados como diagnósticos (Baum 1978). Pueden ser persistentes (*T. ramosissima* Ledeb.*, T. chinensis* Lour.*, T. smyrnensis, T. hohenackeri*) o, como en la mayoría de casos, caedizos al madurar el fruto. Se trata pues, de un buen carácter diagnóstico para el grupo de especies con los pétalos persistentes, aunque no es muy concluyente a nivel específico.

Los ***estambres*** 4-5 (10), 8-10 (15), suelen presentarse en número igual, al de sépalos y pétalos, si bien en algunas especies el número es el doble (*T. pycnocarpa* y especies relacionadas, *T. stricta* Boiss.*, T. octandra*). También es común en algunas especies la presencia de estambres en número mayor al habitual (eg. *T. africana, T. hampeana, T. pycnocarpa*). Los estambres de *Tamarix* consisten en una antera, con dos tecas, mucronada o no, que se une mediante el filamento estaminal a un disco nectarífero. La forma de disponerse los filamentos estaminales con respecto a los lóbulos formados por el disco nectarífero se ha utilizado como carácter diagnóstico (Baum 1978). Generalmente, los filamentos se pueden disponer de manera truncada o progresivamente atenuada sobre los lóbulos del disco (*T. africana*), o bien entre los lóbulos de este (*T. smyrnensis*). Baum (1966, 1978) utilizó una nomenclatura muy precisa para referirse a la morfología de los discos estaminales en *Tamarix,* utilizando diferentes nombres según el número de estambres y su tipo de inserción en el disco. Según la inserción de los filamentos en el disco distinguió tres tipos, a los que otorgó gran importancia como carácter diagnóstico: **holólofo**, con los filamentos estaminales insertos entre los lóbulos del disco; **parálofo**, con los filamentos insertos de manera truncada sobre los lóbulos; **sínlofo**, con los filamentos estaminales confluyentes sobre los lóbulos del disco. Sin embargo, se ha observado una amplia variabilidad intra-específica entre las tres morfologías mencionadas, así como la existencia de formas intermedias de difícil asignación a cualquiera de ellas. Como ya hicieran algunos autores posteriores a Baum (1966, 1978) (Zohary 1987, Yang & Gaskin 2007), en la presente Tesis Doctoral, se ha optado por no utilizar esta nomenclatura. Así pues, se ha descrito en cada caso el tipo de inserción de los filamentos estaminales sobre el disco.

El ***gineceo*** es unilocular, generalmente con tres carpelos, a veces cuatro, raras veces cinco o más. Presenta estilos libres con forma de clavo o maza, en número igual al de los carpelos. Al madurar, produce un fruto seco, dehiscente por 3 (4) valvas que se abren al madurar, de tamaño variable según las especies, entre 3 y 15 mm de longitud.

Las ***semillas*** presentan forma oval, entre 0.5 y 1.5 mm de longitud, con un vilano formado por pelos simples huecos con excavaciones en su base que favorecen la dispersión aérea (figura 2). El vilano está unido a la testa seminal, desprendiéndose ambos de manera conjunta al inicio de la germinación.

El número cromosómico más comúnmente citado para las especies del género es n=12 (Baum 1978, Yang & Gaskin 2007). Sin embargo, recientemente Samadi & al. (2013) han encontrado individuos triploides (n=18) y tetraploides (n=24), que han sido asignados a especímenes híbridos o a autopoliploidías.

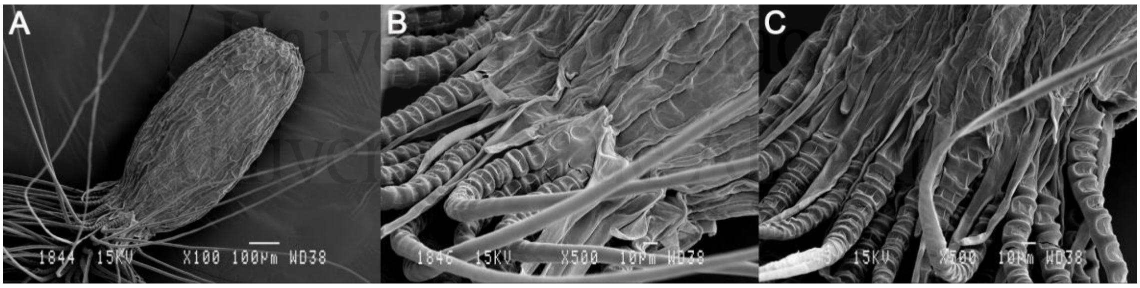

Figura 2. Detalle de la semilla (A) y base de los pelos del vilano (B) en *T. boveana* (ABH 54185) y (C) *T. boveana* (ABH54330).

Distribución mundial

El género *Tamarix* comprende entre 54 y 90 especies, según autores (Baum 1978, Zohary 1987, Yang & Gaskin 2007), originarias de Eurasia y África. Habitan principalmente en zonas áridas, desérticas o subdesérticas, en regiones templadas o subtropicales (Zohary 1987). Secundariamente, algunas especies de *Tamarix* han colonizado América y Oceanía (Gaskin & Schaal 2003).

Atendiendo a las investigaciones de Zhang & al. (2014), la familia *Tamaricaceae* pudo haber habitado las zonas áridas y salinas asociadas al Paratetis (hace 70 m.a.). El género *Tamarix* se habría expandido, con la progresiva retirada del Paratetis, hacia sus límites geográficos actuales: al oeste, las costas atlánticas del sur de Europa y el noroeste de África; al este, la costa pacífica de Asia; al norte las estepas y desiertos fríos asiáticos de Mongolia y Kazajistán; al sur, llegando al extremo más meridional del continente africano. La llegada del género al sur de África se relaciona probablemente con el llamado "pasillo árido de Balinsky", que habría conectado el este y el sur de África en varias ocasiones durante los últimos 20 m.a. (Balinsky 1962), dando lugar a las dos especies nativas de dicha zona, *T. usneoides* y *T. angolensis* Nied, ambas con características morfológicas muy similares a *T. aphylla* y *T. dioica* que crecen en áreas subtropicales del hemisferio norte.

Tamarix es abundante principalmente en las regiones Mediterránea, Irano-Turaniana e Índica, en las que se concentra el mayor número de especies, y donde se encuentran los dos centros principales de diversidad, localizados, según Baum (1978), en el contacto de las regiones Irano Turaniana e Índica y en el Mediterráneo Oriental. Desde estos dos centros, alcanza las regiones Eurosiberiana, Indochina, Asiática-Oriental, Saharo-Arábiga, Sudano-Zambeziana, Capense, Karoo-Namibia y Macaronésica (Takhtajan 1986), si bien la diversidad de especies es mucho menor en las zonas periféricas del área de distribución.

La presencia actual de *Tamarix* en América y Oceanía como género alóctono no es meramente testimonial. Desde el siglo XIX se utilizó como planta ornamental, fijadora del suelo o barrera contra los vientos, llegando a convertirse posteriormente en una de las mayores plantas invasoras de América del Norte (Baum 1967, Di Tomaso 1998, Stromberg 1998, Gaskin & Schaal 2003, Csurhes 2008).

Contexto histórico

El género *Tamarix* es conocido desde los orígenes de la civilización. Ya en el antiguo testamento se menciona en varias ocasiones (NIV: Gn 21.33, Sl 22.6; 31.13), originalmente bajo la voz hebrea "ethel" o "eshel". También es mencionado de manera indirecta como "Maná", que según varios autores (United Bible Societies 1980, Baum 1978, Musselman 2007) corresponde, al menos en parte, a la secreción dulce que producen ciertos insectos (*Coccus manniparus* Hemprich & Ehrenberg *in* Ehrenberg*,* 1829) que se alimentan de la savia de los *Tamarix*, en especial de *Tamarix mannifera* (Ehrenb.) Bunge (= *T. nilotica*). Así mismo, también se hace referencia a *Tamarix* en el Corán (Sura 34:15-16, Ali), donde narra la destrucción de una presa que causó desertificación en el pueblo de Al-rim, sustituyendo los jardines por *Tamarix* y espinos.

Fuera del contexto de los textos religiosos, los tratados científicos más antiguos que se han encontrado en la bibliografía, con referencias a *Tamarix,* se remontan a los siglos III y IV a.C., mencionado como “Myrica” por Teofrasto (Stapel & al. 1644). Posteriormente, ya en el siglo I de nuestra era, Dioscórides habla de un *Tamarix* (“Myrica” en la traducción al latín de Rvelio (1554); “Tamarisco” en la traducción al castellano de Laguna (1563)) que crece domesticado abundantemente en Siria y Egipto, y enumera algunas de sus propiedades curativas. En la misma época, Plinio el Viejo (Harduinus 1723) también lo recoge como “Myrice” en su tratado de Historia Natural (Libro XIII, sección 37), indicando además que en Italia lo llaman “Tamarice”.

Los autores prelinneanos también reconocen el género *Tamarix.* Inicialmente, bajo el nombre de Myrica se pueden encontrar referencias en las obras de Cesalpino (1583) y Mattioli (1562). Este último realizó observaciones principalmente sobre usos médicos tradicionales, ampliando ligeramente la información extraída de los escritos antiguos de Dioscórides y Galeno. También Clusius (1576) utilizó este nombre (*Myrica silvestris*). Atendiendo a la descripción, a la iconografía aportada y a la amplia distribución mencionada, que incluye España, Grecia, Siria y Egipto, parece claro que Clusius se refería al género *Tamarix* en una interpretación muy próxima a la actual. Incluso recoge algunos nombres autóctonos, reconociendo para el territorio español la voz “Taray”, que se sigue utilizando hoy en día para referirse a las especies locales de *Tamarix*.

Tournefort (1719) ya lo menciona como *Tamariscus,* distinguiendo entonces dos especies: “*Tamariscus Narbonensis”* y “*Tamariscus Germanica”*, ambas asignadas a L’Obel (1591) quien, de hecho, había reproducido ilustraciones previas de ambos táxones, publicadas por Dalechamps (1586), donde ya aparecían referidos como “*Tamarix Germanica*” y “*Tamarix Narbonensis*”, siendo esta la referencia más antigua que se ha encontrado del uso del término “*Tamarix”* para referirse a este grupo de plantas. A este respecto, el primer diccionario de lengua española (Covarrubias 1611) recogía entradas para *“Tamariz”* y *“Taray”.*

Linneo (1753) incluyó en *Tamarix* los dos táxones que se venían utilizando comúnmente con anterioridad: *Tamarix gallica*, que autores previos habían llamado *T. narbonensis* y *Tamarix germanica* (≡ *Myricaria germanica*). *Tamarix aphylla*, pasó inicialmente desapercibida al incluirla Linneo, seguramente por estudiar un espécimen sin racimos, dentro del género *Thuja*.

No fue hasta la segunda mitad del siglo XVIII cuando varios autores comenzaron a describir nuevas especies: *Tamarix orientalis* Forsk. *T. pentandra* Pall., *T. tetrandra* Pall. ex M. Bieb.*, T. africana*, *T. chinensis* Lour., *T. indica* y *T. ericoides.*

El primer autor que planteó un estudio detallado fue Willdenow (1816), que en su *Beschreibung der Gattung Tamarix* (Descripción del género *Tamarix*), recopiló las nueve especies que se habían descrito hasta el momento y añadió otras siete. Por aquel entonces, *Tamarix* incluía también las especies que actualmente se clasifican en *Myricaria* y *Reaumuria.* Así pues, el número de especies reconocidas por Willdenow, dentro del concepto actual de *Tamarix,* asciende a 11, describiendo como nuevas las siguientes: *T. hispida* Willd., *T. canariensis, T. gracilis* Willd*.* y *T. laxa* Willd*.* En esta obra, Willdenow consideró *T. pentandra* como un sinónimo de *T. gallica* y otorgó la autoría de *T. africana* a Desfontaines (1798), aunque Poiret (1789) ya había usado este nombre con anterioridad para describir la misma especie.

La segunda década del siglo XIX fue muy activa en cuanto al estudio del género. Desvaux (1824) fue el primero en reconocer *Myricaria* como un género independiente de *Tamarix*. Sin embargo, de acuerdo con Baum (1978), parece ser que Desvaux desconocía la existencia del trabajo previo de Willdenow. Así pues, Desvaux reconoció nueve especies dentro de *Tamarix,* de las cuales: *T. songarica* corresponde a *Reaumuria songarica* Pall., *T. canescens* Desv. corresponde a *T. hispida* Willd., y *T. pallasii* Desv. fue descrita para reemplazar a *T. pentandra* Pall., nombre que había sido considerado como superfluo por Bieberstein (1808) y por Willdenow (1816).

Posteriormente, Ehrenberg (1827) profundizó en las diferencias entre *Myricaria* y *Tamarix.* Aunque su tratamiento taxonómico resultó algo confuso, fue el primero en crear tres subgéneros en *Tamarix.* En el primero (*T.* subgen. *Oligadenia* Ehrenb.) incluyó aquellos táxones con cuatro filamentos estaminales: *T. tetrandra, T. laxa, T. laxa* var. *racemosa* Ehrenb. y *T. laxa* var. *subspicata* Ehrenb (= *T. parviflora*). En el segundo (*T.* subgen. *Decadenia* Ehrenb.), incluyó aquellos táxones con cinco filamentos estaminales, combinando un buen número de las especies previamente descritas como variedades de *T. gallica* (*T. gallica* var. *chinensis* (Lour.) Ehrenb.*, T. gallica* var. *indica* (Willd.) Ehrenb.*, T. gallica* var. *canariensis* (Willd.) Ehrenb.*, T. gallica* var. *arborea* Sieber ex Ehrenb.), e incluso algunas descritas por él mismo (*T. gallica* var. *nilotica* Ehrenb.*, T. gallica* var. *mannifera* Ehrenb.*, T. gallica* var. *heterophylla* Ehrenb.*, T. gallica* var. *subtilis* Ehrenb.), así como *T. africana* o *T. articulata* Vahl. (= *T. aphylla*). Llama la atención la inclusión en este subgénero de especies que presentan principalmente cuatro estambres (*T. tetragyna*, *T. effusa* Ehrenb. y *T. gracilis*). En el tercer subgénero (*T.* subgen. *Polyadenia* Ehrenb.), incluyó aquellas especies con 10 filamentos estaminales: *T. ericoides, T. amplexicaulis*, *T. passerinoides* Delile*, T. passerinoides* var. *macrocarpa* Ehrenb., *T. passerinoides* var. *divaricata* Ehrenb. y *T. passerinoides* var. *hammonis* Ehrenb.

Así mismo, Candolle (1828) trató el género en su *Prodromus*, reconociendo 17 especies, de las cuales tres fueron descritas por él (*T. parviflora*, *T. pycnocarpa*, *T. senegalensis* DC.). Candolle no aportó nombres a nivel subgenérico, si bien clasificó las especies en "pentapétalas y pentandras", "tetrapétalas y tetrandras" y "pentatetrapétalas con el doble de estambres”. El tratamiento de Candolle fue bastante acertado desde el punto de vista de la recopilación de especies publicadas con anterioridad, si bien por su proximidad en el tiempo con la contribución de Ehrenberg, no incluía los nuevos táxones descritos por este último.

Ledebour (1829), con la supervisión de C. A. Meyer y A. Bunge, incluyó cuatro especies, tres de ellas nuevas, en su *Flora Altaica*, adoptando para las especies incluidas los subgéneros propuestos por Ehrenberg: Oligadenia (*T. elongata* y *T. laxa*) y Decadenia (*T. cupressiformis* Ledeb. y *T. ramosissima*).

Roxburgh (1832) incluyó en su *Flora Indica* solo dos especies, *T. indica* y *T. dioica,* esta última descrita por él mismo. También sobre las especies del subcontinente indio trabajaron Wight y Walker-Arnott (1834), que excluyeron *T. ericoides* de *Tamarix* y lo ubicaron en el nuevo género *Trichaurus* Wight & Walker-Arnott.

Anteriormente, Bunge (1833) había descrito la primera de las muchas especies de *Tamarix* que llevan su autoría: *T. juniperina* Bunge (= *T. chinensis*).

Decaisne (1835) recalcó la importancia del disco estaminal, realizando observaciones sobre su configuración como carácter diagnóstico. Posteriormente, el propio Decaisne (1844) describió *Trichaurus aucherianus* Decne. (≡ *Tamarix aucheriana* (Decne.) B. R. Baum).

Por las repercusiones que tendría posteriormente como flora invasora, es destacable la temprana referencia del cultivo ornamental de especies de *Tamarix* en Estados Unidos, donde ya en 1837, se ofertaban ejemplares de *T. gallica* a 50 centavos (Catálogo del vivero de Prince & sons). Atendiendo a los datos conocidos sobre especies de *Tamarix* naturalizadas en Norteamérica, es más que probable que hubiese otras especies bajo esa denominación.

Webb y Bertheolt (1840), y posteriormente Webb (1841), pusieron de manifiesto con sus interpretaciones la dificultad de clasificar algunas especies de *Tamarix.* Webb tuvo grandes problemas con las diferencias entre *T. gallica-T. canariensis.* Lo que le llevó a un resultado un tanto confuso que incluye la descripción de una nueva especie *T. anglica* Webb.

Así mismo, es destacable la precisa recopilación de Walpers (1843). Este utilizó los subgéneros propuestos por Ehrenberg (1827), aunque los llamó secciones, e incluso añadió una subdivisión (*parviflorae*) en *T.* sect. *Decadenia* (Ehrenb.) Walp. para incluir las especies de flores pequeñas (*T. orientalis* y *T. gallica,* con sus múltiples variedades). Así pues, Walpers incluyó hasta 30 táxones a nivel específico o como variedades, contando con *T. ericoides, T. pycnocarpa* y *T. aucheriana,* incluidas en *Trichaurus* (*T.* subgen. *Polyadenia* sensu Ehrenberg). Sin embargo, si utilizó *T.* sect.

Polyadenia (Ehrenb.) Walp. para incluir a *T. amplexicaulis* y *T. passerinoides.* Siguiendo un criterio similar al de Ehrenberg, mantuvo *T. tetragyna* y *T. effusa* en *T.* sect. *Decadenia*, e incluyó nueve variedades dentro de *T. gallica,* varias de las cuales han sido posteriormente consideradas como especies válidas, o al menos diferentes a *T. gallica* (*T. chinensis, T. nilotica, T. mannifera, T. indica* y *T. canariensis* entre otras).

De nuevo Ledebour (1843) trató el género dentro de su *Flora Rossica*, utilizando *T.* subgen. *Oligadenia* y *T.* subgen. *Decadenia* para clasificar las especies incluidas en el área de estudio abarcada por su trabajo. Dentro de *Oligadenia* describió *T. polystachya* Ledeb., mientras que mantuvo *T. tetragyna T*. subgen*. Decadenia*. En este trabajo, Ledebour reconocía diez especies para Rusia, sin embargo su interpretación de *T. gallica* es discutible. Ledebour describió tres variedades nuevas (*T. gallica* var. *vulgaris* Ledeb*., T. gallica* var. *pycnostachys* Ledeb*.,* y *T. gallica* var. *micrantha* Ledeb.), en las que incluyó todos los nombres previos (*T. pallasii, T. pentandra, T. ramosissima* y *T. eversmanni* Presl. entre otros) que hacen referencia, según nuestro criterio, a *T. ramosissima* en sentido amplio, y que se diferencian de *T. gallica* por sus pétalos persistentes y por la configuración de su disco nectarífero, con los filamentos estaminales insertos entre los lóbulos. Además, *T. gallica* es propia del Mediterráneo Occidental y algunas zonas del oeste de Europa.

Boissier (1849) publicó tres nuevas especies, todas ellas dentro de *T.* sect. *Oligadenia*: *T. hampeana* Boiss & Heldr. ex Boiss, de las costas continentales mediterráneas de Grecia y Turquía, *T. meyeri* Boiss. y *T. deserti* Boiss., las dos últimas muy próximas morfológicamente a *T. tetragyna.* Según los comentarios de Boissier en la descripción de *T. meyeri,* se puede interpretar que en ese momento se consideraba *T. tetragyna* como una especie pentámera. De ahí que muchos autores anteriores la hubieran incluido en *T.* sect. *Decadenia.*

Posteriormente, Bunge (1851) trató *Tamarix* entre los géneros incluidos en las recolecciones de Alexander Lehmann en las estepas de Asia Central. Sin embargo, Bunge excedió los límites geográficos de dicha obra. Por ejemplo, describió *T. boveana* Bunge (sobre especímenes recolectados por Bové en Argelia), dentro de los comentarios sobre la morfología de *T. elongata,* a la que se asemeja en varios aspectos. Además, Bunge (1851) obvió los subgéneros propuestos por Ehrenberg, clasificando las especies según varias nuevas secciones: en *T.* sect. *Tetrandrae* Bunge, incluyó *T. elongata, T. boveana, T. tetragyna, T. meyeri, T. laxa y T. polystachya;* en *T.* sect. *Vaginantes* Bunge, incluyó *T. dioica, T. articulata* (= *T. aphylla*) y *T. usneoides*, puntualizando que ninguna de ellas se encontraba entre el material revisado para el dicho estudio; en *T.* sect. *Leptostachyae* Bunge, incluyó *T. leptostachya* Bunge y *T. karelinii* Bunge, ambas especies nuevas; por último, en *T.*

sect. *Paniculatae* Bunge, incluyó *T. gracilis, T. pallasii* y *T. arceuthoides* Bunge, describiendo muy acertadamente las principales diferencias entre *T. pallasii* y *T. gallica*, que habían sido obviadas por autores anteriores (Ehrenberg 1827, Ledebour 1843, Walpers 1843).

Un año después, Bunge (1852) publicó una obra monográfica que pretendía incluir y clasificar toda la información sobre *Tamarix* publicada hasta ese momento. El propio título de la obra, *Inest Tentamen Generis Tamaricum Species Accuratius Definiendi*, que se podría traducir como "Intento de definir con precisión las especies incluidas en el género *Tamarix*", así como las divergencias en los tratamientos realizados por los predecesores de Bunge, dan idea de las dificultades que plantea la correcta organización de este género. Bunge re-incluyó *Trichaurus* en *Tamarix, y* reconoció 51 especies, 20 de las cuales eran nuevas o previamente descritas por él. Además, incluyó hasta 43 variedades dentro de las especies aceptadas. En esta monografía, Bunge no siguió sus anteriores secciones y estableció solamente dos para todo el género: *T.* sect. *Vernales* Bunge y *T.* sect. *Aestivales* Bunge, que a su vez dividió en numerosos apartados. Las especies descritas por Bunge y sus divisiones a nivel infragenérico se recogen en la Tabla 1.

A pesar de los numerosos cambios que se han producido en la taxonomía de *Tamarix* desde la monografía de Bunge (1852), lo cierto es que su tratamiento del género fue muy importante. La completa recopilación de nombres, la detallada descripción de los táxones aceptados, las precisas referencias del material estudiado y los acertados comentarios expresados al inicio de la obra, hacen de este trabajo, aún pasados 164 años desde su publicación, una referencia indispensable para el estudio detallado de *Tamarix.*

Existe una monografía inédita de *Tamarix* escrita por Gay (1853). Gay nunca llegó a editar dicha obra, quedando solamente sus notas manuscritas, que incluían numerosos nombres nuevos y dibujos, recogidas en un grueso volumen que se conserva en la biblioteca del Real Jardín Botánico de Kew. Casi medio siglo después, varios autores rescatarían y darían uso a algunos de los nombres propuestos por Gay: *T. brachystylis* J. Gay ex Batt & Trab., *T. bounopaea* J. Gay ex Batt & Trab., *T. balansae* J. Gay ex Batt & Trab., *T. pauciovulata* J. Gay ex Batt & Trab. (Battandier & Trabut 1888, Maire 1931).

Poco después, el propio Gay, en una publicación de Blanche y Gaillardot (1854), sinonimizó *T. pallasii* a *T. laxa,* un error que se ha arrastrado hasta nuestros días (Gorschkova 1949, Baum 1978) y que es tratado en el artículo 3 de esta Tesis Doctoral (Villar & al. 2014a).

Boissier (1856), describió tres nuevas especies: *T. noeana* Boiss. (= *T. tetragyna*), *T. hispanica* Boiss. (= *T. africana*) y *T. stricta*. En dicho trabajo, Boissier clasificó sus nuevas especies dentro de las “series” de Bunge, aunque las trató bajo el nombre de secciones. Posteriormente, el propio Boissier (1867), volvió a tratar el género en su *Flora Orientalis*. En esta ocasión, Boissier siguió de manera más estricta las subdivisiones de Bunge (1852), manteniendo como secciones solamente *T.* sect. *Vernales* y *T.* sect. *Aestivales,* y asumiendo a su vez las “series” previamente descritas. Además de cambiar de “serie” alguna especie (*T. tetrandra* de *T.* ser. *Leptobotryae* Bunge a *T.* ser. *Pachybotryae* Bunge), Boissier describió seis nuevas: *T. syriaca* Boiss.*, T. ispahanica* Bunge ex Boiss., *T. jordanis* Boiss., *T. bachtiarica* Bunge ex Boiss., *T. bungei* Boiss. y *T. serotina* Bunge ex Boiss. Si bien todas ellas fueron posteriormente incluidas en la sinonimia de otras que ya existían (Baum 1966).

Thiselton Dyer (1875) reconoció seis especies en India, una de las cuales (*T. salina* Dyer) fue descrita por él. De las otras cinco (*T. gallica, T. dioica, T. articulata, T. ericoides* y *T. stricta*), solo el tratamiento que dio a *T. gallica* puede considerarse confuso, ya que lo utilizó para incluir como variedades *T. pallasii* y *T. indica.* De hecho, *T. gallica* no está presente en dicha región.

Niedenzu (1895) trató de recopilar todas las especies del género, e incluyó 67. Además, propuso una nueva clasificación a nivel infragenérico, que se puede consultar en la Tabla 1. Posteriormente, Niedenzu (1925) aumentó el número a 78. De las descritas por él, solamente *T. angolensis* Nied. es una especie aceptada en la actualidad.

En la obra póstuma de Freyn (1903), basada en recolecciones de Sintenis en Turkmenistán, se describieron dos especies nuevas (*T. askabadensis* Freyn y *T. karakalensis* Freyn), consideradas recientemente como sinónimos de *T. arceuthoides* Bunge (Samadi & al. 2013).

A finales del siglo XIX y principios del XX comenzó a estudiarse en detalle la flora del noroeste africano. Ball (1877) publicó *T. speciosa* Ball (= *T. africana*).

Posteriormente, Battandier y Trabut (1888) trataron el género con cierta perspectiva. Sus observaciones se recogen en el trabajo posterior de Battandier (1909). Battandier y Trabut rescataron algunos nombres de la monografía no publicada de Gay (1853), basados principalmente en recolecciones de Balansa conservadas en el herbario de Cosson (actualmente incluido en P). Así pues, se rescataron algunos nombres que, a falta de estudios más detallados, resultaron ser sinónimos de otros ya publicados. Battandier (1909) reconoció diez especies, dos de ellas nuevas: *T. articulata* (= *T. aphylla*), *T. gallica, T. getula* Batt. (= *T. africana*), *T. bounopaea* (= *T.*

boveana), *T. boveana, T. africana, T. brachystylis* (= *T. gallica*), *T. rubella* Batt. (= *T. parviflora*), *T. balansae* (= *T. amplexicaulis*) y *T. pauciovulata* (= *T. amplexicaulis*).

A partir de este momento, se sucede la publicación de multitud de especies y variedades de *Tamarix* en Marruecos y Argelia, como se detalla a continuación:
Caballero (1911): *Tamarix lagunae* Caball. (= *T. gallica*).
Pau (1924): *T. tingitana* Pau (= *T. africana*), *T. weylerii* Pau (= *T. gallica*).
Sennen (1931): *T. murbeckii* Sennen *nom. nud*. (= *T. gallica*).
Sennen & Mauricio (1934): *T. muluyana* Sennen & Mauricio *nom. nud*. (= *T. gallica*), *Tamarix valdesquamigera* Sennen & Mauricio *nom. nud*. (= *T. gallica*), *T. pulchella* Sennen & Mauricio *nom. nud.* (= *T. gallica*), *T. mauritii* Sennen & Mauricio *nom. nud*. (= *T. africana*).
Maire (1931): *T. leucocharis* Maire (= *T. gallica*), *T. trabutii* Maire (= *T. amplexicaulis*), *T. balansae* var. *longipes* Maire & Trab. ex Maire (= *T. amplexicaulis*), *T. balansae* var. *micrantha* Maire & Trab. ex Maire.
Maire (1933a): *T. ludibunda* Maire (atendiendo al holotipo en MPU, probablemente equivale a una floración tardía de *T. boveana*).
Maire (1933b): *T. oxysepala* Trab. ex Maire (= *T. amplexicaulis*).
Maire (1934): *T. tenuifolia* Maire & Trab. ex Maire (= *T. amplexicaulis*).
Maire (1935): *T. brachystylis* var *fluminensis* Maire (= *T. africana* var. *fluminensis* (Maire) B.R. Baum), *T. malenconiana* Maire (= *T. africana*).
De manera similar, Pau y Sennen, entre otros, describieron numerosos táxones en la primera mitad del siglo XX en la Península Ibérica, aunque ninguno de ellos se considera como especie aceptada en la actualidad.
Pau (1906): *T. jimenezii* Pau (= *T. boveana*).
Pau (1918): *T. segobricensis* (= *T. africana*).
Pau (1922): *T. calarantha* Pau (= *T. africana*).
Pau & Villar (1927): *T. esperanzana* Pau & Villar (= *T. gallica*), *T. matritensis* Pau & Villar (= *T. gallica*), *T. castellana* Pau & Villar (= *T. africana*), *T. viciosoi* Pau & Villar (= *T. africana*).
Sennen (1928): *T. uncinatifolia* Sennen (= *T. africana*), *T. celtiberica* Sennen & Elias ex Sennen (= *T. africana*), *T. lucronensis* Sennen & Elias ex Sennen (= *T. parviflora*), *T. riojana* Sennen & Elias ex Sennen (= *T. gallica*).
Sennen (1932): *T. brachylepis* Sennen (= *T. gallica*).

También en la primera mitad del siglo XX se realizaron importantes estudios taxonómicos en el este de Europa y la URSS. La contribución más destacable fue el tratamiento del género que realizó Gorschkova (1949) para la Flora de la URSS (traducción al inglés, Shinners 1957), donde se incluían 25 especies clasificadas en dos subgéneros, dos secciones y diez series, que pueden ser consultados en la Tabla 1. Sin embargo, su tratamiento taxonómico resulta confuso en términos generales. En *T.* subgen. *Eutamarix* incluyó *T.* sect. *Vernales* y *T.* sect. *Aestivales* de Bunge, proponiendo numerosas series, en muchos casos monoespecíficas, así como otras que incluían especies con características morfológicas muy diferentes (e.g. *Tamarix* ser. *Ramosissimae* Gorschk., ver Tabla 1). En dicho trabajo también se incluyen las especies descritas con anterioridad por Gorschkova: *T. komarovii* Gorschk., *T. litwinowii* Gorschk. y *T. araratica* (Bunge) Gorschk. (= *T. kotschyi*). Además, Gorschkova (1949) incluyó un apartado final con especies que fueron consideradas como "de origen híbrido", en su mayoría propuestas por Rusanov (1949): *T. kashakorum* Gorschk. = *T. leptostachya* x *T. ramosissima, T. karelinii = T. ramosissima* x *T. hispida, T. ewersmannii = T. ramosissima* x *T. leptostachya, T. korolkowii* Regel & Schmalah = *T. ramosissima* x *T. leptostachya, T. komarovii = T. ramosissima* x *T. passerinoides.*

En el Medio Oriente, Gutmann (1947) aceptó para Palestina la presencia de cinco especies (dos de ellas nuevas), que incluyó en tres grupos, aunque no mencionó un rango concreto para ninguno de ellos: *Vernales* (*T. tetragyna* var. *meyeri*), *Vernali-Aestivales* (*T. jordanis xeropetala* Gutm.), *Aestivales* (*T. maris-mortui* Gutm., *T. pseudo-pallasii* Gutm. y *T. articulata*).

Schiman-Czeika (1964) trabajó el género *Tamarix* para la *Flora Iranica*, aceptando 35 especies para el área de estudio, que trasciende las fronteras de Irán para incluir todo el territorio de Afganistán, así como partes de Irak, Pakistán, Turkmenistán y Azerbayán. En su tratamiento, Schiman-Czeika utilizó las secciones de Bunge (*T.* sect. *Vernales* y *T.* sect. *Aestivales*) y adaptó grupos del mismo autor nombrándolos como subsecciones (*T.* subsect. *Anisandrae* (Bunge) Gorschk., *T.* subsect. *Pachybotryae* (Bunge) Gorschk., *T.* subsect. *Leptobotryae* (Bunge) Gorschk., *T.* subsect. *Xeropetala* (Bunge) Gorschk., *T.* subsect. *Vaginantes* (Bunge) Gorschk. y *T.* subsect. *Pleiandrae* (Bunge) Gorschk.).

Solo dos años después, Baum (1966) publicó el último monográfico global sobre *Tamarix*. Dicha obra, que fue inicialmente publicada como Tesis Doctoral, así como informe final de un proyecto de investigación financiado por el USDA, fue re-editada con mínimos matices en una segunda versión (Baum 1978), entre los que destaca la validación de las nuevas series y secciones propuestas. En su monográfico, Baum aceptó 54 especies en *Tamarix,* dos de ellas (*T. dalmatica* B. R. Baum y *T. bengalensis* B. R. Baum) nuevas. Baum (1966, 1978) clasificó las especies en secciones y series descritas por autores anteriores, o bien de nueva creación, tal y como se puede consultar en la Tabla 1.

El trabajo de Baum es destacable desde muchos puntos de vista. La recopilación bibliográfica es muy completa, lo que permitió al autor incluir prácticamente todos los nombres publicados hasta ese momento, creando extensas sinonimias en algunos nombres. Sin embargo, el propio autor señaló la existencia de aspectos taxonómicos pendientes de resolver. La agrupación de las especies en secciones y series se ha demostrado artificial de acuerdo a estudios posteriores (Gaskin & Schaal 2003, Villar & al. 2015). La tarea de presentar una clave para el género a escala global es muy complicada, debido a las escasas diferencias entre algunas especies, así como a la elevada variabilidad morfológica que presentan algunos táxones. La clave dicotómica de Baum presenta a veces, tendencia hacia ciertas especies (e.g. *T. tetragyna, T. dalmatica* y *T. rosea*) y lo contrario en otras (e.g. *T. pycnocarpa* y *T. boveana*). El uso generalizado de la clave de Baum desde su publicación (Pignatti 1982, Baum 1990, Cirujano 1993, De Martis & al. 1984, Venturella & al. 2007, Salazar & Quesada 2009), ha llevado en algunos casos a identificaciones erróneas y extensiones exageradas de las áreas de distribución de ciertas especies como *T. mascatensis* y *T. dalmatica* (De Martis & al. 1984, 1986a, 1986b), o *T. meyeri* (Venturella & al. 2012).

Poco después de la publicación de la primera versión de su monografía, Baum (1966) describió una nueva especie (*T. kermanensis* B. R. Baum) próxima morfológicamente a *T. aphylla.*

Zohary (1987 (1ª ed. 1972)) en su *Flora Palaestina*, aceptó 13 especies presentes en dicha área, varias de ellas descritas previamente por él mismo: *T. negevensis* Zohary (= *T. arborea?*), *T. gennessarensis* Zohary (= *T. tetragyna?*), *T. aravensis* Zohary. Zohary (1972), que reconocía unas 90 especies en *Tamarix,* discrepó con Baum (1966) en la sinonimización que realizó este último de todas sus especies, así como en su interpretación de algunos nombres como *T. palestina* y *T. jordanis*. Además Zohary realizó interesantes observaciones en el grupo de *T. nilotica,* en el que incluyó como sinónimos o variedades *T. arborea, T. mannifera* y *T. arabica* Bunge, relativizando así la importancia de la estructura del disco como carácter diagnóstico en ciertos grupos de especies. También incluyó *T. meyeri* y *T. desertii* como variedades de *T. tetragyna,* y *T. sodomensis* Zohary, incluida por Baum (1968) entre los sinónimos de *T. arborea,* como variedad de *T. parviflora.*

Otra contribución destacable a la taxonomía de *Tamarix* la hizo Qaiser (1981), quien reconoció 26 especies para Pakistán, cinco de ellas nuevas: *T. pakistanica* Qaiser, *T. alii* Qaiser, *T. baluchistanica* Qaiser, *T. sultanii* Qaiser y *T. sarenensis* Qaiser. Qaiser no utilizó series ni secciones, si bien realizó un trabajo muy completo incluyendo tipos, sinónimos y algunas decisiones críticas con la monografía de Baum, como por ejemplo, la desvinculación de *T. smyrnensis* y *T. hohenackeri,* que también se trata en los artículos 4 y 6 de la presente Tesis Doctoral (Villar & al. 2014b, 2014c).

Zieliński (1994) hizo interesantes aportaciones, mencionando la escasa delimitación morfológica entre algunas especies, así como a los frecuentes casos de hibridación, aunque no entró a detallar este aspecto. Así pues, Zieliński (1994) usó un concepto amplio de especie, tratando solo aquellas que consideró más características y bien reconocibles. Esto le llevo, por ejemplo, a incluir *T. parviflora* en la sinonimia de *T. tetrandra* o bien, *T. pycnocarpa, T. macrocarpa* y *T. aucheriana* en la sinonimia de *T. passerinoides.*

En el último cuarto del siglo XX, se publicaron varias especies nuevas descritas de distintas zonas de China: *T. taklamakanensis* M. T. Liu (Liu 1979), *T. gansuensis* H. Z. Zhang ex P. Y. Zhang & M. T. Liu., *T. tarimensis* P. Y. Zhang & M. T. Liu., *T. jintaensis* P. Y. Zhang & M. T. Liu. y *T. sachensis* P. Y. Zhang & M. T. Liu. Todas ellas se recogen en *Flora of China* (Yang & Gaskin 2007).

Las especies de *Tamarix* publicadas más recientemente son *T. duezenlii* Çakan & Ziel. (2004) y *T. minoa* Villar & al. (2015), que se trata en el artículo 7 de esta Tesis Doctoral.

A continuación, la Tabla 1 recoge las clasificaciones infragenéricas propuestas para *Tamarix* por: Bunge (1852), Niedenzu (1895), Gorschkova (1949) y Baum (1978).

Tabla 1: Divisiones infragenéricas propuestas por varios autores

Autor y año	**BUNGE 1852**									
Sección	***Vernales*** Bunge: Racimos en ramas leñosas. Flores principalmente tetrámeras, mezcladas con algunas pentámeras, en pocas especies todas pentámeras					***Aestivales*** Bunge: Racimos en ramas de crecimiento en el propio año, terminales (raramente todos en *T. juniperiana* y *T. hohenackeri*, o al menos los primarios en *T. gallica* y *T. gracilis* surgiendo de yemas en ramas leñosas laterales), casi todos en racimos compuestos dispuestos en paniculas. Flores siempre pentámeras				
Subsección Bunge no definió estos grupos como subsecciones						**Fl. pentandri**, folia sessilia			**Fl. pentandri**, folia vaginantia	**Flores 10 (8-13) andri**, folia amplexicaulia vel vaginantia
Serie	***Anisandrae*** Bunge: Flores 4-meras o 5-meras, estambres en número mayor que el de los sépalos	***Pachybotryae*** Bunge: Flores 4-meras, estambres en número igual a los sépalos, racimos en antesis de 3 líneas (6.75 mm) de ancho, estilos 4, ligéramente alargados, hojas grandes	***Macrobotrya*** Bunge: Como *Pachybotryae* salvo por los estilos, 3 sésiles	***Leptobotryae*** Bunge: La mayoría de flores 4-meras, estambres en número igual a los sépalos, racimos de hasta 2 lin. (4.5 mm) de ancho por 2 pulg. de largo, estilos raramente 4, a menudo 3, hojas pequeñas	***Macrostyla*** Bunge: Flores 5-meras, estambres en número igual a los sépalos, racimos gruesos y densos, estilos casi tan largos como el ovario	***Pycnocarpae*** Bunge: Cápsula ovado-piramidal de mas de 3 lineas (6.75 mm) de largo	***Xeropetalae*** Bunge: Pétalos persistentes al madurar el fruto. Filamentos de base filiforme profundamente inmersos en los lóbulos del disco. cápsulas estrechas de hasta 2 lineas (4.5 mm) de largo. A: racimos laterales simples; B: racimos paniculados	***Piptopetalae*** Bunge: Petalos deciduos tras la floración. Cápsulas estrechas de hasta 2 lineas de longitud, raramente mayores, en ese caso estrechísimas. A: filamentos de base filiforme y profundamente inmersos en los lóbulos del disco; B: de base ensanchada confluente sobre los lóbulos; C: disco pentágono pequeño,con 5 lóbulos profundos atenuados en los estambres	***Vaginantes*** Bunge	***Pleiandrae*** Bunge
Especies incluidas *descritas por el autor Negrita: comúnmente aceptadas	***T. octandra****, ***T. dubia****, ***T. rosea****, ***T. hampeana.***	***T. tetragyna***, ***T. meyeri***, ***T. boveana****, ***T. brachystachys****, ***T. szovitsiana****	***T. elongata***	***T. tetrandra***, ***T. kotschyi****, *T. cupressiformis*, ***T. parviflora***, *T. cretica**, ***T. laxa***, *T. affinis**, *T. florida**	***T. africana***	***T. gracilis***, *T. effusa*	**A:** ***T. hohenackeri****, *T. juniperiana**; **B:** ***T, chinensis***, *T. aodessana*, *T. ewesmanni*, ***T. pallasii*** (incl. *T. ramosissima*), ***T. smyrnensis****	**A:** ***T. nilotica***, ***T. arabica****, ***T. indica***, ***T. senegalensis***, ***T. arceuthoides****, ***T. aralensis****; **B:** ***T. mascatensis****, ***T. gallica***, *T. mannifera*; **C:** *T. anglica*, ***T. arborea***, ***T. karelinii****, ***T. hispida***, ***T. leptostachya****, *T. leptopetala**	*T. articulata* (= ***T. aphylla***), ***T. usneoides***, ***T. dioica***	***T. amplexicaulis***, ***T. passerinoides***, ***T. pycnocarpa***, ***T. macrocarpa***, ***T. ericoides***

Autor y año	**NIEDENZU 1895**									
Subgénero	***Sessiles*** Nied.: Hojas sentadas (a veces lig. decurrentes), rara vez amplexicaules en más de medio tallo								***Amplexicaules:*** Anchamente acorazonadas o envainantes. Abrazando casi todo el tallo	
Sección	***Obdiplostemones*** Nied.: Estambres internos más largos que los externos. Brácteas linear-lanceoladas. Pedúnculo corto. Racimos en ramas del año anterior	***Haplostemones*** Nied.: Estambres antisépalos (a veces 1 o 2 antipétalos)							**Obdiplandrae** (=*Pleiandrae* Bunge)	***Haplandrae*** (= *Vaginantes* Bunge)
Subsección		***Anisomerae*** Nied.: Cáliz, corola y androceo isómeros, generalmente con 5 piezas. Gineceo oligómero, generalmente con 3 piezas						***Isomerae*** Nied.: (= *pachybotryae* Bunge)		
Serie: Niedenzu (1895) no definió los grupos descritos por debajo de subsección como series o subseries, sino como grupos y subgrupos, con varios apartados.		***Coristylae*** Nied. ***aestivales:*** Con racimos en ramas del propio año			***Coristylae*** Nied. ***vernales:*** Con racimos en ramas del año anterior		***Systylae*** Nied.			
Subserie		***Astylae***	***Stylosae-epidiscus***	***Stylosae-mesodiscus***	***Brachystylae***	***Metriostylae***				
Especies incluidas * descritas por el autor Negrita: comúnmente aceptadas	***T. dubia*, *T. octandra***	***T. gracilis***	***T. karelinii***, *T. anglica*, ***T. arborea***, *T. leptopetala*, ***T. leptostachya***, *T. serotina*, ***T. hispida***	I: ***T. chinensis***, *T. odessana*, *T. ewersmanni*; II: ***T. mascatensis***, ***T. aralensis***, ***T. pallasii***, ***T. smyrnensis***; III: *T. mannifera*, ***T. gallica***, ***T. arceuthoides***, *T. bungei*, ***T. nilotica***, ***T. senegalensis***; IV: ***T. arabica***, ***T. indica***	a: ***T. elongata***; b1: ***T. laxa***, ***T. parviflora***; b2: ***T. rosea***, ***T. hampeana***, *T. syriaca*, *T. ispahanica*, *T. cupressiformis*, *T. affinis*, *T. florida*; b3: ***T. kotschyi***	a: ***T. parviflora***; b1: *T. jordanis*, ***T. hohenackeri***, *T. bachtiarica*; b2: *T. juniperiana*	*T. effusa*, *T. brachystylis*, *T. africana* Desf.	A: ***T. bounopaea***, ***T. boveana***, ***T. meyeri***, ***T. brachystachys***, ***T. szovitsiana***, ***T. tetragyna***; B: ***T. tetrandra***	A: ***T. ericoides***; B: ***T. pycnocarpa***, ***T. macrocarpa***, ***T. amplexicaulis***, ***T. passerinoides***, *T. pauciovulata*, ***T. stricta***	A: *T. articulata* (= ***T. aphylla***), ***T. usneoides***, ***T. salina***; B: ***T. dioica***, *T. balansae*, *T. korolkowii*

Tabla 1. Continuación

Autor y año	**GORSCHKOVA 1949**										
Subgénero	***Eutamarix*** Gorschk.: Flores pequeñas. Cáliz de 0.5-1 (2.3) mm de largo. Pét. De 1-2.5 (3-4) mm de largo. Estambres 4-5 (raramente 6-8), iguales. Hojas semiamplexicaules										***Trichaurus*** Arn. (Gorschk.): Fl. Grandes, Caliz 1-3 mm long., Pétalos 2.5-5 mm long., Estambres numerosos (10-14), de distinta longitud. Racimos terminales en panículas simples, raramente laterales. Hojas amplexicaules o envainantes
Sección	***Vernales*** Bunge: Racimos en ramas del año anterior, laterales, rara vez terminales, principalmente de floración temprana. Flores principalmente tetrámeras, raramente pentámeras					***Aestivales*** Bunge: Racimos en ramas del propio año, terminales, raraemnte laterales, principalmente de floración tardía. Flores principalmente pentámeras, raramente tetrámeras					
Serie	***Elongatae*** Gorschk.: Racimos largos, 9-20 cm x 0.4-1 cm de ancho. Brácteas anchamente lineares o lineares, igualando o superando al perianto. Estambres 4-8	***Tetrandrae*** Gorschk.: Racimos más o menos largos, hasta 7 cm x 3-8 mm de ancho. Brácteas triangular-lanceoladas, mas cortas o igualando el cáliz. Estambres 4 (5-6)	***Laxiusculae*** Gorschk.: Racimos cortos (0.7-5 cm) y finos (2-4 (5) mm). Pedúnculos con brácteas. Bráct. oblongas u ovado-lanceoladas, superando o no el pedicelo, a veces superando el cáliz. Estambres 4	***Laxae*** Gorschk.: Racimos acortados y gruesos (0.5-3 cm por 4-9 mm). Bráct. oblongas u oblongo-lanceoladas, 2-3 veces mas cortas que el pedicelo. Estambres 4 (5-6)	***Floridae*** Gorschk.: racimos largos (5-9 cm). Flores 5-meras. Bráct. anchamente ovadas a linear-oblongas, superando el pedicelo pero no el cáliz. Estambres 5	***Graciles*** Gorschk.: Racimos terminales, raramente laterales, 1-3 (6) cm x 3-5 mm Flores 4-5-meras. Estambres 4-5. Disco con 4-5 lóbulos unidos a las bases ensanchadas de los filamentos	***Hispidae*** Gorschk.: Plantas cubiertas de pelos cortos y erectos. Disco con 5 lóbulos unidos a la base ensanchada de los filamentos	***Bungeanae*** Gorschk.: Racimos espiciformes, densos, 0.7-3 cm x 3-5 mm, en panículas compuestas. Estambres 5. Disco con 5 lóbulos sobre los que se unen los delgados filamentos	***Micranthae*** Gorschk.: Racimos finos, simples, largos, 4-15 cm x 2-3 mm, en panículas densamente compuestas. Disco con 5 lóbulos, unidos a las bases ensanchadas de los filamentos	***Ramosissimae*** Gorschk.: Racimos 1-6 (9) mm x 3-5 mm, en panículas densas o más o menos abiertas. Estambres 5. Disco con 5 o 10 lóbulos. Filamentos insertos entre los lóbulos	
Especies incluidas * descritas por el autor Negrita: comúnmente aceptadas	***T. octandra***, ***T. meyeri***, ***T. elongata.***	***T. tetrandra***	*T. araratica*, ***T. litwinowii****, ***T. androssowii***, ***T. kotschyi***	***T. laxa***	***T. hohenackeri***, *T. florida*	***T. gracilis***, *T. leptopetala*	***T. hispida***	*T. bungei*	***T. leptostachya***	***T. ramosissima***, ***T. arceuthoides***, *T. karakalensis*	***T. passerinoides*** (incl. *T. pycnocarpa*, *T. macrocarpa*, *Trichaurus aucherianus*)

Autor y año	**BAUM 1978**								
Sección	***Tamarix*** B.R. Baum: Hojas sésiles con base estrecha, auriculadas o vaginadas. Racimos 3-5 mm de ancho, excepto en algunas especies dioicas (5-7 mm). Brácteas superando los pedicelos. Flores 5-meras u ocasionalmente 4-5-meras, o 4-meras solo en racimos vernales. Pét. 1-2.25 mm de largo. Androceo haplostémono, (4-) 5 estambres antisépalos y diversas estructuras del disco, sin estambres antipétalos			***Oligadenia*** (Ehrenb.) Endl.: Hojas sésiles con base estrecha, raramente amplexicaules con base decurrente (*T. kotschyii*). Racimos 3-12 mm de ancho, o 3-5 mm de ancho y entonces flores puramente tetrandras. Brácteas superando o no el pedicelo. Flores tetrameras, tetra-pentámeras, pentámeras o mezcladas en el mismo racimo. Pétalos 2-6 mm de largo. Androceo haplostémono, parcialmente diplostémono o diplostémono, con 4-5 estambres antisépalos y 0-4 antipétalos mas cortos, y varias estructuras del disco				***Polyadenia*** (Ehrenb.) B.R. Baum: Hojas amplexicaules o casi, excepto en algunas especies (sésiles con base estrecha o vaginadas). Racimos 6-10-(15) mm de ancho. Bract. superando o no los pedicelos. Flores 5-meras. Pét. 2.5-6 (7) mm de largo, si 2-2.5 mm entonces hojas vaginadas (*T. stricta*) o disco para-sinlófico (*T. komarovii*). Androceo diplostémono, parcialmente diplostémono, triplostémono, parcialmente triplostémono o, raramente haplostémono (*T. salina*); cinco estambres antisépalos largos, (0) 1-10 estambres antipétalos con filamentos más cortos. Discos álofos, con la excepción de *T. komarovii*	
Serie	***Gallicae*** B.R. Baum: Completamente glabros, sin papilas. Hojas normalmente sésiles con base estrecha, excepto en *T. mascatensis* (fuertemente envainantes)	***Leptostachyae*** (Bunge) B.R. Baum: Al menos las partes más jóvenes pelosas, papilosas o papilulosas. Hojas sésiles con base estrecha a auriculadas o más o menos envainantes	***Vaginantes*** Bunge: Enteramente glabros, sin papilas presentes. Hojas vaginadas o pseudo-vaginadas	***Laxae*** Gorschk.: Bracteas, al menos las inferiores en racimos vernales, más cortas o tan largas como los pedicelos. Flores 4-5-meras; androceo haplo a parcialmente diplostémono, con no más de un estambre antipétalo	***Anisandrae*** Bunge, p. maj. p.: Bráct. superando el cáliz, o si menores que el pedicelo, pét. parabólicos. Flores 4-5-6-meras. Pét. mayores de 2.25 mm de largo. Estambres 4-8 (4-5 antisépalos y 0-4 antipétalos). Androceo haplo a diplostémono	***Arbusculae*** B.R. Baum: Brácteas ligeramente más cortas o más largas que los pedicelos. Flores 4-meras, tetrandras. Pét. 2-2.25 mm de largo. Racimos simples, 3-5 mm de ancho	***Fasciculatae*** B.R. Baum: Brácteas mucho más cortas que los pedicelos o igualándolos. Fl. 4-meras, tetrandras. Pét. 2-2.25 mm de largo. Racimos 3-6 mm de ancho con las flores superiores contraidas en un fascículo apical umbeliforme	***Arabicae*** B.R. Baum: Androceo de algunas flores en cada racimo parcialmente triplostémono a triplostémono	***Pleiandrae*** Bunge: Androceo parcialmente diplostémono a diplostémono, raramente haplostémono, y entonces las flores superiores del racimo con uno o más estambres antipétalos
Especies incluidas * descritas por el autor Negrita: comúnmente aceptadas	***T. arceuthoides***, ***T. gallica***, *T. korolkowii*, ***T. mascatensis***, ***T. palaestina***, ***T. ramosissima***, ***T. smyrnensis***	***T. arabica***, *T. aralensis*, ***T. arborea***, ***T. canariensis***, ***T. hispida***, ***T. indica***, *T. karakalensis*, ***T. leptostachya***, *T. mannifera*, ***T. nilotica***, ***T. senegalensis***	***T. angolensis***, ***T. aphylla***, *T. bengalensis**, ***T. dioica***, ***T. usneoides***	***T. chinensis***, ***T. gracilis***, ***T. laxa***, ***T. szovitsiana***	***T. africana***, ***T. boveana***, ***T. brachystachys***, ***T. dalmatica****, ***T. elongata***, ***T. hampeana***, ***T. meyeri***, ***T. octandra***, ***T. rosea***, ***T. tetragyna***, ***T. tetrandra***	***T. androssowii***, ***T. kotschyi***, ***T. parviflora***	***T. polystachya***, ***T. litwinowii***	***T. pycnocarpa***, *T. aucheriana*	***T. amplexicaulis***, ***T. dubia***, ***T. ericoides***, ***T. komarovii***, *T. ladachensis* (= ***Myrtama elegans***), ***T. macrocarpa***, ***T. passerinoides***, ***T. salina***, ***T. stricta***

Estudios moleculares

Hasta principios del siglo XXI no se publicaron los primeros estudios moleculares sobre *Tamarix.* La primera filogenia con cierto número de especies la publicaron Gaskin & Schaal (2003). En ella utilizaron los marcadores ITS (ADN nuclear) y *trnS-trnG* (ADN plastidial), destacando las diferentes topologías generadas por las regiones de ADN nuclear y plastidial, así como la no correspondencia entre las secciones propuestas por Baum (1978) y los grupos obtenidos en los análisis filogenéticos. También desde los primeros años del siglo XXI, se han utilizado diferentes técnicas moleculares para la detección de híbridos (Gaskin & Schaal 2002, Gaskin & Shafroth 2005, Gaskin & Kazmer 2009, Mayonde & al. 2015). Recientemente se han diseñado microsatélites para la identificación de especies y se han usado para la caracterización genética de poblaciones mixtas de *Tamarix* en Italia (Terzoli & al. 2010, 2014).

En la presente Tesis Doctoral, los estudios moleculares se han enfocado hacia una filogenia basada en la secuenciación y análisis de secuencias obtenidas mediante la amplificación de regiones no codificantes de ADN plastidial y nuclear. Previamente a la selección de las cuatro regiones utilizadas finalmente (ITS, *trnQ-rps16, trnS-trnG* y *ndhF-rpl32*), otras fueron probadas y descartadas (*petG-trnT, trnD-trnT, rpl32-trnL, psbD-trnT, psbA-trnH, trnT-trnL, rpl20-rps12*), principalmente, a causa de dificultades para su amplificación o por su escasa variabilidad. De entre las descartadas, *rpl32-trnL* mostraba una variabilidad destacable, pero fue abandonada por su excesiva longitud (más de 1600 pares de bases), que dificultaba el ensamblaje de las cadenas complementarias al recibir los resultados de secuenciación.

La utilización de estas técnicas ha permitido la obtención de resultados muy interesantes para la taxonomía del género, como por ejemplo: el apoyo a la descripción de una nueva especie, la separación entre *T. canariensis* y *T. gallica,* o la constatación de que las divisiones infragenéricas no corresponden a grupos naturales. Los resultados de los estudios moleculares llevados a cabo durante la realización de esta Tesis Doctoral se comentan en detalle en los artículos 7 y 8, donde se dan a conocer interesantes resultados con futuras implicaciones para la taxonomía del género.

Los artículos de la sección I tratan aspectos nomenclaturales y de tipificación no resueltos con anterioridad. Estos trabajos son el resultado de las visitas realizadas a diferentes herbarios durante los años previos a la defensa de esta Tesis Doctoral.

El artículo 1 se centra en las tipificaciones de los *Tamarix* descritos por Freyn en su obra póstuma de 1903. Esto incluye *T. karakalensis,* con cuatro variedades (incluyendo la variedad típica), y *T. askabadensis.* Resulta interesante el hecho de que Freyn indicó holotipos para algunos de estos casos, mencionando los especímenes depositados en su herbario personal. Sin embargo, su prematuro fallecimiento provocó que dichos especímenes nunca llegaran al herbario de Freyn (actualmente en BRNO), por lo que fue necesario seleccionar otros especímenes, dando prioridad, cuando fue posible, a los que presentan etiquetas con caligrafía de Freyn. De acuerdo con la bibliografía existente (Baum 1978, Samadi & al. 2013) y nuestras propias observaciones, tanto *T. karakalensis* como *T. askabadensis* son sinónimos de *T. arceuthoides*.

En el artículo 2 se recogen tipificaciones o aclaraciones sobre los tipos de 19 nombres de *Tamarix.* En concreto se escogen los lectotipos de cuatro nombres, un epitipo, se corrige la denominación de holotipo a lectotipo en cinco casos, siete lectotipificaciones previas son concretadas en un solo espécimen y por último, en otros dos casos, se realizan puntualizaciones menores.

Por último, en el artículo 3 se trata un caso complejo nomenclatural. Se propone la conservación de *T. ramosissima* sobre el prioritario *T. pentandra,* descartado desde antiguo por haberse considerado que su autor (Pallas 1789) lo incluyó en la sinonimia de *T. gallica,* hecho que no se considera probado en este trabajo*.* Además, se destaca la errónea sinonimización de *T. pallasii* a *T. laxa* (Blanche & Gaillardot 1854)*,* que se venía arrastrando desde mediados del siglo XIX. Este caso en particular es curioso, ya que numerosos herbarios han almacenado los pliegos de *T. pallasii* (= *T. ramosissima sensu* Villar & al. 2014a) en carpetas de *T. laxa*, por haberse considerado como tipo de *T. pallasii* un pliego en conflicto con el protólogo.

En conjunto, estos tres primeros artículos ilustran la complejidad nomenclatural existente en *Tamarix.* La caracterización de los tipos nomenclaturales es un trabajo necesario para poder acometer futuros tratamientos taxonómicos sustentados en una base sólida. El hecho de que muchos táxones fueran descritos sobre materiales pertenecientes a una o varias recolecciones, en ocasiones de localidades diferentes, y compuestas por numerosos pliegos de herbario, resulta beneficioso desde el punto de vista de la disponibilidad de material original, pero también puede generar confusiones.

El caso del material tipo de *T. arborea* es ilustrativo de esta situación, ya que contiene en proporciones similares, tanto especímenes que corresponden con la descripción original, como otros que se ajustan mejor a la morfología de *T. nilotica*. En un género como *Tamarix,* en el que muchos nombres hacen referencia a táxones de similar morfología y en el que existen tantos sinónimos, parece recomendable pues, fijar los tipos nomenclaturales en especímenes concretos, si bien esta práctica no es obligatoria según el Código Internacional de Nomenclatura (ICN, McNeill & al. 2012).

Los artículos incluidos en la sección II son ejemplo de la problemática taxonómica que arrastra el género en los últimos tiempos.

En el artículo 4 se descartó la presencia de *T. dalmatica* en la Península Ibérica, mediante un análisis crítico de las citas de esta especie en las últimas décadas, así como del material tipo de la especie en cuestión. Del mismo modo, se pone de manifiesto cierta plasticidad morfológica, anteriormente no considerada, de las especies locales que habían sido confundidas con *T. dalmatica.*

En el artículo 5 se proporciona una primera cita de *T. hohenackeri* para el continente americano, basada en la correspondencia de los especímenes encontrados con la del material tipo de la especie. Por otra parte, destaca el rechazo a la sinonimización de *T. hohenackeri* a *T. smyrnensis*, que puede haber dificultado la identificación de la primera con anterioridad a nuestras observaciones.

En el artículo 6 se presenta un estudio crítico de las especies de *Tamarix* presentes en la isla de Creta. En este sentido, se puede comprobar como la falta de citas previas había provocado que se pasara por alto la existencia de una especie muy abundante, *T. nilotica* (Dimopoulos & al. 2014), ampliamente confundida con *T. smyrnensis,* también presente en la isla.

En conjunto, los artículos 4, 5 y 6, ilustran las dificultades que presenta *Tamarix* incluso a la hora de obtener identificaciones precisas. Se trata de tres ejemplos en tres lugares muy diferentes, en los que la información existente había llevado a sobreestimar la presencia de ciertas especies, o a que pasara desapercibida la existencia de otras. El caso de las citas de *T. dalmatica* en España, es un ejemplo claro de la falta de información al respecto de la plasticidad morfológica y las variaciones que muestran a lo largo del año las especies locales. Esto, unido a cierta tendencia hacia *T. dalmatica* (Villar & al. 2012) de la clave a escala global más reciente disponible (Baum 1978), provocó la mencionada confusión. De forma similar, la ausencia de citas previas de *T. nilotica* en Creta y otras islas egeas, ha provocado que no se haya reportado la presencia de esta especie hasta el año 2013 (Dimopoulos & al. 2013, Villar & al. 2014b).

En los tres artículos de esta sección, el examen de material tipo de las especies tratadas ha sido básico para la resolución de los problemas planteados. De hecho, casos similares pueden ser fácilmente solucionables en el futuro cercano.

En los artículos de la sección III se incluyen estudios que se apoyan en filogenias moleculares.

En el artículo 7 se describe una nueva especie, *T. minoa,* encontrada en Creta. Se presenta una filogenia parcial que apoya la independencia de esta nueva especie que había sido previamente confundida con *T. hampeana* o *T. tetragyna* y cuya morfología se asemeja, de hecho, a *T. africana.*

El artículo 8 incluye los resultados filogenéticos más completos presentados hasta ahora para *Tamarix*. Para ello, se realizaron numerosas recolecciones y se obtuvieron muestras pertenecientes a los diferentes herbarios visitados durante la realización de la Tesis Doctoral. Los resultados obtenidos son destacables. Por un lado, se observan interesantes diferencias entre las filogenias de origen nuclear y plastidial, sugiriendo un patrón de evolución reticulada del género, en el que ya se ha descrito la hibridación como un proceso común. Por otro lado, se demuestra la independencia de algunas especies consideradas próximas o incluso sinónimas, como son las parejas formadas por *T. gallica* y *T. canariensis, T. tetrandra* y *T. parviflora o T. hispida* y *T. karelinii,* estas últimas manteniendo un estrecho parentesco*.* Así mismo se muestran inesperadas relaciones entre especies con diferente morfología, como *T. gallica* y *T. boveana o T. indica* y *T. minoa*. Además, la posición de algunas especies como *T. kermanensis* o *T. octandra* hace pensar que ciertos caracteres (hojas vaginadas o diversos números de estambres) pueden haber aparecido en varios momentos diferentes de la historia evolutiva de *Tamarix.*

En general, los temas tratados en esta Tesis Doctoral representan solo una pequeña parte de la problemática taxonómica que acarrea el género. Aún quedan pues, numerosas vías de investigación por recorrer antes de poder tener una imagen realmente precisa de la taxonomía de *Tamarix*. Aparte de los numerosos aspectos en los que se puede profundizar siguiendo con el mismo esquema de trabajo de esta Tesis (solución de problemas taxonómicos a escala local, estudio y precisión del material tipo de referencia y ampliación y mejora de los estudios filogenéticos), también existen vías de investigación abiertas en relación a los procesos de hibridación en el género, que podrían haber tenido un papel importante en la aparición de nuevas especies. Es necesario identificar y describir adecuadamente los híbridos, comprobar si se dan con regularidad entre las especies que comparten hábitat, si ciertas especies son más propensas que otras a la hibridación, si los híbridos son viables, si las poliploidías son comunes en estos casos, etc. Así pues, el contenido de esta Tesis Doctoral puede ser considerado como un nuevo paso hacia el entendimiento del género *Tamarix*. En su caso, parece clara la necesidad de conjugar los estudios taxonómicos morfológicos, que nos permiten identificar y nombrar correctamente a los especímenes objeto de estudio, con los estudios moleculares, que cada vez nos permiten obtener resultados más precisos.

A.P.G. III. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society* 161: 105-121.

Balinsky, B. 1962. Patterns of animal distribution of the African continent. *Annals of the Cape Provincial Museums* 2: 299-310.

Ball, J. 1877. Spicilegium Florae Maroccanae. *Journal of the Linnean Society* 16: 372-373.

Battandier, J. A. & Trabut, L. 1888. *Flore de l'Algerie*. 321-323.

Battandier, J. A. 1909. Revision des *Tamarix* algériens et description de deux espèces nouvelles. *Bulletin de la Société Botanique de France* 54: 252-257.

Baum, B. R. 1966. *Monographic Revision of the genus Tamarix*. Final research report for the USDA. Department of Botany. Hebrew University. Jerusalem, 193 pp.

Baum, B. R. 1967. Introduced and naturalized tamarisks in the United States and Canada. *Baileya* 15: 19-25.

Baum, B. R. 1968. A new species of *Tamarix* from South-Eastern Iran. *Oesterreichische Botanische Zeitschrift* 114: 379-382.

Baum, B. R. 1978. *The genus Tamarix.* Israel Academy of Sciences and Humanities. Jerusalem. 209 pp.

Baum B. R. 1990. *Tamarix* L. In: Tutin T. G., Heywood, V. H., Burges, N. A., Moore, D. M., Valentine, D. H., Walters, S. M. & Webb, D. A. (eds.). *Flora Europaea* 2. Cambridge University Press. 292-294.

Bieberstein, M. 1808. *Flora Taurico-Caucasica* 1. Krakovia. 246-248.

Blanche, I. & Gaillardot, C. 1854. *Catalogue de L'herbier de Syrie.* Dondey-Dupré. Paris. 10.

Bunge, A. 1833. Enumeratio Plantarum quas in China Boreali collegit Dr. Al. Bunge. *Mémoires présentés à l'Académie Impériale des Sciences de St.-Pétersbourg par Divers Savants et lus dans ses assemblées* 2: 75-147.

Bunge, A. 1851. Alexandri Lehmann reliquiae botanicae. *Mémoires présentés à l'Académie Impériale des Sciences de St.-Pétersbourg par Divers Savants et lus dans ses assemblées* 7: 290-296.

Bunge, A. 1852. *Tentamen Generis Tamaricum Species Accuratius Definiendi.* J.C. Schuenmanni & C. Mattieseni. Dorpati. 84 pp.

Boissier, E. 1849. *Diagnoses Plantarum Orientalium Novarum*, ser. 1, 10. M. Ducloux et Cons. Paris. 8-10.

Boissier, E. 1856. *Diagnoses Plantarum Orientalium Novarum*, ser. 2, 2. M. Apud B. Herrmann. Leipzig. 56-58.

Boissier, E. 1867. *Flora Orientalis* 1. H. Georg. Gèneve. 763-779.

Caballero, A. 1911. Enumeración de las plantas herborizadas en el Rif. *Memorias de la Real Sociedad Española de Historia Natural* 8: 256-257.

Çakan, H. & Zieliński, J. 2004. *Tamarix duezlenlii* (Tamaricaceae) – a species new to science from southern Turkey. *Acta Societatis Botanicorum Poloniae* 73: 53-55.

Candolle, A. P. 1828. *Prodromus Systematis Naturalis Regni Vegetabilis* 3. Treuttel & Würtz. Paris. 95-98.

Cesalpino, A. 1583. *De plantis libri* XVI (cap. 47). Gregorium Marescottum. Florencia. 126.

Cirujano, S. 1993. Tamarix L. In: Castroviejo, S. & al. (eds.). *Flora Iberica* 3. Real Jardín Botánico, CSIC. Madrid. 437-443.

Clusius, C. 1576. *Rariorum aliquot stirpium per hispanias observarum historia*. Christophori Platini. Antwerpen (Amberes). 104-107.

Covarrubias, S. 1611. *Tesoro de la Lengua Castellana o Española* 2. Luis Sánchez. Madrid. 38-39.

Csurhes, S. 2008. *Pest plant risk assessment: Athel pine Tamarix spp*. The State of Queensland. Department of Primary Industries and Fisheries. Brisbane. Australia. 10 pp.

Dalechamps, J. 1586. *Historia Genaralis Plantarum* 2. Guilielmum Rouilium. Lugduni (Lyon). 789.

Decaisne, J. 1835. Florula sinaica. *Annales des Sciencies Naturelles* 2 (3). 260-261.

Decaisne, J. 1844. Plantae rariores quas in India Orientali colleggit Victor Jaquemont. *Voyage dans l'Inde pendant les annees 1828 a 1832* 4 (Bot.). Firmin Didot freres. Paris. 58-60.

De Martis, B., Loi, M. C. & Polo, M. B. 1984. Il genere *Tamarix* L. (Tamaricaceae) in Sardegna*. Webbia* 37(2): 211-235.

De Martis, B., Loi, M. C. & Polo, M. B. 1986a. Contribution to a better understanding of the genus *Tamarix* in Portugal. *Candollea* 41: 293-298.

De Martis, B., Loi, M. C. & Polo, M. B. 1986b. *Tamarix mascatensis* Bge. (Tamaricaceae) in Portogallo, nuova per la flora d'Europa. *Boletim da Sociedade Broteriana* 58: 215-217.

Desvaux, M. 1824. Sur la nouvelle famille de plantes fondée sur le genere *Tamarix*. *Annales des Sciences Naturelles. Botanique. Paris.* 4: 344-350.

Desfontaines, R. L. 1798. *Flora Atlantica sive Historia Plantarum, quae in atlante, agro Tunetano et algeriensi crescunt* 1. L.G. Desgranges. Paris. 269.

Dimopoulos, P., Raus, Th., Bergmeier, E., Constantinidis, Th., Iatrou, G., Kokkini, S., Strid, A. & Tzanoudakis, D. 2013: Vascular plants of Greece: An annotated checklist. Berlin: Botanischer Garten und Botanisches Museum Berlin-Dahlem; Athens: Hellenic Botanical Society. *Englera* 31. 372 pp.

Di Tomaso, J. 1998. Impact, biology and ecology of saltcedar (*Tamarix sp.*) in southwestern United States. *Weed Technology* 12: 326-336.

Ehrenberg, C. G. 1827. Über die Manna-Tamariske nebst allgemeinen Bemerkungen über die Tamariscineen. *Linnaea* 2: 241-344.

Freyn, J. 1903. Plantae ex Asia Media. *Bulletin de l´Herbier Boissier,* sér. 2, 3: 1058-1068.

Gaskin, J. F. & Schaal, B. 2003. Hybrid *Tamarix* widespread in U.S. invasion and undetected in native Asian range. *PNAS* 99 (17): 11256-11259.

Gaskin, J. F. & Schaal, B. 2003. Molecular phylogenetic investigation of U.S. invasive *Tamarix*. *Systematic Botany* 28 (1): 86-95.

Gaskin, J. F. & Shafroth, P. B. 2005. Hybridization of *T. ramosissima* and *T. chinensis* (saltcedars) with *T. aphylla* (athel) (Tamaricaceae) in the Southwestern USA determined from DNA sequence data. *Madroño* 52: 1-10.

Gaskin, J. F. & Kazmer, D. J. 2009. Introgression between Invasive Saltcedars (*Tamarix chinensis* and *T. ramosissima*) in the USA. *Biological Invasions* 11: 1121-1130.

Gay, J. 1853. *Tamariscinae, Études sur le genere Tamarix*. Manuscrito inédito. Bibioteca de RBG Kew. Londres.

Gorschkova, S. G. 1949. Tamaricaceae. In: Komarov, V. L. (ed.), *Flora URSS* 15. Moscow-Lenningrad. 290-327.

Gutmann, H. 1947. The genus *Tamarix* in Palestine. *Palestine Journal of Botany* 4: 46-54.

Harduinus, J. 1723. *Caii Plini Secundi Historiae Naturalis*. Antonii-Urbani Coustelier. Paris. 697.

Laguna, A. 1563. *Pedacio Dioscorides Anazarbeo, Acerca de la Materia Medicinal, y de los venenos mortíferos*. Libro 1. Mathias Gast. Salamanca. 71-72.

Ledebour, C. F. 1829. *Flora Altaica* 1. G. Reimeri. Berlin. 421-426.

Ledebour, C. F. 1843. *Flora rossica, sive enumeratio plantarum in totius imperii Rossici provinciis Europaeis, Asiaticis, et Americanis hucusque observatarum* 2 (4). E. Schweizerbart. Stuttgart. 130-138.

Linnaeus, C. 1753. *Species plantarum* 1. Holmiae. Laurentii Salvii. 560 pp.

Liu, M. T. 1979. A new species of Tamarix from Xinjiang. *Acta Phytotaxonomica Sinica* 17 (3): 120-121.

L'Obel, M. 1591. *Icones stirpium* 2. Amberes. 218.

Maire, R. 1931. Contribution à l'étude de la Flore de l'Afrique du Nord 17(1). *Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord* 22: 34-36.

Maire, R. 1933a. Études sur la Flore et la Végétation du Sahara central. *Mémoires de la Société d'Histoire Naturelle de l'Afrique du Nord* 3: 155-160.

Maire, R. 1933b. Plantae maroccanae novae. Rabat. 2 pp.

Maire, R. 1934. Contributions à l'étude de la Flore de l'Afrique du Nord 22. *Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord* 25: 296.

Maire, R. 1935. Contributions à l'étude de la Flore de l'Afrique du Nord 23. *Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord* 26: 192-195.

Mayonde, S. G., Cron, G. V., Gaskin, J. F. & Byrne, M. J. 2015. Evidence of *Tamarix* hybrids in South Africa, as inferred by nuclear ITS and plastid *trnS-trnG* DNA sequences. *South African Journal of Botany* 96: 122-131.

Mattioli, P. A. 1562. *Comentarii denuo aucti, in libros sex Pedacii Dioscoridis Anzarabei de medica materia*. Gabrielem Coterium. Lugduini (Lyon). 127.

McNeill, J., Barrie, F. R., Buck, W. R., Demoulin, V., Greuter, W., Hawksworth, D. L., Herendeen, P. S., Knapp, S., Marhold, K., Pardo, J., Prud'homme van Reine, W. F., Smith, G. F., Wiersema, J. H. & Turland, N. J. 2012. *International code of nomenclature for algae, fungi and plants (Melbourne Code), adopted by the 18th Int. Bot. Congr. Melbourne, Australia, Jul 2011*. Regnum Vegetabile 154. Koeltz Scientific Books.

Musselman, L. J. 2007. *Figs, dates, laurel, and myrh: plants of the Bible and the Quran.* Timber press. Portland. Oregon. 336 pp.

Niedenzu, F. 1895. In: Engler, A. & Prantl, K. (eds*.). Die natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigeren Arten* 3 (6). Leipzig. 289-297.

Niedenzu, F. 1925. In: Engler, A. & Prantl, K. (eds.). *Die natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigeren Arten* 2. Berlin. 282-289.

Pallas, P. S. 1789. *Flora rossica, seu stirpium Imperii Rossici per Europam et Asiam indigenarum descriptiones et icones* 1 (2). E Typographia imperiali J.J. Weitbrecht. Petropoli. 72-73.

Pau, C. 1906. Synopsis formarum novarum hispanicarum cum synonimin nonnullis accedentibus. *Bulletin de l'Académie Internationale de Géographie Botanique* 206: 73-77.

Pau, C. 1918. Una ligera visita botánica a Tous. *Butlletí de la Institució Catalana d'Història Natural* 18: 158-161.

Pau, C. 1922. Nueva contribución al estudio de la flora de Granada. *Memòries del Museu de Ciències Naturals de Barcelona. Sèrie Botànica* 1 (1): 74 pp.

Pau, C. 1924. Plantas del noste de Yabala (Marruecos). *Memorias de la Real Sociedad Española de Historia Natural* 12 (5): 263-401.

Pau, C. & Villar, H. 1927. Novae Tamaricis in Hispania centrali. *Broteria* 23: 101-113.

Pignatti, S. 1982. *Flora d'Italia* 2. Edagricole. Bologna. 133-134.

Poiret, J. 1789. *Voyage en Barbarie* 2. J. B. F Née de la Rochelle. Paris. 139.

Prince, W. & sons. 1837. Annual catalogue of trees and plants cultivated at the Linnean Botanic Garden and Nurseries. New York, USA. 2-4, 50.

Qaiser, M. 1981. The genus *Tamarix* Linn. (Tamaricaceae) in Pakistan. *Pakistan Journal of Botany* 13: 107-158.

Roxburgh, W. 1832. *Flora Indica; or descriptions of Indian plants* 2. W. Tacker and Co. Calcuta and Parbury; Allen and Co. London. 100-102.

Rusanov, F. N. 1949. *Sredniyeaziatskie Tamariksi*. Tashkent.

Rvelio, I. 1554. *Pedanii Dioscoridis Anzarbei, De Medica Materia* 6 (1). Iacobum Faure. Lyon. 75.

Samadi, N., Ghaffari, S. M. & Akhani, H. 2013. Meiotic behaviour, karyotype analyses and pollen viability in species of *Tamarix* (*Tamaricaceae*). *Willdenowia* 43: 195-203.

Salazar, C. & Quesada, J. 2009. Tamarix L. In: Blanca, G. & al. (eds.). *Flora vascular de Andalucía Oriental* 2. Consejería de Medio Ambiente. Junta de Andalucía. Sevilla. 190-193.

Schiman-Czeika, H. 1964. Tamaricaceae. In: Rechinger, K. H. (ed.). *Flora Iranica* 4. Akademische Druck. Graz. 17 pp.

Sennen, F. 1928. Plantes d'Espagne, par le Fr. Sennen-Diagnoses et comentaires. *Boletín de la Sociedad Ibérica de Ciencias Naturales* 27: 66-67.

Sennen, F. 1931. Campagne botanique au Maroc. *Bulletin de la Société Botanique de France* 78: 182-194.

Sennen, F. 1932. Brèves diagnoses des formes nouvelles parues dans nos exsiccata "Plantes d'Espagne-F. Sennen". *Butlletí de la Institució Catalana d'Història Natural* 32: 90.

Sennen, F. & Mauricio, F. 1934. *Catálogo de Flora del Rif oriental*. La Ibérica. Melilla. 42-43.

Shinners, L. H. 1957. Salt cedars (*Tamarix*, Tamaricaceae) of the Soviet Union by S. G. Gorschkova. *The Southwestern Naturalist* 2 (2-3): 48-73.

Stapel, I. B., Scaligeri, I. C. & Constantini, R. 1644. *Theophrasti Eresii de Historia Plantarum Libri Decem*. Amsterdam. 408-410.

Stromberg, J. 1998. Dynamics of Fremont cottonwood (*Populus fremontii*) and saltcedar (*Tamarix chinensis*) populations along the San Pedro River, Arizona. *Journal of Arid Environments* 40: 133-155.

Takhtajan, A. 1986. *Floristic regions of the world*. University of California Press. Berkeley-Los Angeles-London. 522 pp.

Terzoli, S., Beritognolo, I., Sabatti, M. & Kuzminsky, E. 2010. Development of a novel set of EST-SSR markers and cross-species amplification in *Tamarix africana* (Tamaricaceae). *American Journal of Botany* 97 (6): e45-47.

Terzoli, S., Abbruzense, G., Beritognolo, I., Sabatti, M., Valentini, R. & Kuzminsky, E. 2014. Genetic characterization of a *Tamarix spp*. germoplasm collection in Italy. *Botany* 92 (5): 360-369.

Thiers, B. 2008+ [continuously updated]. *Index herbariorum: a global directory of public herbaria and associated staff*. New York Botanical Garden. Published at http://sweetgum.nybg.org/ih.

Thiselton Dyer, W. T. 1875. Tamariscineae. In: Hooker, J. D. (ed.). *Flora of the British India* 1. L. Reeve. London. 248-250.

Tournefort, J. P. 1719. *Institutiones Rei Herbariae* 1 (3 ed.). Typographia Regia. Paris. 661.

United Bible Societies. 1980. *Helps for Translators: Fauna and Flora of the Bible*. United Bible Societies. New York. 2ª ed. 224 pp.

Venturella, G., Baum, B. R. & Mandracchia, G. 2007. The genus *Tamarix* (Tamaricaceae) in Sicily: first contribution. *Flora Mediterranea* 17: 25-46.

Venturella, G., Gargano, M. L. & Mandracchia, G. 2012. First record of Tamarix meyeri (Tamaricaceae) for western Europe*. Plant Biosystems* 146: 484-489.

Villar, J. L., Alonso, M. A., Juan, A. & Crespo, M. B. 2012. Does *Tamarix dalmatica* (Tamaricaceae) occur in Spain? *Anales del Jardín Botánico de Madrid* 69: 253-258.

Villar, J. L., Alonso, M. A., Juan, A., Gaskin, J. F., & Crespo, M. B. 2014a. Proposal to conserve the name *Tamarix ramosissima* against *T. pentandra* (*Tamaricaceae*). *Taxon* 63 (5): 1140-1141.

Villar, J. L, Juan, A. & Alonso, M. A. 2014b. *Tamarix hohenackeri* Bunge, a new record for the flora of Mexico. *Acta Botánica Mexicana* 106: 117-128.

Villar, J. L., Alonso, M. A., Vicente, A., Juan, A. & Crespo, M. B. 2014c. The genus *Tamarix* (*Tamaricaceae*) in Crete (Greece). *Willdenowia* 44: 321-326.

Villar, J. L., Turland, N. J., Juan, A., Gaskin, J. F., Alonso, M. A. & Crespo, M. B. 2015. *Tamarix minoa* (*Tamaricaceae*), a new species from the island of Crete (Greece) based on morphological and plastid molecular sequence data. *Willdenowia* 45: 161-172.

Walpers, G. G. 1843. *Repertorium Botanices Systematicae* 2. Leipzig. 114-117.

Webb, P. B. & Berthelót, S. 1840. Historie naturelle des Iles Canaries 3 (2). *Phytographia canariensis*, Sect. 1. Paris. 170-172.

Webb, P. B. 1841. Observations sur le Tamarix gallica de Linné. *Annales des Sciences Naturelles* 2 (16): 257-266.

Wight, R. & Walker-Arnott, G. A. 1834. *Prodromus Florae Penínsulae Indiae Orientalis* 1. Parbury, Allen and Co. London. 39-40.

Willdenow, C. L. 1816. Beschreibung der Gattung Tamarix. *Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin 1812–1813*. 76-86.

Yang, Q. & Gaskin, J. F. 2007. *Tamarix.* In: Zhengyi, W. and Raven, P. H. (eds.). *Flora of China* 13. Science Press; Missouri Botanical Garden Press. 59-65.

Zhang, M., Hao, X., Sanderson, S. C., Vyacheslav, B. V., Sukhorukov, P. & Zhang, X. 2014. Spatiotemporal evolution of *Reaumuria* (Tamaricaceae) in Central Asia: insights from molecular biogeography. *Phytotaxa* 167 (1): 89-103.

Zieliński, J. 1994. *Tamarix* L. In: Browicz, K. (ed.). *Chorology of trees and shrubs in south-west Asia and adjacent regions* 10. Ponzań. Bogucki Wydawnictwo Naukowe. 30-34.

Zohary, M. 1987. *Tamarix* L. In: Zohary, M. (ed.). *Flora Palaestina* 2. Reimpresión (1ª ed. 1972). Israel Academy of Sciences and Humanities. 350-362.

Conclusions

1. Se descarta la presencia de *Tamarix dalmatica* en la Península Ibérica, las citas atribuidas a este taxon han sido corregidas a *Tamarix boveana* o *Tamarix africana* según los casos. Así mismo se ha aportado información al respecto de la variabilidad morfológica de estas dos especies, que ayudará a evitar nuevas confusiones.
2. Se cita por primera vez *Tamarix hohenackeri* en México y se reafirma su independencia frente *Tamarix smyrnensis*, ya puesta de manifiesto por algunos autores.
3. El estudio de los *Tamarix* de la isla de Creta (Grecia), pone de manifiesto la confusión entre *Tamarix smyrnensis* y *Tamarix nilotica*, lo que ha supuesto la ausencia de citas de *Tamarix nilotica* hasta fechas recientes.
4. Se propone la conservación del nombre *Tamarix ramosissima* frente al prioritario *Tamarix pentandra,* debido al uso generalizado de *Tamarix ramosissima* en la actualidad.
5. *Tamarix pallasii* es rescatado de la sinonimia de *Tamarix laxa,* dos especies que presentan evidentes discrepancias morfológicas.
6. Se destaca la importancia de precisar los tipos nomenclaturales de los numerosos táxones descritos en *Tamarix*, como se ha llevado a cabo para 23 casos en este trabajo.
7. La problemática en cuanto a la separación de *Tamarix gallica* y *Tamarix canariensis*, queda resuelta en parte con la restricción del área de distribución de *Tamarix canariensis* a las Islas Canarias, apoyada por los análisis filogenéticos.
8. Los análisis filogenéticos muestran el parentesco entre *Tamarix gallica,* con *Tamarix boveana* y *Tamarix tetragyna*, hasta el punto de no haberse encontrado diferencias en las regiones moleculares utilizadas, a pesar de su evidente diferenciación a nivel morfológico.
9. Los estudios moleculares, en conjunción con los morfológicos, han demostrado su utilidad para la detección de nuevas especies, como en el caso de *Tamarix minoa*.
10. Es difícil establecer una clasificación infragenérica en la que los grupos morfológicos se vean reflejados en clados monofiléticos en las filogenias. Este hecho se relaciona con procesos de evolución reticulada, lo que se vería apoyado por la contrastada capacidad de hibridación de especies de morfología muy diferente dentro del género.

11. La existencia de híbridos hace necesaria la apertura de vías de investigación destinadas a su detección y descripción morfológica. De hecho, no se puede descartar la posibilidad de que algunos de los numerosos nombres publicados en *Tamarix* se hayan podido describir sobre ejemplares híbridos.

Sección I:
Aspectos nomenclaturales

Artículo 1

Villar J. L., Juan A., Alonso M. A. & Crespo M. B. 2014. Type specimens of *Tamarix* (Tamaricaceae) described by Josef Franz Freyn in 1903. *Phytotaxa* 172 (3): 289-292.

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Type specimens of *Tamarix* (Tamaricaceae) described by Josef Franz Freyn in 1903

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Five *Tamarix* taxa were described in Freyn's posthumous publication (Freyn 1903): *Tamarix askabadensis* Freyn (1903: 1059), *Tamarix karakalensis* Freyn (1903: 1060), *T. karakalensis* var. *scoparia* Freyn (1903: 1062), *T. karakalensis* var. *verrucifera* Freyn (1903: 1062), and *T. karakalensis* var. *myriantha* Freyn (1903: 1062). This publication comprised an enumeration of the plants collected by Paul Sintenis in "*Tauria, 1900–1901*" (in the Sintenis's voucher labels as "*Iter transcaspico-persicum 1900–1901*"), by Ove Paulsen in "*regione caspica, transcaspica, praesertium in altiplanitie Pamir, 1898–1899*", and by Victor Ferdinand Brotherus "*in Turkestania, 1896*". However, all *Tamarix* taxa treated in that work belong to those collected by Sintenis. It is important to point out that Sintenis was mostly a plant collector who sold his vouchers to many different herbaria: ANK, BHUPM, BREM, G, GH, HAC, JE, LD, PAL, PR, TUB, VT, W, WAG, and WU (acronyms according to Thiers 2014). However, his personal herbarium (ca. 80000 vouchers of 18000 species) was acquired by the Herbarium of the Botanical Museum of Lund (LD) in 1921–1922 (Patrik Frödén pers. comm.).

Sintenis's labels are printed, bearing the name of the new *Tamarix* species and varieties, together with the quotation "determ. J. Freyn". Accordingly, it can be assumed that Freyn personally examined and identified the Sintenis collections before the labels were printed and the vouchers distributed. In the protologue of each variety of *T. karakalensis*, Freyn (1903: 1062) referred clearly to the specimens kept at his personal herbarium, which is currently conserved at the Moravian Museum of Brno (BRNM), whereas no specific mention was made to *T. karakalensis* or *T. askabadensis*. Therefore, those vouchers kept at BRNM should have been considered as the holotypes for the three described varieties, though Baum (1966: 62) reported the holotypes of *T. karakalensis* var. *scoparia* and *T. karakalensis* var. *myriantha* at the herbarium of the Conservatoire et Jardin botaniques de la Ville de Genève (G). Surprisingly no specimen of *T. askabadensis, T. karakalensis* or any of its varieties is currently found in Freyn's herbarium at BRNM. It turns out that Freyn examined personally the Sintenis's 1900–1901 collections in 1902 (Karel Sutorý pers. comm.). But after Freyn's early dead in January 1903, it might be assumed that those examined vouchers were not sent to him, and they still remain at Sintenis's herbarium, which is currently conserved at LD. Some of those *Tamarix* specimens at LD were personally examined by Freyn, since there is one copy of each taxa that bears Freyn's handwriting, indicating even the precise day he examined them. Consequently, these vouchers would be considered as the best choice for typification of each of the *Tamarix* taxa [Art. 9.3(a) of the ICN, McNeill *et al.* 2012], and they have been given priority when possible.

According to the printed labels of the original collections of *T. askabadensis, T. karakalensis* and its three varieties, the authorship appears to be attributed to Freyn and Sintenis. It is probable that they agreed to publish the new taxa discovered amongst the Sintenis's 1900–1901 collections sharing the authorship. Nevertheless, Freyn (1903: 1059, 1060, 1062) indicated the new taxa only as "*n. sp.*", and "*n. var.*", hence the valid authorship belongs only to Freyn (Art. 46.8 of the ICN), and the shared authorship (Freyn et Sint.) remains only on the voucher labels ("*in sched.*").

Although type specimens for almost every *Tamarix* species, subspecies or varieties described until 1966 were included in Baum's monograph about this genus (Baum 1966), those *Tamarix* taxa described by J.F. Freyn were proven to need some clarification after studying the materials kept at some important herbaria (B, G, JE, LD, MO, P, PR, PRC, and W). In the present contribution, the information of the labels is always given between inverted commas. The handwritten text has been transcribed to italics, and the typewritten text is maintained as standard font. Material from JE, LD, and WU has been studied from digital images. The "_a" and "_b" besides G herbarium numbers refer to a second and third sheet under the same herbarium number.

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Typifications

Tamarix askabadensis Freyn (1903: 1059).

Lectotype (First step: Baum, 1966, Monogr. Rev. Gen. Tamarix: 33. Second step: designated here):—TÜRKMENISTAN. "P. SINTENIS: Iter transcaspico-persicum 1900–1901. Nº 295. Tamarix askabadensis Freyn et Sint. n. sp. Regio transcaspica; Aschabad: prope Koosen. 19. V. 1900. determ. J. Freyn" (G-00359261!).

Notes:**—***Tamarix askabadensis* was described on the basis of the collection *Sintenis 295*, from "*Askabad, pr. Kösen ad ripas et loca humida subsalsa, 19.V.1900, in Blüthenfülle*". Vouchers belonging to *Sintenis 295* were found at G, JE and LD, which are to be regarded as syntypes (Art. 9.5 Ex.3 of the ICN). Regarding the two copies kept at LD, one of them (barcode 1210404) bears a label handwritten by Sintenis and later by Freyn, indicating that Freyn studied that voucher on April 15th 1902. All other copies from that exsiccata bear typewritten labels that were printed before the distribution of the specimens. Therefore, the cited specimen at LD would have been the most appropriate choice for lectotypification, as it was directly examined by Freyn. However, Baum (1966: 33) indicated that the holotype was kept at G, and also mentioned the existence of isotypes at G, P, W and WU. Following the ICN (Art. 9.9), the use of term "holotype" by Baum (1966: 33) should be corrected to "lectotype". Once the correction is done, it has to be considered as a valid lectotypification (Art. 7.9, and 7.10 of the ICN), though Baum's selection has to be narrowed to one of the specimens held at G. The specimen labelled as G00359261 is here selected as a second step lectotype (Art. 9.17 Ex. 12 of the ICN), and consequently any other copies of *Sintenis 295* must be considered as isolectotypes. According to Baum (1966: 31), *T. askabadensis* is currently regarded as a synonym of *T. arceuthoides* Bunge*,* a synonymization which is supported by our own observations.

Additional specimens examined:**—**TÜRKMENISTAN. Regio transcaspica, Aschabad, prope Koosen, 19 May 1900, leg. *Sintenis 295*, det. *Freyn* (G-00359261!, G-00359261_a!, G-00359262!, G-00359262_a!, JE-00016587, LD-1210404, LD-1210344).

Tamarix karakalensis Freyn (1903: 1060).

Lectotype (designated here):—TÜRKMENISTAN. (handwritten): "*1966* ^{b}*. Tamarix. Karakala: prope Arabadschik in valle fluvii Sumbar. 24/6. 01* " (Sintenis's handwritting), "*Karakalensis n. sp. ! 20/4 02 Freyn*" (Freyn's handwritting); (Typewritten): "P. Sintenis: iter transcaspico persicum 1900–1901. Nº 1966^{b}. *Tamarix karakalensis* Freyn et Sint. n. sp. Regio transcaspica; Kisil Arwat; Karakala: in valle fluvii Sumbar. 24.VI.1901. Determ. J. Freyn" (LD-1210584! [digital photo]).

Notes:**—**In the protologue of *Tamarix karakalensis,* Freyn (1903: 1060) mentioned two exsiccata, collected in different locations and dates: (1) "*Karakala prope Arabadschik in valle fluvii Sumbar, 24-VI-1901 (Sintenis 1966b)*" and; (2) "*Nurgeli chan ad rivum, 28-VI-1900 (Sintenis 1966a)*". Vouchers of *Sintenis 1966b* collection have been found at G, LD, MO, P and W, and Baum (1966: 62) also reported isotypes at E, W and WU. Conversely, the only copy of *Sintenis 1966a* that we were able to trace is kept at LD, though this collection was not mentioned by Baum (1966). A lectotype is to be selected from the pull of syntypes of these two collections (Art. 9.5, 9.11, and 9.12 of the ICN). Among those vouchers belonging to *Sintenis 1966b*, only that one present at LD bears a handwritten label (with both Sintenis's and Freyn's handwritting) matching exactly the protologue, alongside with the printed label that is shared with the other copies. The "*b*" letter besides the collection number 1966 is missing in the printed labels of most of the found vouchers (P, MO and W), and it was handwritten in the others (G and LD). However, they can be easily assigned to *Sintenis 1966b* by matching the locality and the collection date printed in the labels. Among all the existing material, the *Sintenis 1966b* voucher LD1210584 is here selected as lectotype. It is the only one whose label perfectly matches the information in the protologue and it was personally examined by Freyn, since his handwriting clearly appears in the label. Any other voucher belonging to *Sintenis 1966b* collection, including those without "*b*" but matching the location and date, must be considered isolectotype. Any voucher belonging to *Sintenis 1966a* collection must be considered as syntype.

T. karakalensis was accepted as an independent species by Baum (1966: 60), though it is morphologically very similar to *T. arceuthoides,* as it has been recently suggested by Samadi *et al*. (2013: 196). Accordingly, we consider both taxa to be synonyms, *T. arceuthoides* having the priority.

Additional specimens examined:—TÜRKMENISTAN. Regio transcaspica; Kisil Arwat; Karakala: in valle fluvii Sumbar, 24. June 1901, det. J. Freyn, *Sintenis 1966b* (G-00359275!, G-00359275_a!, LD-1210584, MO-5414457!, P-04958261!, W-1902-5367!). Karakala: Nurgeli chan, ad rivum, 28 June 1901, det. J. Freyn, *Sintenis 1966a* (LD-1210464).

Tamarix karakalensis var. ***scoparia*** Freyn (1903: 1062).

Lectotype (First step: Baum, 1966, Monogr. Rev. Gen. Tamarix: 62. Second step: designated here):—TÜRKMENISTAN. "P. Sintenis: Iter transcaspico persicum 1900–1901. Nº 646 b. Tamarix Karakalensis Freyn et Sint. n. sp. var. scoparia Freyn et Sint. Regio transcaspica; Aschabad; Suluklü (Saratowka); ad fines Persiae: inter Mergen Ulja et Kalkulap [sic, for Kulkulab]. 20. VII. 1900. determ. J. Freyn." (G-00359282!).

Notes:—*Tamarix karakalensis* var. *scoparia* was described based on the *Sintenis 646b* collection (Freyn, 1903: 1062). Baum (1966: 62) reported that the holotype was kept at G. As it was explained in the case of *T. askabadensis,* Baum's typification must prevail (Artt. 7.9, and 7.10 of the ICN), but the use of the term "holotype" has to be corrected to "lectotype" (Art. 9.9 of the ICN). However, two vouchers of *Sintenis 646b* are kept at G, and some additional ones are known to be conserved at LD, P and W, they all being syntypes (Art. 9.5 of the ICN). Hence the selection of lectotype has to be narrowed to one of the specimens at G (Art. 9.17 of the ICN), since none of them is clearly marked as holotype. Therefore, the voucher G00359282 is here selected as lectotype, since it is well conserved. Any other copy of *Sintenis 646b* must be considered as isolectotype. In our opinion the phenotypic variability of the nominal variety completely includes that of var. *scoparia*. We agree with Baum (1966: 33) in synonymizing the names.

Additional specimens examined:—TÜRKMENISTAN. Regio transcaspica: Aschabad, Sulukl¨, as fines Persiae, inter Merjen Ulja et Kulkulab , 20. July 1900, det. J. Freyn, *Sintenis 646b* (G-00359282!, G-00359283!, G-00359283_a!, LD-1618152, LD-1617256, P-04958259!, W-1902-5368!).

Tamarix karakalensis var. ***myriantha*** Freyn (1903: 1062).

Lectotype (First step: Baum, 1966, Monogr. Rev. Gen. Tamarix: 62. Second step: designated here):—TÜRKMENISTAN. "P. Sintenis: Iter transcaspico persicum 1900–1901. Nº 467. Tamarix Karakalensis Freyn et Sint. n. sp. var. miryantha Freyn et Sint. Regio transcaspica; Aschabad; versus Besmen. 4. VI. 1900. determ. J. Freyn." (G-00359278!).

Notes:—Freyn (1903:1062) described *T. karakalensis* var. *myriantha* based on the *Sintenis 467* collection, though it appears referenced to *Sintenis 477*. That seems to be a typing mistake, as the number 467 occurs in the labels of all syntypes found at G, LD, P, PR and W, even in the voucher that was personally examined by Freyn (LD-1666462). We have not found any sheet numbered *Sintenis 477* from the "Iter transcaspico persicum 1900–1901" in any of the studied herbaria. As in the previous case, Baum (1966: 62) said that the holotype of this taxon to be at G, and this selection must prevail (Art. 7.9, and 7.10 of the ICN). The use of "holotype" has to be corrected to "lectotype" (Art. 9.9 of the ICN), and the selection of lectotype has to be narrowed (Art. 9.17 Ex. 12 of the ICN), as more than one voucher is kept at G, and none of them is clearly marked as holotype. The voucher G-00359278 is here selected as lectotype, as it is a complete and well preserved specimen. Any other copy of the *Sintenis 467* collection must be considered as isolectotype. According to our observations, the morphological variability of the var. *myriantha* is completely included in that of the nominal variety. We agree with Baum (1966: 33), who synonymized the names.

Additional specimens examined:—TÜRKMENISTAN. Regio transcaspica: Aschabad, versus Besmen, 4. June 1900, det. J. Freyn, *Sintenis 467* (G-00359276!, G-00359276_a!, G-00359277!, G00359277_a!, G-00359277_b!, G-00359278!, G-00359279!, LD-1633435, LD-1666462, P-04958258!, P-04958260!, PR-376106!, PR-2998!, W-1902-5369!).

Tamarix karakalensis var. ***verrucifera*** Freyn (1903: 1062).

Lectotype (designated here):—TÜRKMENISTAN. (typewritten) "P. Sintenis: iter transcaspico persicum 1900–1901. Nº 646^{a}. Tamarix Karakalensis Freyn et Sint. n. sp. var. verrucifera Freyn et Sint. Regio transcaspica; Germab: in paludosis salsis prope pagum Skobelewka. 29. VI. 1900. Determ. J. Freyn."; (handwritten by Sintenis, with later annotations by Freyn): "646^{a}, *Tamarix karakalensis β verrucifera n. var. Tamarix verrucifera n. spec. ! 17/4 02 J Freyn, Germab: prop. pag. Skobelewka, 29/6-00*" (LD-1667358! [digital photo]).

Notes:—Freyn (1903: 1062) based the original description of *T. karakalensis* var. *verrucifera* on the *Sintenis 646a* collection. Only two vouchers of this collection (B-100278715 and LD-1667358) have been found among all the studied materials. According to the existing handwriting on the original label, we guess that the voucher at LD was personally checked by Freyn in April 1902. Hence, the specimen LD-1667358 is selected here as lectotype. The voucher B-100278715 must be considered as isolectotype. Further investigation is needed to verify if the var. *verrucifera* is synonym the nominal variety.

Baum (1966: 33) considered the name of this variety as a *nomen illegitimum*, on the basis of the occurrence of galls on the exsiccatum. Baum's nomenclatural interpretation is not correct, and the name *T. karakalensis* var. *verrucifera* is legitimate according to the ICN (McNeill *et al.* 2012).

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References

Baum, B. (1966) *Monographic Revision of the genus Tamarix*. Final research report for the USDA. Department of Botany, Hebrew University, Jerusalem, 193 pp.

Freyn, J. (1903) Plantae ex Asia Media. *Bulletin de l´Herbier Boissier* sér. 2, 3: 1058–1068.

McNeill, J., Barrie, F.R., Buck, W.R., Demoulin, V., Greuter, D.L., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Marhold, K., Prado, J., Proud'Homme van Reine, W.F., Smith, J.F. & Wiersema, J.H. (eds.) (2012) International Code of Nomenclature for algae, fungi and plants (Melbourne Code): Adopted by the Eichteenth International Botanical Congress, Melbourne, Australia, July 2011. *Regnum Vegetabile* 154: 1–274.

Samadi, N., Seyed, M. & Akhani, H. (2013) Meiotic behaviour, karyotype analyses and pollen viability in species of *Tamarix (Tamaricaceae)*. *Willdenowia* 43: 195–203.
http://dx.doi.org/10.3372/wi.43.43121

Thiers, B. (2014) continuously updated. *Index Herbariorum: A global directory of public herbaria and associated staff*. New York Botanical Garden's Virtual Herbarium. Available from: http://sweetgum.nybg.org/ih. (Accessed: 7 March 2014).

Artículo 2

Villar J. L., Alonso M. A., Juan A. & Crespo M. B. 2015. Remarks on typification of nineteen names in *Tamarix* L. (*Tamaricaceae*). *Nordic Journal of Botany* 33: 591-600.

Remarks on typification of nineteen names in *Tamarix* L. (*Tamaricaceae*)

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Abstract

The earlier typifications of 12 names of *Tamarix* (*T. arabica, T. aralensis, T. boveana, T. chinensis, T. hohenackeri, T. karelinii, T. kotschyi, T. leptopetala, T. laxa* var. *araratica, T. laxa* var. *subspicata, T. mannifera* var. *persica* and *T. pycnocarpa*) are discussed. In eight cases, a second-step lectotype was selected, because several specimens of the type collection were found at the herbaria where the first-step lectotypes were indicated. Five previous indications of holotypes were corrected to lectotype designations, as no concrete specimens had been mentioned in the protologue. The typifications of *T. hampeana* and *T. mascatensis* are only commented to provide some clarification. Moreover, four additional names (*T. bengalensis, T. gallica* var. *arborea, T. mannifera* var. *purpurascens* and *T. passerinoides* var. *macrocarpa*) are here lectotypified, and an epitype is selected for *T. pallasii* var. *macrostemon*. Lectotypes are designated from the material present at G-BOIS, P, P-LOUR, PRC, and W. Most of the 19 names treated in this work were described in the 18th and 19th centuries by important European botanists such as Bunge (12), Boissier (1), Candolle (1), Ehrenberg (3), and Loureiro (1).

Introduction

Since Linnaeus (1753) published the name *Tamarix gallica* L., about 200 taxa, including species, subspecies, varieties and forms have been described in the *Tamarix* genus. To date, no general consensus exists on the taxonomic treatment of all of these taxa, and between 54 and 90 species are recognized depending on the authors (Baum 1978, Yang and Gaskin 2007). This has generated a large number of synonyms in some of the currently accepted species. Therefore, it is important to clarify the type material for every name that was validly published, so that the taxonomic treatment of this genus can be properly organised. However, most of the *Tamarix* taxa were published before the 20th century (Pallas 1789, Willdenow 1816, Desvaux 1824, Candolle 1828, Ehrenberg 1827, Ledebour 1843, Bunge 1851, 1852, Boissier 1849, 1867), that is before the date when it became mandatory to indicate a type in publication of new names (ICN, Art. 40.1 and 40.2; McNeill et al. 2012). In many cases, the original descriptions of *Tamarix* taxa were based on one or a few different gatherings, comprising several specimens which were sent to different herbaria. Consequently, a high number of isotypes and syntypes can be found for some names.

The global monograph of *Tamarix* by Baum (1966) included almost every taxon known by that time, and also a complete bibliographical compilation. As such, it is a key reference for anyone who wants to study *Tamarix* in depth. Baum (1966) mentioned type material for almost every name included in his work, even those put into the synonymy of accepted species names, and therefore, his publication must be considered as effective typification in most cases (ICN, Art. 7.9, 7.10). However, some type designations were found in need of restriction, and some mistakes should be corrected in order to achieve precision in certain type designations. It is important to note that Baum's monograph was first published in 1966, as a final research report for the United States Department of Agriculture (USDA). Another version with minor textual changes was published 12 years later by the Israel Academy of Sciences and Humanities (Baum 1978). This later version has been referred to as the place of valid publication of some names (Cirujano 1993, De Martis et al. 1984, Villar et al. 2012). However, the first version (Baum 1966) was distributed to main botanical research centres and libraries and thus was effectively published. Hence, all the nomenclatural novelties (new names, typifications) made by Baum must be accepted in the 1966 version as has been done in Villar et al. (2014a, 2014b).

The revision of various *Tamarix* taxa during the inspection of material from some important herbaria (B, G, K, MA, MO, MPU, P, PR, PRC, W) revealed the need to restrict the typifications of several names. Four names (*T. bengalensis, T. gallica* var. *arborea, T. mannifera* var. *purpurascens* and *T. passerinoides* var. *macrocarpa*) are lectotypified here. An epitype is selected for *T. pallasii* var. *macrostemon.* Seven more new type designations (*T. arabica, T. aralensis, T. boveana, T. hohenackeri, T. kotschyi, T. laxa* var. *subspicata* and *T. mannifera* var. *persica*) are second-step lectotypifications (ICN, Art. 9.17), since at least two specimens from the same gathering were found in the same herbarium, where the holotype or lectotype specimens were indicated by Baum (1966). For seven of the second-step lectotypes, as well as for five additional names (*T. chinensis, T. karelinii, T. laxa* var. *araratica, T. leptopetala* and *T. pycnocarpa*), correction from holotype to lectotype is also needed, as no particular specimen was designated by the original authors and syntypes exist (ICN, Art. 9.1, 9.5, 9.9). Finally, we have also included two cases (*T. hampeana* and *T. mascatensis*) in need of minor clarifications.

The studied *Tamarix* names are not necessarily currently accepted, and we have clarified typifications of synonyms of some widely accepted taxa. In advance of forthcoming taxonomic arrangements currently accepted species names have been included for each case, either following the bibliographic references or according to our own assessment. Some comments and considerations have also been discussed for names in which the taxonomical placement is more complicated.

Due to the complex taxonomy of the genus, we have not included in the text any specimens seen only as digital images from virtual databases (Jstor 2014, virtual herbaria 2014). Consequently, the cited material includes only those type specimens that were examined by the authors themselves. Labels of isolectotypes and syntypes are literally transcribed only when they show relevant differences with information provided in the text. Bunge was the author of twelve of the names here studied, as well as three additional combinations of names first described by Ehrenberg.. Consequently, it is important to note that while a significant part of Bunge's collections is kept at LE, the primary set containing his personal herbarium was acquired by Cosson and is now kept at P (Stafleu and Cowan, 1976). Following Baum (1966), we also used that set in our typifications.

Typifications were conducted following the International Code of Nomenclature (ICN) (McNeill et al., 2012). Particular issues concerning possible holotype specimens were also considered following McNeill (2014). The acronyms of the cited herbaria are according to the Index Herbariorum (Thiers 2014). The abbreviations of author names follow those proposed by Brummitt and Powell (1992), with amendments in IPNI (2014). All information shown on the label transcriptions is given between double quotation marks. Any handwritten text has been italicised, whereas the typewritten text is provided in standard font. The studied names are listed alphabetically.

Typifications

Tamarix arabica Bunge (1852, p. 55)

Lectotype (First step: Baum 1966, p. 71. Second step: designated here): Label 1: "HERB. MUS. PARIS. "Voyage de Mr Botta dans l´Arabie Yemen 1837. *Tamarix. Tehama"*. Revision label: "*Tamarix arabica Bge. Determinavit: B. Baum, 1967"* (P04958264). **Isolectotypes:** G (G unnumbered), K (K000641920), P (P04958265, P04958267 (only the specimen on the right), P04958263).

Tamarix arabica was described by Bunge (1852) on a gathering made by Botta in "Habitat in Tehama Arabia felicis", currently in Yemen. Baum (1966) indicated the "holotype" at P, as well as isotypes at G, K and P. Nevertheless, the use of the term holotype is not correct, as Bunge (1852) only referred to Botta's gathering but not to a specific sheet, and several duplicates exist. Consequently, those duplicates are to be considered as syntypes (ICN, Art. 9.5). According to ICN (Art. 9.9), we have to consider that Baum effectively selected a lectotype. However, four different syntypes can be found at P with different accession numbers. None is labelled as the type, but one of them includes an original revision label from Baum (P04958264). Therefore, the latter specimen is selected here as a second-step lectotype (ICN, Art. 9.17), due to its completeness and good state of preservation. Any other specimen from Botta's gathering in Tehama must be considered as an isolectotype. One of those isolectotypes (P04958267) is mounted in a mixed sheet alongside a specimen coming from a different gathering. In this case, the isolectotype corresponds only to the specimen mounted on the right side of the sheet.

According to Baum (1966), *T. arabica* is an accepted species name. However, its relations with similar taxa such as *T. nilotica* (Ehrenb.) Bunge. are still unclear. See also comments on *T. gallica* var. *arborea* Sieber ex Ehrenb.

Tamarix aralensis Bunge (1852, p. 59)

Lectotype (First step: Baum, 1966, p. 50. Second step: designated here): "*Nordküste der Aralsee, 30 jun 41. Reliquiae Lehmanninae. Herb. Al. de Bunge"* (P04958218). **Isolectotype:** P (P04958217).

Bunge (1852) described *Tamarix aralensis* based on material collected by Lehmann on the northern coast of the Aral Sea ("littus septentrionale lacus Aralensis"), currently in Kazakhstan. Baum (1966) reported the "holotype" at P, as well as an isotype at P and a *fragmentum typi* at the J. Gay's herbarium (K). There are currently two specimens at P that could belong to the mentioned type collection. However, only one of them (P04958218) is properly labelled according to the protologue (Bunge, 1852). The second one (P04958217) only shows that it was collected by Lehmann and belonged to Bunge's own herbarium. The use of holotype by Baum (1966) is here corrected to lectotype (ICN, Art. 9.9), as Bunge (1852) did not mention a concrete specimen and syntypes exist (ICN, Art. 9.1, 9.5). Baum's reference (1966) is considered an effective first-step lectotypification, and the specimen selected here is to be treated as a second-step lectotype (ICN, Art. 9.17).

Baum (1966) treated *T. aralensis* as an accepted species. However, as recently suggested by Samadi et al. (2013), we think that it should be included in the synonymy of *T. arceuthoides* Bunge.

Tamarix bengalensis B.R.Baum (1966, p. 180)

Lectotype (designated here): "*Herb Ind Or Hook, fil &. Thomson. Tamarix gallica, L. Hab. Bengal Or. Regio Trop. Alt.-Coll. JDH"* (W-Rchb.1889-168081). **Isolectotypes:** B (B10 0278713), P (P04957926, P05145043), W (W-Rchb.1889-6421, W0031783).

Tamarix bengalensis was described by Baum (1966), based on specimens from Hooker and Thomson´s India Orientalis Herbarium, collected by J.D. Hooker at "Bengal Or. reg. trop." In the protologue, Baum cited the type locality as "Bengal or. reg. temp.", but this seems to be a typographical mistake. In every studied specimen from the original material, the label clearly shows the text "reg. trop.", and no duplicate has been seen bearing a "reg. temp." label. Baum (1966) mentioned that the holotype was at W as well as isotypes at B, BM, CGE, G, K, OXF, P, S, U and W. However, three different specimens bearing the same collection label are found in W (W-Rchb.1889-6421, W0031783, W-Rchb.1889-168081), none of them marked as holotype. Considering that Baum did not make a precise indication of any of the specimens present at W, and no particular note is found on any of them, we could treat all the sheets at W designated as lectotype (thus constituting the first step of typification), and a second-step lectotype may be selected from those specimens (ICN, Art. 9.2, 9.3). Based on its state of preservation and accurate matching with the protologue, the specimen W-Rchb.1889-168081 is here selected as lectotype. Other specimens belonging to the original material should be considered as isolectotypes.

In this case, we agree with the treatment made by Qaiser (1981), who proposed the inclusion of *T. bengalensis* as a synonym of *T. indica* Willd.

Tamarix boveana Bunge (1851, p. 291)

Lectotype (First step: Baum 1966, p.98. Second step: designated here): Label 1: “Tamarix. Près de La Macta. Avril 1830. Bové. Herb. Al de Bunge”*;* Label 2: “Herb. Al. de Bunge. *Tamarix boveana Bge. Algeria”* (P00166715). **Isolectotypes:**“Tamarix. Près de La Macta. Avril 1830. Bové”, B (B10 0165200, B10 0165201), G (G 2 unnumbered sheets), K (K000242695, K000614109), P (P00166717, P05038533), W (W 0031775).

Tamarix boveana was described by Bunge (1851), who highlighted the resemblance of this species to *T. elongata* Ledeb. The description was based on a gathering by Bové in “Africa boreali: Près de la Macta. Avril, 1839”, currently in the Northwestern coast of Algeria. One year later, the description was expanded by Bunge (1852) and the collection date was corrected to “30 Avril 1830”. In our opinion, the latter change would imply the correct year reference, although it is difficult to distinguish between the numbers 0 and 9 on the Bove’s gathering labels.

Baum (1966) mentioned the “holotype” at P, as well as isotypes at B, FI, G, K, W and WU. Baum’s indication of holotype must be corrected to lectotype (ICN, Art. 9.9), since Bunge (1851) did not refer to any single specimen and many syntypes are known (ICN, Art. 9.1, 9.5). In addition, three sheets bearing Bove’s original collection label are found at P (P00166715, P00166717, P05038533). A second-step lectotype may be selected in order to narrow Baum´s typification to a single specimen (ICN, Art. 9.17). The sheet P00166715 is selected here as second-step lectotype because it bears original labels from Bunge’s herbarium, and therefore it was probably examined by him. The third specimen studied at P (P05038533) is mounted on a mixed sheet alongside a 1856 Cosson collection in Oran (close to La Macta). Other copies from the gathering of Bové in La Macta (Algeria) must be considered as isolectotypes.

Tamarix boveana is at present a widely accepted name. However, it belongs to a group of species whose morphological boundaries are still unclear. Further studies must be carried out to properly clarify the taxonomic identity of this species and its close relatives (Zielinsky 1994): e.g. the currently accepted *T. tetragyna* Ehrenb., *T. meyeri* Boiss., *T. elongata* Ledeb., and *T. brachystachys* Bunge; as well as some of the synonyms of those five species: *T. bounopoea* J. Gay ex Batt. & Trab., *T. jimenezii* Pau, *T. noëana* Boiss., *T. effusa* Ehrenb., *T. deserti* Boiss., and *T. genessarensis* Zohary.

Tamarix chinensis Lour. (1790, p.182)

Lectotype (Baum, 1966, p. 86): Label 1: “*Tamarix Sinica. Pentandr. 3-gynia.” (probably Loureiro’s handwritting);* Label 2: “*Tamarix chinensis Lour.”*; Label 3: “HERB. MUS. PARIS. ex Herb. Cochinchinensi LOUREIRO” P-LOUR (P00150890). **Isolectotype?:** Label 1: “*Tamarix e China (W.)”* (Willdenow’s handwriting), Label 2: “*T. (gallica) chinensis Ehrbg”* (Ehrenberg’s handwriting) B (B-W 06064).

This name was published by Loureiro (1790), who described the habitat as “in provincia Cantonensi Sinarum”, in the southwestern coast of China. According to Baum (1966), the holotype is kept at P, as well as an isotype or a fragment of the holotype at B (B-W06064), that would be a syntype (ICN, Art 9.5). Moreover, Loureiro (1790) did not mention a concrete specimen, so no holotype can be directly recognized (ICN, Art. 9.1). The specimen kept at B is only a small fragment belonging to the Willdenow herbarium. Moreover, this specimen is a very small twig with only one raceme almost lacking flowers and consequently, would not be very useful for further taxonomic and morphological studies. In addition, we have not found any clear reference about this material being originally collected by Loureiro (Willdenow 1814, Ehrenberg 1827). Nonetheless, were it properly referenced, it should be considered as an isolectotype.. The specimen P00150890 belongs to Loureiro’s Herbario Cochinchinensi, bearing a label probably handwritten by Loureiro and thus, it has been labelled as “holotypus”, probably according to Baum (1966). Therefore, this sheet is the proper specimen to be designated as the lectotype. Baum’s use of holotype (1966) is here corrected to lectotype (ICN, Art. 9.9) and, hence, he made an effective lectotypification (ICN, Art. 7.9, 7.10).

Tamarix chinensis is generally accepted at species rank. Nevertheless, further studies are being carried out in order to clarify its relationships with similar taxa (see comments on *T. hohenackeri*).

***Tamarix gallica* L. var. *arborea* Sieber ex Ehrenb. (1827, p. 269)**

Based on the same type: *Tamarix arborea* (Sieber ex Ehrenb.) Bunge. (1852, p. 67)

Lectotype (designated here): “Tamarix gallica L. (arborea), Cairo, Sieber” (PRC452688). **Isolectotypes:** PRC (PRC452690), W (W-Rchb. 1889-0320247, W-Rchb. 1889-0320297, W0031722, W0031723).

Tamarix gallica var. *arborea* was originally described by Ehrenberg (1827) from a Sieber’s gathering in “Cairo” (Cairo, Egypt). Sieber’s gathering is titled “Sieber, Franz Wilhelm; Herb. Fl. Aegypt.”, and it was indeed collected by Franz Wilhem Sieber and Franz Kohaut between 1817 and 1818 (A. F. Igersheim, 2011, *in sched*.). Ehrenberg (1827) ascribed this varietal name to Sieber. In fact, the original labels from Sieber’s gathering bear “Tamarix gallica L. (arborea),” pointing out that he had already suggested the name. It was later elevated to the rank of species by Bunge (1852), based on the original material from Sieber “Prope Cahiram” and another gathering (*Kotschy 1002*) that is not relevant for typification.

Baum (1966) stated that the lectotype was at PRC as well as isolectotypes at G, K, OXF, P, PRC and W. However, all six specimens extant at PRC are marked as “isolectotypus”, and bear different accession numbers. Moreover, as Bunge (1852) pointed out, Sieber’s collection is heterogeneous; some sheets are referable to *T. arborea* and some others to *T. nilotica* (Ehrenb.) Bunge. Among all the specimens kept at PRC, only two could clearly be considered as *T. arborea* (PRC452688 and

PRC452690) because the others (PRC452687, PRC452689, PRC452691 and PRC452701) are closer to *T. nilotica* in respect of the configuration of the nectariferous disc. As the previous selection of lectotype (Baum, 1966) was found to belong to two different taxa, a new lectotypification is needed (ICN, Art. 9.11). The specimen PRC452688 is selected here as lectotype because it is well preserved and shows the main morphological characters of this species. Any other specimen belonging to Sieber's collection from Cairo should be considered as an isolectotype, except those that belong to *T. nilotica*. Finally, the only specimen we were able to examine from *Kotschy 1002* at W corresponds to *T. nilotica*. Indeed, Baum (1966) mentioned that this gathering would correspond to *T. nilotica.*

According to Baum (1966), *T. arborea* is an accepted species. As we can deduct from the heterogeneous type collections, the taxonomic identity of this species is rather obscure, and many morphotypes with intermediate morphology exist between *T. nilotica* and *T. arborea.* The main diagnostic character used for the separation of these two species is the structure of the nectariferous disc: staminal filaments inserted between the disc lobes in *T. nilotica* and rising from the top of disc lobes in *T. arborea*. Zohary (1987) placed *T. arborea* in the synonymy of *T. nilotica,* as he also did with the names *T. mannifera* (Ehrenb.) Bunge and *T. arabica* Bunge. Indeed, he disregarded the use of disc configuration as a diagnostic character in *Tamarix*, as it has also been suggested recently by Villar et al. (2012). In the light of these findings, further studies will be needed to achieve a proper solution for the taxonomy of this group.

***Tamarix hampeana* Boiss. & Heldr. in Boiss. (1849, p. 8)**

Lectotype (Baum, 1966, p. 107): "*64. Tamarix Africana Desf. Palère au bord des fosses 14.Avril.1844, de Heldreich 1845*" G-BOIS (G00330259). **Syntypes:** "Phalareus, various years, Sprunner", G-BOIS (G00330260, G00380106, G00380107, G00380108); "Astros ad mare, 1842 apr., Boissier", G BOIS (G00330258); "ad phalerum, Heldreich, 1844", (P06618760); "grece phalere, Heldreich, 1846", (P05144597); "in maritimis ad phalerum, de Heldreich. Apr. 1844", (G00380104, G00380104_a, G00380105, K000641864, P06618759); "Attica, apr 1844 Tamarix africana, de Heldreich", (P06618441); "De Heldreich Herbarium Graecum Normale, Attica: in subpaludosis et ad ripas in halipedo Phaleri, 8 April 1847" (MA78790).

Boissier (1849) described *Tamarix hampeana* on several gatherings from the Attica region (Greece), collected independently by Heldreich and by Spruner at "Phalerum", as well as by Boissier in "Astros". All gatherings mentioned by Boissier are syntypes (ICN, Art. 9.5). Baum (1966) selected a specimen at G as the lectotype, bearing the label "*Heldreich 64*, Palère au bord des fosses 14.4.1844", and also reported isotypes at G, FI, K, OXF, P and W. No specimen matching that label is found in the general collection of G. A specimen of Heldreich's (G00380104) collected during April of 1844 "in maritimis ad Phalerum" bears a label indicating that it is the lectotype. However, that indication is wrong, as it does not match the protologue or Baum´s typification. The specimen G00330259, present at Boissier´s herbarium (G-BOIS), is indeed the only one at G matching exactly the protologue and Baum´s lectotype indication (Baum 1966). Therefore, it must be considered as the lectotype of *T. hampeana,* and is here cited as such in order to clarify this case. Any other specimen from *Heldreich 64* must be considered as isolectotype. Any other specimen from the original material, collected before 1849 by Heldreich or Sprunner at “Phalerum” (“Phalareus”, “Phaleri”or “Phalere”), or by Boissier at “Astros”, remain syntypes.

Tamarix hampeana is widely accepted as a separate and well-characterized species.

Tamarix hohenackeri **Bunge (1852, p. 44)**

Lectotype (First step: Baum, 1966, p. 47. Second step: designated here): “*Tamarix angustifolia* Ledeb. Unio Itiner. 1838. Ad rivulos prope Helenendorf Georg. R.F. Hohenacker. Cauc. Jun”. Label 2: “Herbier E. Drake” (P04957847). **Isolectotypes:** Bearing the original typewritten label by Hohenacker: “*Tamarix angustifolia* Ledeb. Unio Itiner. 1838. Ad rivulos prope Helenendorf Georg. R.F. Hohenacker. Cauc. Jun.”, G (G-Boiss, 3 unnumbered sheets), K (K000641905, K000641906, K000641907), , P [P04958357, P04957848, P04957850, P04958294 (only the branch on the right)], PRC (PRC452707, PRC453708), W (W1889-880289, W0227453). Bearing a handwritten label: “*Tamarix angustifolia Ledeb. Helenendorf. R.F. Hohenacker”*, P (P04957849); “*Tamarix angustifolia Ledeb. Ad rivulos prope col. Helenendorf. in terr. Elisabethpol. Armen. Or. R.F. Hohenacker”,* P (P05113398). **Syntypes:** “Szovits 111. *Tamarix angustifolia*. In sylvaticis ad fl. Chram. Herb. Al. de Bunge”, P [P04957846 (branch on the right side, alongside two other probable syntypes)].

Tamarix hohenackeri was described by Bunge (1852) from several gatherings: *Wilhelms s.n.* “in Iberia Caucasica” (Georgia); *Hohenacker s.n. “*in salsis territorii Elisabethpol prope Helenendorf” (Göygöl, Azerbaijan); *Szovits 111* “in sylvaticis ad fl. Chram” (Khrami river, Georgia); and *Wittmann s.n. “*prope Tiflis et Soghum” (Tbilisi and Sukhumi, Georgia). All these gatherings are syntypes (ICN, Art. 9.5), and would have been eligible for lectotypification. Among those, Baum (1966) selected a lectotype from Hohenacker’s collection that was kept at P, with isolectotypes at BM, FI, G, HBG, K, L, OXF, P, PRC, S, US and W. However, there are five specimens from Hohenacker’s collection at P with different accession numbers (P04958357, P04957847, P04957848, P04957850, P04958294), and none of them is clearly identified as the lectotype. Moreover, specimen P04958294 is mounted on a mixed sheet alongside *Kotschy 157*, so only the specimen on the right side is original material of *T. hohenacheri.* A second-step lectotypification (ICN, Art. 9.17) may apply in order to narrow the lectotype selection to a single specimen. The sheet P04957847 is here selected as lectotype since the specimen is well preserved and perfectly matches the original description. It is important to note that Hohenacker (1838) used the name “*Tamarix angustifolia* Ledeb.” for the same specimens collected near “Helenendorf” that Bunge used for his description of *T. hohenackeri*, so the former name is always found on the labels of this gathering. The remaining specimens from Hohenacker’s gathering, labelled as “*Tamarix angustifolia* Ledeb.”, must be considered as isolectotypes. In addition, the above-mentioned specimens from *Wilhelms s.n.*, *Szovits 111* and *Wittmann s.n.* should be considered as syntypes.

The taxonomical position of the *T. hohenackeri* has recently been supported as a separate species (Qaiser 1981, Yang and Gaskin 2007, Villar et al. 2014c, 2014d), though Baum (1966) cited this name as a synonym of *T. smyrnensis*. Nonetheless, further research is needed on the following group of species: *T. hohenackeri, T. ramosissima, T. austromongolica, T. smyrnensis* and *T. chinensis*, as well as their subspecific taxa and possible hybrids that have already been proven (Gaskin and Kazmer 2009). These species share, amongst other features, persistent petals and hololophic nectariferous discs.

Tamarix karelinii **Bunge (1851, p. 294)** ("*karelini*")

Lectotype (Baum, 1966, p. 58): Label 1: "*Herbarium Bungeanum. Tamarix Karelini mihi. in insula Ogurtschinsk maris Caspii. ad lit. orient. (T. ramosissima Kar. Enum. Turcom.)"* (Bunge's handwritting). Label 2: "HERB. MUS. PARIS. *Tamarix Karelini Bunge. Région Caspienne*" (P04957963).

Bunge (1851) described the species *Tamarix karelinii* based on material collected by Karelin in the Ogurtschinsk [Ogurja] Island, which is off the southeast coast of the Caspian Sea, in Turkmenistan. The same material had previously been referred as *Tamarix pallasii* var. *ramosissima* by Karelin (1839). Baum (1966) combined it as *Tamarix hispida* var*. karelinii* (Bunge) Baum, and he also cited the holotype of this name at P, as well as isotypes at G, LE and P, to which Qaiser (1981) added another duplicate kept at K. However, Bunge (1851) did not mention a single specimen, and we know about the existence of several syntypes belonging to the Karelin's gathering (ICN, Art. 9.1, 9.5). Therefore, Baum's (1966) use of holotype must be corrected to lectotype (ICN, Art. 9.9), as already noted by Qaiser (1981). We have only found one specimen at P, which was not labelled as typus, but the main label seems to be handwritten by Bunge. According to ICN, Art. 7.9, 7.10, the reference in Baum (1966) can be considered as effective lectotypification. Other specimens belonging to Karelin's collection in the "Ogurtschinsk" Island are to be considered as isolectotypes.

Baum (1966) combined the name as *T. hispida* Willd. var. *karelinii* (Bunge) B.R.Baum, placing it as a glabrescent variety of *T. hispida*. As several intermediate morphotypes are known to exist, we agree with Baum's treatment in this case.

Tamarix kotschyi **Bunge (1852, p. 30)**

Lectotype (First step: Baum, 1966, p. 120. Second step: designated here): Label 1: "*Tamarix kotschyi Bung."*; Label 2: "*Th. Kotschy.* Pl. Pers. Austr. Ed. *R. F. Hohenacker. 1845.* 100. Tamarix tetrandra *Pall.* var. parviflora. DC. --- Boiss. Ad rivulos in montibus pr Gere. D 24. Mart. 1842." (P02433872). **Isolectotypes** G (G-BOIS 1-770 (13)), K (K000641894, K000641895, K000641896), P (P04958572, P02433873, P02433874, P02433875), PRC (PRC452681, PRC452682, PRC452683, PRC452684), W (W1889-6411, W0031782, W1889-320256).

This taxon was described by Bunge (1852) on the basis of *Kotschy 100*, which was collected “ad rivulos in montibus prope Gere Persiae australis. D 24 mart 1842”. This gathering corresponds to a large set of duplicates which were distributed to many herbaria, all of which are syntypes (ICN, Art. 9.5). According to Baum (1966), the “holotype” is at P, as well as isotypes at B, CGE, FI, G, K, OXF, P, PRC, S, UPS and W. Five different specimens can be found at P (P04958571, P02433872, P02433873, P02433874, P02433875). However, according to ICN, Art. 9.1 no holotype exists. Therefore, Baum’s previous designation must be corrected to lectotype (ICN, Art. 9.9), and a second-step lectotype (ICN, Art. 9.17) may be designated amongst the material included at P since the type indication of Baum (1966) is to be considered as effective lectotypification (ICN, Art. 7.9, 7.10). The specimen P02433872 is selected here as a second-step lectotype because it is considered the best-preserved and most-complete amongst those present at P. Although the lectotype is in good condition, all the five specimens at P are mostly or entirely leafless, showing mostly racemes and flowers. In case of *T. kotschyi*, the leaves are an important morphological feature for the identification of the species, so any specimen from the original material showing a greater number of leaves would have been a better option for typification. The isolectotypes kept at G, PRC and W are a nice example of that, as they show a more complete representation of the morphology of this species than those present at P. Nonetheless, no need exists for an epitype selection (ICN. Art. 9.8), because the lectotype at P is not ambiguous and can undoubtedly be identified as *T. kotschyi*. Any other specimens belonging to *Kotschy 100* must be considered as isolectotypes.

We agree with Baum (1966) in considering *Tamarix kotschyi* an accepted species.

***Tamarix laxa* Willd. var. *araratica* Bunge (1852, p. 35)**

Lectotype (Baum, 1966, p. 120): “*114 T. tetrandra Pall. Am Araxes Ufer, 21 apr. 47. Iter Persicum. Buhse. 1847–1849. Herb. Al. de Bunge”* (P04958015, two branches on the left side of the sheet).

This variety was described by Bunge (1852) based on two different gatherings by Buhse in “regionibus transcaucasicis, Ad Araxen fluvium” and “regionibus transcaucasicis, ante vallem Arghuri”, which refer to the Aras river (probably its upper course) and in front of the Arghuri (formerly Akori, currently Yenidoğan) valley, in the north eastern slope of Mount Ararat, Igdir, Turkey. Baum (1966) placed it into the synonymy of *T. kotschyi*, and cited the “holotype” to be at P, as well as isotypes at K and LE. Given that Bunge (1852) made reference to two gatherings and the known existence of additional syntypes, Baum’s use of holotype must be corrected to lectotype (ICN, Art. 9.5, 9.9), and hence the indication of Baum (1966) can be considered effective lectotypification. One specimen can be found at P (P04958015) matching the protologue information, and this sheet may be accepted as the lectotype. This specimen is mounted on a mixed sheet, together with a different gathering (*Tamarix laxa W. Desert. wolg. Klaus. 36. Herb. Al. de Bunge*) that is irrelevant for typification purposes. Other specimens from the original material are to be considered as isolectotypes.

According to Baum (1966), *T. laxa* var. *araratica* is a synonym of *T. kotschyi.*

***Tamarix laxa* Willd. var. *subspicata* Ehrenb. (1827, p. 254)** (“*suspicata*”)

Based on the same type: *Tamarix cretica* Bunge (1852, p. 33)

Lectotype (First step: Baum, 1966, p. 122. Second step: designated here): Original Label: “Tamarix. gallica L., Armiro. *Sieber. Hb Portenschlag”.* Additional label: “*Tamarix cretica mihi. Bunge. Bunge*.” (Handwritten by Bunge) (W0031737). **Isolectotypes:** G-BOIS (G unnumbered), MO (MO3728838), P (P05171492), PR (PR616956), PRC (PRC452710, PRC452711, PRC452712, PRC452713), W (W0031736, W0031738).

This taxon was described by Ehrenberg (1827) on the basis of material collected by Sieber in “Armiro” (which probably makes reference to the Gulf of Almiro, Northwestern Crete, Greece). The original Sieber’s collection labels bear only “*T. gallica* L., Armiro, Sieber”. It seems to be a gathering from Sieber’s Herbarium florae Creticae, which was collected by Sieber and Kohaut in 1817 (Igersheim 2012, *in sched*.). According to Baum (1966), specimens from this gathering can be found at K, OXF, P, PRC and W. They have also been observed by us at G-BOIS, MO and PR. No single specimen was indicated by Ehrenberg (1827) and, consequently, all those mentioned above must be considered syntypes (ICN, Art. 9.1, 9.5) Baum (1966) said that the “holotype” was a specimen at W, but in fact three syntypes are found there, bearing different herbarium numbers (W0031736, W0031737, W0031738), and none of them is clearly marked as holotype. In this case, Baum’s indication must be corrected to lectotype (ICN, Art. 9.9). Once this correction is made, Baum’s typification (1966) can be considered as first-step lectotypification, which may be narrowed to a single specimen selected amongst those kept at W. Accordingly, the specimen W0031737 is selected here as second-step lectotype (ICN, Art. 9.17), based on its preservation state and accurate match with the protologue. Any other specimen from Sieber’s original gathering must be considered an isolectotype.

The varietal name was published as “*suspicata”* by Ehrenberg (1827), but this has to be interpreted as a typing error (missing a “b”), as later in the text this taxon is described as “Flores subspicatos trennen lässt”. This collection is also the type for *Tamarix cretica,* which was described by Bunge (1852) based on the same gathering by Sieber. Bunge (1852) stated that Ehrenberg’s variety was a mere synonym of this new species. Nowadays, *T. cretica* is widely accepted as a synonym of *T. parviflora* DC. (Baum 1966, 1978, 1990). The taxonomic status of *T. parviflora* is currently under discussion, as some authors considered it a synonym of *T. tetrandra* Pall. (Zielinski 1994). However, we are still lacking sufficient data to understand the taxonomic relationships between *T. tetrandra* and *T. parviflora*, and further detailed studies are required.

***Tamarix leptopetala* Bunge (1852, p. 72)**

Lectotype (Baum, 1966, p. 120): Label 1: "*Tamarix leptopetala m. habitat in valle Loura montium Elbrus. Pers. boreali. Kotschy. N. 728"* (Bunge´s handwritting) *"*Herb. Al. de Bunge"*;* Label 2: "*Ky 728*. *Tamarix leptopetala Bge. In monte Elbrus pr. Derbent (Persia). Kotschy"*; Label 3: "*Tamarix kotschy* Bunge. Rev: S. Toofani 14-8-2009". (P02433880, a single branch on the right upper side of the sheet). **Isolectotypes:** "*Kotschy N. 728"*, G (G-BOIS 1-774(24)), W (W0031781).

Tamarix leptopetala was described by Bunge (1852) based on *Kotschy 728,* "Persia boreali: in parte septentrionali montium Elbrus in valle Loura", currently in Alborz Province, Iran. Bunge (1852) clearly cited *Kotschy 728* but made no indication of a single specimen that could be considered the holotype. Consequently, all existing specimens of Kotschy's gathering are syntypes (ICN, Art. 9.5). Baum (1966) said that the "holotype" was kept at P, as well as isotypes at G and UPS. Another specimen was later found at W (W0031781). The use of holotype by Baum (1966) for the specimen kept at P (P02433880) must be corrected to lectotype, and then Baum's typification can be considered as effective (ICN, Art. 7.9, 7.10, 9.9). However, it is worth mentioning that the specimen at W is the most complete among those that we were able to study. Both specimens at P and W bear labels handwritten by Bunge. The remaining specimens belonging to *Kotschy 728* must be considered isolectotypes.

Tamarix leptopetala was considered by Baum (1966) as a synonym of *T. kotschyi* Bunge. This taxon was described as a species with pentamerous flowers (Bunge, 1852), the morphological feature accounting for the main difference from *T. kotschyi,* a species with tetramerous flowers. However, Baum (1966) pointed out that racemes with a certain number of pentamerous flowers are commonly found in *T. kotschyi*, mainly in late or secondary bloom. In addition, we have confirmed the presence of tetramerous flowers in specimens of *Kotschy 728*, as previously reported by Baum (1966, 1978). This would mean that *Kotschy 728* corresponds to a late bloom (presenting pentamerous flowers) of *T. kotschyi.* Although Qaiser (1981) disregarded Baum´s synonymization and considered *T. leptopetala* as a synonym of *T. mascatensis,* our observations suggest that the morphological evidences are clear enough to maintain *T. leptopetala* as a synonym of *T. kotschyi*.

***Tamarix mannifera* (Ehrenb.) Bunge var. *persica* Bunge (1852, p. 64)**

Lectotype (First step: Baum, 1966, p. 50. Second step: designated here): "*Th. Kotschy.* Pl. Pers. Austr. Ed. *R.F. Hohenacker. 1845.* Nro. 0. Tamarix gallica *L.* var. mannifera Ehrenb. – Boiss. Prope urbem Schiras. Majo. M. ? 1842" (P04957874). **Isolectotypes:** "Th. Kotschy Nro 0", G (G unnumbered), P (P04958035, P04958030, P04958029), PR (PR616951-(5658)), W (W1889-320287).

Tamarix mannifera var. *persica* was described by Bunge (1852), based on *Kotschy 0* that was collected "in Persia australi prope urbem Schiras" (Schiraz, Iran).

According to Baum (1966), the “holotype” is kept at P, as well as isotypes at several herbaria: B, CGE, FI, G K, L, OXF, P, POM, S, UPS and W, and we have also found another specimen of this collection at PR. No particular specimen within the *Kotschy 0* gathering was originally indicated by Bunge (1852). Accordingly, all specimens from *Kotschy 0* are considered to be syntypes and the use of “holotype” by Baum (1966) must be corrected to lectotype (ICN, Art. 9.5, 9.9). However, four different specimens of *Kotschy 0* are kept at P (P04957874, P04958035, P04958030, P04958029), none of which is labelled as type material. Consequently, a second-step lectotype (ICN, Art. 9.17) may be selected amongst these four sheets at P. The specimen P04957874 is selected here, considering its good state of preservation as well as the existence of fragments having all diagnostic morphological features. All other specimens of *Kotschy 0* must be considered as isolectotypes.

Baum (1966) treated *Tamarix mannifera* var. *persica* as a synonym of *T. aralensis.* According to our observations, both names are indeed synonyms of *T. arceuthoides.*

Tamarix mannifera **(Ehrenb.) Bunge var*.* *purpurascens*** **Bunge (1852, p. 64)**

Lectotype (designated here): “*329. Tamarix (gallica) mañifera Ehrbg. Arabice: Trpha. in Arabia petrea loco “Nafch”. ll. i. 1835 d. 16. Mai leg. W. Schimper”* (probably Bunge’s handwriting) “Herb Al de Bunge” (P04958039). **Isolectotypes:** “*Schimper* 329”, K (K000318347), P (P04958041, P04958036, P04958037, P04958038), PR (PR616950), PRC (PRC452671, PRC452693), W (W0031777, W0031778, W1889-320226, W1889-6416). **Syntypes:** “*Schimper* 299”, P (P0495802, P0495803), W (W 0031776); “*Bové*, Arabie petrea”, K (K000318349), P (P04958057). “*Bové,* Env. d. Tor. Cote de la mer rouge”, P (P04958056); mixed sheet, W (W-Rchb 1889-0320288, three out of four fragments correspond to original material, see below).

This variety was described by Bunge (1852) on the basis of several gatherings: *Schimper 299* “pl. exs. Arab. petr. prope Dahabb” (Dahab, South Sinai, Egypt), *Schimper 329* “in loco Nafch”(southern Syria), *Ehrenberg s.n* “Arabia petraea: ad montem Sinai” (South Sinai, Egypt), and *Bové s.n.* “Arabia petrea: prope Tor in littore mari rubri” (El Tor, South Sinai, Egypt). The specimens belonging to those four gatherings are syntypes (ICN, Art. 9.5), and we have studied those found at P, PR, PRC and W. The specimen P04958039 (*Schimper 329*) is selected here as lectotype, due to its good state of preservation and because it belongs to Bunge’s personal herbarium, so we might assume that he studied it before publishing the variety. The few studied specimens of *Schimper 299* (W0031776, P0495802, P0495803) lacked flowering racemes and showed only leaves, sometimes more distinctly amplexicaul than the other type material of this variety. Any other specimen of *Schimper 329* must be considered as an isolectotype and other original materials must remain as syntypes. Among the studied specimens, we have found a mixed sheet at W (W-Rchb 1889-0320288) that contains four different gatherings: the upper left side corresponds to an isolectotype from *Schimper 329*; the lower left side is a syntype from *Schimper 299*; the lower right side is probably a syntype from Ehrenberg’s gathering; and the last specimen, on the upper right side, could not be properly identified as original material of *T. mannifera* var. *purpurascens*.

According to our observations, *T. mannifera* var. *purpurascens* is a synonym of *T. nilotica.*

Tamarix mascatensis **Bunge (1852, p. 60)**

Holotype (except for the left and the lower specimens, labelled as *T. pallasii* var. (2)): Label 1: "*Regn. Mascatensi secus torrentes.* Aucher-Eloy-Herbier d´Orient Nº 4512"; Label 2: "*N1 Tamarix mascatensis m. N2 T. pallasii var. Bunge"* (Bunge's handwriting); Revision label: "Typificavit J. Walter (W) 2012-02 Syntypus for specimen 1" (W0031779). **Isotypes:** *Regn. Mascatensi secus torrentes.* Aucher-Eloy-Herbier d´Orient Nº 4512. G (G-BOIS 1-774 (25)), K (K000641919), P (P04958061).

Tamarix mascatensis was described by Bunge (1852) on the basis of Aucher Eloy's gathering "in Regno Mascatensi (Oman) secus torrentes". In the protologue, Bunge (1852) clearly cited a particular specimen with the following notes: "ex herb. Mus. Vindob." (Natural History Museum of Wien, W), which is mounted on a sheet at W (W0031779) together with plant material belonging to a variety of *T. pallasii.* In this case, there is no need for lectotypification, as a single specimen was cited clearly by Bunge (1852) (ICN, Art. 9.1). Moreover, this type material was also mentioned by Baum (1966). The sheet (W0031779) on which the holotype is mounted, currently bears a typification label classifying it as a syntype, which is not correct. The right, central and upper left fragments (marked by Bunge with number 1) of the sheet W0031779 have to be considered as the holotype of *T. mascatensis*. In addition, the collection number of Aucher Eloy, cited by Bunge (1852) as 4912, might be in fact the number 4512, as was already noted by Boissier (1867). This number can be seen in the isotypes present at G and P, as well as in the holotype at W. Paying attention to the handwriting on other Aucher Eloy's collection labels, we believe that the correct number is 4512.

We agree with Baum (1966) in considering *Tamarix mascatensis* an accepted species.

Tamarix pallasii **Desv. var.** ***macrostemon*** **Bunge (1852, p. 50)**

Lectotype (Qaiser. 1981, p. 126): "*1157. T. pallasii. Desv. var. macrostemon. sepal. obtusis. ad fl. Alasan in prov. Scheki Trans Cauc. Kolenati.* Herb. Al. de Bunge" (P0495864). **Epitype** (designated here): Bearing a compound label: "*Nº 241. Tamarix. In salsis campestribus ad pag. Tschorbula distr. Khoi prov. Aderbeidzan. 17 Mai 1828"* (handwritten by Bunge). "Herb. Al. de Bunge*. Tamarix pallasii Desv. Persia borealis. Szovitz"* (P04958567). **Syntypes:** "*Tamarix sp. In salsuginoso-limosis inter Buchara et Samarkand. 24 Aug 42. Reliquiae Lehmannianae. Herb. Al. de Bunge"* (P04958188); "Szovits 364. *Tamarix pallasii. In glareosis ad torrentem Avrin prope Badalan. Distr.*

Khoi prov. Aderbeidzan. 7 juni 1828" (P02433882, W1889-81064). "Guebhard 50, ad ripas fl. Sireth" (W0027458).

Tamarix pallasii var. *macrostemon* was described by Bunge (1852) on the basis of several gatherings: *Guebhard 50* "ad ripas fl. Sireth" (Siret river, Romania); *Parreys 443* "in Tauria" (Crimea); *Patrin s.n*. "ad mare Caspium", a specimen kept at B; *A. Meyer s.n.* "frequens in locis humidis ad fossarum rivulorum et fluviorum margines"; *Bunge s.n.* "in Caucaso"; *Hohenacker s.n.* "ad rivos in territorio Elisabethpolensi in valle Gandscha prope Helenendorf" (Göygöl, Azerbaijan); *Kolenati 1157* "ad fluvium Alasan in provincia transcaucasica Scheki [Shaki]" (Alazani river, Azerbaijan, in the border with Georgia); *Szovits 136* "in salsis ad Ziwinsk" (Süngütaşı, formerly Zivin, Kars Province, Turkey); *Hohenacker s.n.* "in humidis prope Lenkoran" (Lankaran, Azerbaijan); *Szovits 241* "in salsis campestribus ad pagum Tschorbula, districti Khoi provinciae Aderbeidschan" (Khoy district, West Azerbaijan province, Iran); *Szovits 364* "in glareosis ad torrentem Avrin prope Badalan districti Khoi provinciae Aderbeidschan" (Khoy district, West Azerbaijan province, Iran); *Kotschy 545* "ad flumen vallis Loura montium Elbrus"(Alborz Province, Iran); *Al. Lehmann s.n.* "versus mare Caspium prope Gurjew" (Atyrau, formerly Guryev, Kazakhstan); *Karelin s.n.* "in Turcomania"; *Al. Lehmann s.n.* "in salsuginoso-limosis inter Buchara et Samarkand" (between Buxoro and Samarqand, Uzbekistan). The gatherings and specimens cited above are syntypes (ICN, Art. 9.5).

Qaiser (1981) selected *Kolenati 1157* kept at P (P0495864) as lectotype. However, the present state of preservation of the lectotype is very poor (see P virtual herbarium), and it cannot be critically identified for purposes of the precise application of the name (ICN, Art. 9.8). Consequently, we designate here the sheet P04958567, belonging to *Szovits 241,* as an epitype to serve as an interpretative type of the name. The epitype is one of the syntypes appearing in the protologue, its state of preservation is optimal, and it shows all morphological features necessary for an unequivocal identification.

Tamarix pallasii var. *macrostemon* is widely treated (Baum 1966, Qaiser 1981) as a synonym of *T. smyrnensis* Bunge.

***Tamarix passerinoides* Delile ex Desv. var. *macrocarpa* Ehrenb. (1827, p. 276)**

Based on the same type: *Tamarix macrocarpa* (Ehrenb.) Bunge (1852, p. 79)

Lectotype (designated here): "*T. (passerinoides) macrocarpa*, In Aeg. Inter Sah et Salieh, 1820-1826 (apr). Ehrenberg leg." (W0028988). **Isolectotypes:** K (K000242696), P (unnumbered).

Ehrenberg (1827) described *Tamarix macrocarpa* as a variety of *T. passerinoides* Delile ex Desv. based on his own gathering from Egypt. It was later raised to the rank of species by Bunge (1852), who cited Ehrenberg's original material, as well as plants from Iran (“Persia australi prope Dalechi”) collected by Kotschy, which are not relevant for the typification purposes. Baum (1966) mentioned some duplicates from Ehrenberg’s gathering at K, L, P, UPS and W as “isotypes”, but he did not select a lectotype. Given that Ehrenberg (1827) made no precise mention of a specimen but only a provenance, no holotype exists and the “isotypes” cited by Baum would instead be syntypes (ICN, Art. 9.1, 9.4, 9.5). The syntypes kept at K (K000242696), P (unnumbered) and W (W0028988) have been studied, and the specimen at W is selected here as the lectotype because it is well preserved and is a good representative of the species. The remaining syntypes should be considered as isolectotypes.

According to Baum (1966), *T. macrocarpa* is an accepted name.

Tamarix pycnocarpa DC. (1828, p. 97)

Lectotype (Baum, 1966, p.133): Label 1: “Ex. HERB. MUS. PARIS. Voyage d´Olivier et Bruguière en Orient”. Label 2: “*Tamarix pycnocarpa DC*.”(Candolle´s handwritting) “*Trichaurus ____ Dne. in Jackmn”* (Decaisne´s handwritting?). “*De Bagdag a Kermacha Olivier et Bruguiere”.* “*De Candolle Sept, Tamarix pycnocarpa DC.”* (Directly handwritten on the sheet). Rev. Label: *“it can be as the isotype of T. pycnocarpa DC. S. Toofani. 23-8-2009”* (P00760171). **Isolectotypes:** “*Tamarix, st.10, de Bagdag a Kermancha le long des chemins, herb. D´Olivier, 1822”,* G (G-DC G00326424); “*De Bagdag a Kermacha Olivier et Bruguiere”* P (P00835761, P00760172, P00760173), PRC (PRC452702).

Tamarix pycnocarpa was described by Candolle (1828) based on an 1822 gathering collected by G.A. Olivier and J.G. Bruguière, “In Oriente secùs vias inter Baghdag et Kermancha. (v.s.)” (Iraq). Specimens of that gathering have been seen at G-DC, P and PRC. Baum (1966) cited the “holotype” at P, as well as the specimens at G-DC, P and PRC as isotypes. Usually, Candolle´s indication “v.s.” in his *Prodromus* would have designated the specimen in his personal herbarium (G-DC 00326424) as the holotype, in the case it would have been the only specimen used by him (ICN, Art. 9.1). Nevertheless, Candolle´s handwriting “*Tamarix pycnocarpa DC*.” on the specimen at P selected by Baum (P00760171) is exactly the same as that on the specimen G-DC 00326424. Therefore, following McNeill (2014) none of the available material can be established as holotype. All these facts undoubtedly indicate that Candolle had at least studied both specimens when he described *T. pycnocarpa* in 1828, and hence they must be treated as syntypes, as well as all specimens from the Olivier and Bruguière’s original collection (ICN, Art. 9.5, 40 Note 1). Furthermore, according to the ICN (art. 9.9), Baum´s use of “holotype” should be first corrected to lectotype, and subsequently, must be considered as effective lectotypification (ICN, Art. 7.9, 7.10).

Four specimens matching Olivier and Brugière’s collection and bearing different herbarium numbers have been found at P (P00835761, P00760171, P00760172, P00760173). Nonetheless, Baum (1966) stated precisely that the “holotype” was the one labeled as “*Tamarix pycnocarpa*” in Candolle’s own handwritting, and bearing a label with Decaisne’s handwritting “*Trichaurus pycnocarpus* Decne, in Jacquemont”. Accordingly, the specimen numbered P00760171 is accepted here as lectotype given that it is the only one which matches both labels mentioned by Baum (1966). The remaining duplicates of Olivier and Brugière’s collection, including the one at G-DC, must be considered isolectotypes.

We agree with Baum (1966) in considering *Tamarix pycnocarpa* an accepted species.

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References

Baum, B. 1966. Monographic Revision of the genus *Tamarix*. Final research report for the USDA. – Department of Botany, Hebrew University. Jerusalem.

Baum, B. 1978. The genus *Tamarix*. – Israel Academy of Sciences and Humanities. Jerusalem.

Baum, B. 1990. *Tamarix* L. – In: Tutin, T.G. et al. (eds.), Flora Europaea 2. Cambridge University Press, pp. 292–294.

Boissier, E. 1849. Diagnoses Plantarum Orientalium Novarum, ser. 1, 10. – M. Ducloux et Cons. Paris.

Boissier, E. 1867. Flora orientalis 1. – H. Georg. Gèneve.

Bunge, A. 1851. Alexandri Lehmann reliquiae botanicae. Mém. Acad. Imp. Sci. St.-Pétersbourg Divers Savans 7: 290–296.

Bunge, A. 1852. Tentamen Generis Tamaricum Species Accuratius Definiendi. – J.C. Schuenmanni & C. Mattieseni. Dorpati.

Brummitt, R. K. and Powell, C. E. 1992. Authors of plant names. – Royal Botanic Gardens. Kew.

Candolle, A. P. de 1828. Prodromus Systematis Naturalis Regni Vegetabilis 3. – Treuttel & Würtz. Paris.

Cirujano, S. 1993. *Tamarix* L. – In: Castroviejo, S. et al. (eds.), Flora iberica 3. Real Jardín Botánico Madrid, CSIC, pp. 43–443.

De Martis, B. et al. 1984. Il genere *Tamarix* L. (Tamaricaceae) in Sardegna. – Webbia 37: 211–235.

Desvaux, M. 1824. Sur la nouvelle famille de plantes fondée sur le genere *Tamarix*. – Ann. Sci. Nat., Bot., ser. 1, 4: 344–350.

Ehrenberg, C. G. 1827. Über die Manna-Tamariske nebst allgemeinen Bemerkungen über die Tamariscineen. – Linnaea 2: 241–344.

Gaskin, J. F. and Kazmer, D. 2009. Introgression between invasive saltcedars (*Tamarix chinensis* and *T. ramosissima*) in the USA. – Biol. Invasions 11: 1121–1130.

Hohenacker, R. F. 1838. Enumeratio Plantarun quas in Provincia Talysch Collegit R. Fr. Hohenacker. – Bull. Soc. Imp. Naturalistes Moscou 11(6): 337–414.

Karelin, G. 1939. Enumeratio Plantarum quas in Turcomania et in Persia Boreali. – Bull. Soc. Imp. Naturalistes Moscou (2): 141–177.

Ledebour, C. F. 1843. Flora rossica, sive enumeratio plantarum in totius imperii Rossici provinciis Europaeis, Asiaticis, et Americanis hucusque observatarum 2(4). – E. Schweizerbart, Stuttgart.

Linnaeus, C. 1753. Species plantarum 1. – L. Salvius, Stockholm.

Loureiro, J. 1790. Flora Cochinchinensis I. – Academia Real Das Scientias. Lisbon.

McNeill, J. 2014. Holotype specimens and type citations: General issues. – Taxon 63: 1112–1113.

McNeill, J. et al. 2012. International Code of Nomenclature for algae, fungi, and plants (Melbourne Code), adopted by the Eighteenth International Botanical Congress Melbourne, Australia, July 2011. [Regnum Vegetabile 154]. Koeltz Scientific Books. Königstein.

Pallas, P. S. 1789. Flora rossica, seu stirpium Imperii Rossici per Europam et Asiam indigenarum descriptiones et icones 1(2). – E Typographia imperiali J.J. Weitbrecht. Petropoli.

Qaiser, M. 1981. The genus *Tamarix* Linn. (Tamaricaceae) in Pakistan. – Pak. J. Bot. 13 (2): 107–158.

Samadi, N. et al. 2013. Meiotic behaviour, karyotypeanalyses and pollen viability in species of *Tamarix* (*Tamaricaceae*). – Willdenowia 43: 195–203.

Stafleu, F. A. and Cowan, R. S. 1976. Taxonomic literature: a selective guide to botanical publications and collections with dates, commentaries and types 1. – Bohn, Scheltema & Holkema. Utrecht. p. 407.

The International Plant Names Index (IPNI). 2014. Published on the Internet <http://www.ipni.org/ > continuously updated; accessed 2 March 2014.

Thiers, B. 2014. Index Herbariorum: A global directory of publicherbaria and associated staff. New York Botanical Garden's Virtual Herbarium. <http://sweetgum.nybg.org/ih/> continuously updated; accessed 2 March 2014.

Villar, J. L. et al. 2012. Does *Tamarix dalmatica* (Tamaricaceae) occur in Spain? – Anales Jard. Bot. Madrid 69: 253–258.

Villar, J. L. et al. 2014a. Proposal to conserve the name *Tamarix ramosissima* against *T. pentandra* (*Tamaricaceae*). – Taxon 53 (5): 1140–1141.

Villar, J. L. et al. 2014b. Type specimens of *Tamarix* (Tamaricaceae) described by Josef Franz Freyn in 1903. – Phytotaxa 172 (3): 289–292.

Villar, J. L. et al. 2014c. *Tamarix hohenackeri* Bunge, a new record for the flora of Mexico. – Acta Bot. Mex. 106: 117–128.

Villar, J. L. et al. 2014d. The genus *Tamarix (Tamaricaceae)* in Crete (Greece). – Willdenowia 44 (3): 321–326.

Willdenow, C. L. 1816. Beschreibung der Gattung Tamarix. Abh. Königl. Akad. Wiss. Berlin 1812-1813, pp. 76–86.

Yang, Q. and Gaskin, J. F. 2007. *Tamarix*. – In: Zhengyi, W. and Raven, P. H. (eds.), Flora of China 13. St. Louis, USA: Science Press, Beijing and Missouri Botanical Garden Press, pp. 59–65.

Zielinski, J. 1994. *Tamarix* L. – In: Browicz, K. (ed.), Chorology of trees and shrubs in south-west Asia and adjacent regions 10. Bogucki Wydawnictwo Naukowe, pp. 30–34.

Zohary, M. 1987. *Tamarix* L. – In: Zohary, M. (ed.), Flora Palestina 2. Reprint. The Israel Academy of Sciences and Humanities. Jerusalem, pp. 350–362.

<http://plants.jstor.org/>, acessed 20 November 2014.

<http://herbarium.univie.ac.at/database/search.php>, acessed 20 November 2014.

Artículo 3

Villar J. L., Alonso M. A., Juan A., Gaskin J. F. & Crespo M. B. 2014. Proposal to conserve the name *Tamarix ramosissima* against *T. pentandra* (*Tamaricaceae*). *Taxon* 63 (5): 1140-1141.

(2330) Proposal to conserve the name *Tamarix ramosissima* against *T. pentandra* (*Tamaricaceae*)

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(2330) ***Tamarix ramosissima*** Ledeb., Fl. Altaic. 1: 424. Nov–Dec 1829, nom. cons. prop.
Lectotypus (vide Baum, Monogr. Rev. Gen. Tamarix: 45. 1966): Kazakhstan ("Kazajstan"), "Tamarix ramosissima Led. Herb. Acad. Petrop. Songaria chin. ad lacum Saisang-Nor.", 1826, *Politow* (K barcode K000341731 [digital image!]; isolectotypi: PRC barcode PRC452672!; W barcode W0031725!).
(=) *Tamarix pentandra* Pall., Fl. Ross. 1(2): 72. 1789, nom. rej. prop.
Lectotypus (vide Baum, Monogr. Rev. Gen. Tamarix: 44. 1966): "Sibiria *P.S. Pallas* 14. d." (BM barcode BM0000999968!).

Tamarix ramosissima Ledeb. is native to Asia, but due to its ornamental use, it is naturalized in many temperate parts of the world, such as Australia, southern Africa, and North and South America. In particular, it has been included among 100 of the "World's Worst" Invasive Alien Species (http://www.issg.org/database/species/search.asp?st=100ss), and it is currently considered the second-worst invasive plant in the U.S.A. (Schaal & al. in J. Heredity 94: 197–204. 2003), where huge efforts have been made for control and eradication (Zavaleta in Ambio 29: 462–467. 2000).

Ledebour described *T. ramosissima* in 1829 from plants collected in Kazakhstan (Lake Noor Zaisan). In the protologue he did not mention *T. pentandra* Pall. or *T. pallasii* Desv. (in Ann. Sci. Nat. (Paris) 4: 349. 1824), two earlier names that apply to the same biological entity, widespread through central and western Asia. During the 19th century, most botanists combined *T. ramosissima* as a variety of *T. pallasii* (e.g., Bunge, Tent. Gen. Tamar.: 51. 1852; Boissier, Fl. Orient. 1: 773. 1867) or treated it as *T. gallica* var. *pallasii* (e.g., Thiselton Dyer in Hooker, Fl. Brit. India 1: 248. 1874). The type of *T. ramosissima* is considered to be a collection by Politow in 1826, sent to Ledebour by Gebler (cf. Baum, l.c. 1966: 44). Specimens of that collection have been seen at PRC! and W!. Baum (l.c. 1966: 45) mentioned a specimen from the Gay herbarium at K (digital image!) as holotype of *T. ramosissima*, and this must be considered as an effective lectotype designation under Art. 9.9 of the ICN (McNeill & al. in Regnum Veg. 154. 2012).

Tamarix pentandra was described by Pallas (l.c.), who mentioned no specific collection in the protologue, but, along with an enumeration of regions and localities, cited previous references (see below) including two illustrations. Therefore, despite Baum's (l.c. 1966: 44) statement that a specimen collected by Pallas in "Sibiria" kept at BM was the holotype, it is clear that this was not "the one specimen" that Pallas used (Art. 9.1 of the ICN, McNeill & al. in Regnum Veg. 154. 2012). However, under Art. 9.9, this specimen (barcode BM0000999968!) must be considered the lectotype of *T. pentandra*. In the protologue, Pallas (l.c.) adopted the phrase name "*Tamarix floribus pentandris*" citing "*Lin. syst. pl. I. p. 739. sp. 1.*", a reference to the first *Tamarix* species in Reichard (Syst. Pl.: 739. 1779); this is *T. gallica* L., first published in 1753 (Sp. Pl.: 270. 1753). Accordingly, *T. pentandra* was soon considered a superfluous name replacing *T. gallica* (Bieberstein, Fl. Taur.-Caucas. 1: 246. 1808; Desvaux, l.c.), a situation which has prevailed until now (cf. Baum, l.c. 1966; IPNI; Tropicos), *T. pentandra* being cited as illegitimate. Desvaux (l.c.) published *T. pallasii* for the species that Pallas had described, providing clear reference to *T. pentandra*, but renaming it, perhaps because it had by then been widely used (e.g., by Moench, Methodus: 123. 1794, and Bieberstein, l.c.) in the sense of *T. gallica*. Under the interpretation that *T. pentandra* was a replacement name for *T. gallica*, as Pallas did not indicate a type, it would be automatically typified under current rules by the type of the latter. Nevertheless, despite *T. pentandra* being considered a superfluous name for *T. gallica* and in modern terms illegitimate, it has been commonly reported as a synonym of either *T. pallasii* (Bunge, l.c. 1852: 50–51) or *T. ramosissima* (Candolle, Prodr. 3: 96. 1828; Gorschkova in Komarov, Fl. URSS 15: 311. 1949; Gorschkova & Shinners in S. W. Naturalist 2: 64. 1957; Baum, l.c. 1966: 42), and only rarely of *T. gallica* (Bieberstein, l.c.), or, in the case of Moench (l.c.) as an accepted name with *T. gallica* as a synonym. However, neither Pallas's (l.c.) reference to the "phrase name" of *T. gallica,* nor his explicit inclusion of "sp. 1" in Reichard's (l.c.) publication, can in our opinion be considered a "citation of the name itself", i.e., *T. gallica* (Art. 52.2 Ex. 12). In fact, the diagnosis "*Tamarix floribus pentandris*" is quite general, and it was later used at the beginning of the protologue of other *Tamarix* species such as *T. hispida* Willd. (in Abh. Königl. Akad. Wiss. Berlin 1812–13 (Phys. Kl.): 77. 1816), *T. canariensis* Willd (l.c.: 79) or *T. gracilis* Willd. (l.c.: 81). Moreover, at the same citation level, Pallas also included references to Duhamel's adoption of *T. narbonensis* (Traité Arbr. Arbust. 2: 300, t. 85. 1755), an unspecific *Tamarix* drawing (Blackwell, Herb. Blackwell. 4: t. 331, fig. 2. 1754–1757 and Gmelin's (Fl. Sibir. 4: 116. 1769) treatment of *T. germanica* L. (≡ *Myricaria germanica* Desv.). In sum, all four references seem to contextualize the taxonomic knowledge about the genus at that time, given that *Tamarix* was only represented by *T. gallica* and *T. germanica*. Moreover, none of the criteria of Art. 52.2 is fulfilled in the case of *T. pentandra* (no types of any kind existed at that time, nor was the name itself cited), and therefore it should be considered a legitimate name. In that case, *T. pallasii* is illegitimate, as Desvaux (l.c.) made direct reference to *T. pentandra* (Art. 52.1 & 52.2e), and *T. pallasii* (the replacement name) is to be automatically typified by the type of *T. pentandra* (Art. 7.5).

Widely considered superfluous, *T. pentandra* was almost neglected in favour of *T. pallasii* during the 19th and the early 20th centuries (Candolle, l.c.; Bunge in Mém. Acad. Imp. Sci. St.-Pétersbourg Divers Savans 7: 294. 1851; l.c.: 49. 1852; Boissier, l.c.; Niedenzu, Gen. Tamar.: 294. 1895; Gandoger, Fl. Cret.: 38. 1916). The material upon which *T. pallasii* was based was a source of confusion through these years. Gay (in Blanche & Gaillardot, Cat. Herb. Syrie: 10. 1854) suggested that a specimen conserved in Jussieu's Herbarium (P-Jussieu!) and annotated by Desvaux, was the original material of *T. pallasii* and that it belonged to *Tamarix laxa* Willd. It belongs to a Patrin collection from "Sibiria" with copies at P-Jussieu!, P-Lamarck!, G! and K, and the morphology matches *T. laxa*. Despite the evident morphological differences between the two taxa, already reflected in their original descriptions, Gay's assumption received acceptance during the 20th century, and some authors continued to synonymize *T. pallasii* to *T. laxa* (cf. Gutmann in Palestine J. Bot., Jerusalem Ser. 4: 53. 1947; Gorschkova, l.c.; Baum, l.c. 1966: 99). In fact, Baum (l.c. 1966: 99) sought to typify *T. pallasii* on that P-Jussieu! specimen mentioned by Gay (l.c.). Nevertheless, according to our argument above, Baum's typification is not acceptable since *T. pallasii* is automatically typified by the type of *T. pentandra* (Art. 7.4). Hence, *T. pallasii* must necessarily be removed from the synonymy of *T. laxa*, as has been erroneously assumed to be its position.

Tamarix pentandra being considered superfluous and *T. pallasii* synonymized under *T. laxa*, the use of *T. ramosissima* spread in the 20th Century (Gutmann, l.c.; Gorschkova, l.c.) and became consolidated worldwide after Baum's monograph (Baum, l.c. 1966), as found in the main floras published since then (Baum in Tutin & al. (eds.), Fl. Eur. 2: 293. 1968; Cirujano in Castroviejo & al. (eds.), Fl. Iber. 3: 438. 1993; Yang & Gaskin in Wu & al., Fl. China 13: 63. 2007; Qaiser in Fl. Pakistan http://www.efloras.org/florataxon.aspx?flora_id=5&taxon_id=200014313; among others) and in international databases such as The Plant List (http://www.theplantlist.org/tpl1.1/record/kew-2520135). The name *T. ramosissima* has been widely accepted by horticulturists, and it is used in many papers dealing with its invasive behaviour in the Americas (Cleverly & al. in Oecologia 111: 12–18. 1997; Gaskin & Schaal in Proc. Natl. Acad. Sci. U.S.A. 99: 11256–11259. 2002; Shafroth & al. in Environm. Managem. 35: 231–246. 2005; Natale & al. in Bol. Soc. Argent. Bot. 43: 137–145. 2008; Stromberg & al. in Restorat. Ecol. 17: 177–186. 2009; in J. Arid Environm. 74: 1399–1407. 2010; Brownell in Eukaryon 9: 4 pp. 2013; among others). By contrast the usage of *T. pentandra* was never general; it was first substituted by *T. pallasii* and later by *T. ramosissima*. All this, together with its supposed synonymization with *T. gallica*, left *T. pentandra* almost neglected. Only a few publications in the middle of the 20th century (Gorschkova, l.c.; Gorschkova & Shinners, l.c: 48) included the name either as a synonym of *T. ramosissima*, or with doubts about its identity, until Baum (l.c. 1966) appeared to have clarified that question.

As shown before, *T. pentandra* is taxonomically conspecific with and has nomenclatural priority over *T. ramosissima*. However, in the context of the taxonomic complexity of this genus, restoring *T. pentandra* over the well-known *T. ramosissima* would be confusing rather than clarifying, given the currently extended use of the latter in both its native range and those places where it is naturalized. Therefore, in order to avoid disadvantageous nomenclatural displacement of a name that has extensively been used in the last 60 years, the rules should be suspended to conserve the name *T. ramosissima* against the earlier *T. pentandra* in order to best serve stability of nomenclature.

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Sección II:
Aspectos taxonómicos

Artículo 4

Villar J. L., Alonso M. A., Juan A. & Crespo M. B. 2012. Does *Tamarix dalmatica* (Tamaricaceae) occur in Spain? *Anales del Jardín Botánico de Madrid* 69 (2): 253-258.

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Does *Tamarix dalmatica* (Tamaricaceae) occur in Spain?

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Abstract

Villar, J.L., Alonso, M.A., Juan, A. & Crespo, M.B. 2012. Does *Tamarix dalmatica* (Tamaricaceae) occur in Spain? *Anales Jard. Bot. Madrid* 69(2): 253-258.

The presence of *Tamarix dalmatica* in the Iberian Peninsula, and its confusion in Spain with the native species *T. boveana* and *T. africana*, is discussed. A morphological comparison between these three species, and a critical study of the causes for the confusion between them, is presented. This includes an analysis of the variability in some morphological characters used for the identification of these species, together with clarifications of some discrepancies between the original descriptions and our observations of the type material. As a conclusion, *T. dalmatica* is excluded from the Iberian and Balearic floras.

Keywords: *Tamarix dalmatica*, *Tamarix boveana, Tamarix africana,* morphological characters, taxonomy, systematics, Iberian Peninsula.

Resumen

Villar, J.L., Alonso, M.A., Juan, A. & Crespo, M.B. 2012. ¿Es *Tamarix dalmatica* (Tamaricaceae) una planta española? *Anales Jard. Bot. Madrid* 69(2): 253-258 (en inglés).

Se discute la presencia de *Tamarix dalmatica* en la Península Ibérica e Islas Baleares. Se pone de manifiesto la frecuente confusión de esta especie, en el territorio peninsular, con las nativas *T. boveana* y *T. africana.* Se realiza una comparación morfológica entre las tres especies y un estudio crítico de las causas que han provocado dicha confusión. Así mismo, se discute la variabilidad existente en algunos caracteres morfológicos utilizados para la identificación de estas especies, así como algunas discrepancias entre las descripciones originales publicadas y el material tipo. Como conclusión se descarta la presencia de *T. dalmatica* en la flora ibero-balear.

Palabras clave: *Tamarix dalmatica*, *Tamarix boveana, Tamarix africana,* caracteres morfológicos, taxonomía, sistemática, Península Ibérica.

INTRODUCTION

The genus *Tamarix* (Tamaricaceae) includes, according to different authors, between 65 and 90 species (Baum, 1978; Liu Shu, 2007) that are native to Asia, Africa and Europe. Many *Tamarix* species grow in xeric environments with some degree of salinity, and species are common in deserts, coastal sand dunes, salt marshes and ravines, although some species are also able to occur in freshwater habitats such as river banks. The complex taxonomy of this genus has been reported several times since the XIX century (Bunge, 1852; Baum, 1978; Zohary, 1987). Some of the characters that have been used for species separation are in fact variable in individuals of the same species, or even in a single individual (Jahandiez & Maire, 1932; Quézel & Santa, 1963). Of the 14 species included in Flora Europaea (Baum, 1990), four were cited for the Iberian Peninsula and the Balearic Islands: *T. africana* Poir.*, T. gallica* L.*, T. canariensis* Willd. and *T. boveana* Bunge. Since then, additional species have been reported: *T. parviflora* DC. (Baum, 1978), *T. dalmatica* Baum (Cirujano, 1993; Gil & al., 1996; Pérez Badia, 1997; Lendínez & al., 2009; Mota & al., 2009), *T. mascatensis* Bunge (De Martis & al., 1985; Gil & al., 1996), *T. arborea* (Sieb. ex Ehrenb.) Bunge (Gil & al., 1996; Gardano & al., 2009), and *T. meyeri* (Venturella & al., 2012).

In Spain, *T. dalmatica* was first reported in the Flora iberica (Cirujano, 1993) for the provinces of Alicante, Murcia and Majorca. Subsequently, some additional localities have been published: Majorca (Gil & al., 1996); La Marina Alta (Alicante) (Pérez Badia, 1997; Bolòs & al., 2005; Serra, 2009); Almería (Lendínez & al., 2009; Mota & al., 2009). And other species have been used in gardens as ornamentals, and have become naturalized (e.g. *T. parviflora* DC., *T. chinensis* Lour. and *T. ramosissima* Ledeb.).

Tamarix dalmatica was described by Baum (1978) based on specimens collected in the XIX and early XX centuries. It is mainly distributed in the eastern Adriatic and north-eastern Ionian coastland (Albania, Bosnia and Herzegovina, Croatia, and Montenegro). Baum also reported the species from the north-western coast of Italy and Sicily. It was also cited for Sicily by Pignatti (1982), but it recently was not found to occur in that island, as reported in a comprehensive revision on the Sicilian taxa of *Tamarix* (Venturella & al., 2007). It has also been recorded in Sardinia (De Martis & al., 1984) and southern Calabria (Venturella & al., 2008). The morphological similarities between *T. dalmatica* and *T. boveana*, and also *T. africana*, have been reflected in the different identification keys which have attempted to distinguish these taxa for the Iberian Peninsula and the Balearics (e.g., Cirujano, 1993; Bolòs & al., 2005; Mateo & Crespo, 2009; Salazar & Quesada, 2010). The present study is aimed to clarify the relationships between these species.

MATERIAL AND METHODS

For this study around 170 herbarium specimens of *T. africana, T. boveana* and *T. dalmatica* from ABH, HUAL, G, JAEN, K, MA, MPU, PR, PRC, UIB, VAL and W (acronyms according to Thiers, 2011) were examined. These included the holotype (PRC) and two isotypes (W and PR) of *T. dalmatica*, and also isotypes of *T. boveana* (W and G). Some field populations reported as *T. dalmatica* in the Iberian Peninsula were visited, and collections of *T. dalmatica* were made in the spring of 2011 in Albania, Montenegro and Croatia, where the species is widely distributed (deposited at ABH). Furthermore, collections of *T. boveana* were made at the type locality (La Macta, Algeria), and these are also currently conserved at ABH.

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The morphological characters of the studied materials of *T. boveana* and *T. dalmatica* were compared with the original descriptions and with morphological data taken from other studies (Bunge, 1852; Baum, 1978; Cirujano, 1993). For species identification various monographs were used (Bunge, 1852; Baum, 1978; Cirujano, 1993). Author abbreviations follow Brummitt and Powell (1992), and have been updated according to the IPNI (2011). Detailed photographs of *T. africana*, *T. boveana* and *T. dalmatica* were made using a binocular microscope (Olympus SZX12) with adapted camera.

RESULTS

Our study of the herbarium specimens (Appendix 1) identified as *T. dalmatica* in Spain in various reports revealed that most of them correspond in fact to *T. boveana*, and some to *T. africana*, but none was found to correspond to *T. dalmatica*. The reports of *T. dalmatica* in Majorca could not be checked because no vouchers were found in the herbaria consulted. However, since no specimen resembling *T. dalmatica* has been found among the Balearic collections studied, or was collected during the last years of our research, its presence in the Balearic Islands is very unlikely. *Tamarix boveana* and *T. africana* are the two species in the Iberian Peninsula that most resemble *T. dalmatica*. The latter species has often been confused with *T. boveana* due to some similarities in floral morphology, although in the field *T. africana* looks much closer to *T. dalmatica*.

Despite their general similarity, some differences can be highlighted: *T. dalmatica* and *T. africana* have similar leaves, although those of *T. africana* are markedly auriculate, but in both species the longest leaves are shorter than 4 mm, whereas those of *T. boveana* can reach up to 7 mm. The racemes (Fig. 1) of *T. boveana* are longer and wider (up to 12 cm long and 13 mm wide) than those of *T. dalmatica* (up to 6 cm long and 7 mm wide) and *T. africana* (up to 6.5 cm long and 7 mm wide).

Bracts are also quite similar in *T. africana* and *T. dalmatica*, being typically broadly triangular to oblong, obtuse, and usually shorter than 3 mm, almost equalling the calyx or slightly overtopping it. Those in *T. boveana* are also oblong and obtuse, but they are much longer, clearly overtopping the calyx, and frequently reaching 5-6 mm in length (Fig. 2). The flowers of *T. africana* are usually pentamerous, whilst those of *T. boveana* and *T. dalmatica* are usually tetramerous. Although all three species show exceptions, *T. dalmatica* is the most variable in the number of pieces in the floral whorls. The size of the sepals can overlap in all three species, but whilst those in *T. boveana* can reach 3.5(4) mm in some cases, in *T. dalmatica* and *T. africana* they are usually smaller (Fig. 2). Petals are elliptic-oblong to obovate unguiculate in *T. boveana*, whereas they are ovate to elliptical (or oblong-cuneate in var. *fluminensis* Maire) in *T. africana*, and oblong elliptical with a cuneate base in *T. dalmatica* (Fig. 2). The ovary of *T. africana* bears 3 styles, whereas in *T. boveana* it usually has 4 styles (rarely 3). Similarly, *T. dalmatica* usually has 4 styles, but 3-styled ovaries are not uncommon and this species is the most variable of the three with regard to this character.

Some differences can also be found in the habitat requirement. *T. boveana* is hyper-halophilous, whereas *T. dalmatica* and *T. africana* are halo-tolerant, and able to grow near freshwater environments. More complete descriptions of the three species are given below.

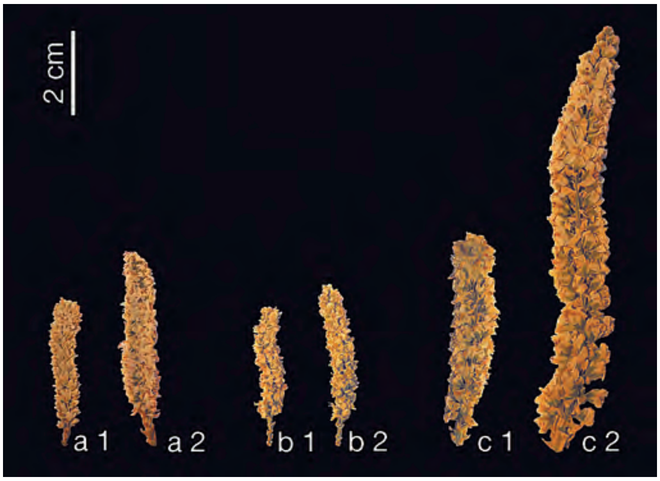

Fig. 1. Racemes of: **a1,** *Tamarix africana* (ABH55366, Valencia, Spain); **a 2,** *T. africana* (ABH57862, Alicante, Spain); **b1, b2,** *T. dalmatica* (ABH57836, Central Dalmatia, Croatia); **c1,** *T. boveana* (ABH58159, Alicante, Spain); **c2,** *T. boveana* (ABH57853, Alicante, Spain).

DISCUSSION

The confusion that led to several erroneous reports of *T. dalmatica* in the Iberian Peninsula was probably due to a number of factors. A widely used character to distinguish between species or groups of species in *Tamarix* is the nectariferous disc (Baum, 1978; De Martis & al., 1984; Cirujano, 1993). Baum (1978) established three types of nectariferous disc according to the fusion of the stamen filaments to the disc: synlophic, paralophic, and hololophic.

Although this is a very useful character, it can be problematical since differences between synlophic and paralophic discs are often very weak. Distinction between paralophic and hololophic discs can also be unclear, particularly when the lobes are not well developed and the disc is circular in shape. Some authors have questioned the reliability of the nectariferous disc shape for some species (Zohary 1987), and in the Flora of China (Liu Shu, 2007), only two types are distinguished: those in which the staminal filaments are inserted on top of the disc lobes, and those in which the filaments are inserted between the lobes. According to the observed variability, the option of using only two types of nectariferous disc seems to work better in the species with marked morphological plasticity. Disc type may have been a reason for some misidentifications. The disc of *T. dalmatica* has been defined as paralophic in several works, whilst *T. africana* and *T. boveana* discs were defined as synlophic (Baum, 1978; Cirujano, 1993). However, this character is especially variable in *T. boveana* (see species description below), and clear assignation to any of those disc types is sometimes extremely difficult.

The number of petals and sepals is an important character to note. *T. boveana* and *T. africana* have been considered quite stable in the number of sepals and petals (tetramerous

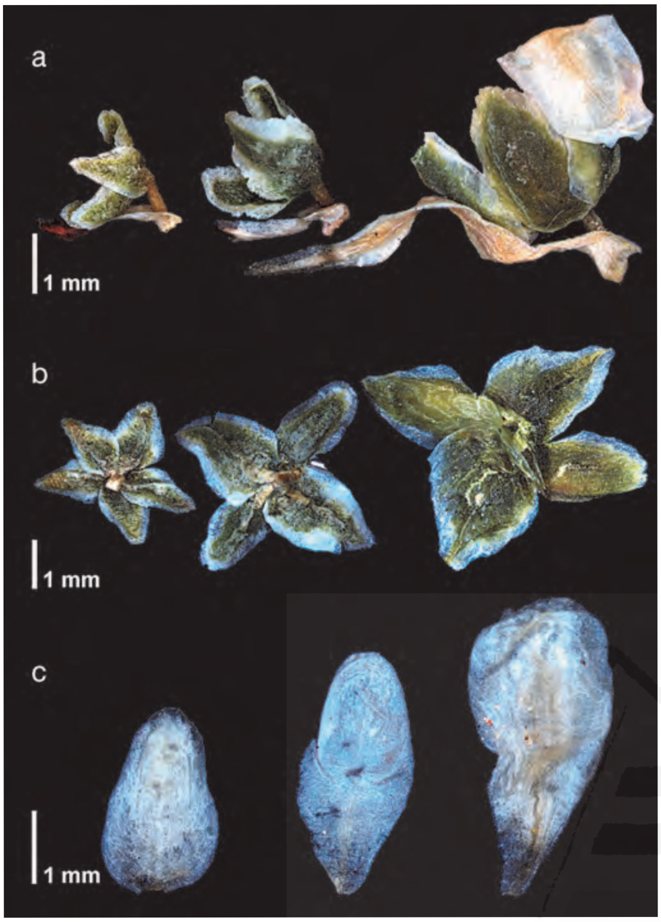

Fig. 2. *Tamarix africana* (left column; ABH55366, Valencia, Spain), *T. dalmatica* (central column; ABH57836, Central Dalmatia, Croatia); *T. boveana* (right column; ABH57853, Alicante, Spain). **a,** bracts and calyx; **b,** outer view of calyx; **c,** petals.

and pentamerous, respectively), whereas *T. dalmatica* was described as a tetra-pentamerous species. This can cause misidentification of *T. dalmatica* with *T. boveana* or *T. africana* in specimens of the latter two species that show flowers with a different sepal number in the racemes. In fact, in most species some flowers can be found that show abnormal features or even morphological aberrations, such as a reduction in the number of sepals (sometimes due to fusion); extra petals or extra sepals (flowers were found with eight well-developed petals and sepals in *T. hampeana* Boiss. & Heldr.); extra bracts located on pedicels, reported by Baum (1978) for *T. rosea* Bunge, but also observed in other species such as *T. boveana* Bunge, *T. chinensis* Lour., *T. hampeana* or *T. hohenackeri* Bunge; extra staminal filaments or stamens, well-developed or not; or intermediate shaped pieces between the sepals and petals. The shape of sepals and their margin are another source of potential confusion. In recent works (Baum, 1978; Cirujano, 1993; Salazar & Quesada, 2010), the two internal sepals of *T. boveana* have been described with a denticulate margin at the apex, whereas the sepal margin in *T. dalmatica* was said to be entire in the original description (Baum, 1978). In the protologue of *T. boveana* (Bunge, 1852), sepals (including the outer ones) were described as having a finely serrulate margin, but according to our own observations, in *T. boveana* the margin of inner and outer sepals can vary from entire to finely serrulate or irregularly denticulate. Surprisingly, despite Baum's original description, no individuals of *T. dalmatica* with entire sepals have been found, including the holotype and two isotypes.

The relative length of bracts with respect to calyx has been another source of confusion. According to the protologue, the bracts in *T. dalmatica* are longer than calyx, but no quantitative measurements were given. In fact, bracts longer than calyces were rare in most specimens of *T. dalmatica* studied by us (including the type material). However, *T. boveana* bracts are almost always longer than the calyx, and clearly larger in size than those of *T. dalmatica*, as emphasized in the descriptions below. It is important to note the convenience of measuring the bract size, even though it is variable in some species. This is because in some cases (e.g. *T. polystachya* Ledeb.) the pedicels continue to elongate after the flowers are open, whereas bracts remain the same size. In such cases, the bracts can be slightly shorter than the calyx when flowers first open, and much shorter than pedicels at fruiting time.

Another confusing character is the size of racemes. According to the original descriptions, *T. dalmatica* and *T. boveana* have racemes that are similar in size. However, *T. boveana* racemes are significantly longer and wider than those in *T. dalmatica.* Yet another source of confusion is the papillosity of the raceme rachis. In *T. boveana* the rachis has been described as papillose, whereas it is glabrous in *T. dalmatica* (Baum, 1978; Cirujano, 1993; Salazar & Quesada, 2010). Whilst most specimens of *T. boveana* show appreciable papillosity all over the rachis, a number of individuals occur in which the raceme rachis appears to be glabrous or only papillose around the insertion of bracts. Moreover, it is necessary to be cautious when using this as a diagnostic character for species segregation. Baum (1978) regarded it as variable in some species, e.g. *T. nilotica, T. macrocarpa, T. arborea,* and *T. passerinoides*, with *T. hispida* Willd. the most extreme example. Two varieties are accepted in the latter: var. *hispida*, with the raceme densely covered with hair-like papillae, and var. *karelinii* (Bunge) Baum, with the raceme almost glabrous, although intermediate forms are common between both extremes.

According to our observations, the presence of *T. dalmatica* in the Iberian Peninsula and the Balearics should be disregarded. And since the variability of morphological characters used for identification is high, it is necessary to use a combination of most of them to ensure accurate identifications.

KEY TO THE STUDIED SPECIES

1. All flowers in the racemes pentamerous, or exceptionally with only a few tetramerous .... ***T. africana***
1. All flowers in the racemes tetramerous, or tetramerous and pentamerous intermixed in similar proportions **2**
2. Racemes 4-12(15) cm long and 7-13 mm wide. Bracts 4-6(7.5) mm long, clearly longer than the calyx .... ***T. boveana***
2. Racemes 2-4(6) cm long and 4.5-5.5(7) mm wide. Bracts 1.25-2.25(3) mm long, usually slightly shorter than the calyx .... ***T. dalmatica***

The following descriptions are included to facilitate further identification of taxa. They are based on our observations of many specimens of the three species, including type materials of both *T. dalmatica* and *T. boveana*:

Tamarix dalmatica Baum

Leaves 1.5-3(4) mm long, narrowly triangular, acute, with narrow decurrent base, the larger slightly auriculate. Inflorescence composed of racemes arranged in unbrached spike-like panicles. Racemes 20-40(60) × 4.5-5.5(7) mm, with a short peduncle (2-3 mm) covered by scarious bracts. Rachis glabrous. Bracts 1.25-2.25(3) mm long, shorter to equalling the calyx, rarely longer, broadly triangular to oblong, patent, slightly concave, with the apex sometimes scarious and incurved, base decurrent and narrow. Pedicels ca. 0.5 mm. Sepals 4 (sometimes 5), 1.2-1.7(2) × 1-1.4 mm, broadly ovate to elliptic, with a hyaline irregular and finely denticulate margin; the 2 external from obtuse to acute, sometimes with prominent central nerve, the 2(3) internal ones obtuse. Petals 4 (sometimes 5), 2.5-3.25(3.5) × 1.2-1.5 mm, oblong-elliptical with a cuneate base to slightly obovate, recurved. Filaments 4(5), inserted on the top of disc lobes, the lobes short and filament insertion truncate (abrupt). Anthers not apiculate. Ovary with 4 styles, rarely 3.

Tamarix boveana Bunge

Leaves 2-4(7) mm long, narrowly lanceolate acute, the larger long triangular with wide base at flowering time, markedly auriculate in late summer and autumn shoots. Inflorescence composed of racemes arranged in unbranched spike-like panicles. Racemes 40-120(150) × 7-13 mm, very large, with a peduncle up to 1 cm long, with some long and wide oblong bracts. Rachis from papillose to almost glabrous. Bracts 4-6(7.5) × 0.5-1 mm, oblong-obtuse, sometimes with scarious incurved apex, base decurrent, divaricate to recurved at fruit stage, with papillose margin and surface, longer to much longer than calyx; exceptionally 1-3 extra bracts* can be found on the pedicels of flowers at the base of racemes, these bracts being triangular linear and usually shorter than 2 mm. Pedicels 0.5-1 mm, sometimes slightly recurved. Sepals 4 (rarely 5, exceptionally 6), (1.8)2-3.5(4) × 1.25-2.5 mm, ovate-elliptical, with a hyaline margin that is entire or finely and irregularly denticulate, the 2 internal obtuse, the 2 external slightly larger, commonly acute (rarely obtuse) to acuminate; when acuminate, the central nerve is strongly developed and the sepals may appear keeled. Petals 4 (rarely 5), 2.5-4(6) × 1.25-2.5 mm, elliptical-obovate to obovate-ungiculate. Filaments 4 (rarely 5, very rarely 6-7), inserted on the top of disc lobes, the lobes short and filament insertion usually cuneate (progressive), sometimes truncate; sometimes the stigmatic disc is very thin and circular, with no clear lobes, and then the insertion of filaments is cuneate. Anthers not apiculate. Ovary with 4 styles, very rarely 3.

*In some specimens these bracts are very close to calyx, and they adopt the shape of a sepal, and so maybe the possible origin of some flowers with a hexamerous calyx.

Tamarix africana Poir.

Leaves 1.5-3(4) mm long, ovate-triangular, acute, auriculate with narrow base. Inflorescence composed of racemes arranged in unbranched spike-like panicles. Racemes 20-50(65) × (5)5.5-7 mm, with a short peduncle (<5 mm) covered by scarious bracts. Rachis usually papillose. Bracts 1.5-3(4)* mm long, sub-equalling to slightly longer than calyx, broadly triangular to oblong, sometimes with scarious incurved apex, usually obtuse, with papillose margin, base narrow decurrent to calcarate, sometimes with 2 small auricles that are also decurrent. Pedicels ca. 0.5 mm. Sepals 5 (rarely 4, exceptionally 6), broadly ovate to oblong, obtuse, with a narrow hyaline margin entire or finely denticulate; the 2 external (1)1.25-2(2.5) mm long, mostly with prominent central nerve, the 2 internal 0.8-1.5 mm long. Petals 5 (rarely 4, exceptionally 6), 2-3(4)* × 0.9-1.5(2) mm, ovate to elliptic (or oblong-cuneate to oblong-unguiculate)**. Filaments 5 (rarely 6-8, and exceptionally 4), inserted on the top of the disc lobes, the insertion cuneate (when extra filaments are present, inserted between lobes). Anthers mostly not apiculate. Ovary always with 3 styles.

*In var. *fluminensis* Maire the bracts, sepals and petals have the largest values for the species.

**Only in var. *fluminensis* Maire.

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REFERENCES

Baum, B. 1978. *The genus Tamarix*. Israel Academy of Sciences and Humanities. Jerusalem, 209 pp.

Baum, B. 1990. *Tamarix* L. In: Tutin, T.G. & al. (eds.), *Flora Europaea* 2: 292-294 (reprint). Cambridge University Press. Cambridge.

Brummitt, R.K. & Powell, C.E. 1992. *Authors of Plant Names*. Royal Botanic Gardens, Kew. 732 pp.

Bunge, A. 1852. *Tentamen Generis Tamaricum Species Accuratius Definiendi*. Dorpati. 83 pp.

Bolòs, O., Vigo, J., Masalles R.M. & Ninot, J.M. 2005. *Flora manual dels Països Catalans*. Pòrtic. Barcelona. 1310 pp.

Cirujano, S. 1993. Tamarix L. In: Castroviejo, S. & al. (eds.), *Flora Iberica* 3: 437-443. Real Jardín Botánico, CSIC. Madrid.

De Martis, B., Loi, M.C. & Polo, M.B. 1984. Il genere *Tamarix* L. (Tamaricaceae) in Sardegna. *Webbia* 37(2): 211-235.

De Martis, B., Loi, M.C. & Polo, M.B. 1986. Contribution to a better understanding of the genus *Tamarix* in Portugal. *Candollea* 41: 293-298.

Gargano, M. L., Mandracchia, G & Venturella, G. 2009. *Tamarix arborea* var. *subvelutina* (Tamaricaceae), new from Spain. *Lagascalia* 29: 320-321.

Gil, Ll., Tébar, F.J. & Boi, M. 1996. Notes florístiques de les illes Balears (VIII). *Bolletí de la Societat d Història Natural de les Balears* 39: 117-128.

IPNI. 2011. *The International Plant Names Index*. Published on the Internet http://www.ipni.org [accessed 10 November 2011].

Jahandiez, E. & Maire, R. 1932. *Catalogue des Plantes du Maroc (Spermatophytes et Ptéridophytes)*. Vol. 2. Algiers. 557 pp.

Lendínez, M.L.; Marchal, F.M.; Quesada, J. & Salazar, C. 2009. Aportaciones al conocimiento de la flora halófila de Andalucía (S. España). *Acta Botanica Malacitana* 34: 275-280.

Liu Shu, C. 2007. *Tamarix.* In: Zhengyi, W. & al. (eds.). *Flora of China* 13: 59-65. Science Press, Beijing & Missouri Botanical Garden Press, St. Louis.

Mateo, G. & Crespo, M.B. 2009. *Manual para la determinación de la flora valenciana*. Ed. 4. [Monogr. Flora Montiber. 5]. Librería Compás, Alicante.

Mota, F., Lahora, A., Pérez-García, F., Garrido, J.A., Posadas, L., Martínez Hernández, F., Medina-Cazorla, J.M. & Mendoza, A.J. 2009. Nuevas citas para la flora de la provincia de Almería (Sureste Ibérico, España). *Anales de biología* 31: 57-58.

Pérez Badia, R. 1997. *Flora vascular y vegetación de la comarca de la Marina Alta (Alicante)*. Instituto de Cultura Juan Gil-Albert. Alicante. 566 pp.

Pignatti, S. 1982. *Flora d'Italia*, 2: 133-134.

Quézel, P. & Santa, S. 1963. *Nouvelle flore de l'Algérie et des régions désertiques méridionales.* 2 CNRS., Paris. 688 pp.

Salazar, C. & Quesada, J. 2009. *Tamarix* L. In: Blanca, G. & al. (eds.), *Flora vascular de Andalucía Oriental* 2: 190-193. Consejería de Medio Ambiente, Junta de Andalucía, Sevilla.

Serra, L. 2007. *Estudio crítico de la flora vascular de la provincia de Alicante: aspectos nomenclaturales, biogeográficos y de conservación.* [*Ruizia*, 19]. Madrid. 1414 pp.

Thiers, B. 2011. *Index Herbariorum: A global directory of public herbaria and associated staff*. [continuously updated]. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/ih/ [accessed November 2011].

Venturella, G., Baum, B.R. & Mandracchia, G. 2007: The genus *Tamarix* (Tamaricaceae) in Sicily: first contribution. *Flora Mediterranea* 17: 25-46.

Venturella, G., Mandracchia, G. & Gargano, M.L. 2008. The tamarisks of southern Calabria (Italy). *Flora Mediterranea* 18: 421-430.

Venturella, G., Gargano, M.L. & Mandracchia, G. 2012. First record of *Tamarix meyeri* (Tamaricaceae) for western Europe. *Plant Biosystems* 146(2): 484-489.

Zohary, M .1987. *Tamarix* L. In: Zohary, M. (ed.), *Flora Palestina* 2: 350-362. Reprint. The Israel Academy of Sciences and Humanities. Jerusalem.

APPENDIX 1

Studied specimens

Tamarix boveana

ALGERIA. Pres de La Macta. IV-1830. *Bové.* (Isotypes of *Tamarix boveana* Bunge, (G (2 vouchers), W). Bords du Chott el Chergui, près de Khrider, cercle de Saïda, 30-V-1852, *Balansa* (isotypus of *Tamarix bounopoea* J. Gay, W1889-66855). Orán, La Macta, saladar con dunas, 30S YE 6064, 1 m, 13-VI-2010, *A. Juan* (ABH56326, ABH56327). M Sila, Chellal, 31S FV 2531, 460 m, *A. Juan* (ABH56332, ABH56333). MOROCCO. Prov. Goulimine, Oued Noun, 13 Km SW of Goulimine on P41 to Tan-Tan, *D. Podelch* (MO-6050185).Saladar próximo a Barrage Mohamed, 30SVD9823, 235 m, 20-IV-2009, *M.A. Alonso, M.B. Crespo, A. Juan, J.L. Villar & al*. (ABH54181, ABH54183, ABH54185). SPAIN. **Alicante:** Jijona, Monnegre, Barranco salinas, 30SYH1663, 260 m, 03-V-2007, *P. Rico, J.C. Cristobal, A. Vicente, A. Guilló & J.L. Villar* (ABH51546). Alicante, campos próximos a Sierra de los Tajos 30SYH0957, 210 m, 20-IV-1998, *E. Camuñas & J.C. Cristobal*. (ABH39056). Elche, Próximo a Sierra de Sancho, 30SYH1142, 90 m, 09-III-1999, *E. Camuñas* (ABH41460). Jijona, Monnegre, Barranco salinas, 30SYH1663, 275 m, 22-IV-1997, *J.C. Cristobal* (ABH33919). Alicante, Cabo Huertas, 30SYH2448, 1 m, 04-V-1997, *E. Camuñas & MB. Crespo* (ABH34309). Jijona, Monnegre, Barranco Salinas, 30SYH1563, 300 m, 26-IV-1997, *J.C. Cristobal* (ABH34012). Denia, Les Deveses, 30SYJ5807, 1 m, 15-III-1997, *M. Signes & J.X. Soler* (MA590335). Elche, Playa del Carabassí, 30SYH174350, 1 m, 26-V-2010, *J.L. Villar* (ABH55442). Cabo de las Huertas, parque arriba de Cala Cantalar, 30SYH253484, 30 m, 13-III-2011, *J.L. Villar & E. Martínez* (ABH57853). Playa de San Juan, junto a edificio Suiza, 30SYH 255492, *J.L. Villar & R.M. García* (ABH57856). Santa Pola, salinas, junto a la torre, 30SYH089289, 1 m, 21-III-2011, *J.L. Villar & I. Aragoneses* (ABH58156). Santa Pola, salinas, 30S YH1029, 1 m, 21-III-2011, *J.L. Villar & I. Aragoneses* (ABH58157, ABH57159). Guardamar del Segura, Desembocadura del Segura, 30SYH053195, 1 m, 21-III-2011, *J.L. Villar & I. Aragoneses* (ABH57854). **Almería**: Cabo de Gata, 3-IV-1876, *E. Hackel* (W). Río Chico, Berja, 30SWF0071, 76 m, 18-III-2006, *M.L. Lendinez, J. Quesada & F.M. Marchal* (JAEN 700428). Pilar de Jaravía, Pulpí, 30SXG1639, 80 m, 18-III-2006, *A. Lahora* (HUAL 22092). Pilar de Jaravía, Pulpí, 30SXG1639, 79 m, 18-III-2006, *J.F. Mota,F.J. Pérez-García & A. Lahora* (HUAL 18130). Vera, Salar de los Carros, 30SXG056203, 3 m, 8-V-2010, *J.L. Villar & E. Martínez* (ABH55342, ABH55343, ABH55344). Salinas de Cabo de Gata, 30SWF684706, 8-V-2010, *J.L. Villar & E. Martínez* (ABH55351). **Granada:** Cúllar, Salado del Margen, 30SWG365672, 840m, 9-V-2010, *J.L. Villar & E. Martínez* (ABH55341, ABH55339). Cúllar, Salado del Margen, 30SWG365664, 840 m, 9-V-2010, *J.L. Villar & E. Martínez* (ABH55340). **Mallorca:** Puerto de Pollensa le long de la routed Alcudia, abords du pré salé, dunes littorales, 2-IV-1977, *J. Duvigneaud* (G159953). **Murcia:** Fortuna, rambla Salada. 100 m, 4-IV-1979, *A. Molina* (G169033). Alhama de Murcia, Los Ventorrillos, 30SHG48, 150 m, 28-III-2006, *M. Cano* (ABH50682).**Tarragona:** Delta del Ebro, frente a Isla del Buda, 31TCF1806, 1 m, 7-V-2009, *J.L. Villar, M.A. Alonso, J.C. Agulló & H. Alvarado* (ABH54332). **Zaragoza:** La salada de Alcañiz, La Sabrosa de Chiprana, 2-V-1887, *Loscos* (G6990/1257). Laguna salada de Chiprana, 30TYL3669, 136 m, 7-V-2009, *J.L. Villar, M.A. Alonso, J.C. Agulló & H. Alvarado* (ABH54330).

Tamarix africana

ALGERIA. Union agricole du Sig, provinced Oran, 1850, *Dulando* (W).Bords de l Oued Biskra, à Biskra, *Balansa 991* (W1889-80151, W1889-320236). Alger, bas-fonds humides au pied des collines du Shael, aus sud de Koléa, 23-III-1960, *A. Dubois & L. Faurel* (W1977-05063). Tizi-Ouzou, El Jecmae, 31SFA1141, 400m, 20-VI-2010, *A. Juan* (ABH56325). FRANCE. Bords de la mer a St.Tropez, 13-4-1861, *Bourgeau* (W).Insula Corsica, in sabulosis maritimis, Ile Rousse, 14-IV.1918, *Mary F. Spencer* (W2009-00736). ITALY. **Sardinia:** Hügel und Küsten s. Alghero, 12.IV-1963, *Krendl* (W1977-19646). Oristano, saladar en Putzultzu, 32TMK489327, 3 m, 20-VI-2009, *J.L. Villar, M.A. Alonso, A. Juan, J.C. Agulló & A. Guilló* (ABH54423). Oristano, Cabras, 32SMK589189, 3m, 21-VI-2009, *J.L. Villar, M.A. Alonso, A. Juan, J.C. Agulló & A. Guilló* (ABH54431, ABH54432). Cagliari, Quartu Santa Elena, 32SNJ1441, 4 m, 24-VI-2009, *J.L. Villar, M.A. Alonso, A. Juan, J.C. Agulló & A. Guilló* (ABH54465, ABH54312, ABH54463). Cagliari, playa en is Canaleddus, 32SNJ312366, 5 m, 24-VI-2009, *J.L. Villar, M.A. Alonso, A. Juan, J.C. Agulló & A. Guilló* (ABH54370). Cagliari, Solanas, 32SNJ377320, 10 m, 24-VI-2009, *J.L. Villar, M.A. Alonso, A. Juan, J.C. Agulló & A. Guilló* (ABH54441, ABH54442). Cagliari, Laguna de Sestu, 32SNJ077536, 55 m, 25-VI-2009, *J.L. Villar, M.A. Alonso, A. Juan, J.C. Agulló & A. Guilló* (ABH55417, ABH56711). Golfo di Cagliari, playa, 32SNJ019337, 2 m, 25-VI-2009, *J.L. Villar, M.A. Alonso, A. Juan, J.C. Agulló & A. Guilló* (ABH55416). Cagliari, rio Chia, 32SMJ899060, 2 m, 25-VI-2009, *J.L. Villar, M.A. Alonso, A. Juan, J.C. Agulló & A. Guilló* (ABH54444). Cagliari, rio Chia, 32SMJ907079, 17 m, 25-VI-2009, *J.L. Villar, M.A. Alonso, A. Juan, J.C. Agulló & A. Guilló* (ABH55360). Cagliari, laguna de Chia, 32SMJ892050, 2 m, 25-VI-2009, *J.L. Villar, M.A. Alonso, A. Juan, J.C. Agulló & A. Guilló* (ABH54443). Cagliari, Sant Antioco, 32SMJ543234, 3 m, 25-VI-2009, *J.L. Villar, M.A. Alonso, A. Juan, J.C. Agulló & A. Guilló* (ABH54366). Oristano, saladar de Santa Giusta, 32SMK645100, 1 m, 26-VI-2009, *J.L. Villar, M.A. Alonso, A. Juan, J.C. Agulló & A. Guilló* (ABH55430, ABH56712). Sassari, Estintino, 32TML356245, 24 m, 26-VI-2009, *J.L. Villar, M.A. Alonso, A. Juan, J.C. Agulló & A. Guilló* (ABH54439). Sassari, Argentiera, 32TML2811, 26-VI-2009, *J.L. Villar, M.A. Alonso, A. Juan, J.C. Agulló & A. Guilló* (ABH54437, ABH54438). Sassari, Lago Baratz, 32TML346032, 26-VI-2009, *J.L. Villar, M.A. Alonso, A. Juan, J.C. Agulló & A. Guilló* (ABH54371). **Sicily:** Plantae siculae, in arenosis Mondello propè Panormum, 26-III-1835, *Huet du Pavillon* (W1889-67485). Selinunte, feuchtestellen un weit der Tempel, 14-IV-1955, *Höpflinger* (W1968-1364). MOROCCO. Beni-Tuzin, bords du rio Kert, 6-V-1934, *Sennen &* Mauricio (W1935-5317, isotypus of *Tamarix mauritii* Sennen). Beni-Tuzin, termas de Rastataf, 9-V-1934, *Sennen & Mauricio* (W). Or, Oujda-Taourirt (Oued Jfrei), 30SWD198231, 325 m, 20-IV-2009, *M.A. Alonso, M.B. Crespo, A. Juan, J.L. Villar & al.* (ABH54445). Proximidades de Debdou, 30SWC006675, 784 m, 20-IV-2009, *M.A. Alonso, M.B. Crespo, A. Juan, J.L. Villar & al.* (ABH54207, ABH54205). TH, carretera de Taza hacia Aknoul, 30SVD533949, 848 m, 21-IV-2009, *M.A. Alonso, M.B. Crespo, A. Juan, J.L. Villar & al.* (ABH54123). TH, Aknoul, 30SVD202307, 925m, 21-IV-2009, *M.A. Alonso, M.B. Crespo, A. Juan, J.L. Villar & al.* (ABH54121). TH, Taza-Guercif, 30SVC328915, 500m, 22-IV-2009, *M.A. Alonso, M.B. Crespo, A. Juan, J.L. Villar & al.* (ABH54191, ABH54192). Carretera costera entre Nador y Al Hoceima, 30SVD876992, 34 m, 23-IV-2009, *M.A. Alonso, M.B. Crespo, A. Juan, J.L. Villar & al.* (ABH54190). Carretera costera entre Nador y Al Hoceima, 30SVD8397, 12 m, 23-IV-2009, *M.A. Alonso, M.B. Crespo, A. Juan, J.L. Villar & al.* (ABH54193, ABH54203). Al Hoceima, 30SVD268951, 25 m, 23-IV-2009, *M.A. Alonso, M.B. Crespo, A. Juan, J.L. Villar & al.* (ABH54193). SPAIN. **Albacete:** In einer sumpfweise nahe E Alcaraz, ca. 700 m, truppweise, 24-V/14-VI-1975, *Polatschek,* (W1976-04119). **Alicante:** Orihuela, Rambla del Trujillao, Río Nacimiento, 30SXG9598, 45 m, 13-III-2008, *P. Rico, M. A. Alonso & al*. (ABH55137). Tibi, entre Xirau y Maigmó, estret roig, junto a carretera de servicio, 30SYH092627, 535 m, 4-V-2009, *J.C. Cristobal* (ABH54301). Alicante, Sierra de los Tajos, Les esmoladores, 30SYH0955, 240 m, 23-III-2007, *L. Serra, J.M: Mondéjar & P. Mateo* (MA784516). San Juan de Alicante, 30SYH22525297, 50 m, 29-III-2011, *J.L. Villar, J.C. Agulló, & E. Martínez* (ABH57862). **Almería:** El Ejido, Balerma, 30SWF097653, 4 m, 9-V-2010, *J.L. Villar & E. Martínez* (ABH55348). **Castellón:** Segorbe, en la rambla seca, V-1918, *Pau 3629* (W1922-15352). **Girona:** Port de la Selva, Cala Tamariua, 31TEG1788, 5 m, 10-IV-2010, *M.B. Crespo & E. Camuñas* (ABH55078). **Granada**: Sierra Nevada zw. Orgiva und Caratauna, 600-700 m, 3-V-1965, *Greuter* (W1966-16337). **Murcia:** Mazarrón, las Chapas, Cañada de Gallego, 30SXG437552, 4 m, 8-V-2010, *J.L. Villar & E. Martínez* (ABH55352). Águilas, Rambla de Minglano, 30SXG213438, 109 m, 8-V-2010, *J.L. Villar & E. Martínez* (ABH55355). **La Rioja:** Logroño, Recajo, sables de l Ebre, 10-V-1923, *Sennen & Elías* (W1926-23534, isotypus of *Tamarix celtiberica* Sennen & Mauricio). **Tarragona:** Cambrils, torrent de Janer, 8-VI-1917, *Sennen 3066* (W1922-15231, isotypus of *Tamarix uncinatifolia* Sennen).**Toledo:** Laguna grande de Villacañas, 30SVJ7285, 650 m, 9-V-2010, *M.D. Vargas & J. Alonso* (ABH55361, ABH55362). **Valencia:** Regn. Valentinum, in arenosis proximis sec. Viam quae ducit ad Cabo S. Anton, 27-IV-1891, *Porta & Kigoiter* (W1892-6724). Villargordo del Cabriel, junto a la carretera, 30SXJ323786, 740 m, 17-V-2010, *J.L. Villar, M.B. Crespo, F. Martínez-Flores & C. Pena* (ABH55366). PORTUGAL. Alto tras os Montes, Mogadouro, Embalse Bemposta, río Douro Internacional, 29TQF1074, 340 m, 14-VI-2010, *M.B. Crespo* (ABH55436). TUNISIA. Tunisien, Oued el Hathob, SW Kairouan, 18-IV-1962, *K. Fitz* (W1979-09956).

Tamarix dalmatica

BOSNIA and HERZEGOVINA. An der Narenta bei Caplijina, V/1892, *F. Fiala* (holotypus PRC 422665, isotypus W 1929-20413, PR). CROATIA. St Stefano pr. Spalato, VI-1872, *Pilcher* (G, 2 vouchers; PR).Dalmacia central, Mündungsebene der Neretva (Posrednica), am linken Neretva-Ufergegenüber von Rogotin (Zwischen Opuzen und Ploçe) nahe Strassenbrücke, 2m, 20-IV-1979, *E. Vitek* (W2003-02919).Dalmacia Central, Slano, 33TYH364407, 16 m, 29-IV-2011, *J.L. Villar & E. Martínez* (ABH58191, ABH58192). Dalmacia central, Omis, 33TXJ376129, 18 m, 30-IV-2011, *J.L. Villar & E. Martínez* (ABH57840). Dalmacia central, Podstrana, 33TXJ283136, 8 m, 30-IV-2011, *J.L. Villar & E. Martínez* (ABH57836). Dalmacia del norte, Sukosan, paseo junto al mar, 33TWJ248777, 1 m, 30-IV-2011, *J.L. Villar & E. Martínez* (ABH58187). MONTENEGRO. Bar, V-1903, *Rohlena* (PR). Bar, al sur de Bar, junto a ctra a Ulcinj, 34TCM432618, 26 m, 27-IV-2011, *J.L. Villar & E. Martínez* (ABH57843). Kotor, Lavsta, Junto a ctra. Budva-Kotor, en llanura aluvial, 34TCM170883, 22m, 27-IV-2011, *J.L. Villar & E. Martínez* (ABH57844, ABH57845). Hercej-Novi, Morinj, desembocadura de río al sur del pueblo, junto al mar, 34TCN070066, 15 m, 28-IV-2011, *J.L. Villar & E. Martínez* (ABH58169, ABH58168).

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TAMARIX HOHENACKERI BUNGE, A NEW RECORD FOR THE FLORA OF MEXICO

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ABSTRACT

Tamarix hohenackeri Bunge is reported here for the first time for the flora of Mexico. It also represents the first record for the American continent. This species, native from Asia, was collected along riversides of the river San Salvador (Ensenada, Baja California). A detailed morphological description of the newly reported taxon is provided, and the taxonomic treatment of *T. hohenackeri* is also discussed. As a result of this study, the presence of six species of the genus *Tamarix* is confirmed for Mexico, and a dichotomous key for the *Tamarix* species in Mexico is presented.

Key words: invasive flora, Mexico, Tamaricaceae, *Tamarix*, taxonomy.

RESUMEN

Se documenta por primera vez la presencia de *Tamarix hohenackeri* Bunge para la flora de México. Se trata, a su vez, de la primera cita para el continente americano. Esta especie, nativa de Asia, ha sido recolectada en los márgenes del río San Salvador (Ensenada, Baja California). Se aporta una descripción morfológica detallada del nuevo taxon citado y se discute, también, su estatus taxonómico. Como resultado del estudio, se indica la presencia de seis especies del género *Tamarix* y además se aporta una clave para la identificación de los representantes de *Tamarix* en México.

Palabras clave: flora invasora, México, Tamaricaceae, *Tamarix*, taxonomía.

INTRODUCTION

Tamarix (Tamaricaceae) is mainly found in Asia, where two main centres of speciation and diversification have been reported (Baum, 1978). The first one would correspond to the Indo-Turanian area, where the oldest species, such as *Tamarix ericoides* Rottl., are mainly located. The second centre is basically placed around the Middle East, extending to the Eastern Mediterranean and Turkey. From both geographical areas, the genus migrated in a southerly and westerly direction towards Africa and Europe, and also in a northerly and easterly direction towards the cold deserts and the Pacific coast of Asia (Baum, 1978).

Most of the vegetative and reproductive morphological characters widely used for the taxonomical identification of the *Tamarix* taxa are rather variable among populations and even within a single individual. This heterogeneity has led to the recognition of a large number of taxa, increasing the taxonomic complexity of this genus. In fact, about 200 taxa have been described since Linnaeus (1753). There is no general consensus on the number of species or on their taxonomic treatment, and consequently between 54 and 90 species are currently recognized (Baum, 1978; Yang and Gaskin, 2007).

The genus *Tamarix* includes trees or shrubs 2-10 m high, branched and mainly glabrous, with a deep root system. Branches are green, reddish brown, dark brown or black. Leaves are alternate, sessile, scale-like, entire, sometimes decurrent, from slightly auriculate to amplexicaul or even vaginate, glabrous, mostly with salt-secreting glands. The inflorescences are racemose, simple or compound, often paniculately branched; and growing on branches of the previous or current year. Flowers are small, tetra or pentamerous and white to pink or purple. Bracts are entire, 1-8 mm length, from sessile to amplexicaul. Sepals vary from triangular-lanceolate to widely ovate; and their lobes are entire or slightly denticulate to dentate. Petals are deciduous or sometimes persistent after anthesis; ovate, elliptic or obovate, and sometimes with an ungiculate or cuneate base. The stamens are 4-15, with filaments inserted on the nectariferous disc. The ovary is mostly conic and with 3-4 styles. Numerous seeds are characterized by an apical sessile hairy pappus.

From an ecological point of view, *Tamarix* species are phreatophytes, which form dense groves growing in ravines, river banks and also in saline soils, mostly located in arid and semi-arid zones. The species have a remarkably high growth rate, reaching their habitual height in a short period of time (Velasco, 2008). Their salt and drought tolerance plus their fast growth, combined with very attractive blooms, have played a key role for the ornamental use of certain *Tamarix* species. Thus, they have also been cultivated to reduce desertification, as wind curtains, or also to stabilize soil in sand dunes (Melgarejo, 2000; Gaskin and Schaal, 2003; Natale et al., 2008).

By the 19th century, some *Tamarix* species were introduced to America and Oceania (Baum, 1967; Di Tomaso, 1998; Stromberg, 1998; Csurhes, 2008; Natale et al., 2008). In the United States, *Tamarix* species have been available in ornamental plant catalogues from the first half of the 19th century, and plant nurseries early offered shipment from the Atlantic coast to any state (Prince and Sons, 1837; Warner Harper, 1903). Since then, some *Tamarix* species have spread to North America and these plants are currently considered as the second worst plant invasion in the United States (Gaskin and Schaal, 2003). As a consequence, much effort has been expended to eradicate the *Tamarix* populations in the United States through national programmes (Anonymous, 2005). Both chemical and mechanical methods have been widely used (Sisneros, 1990), recently complemented by biological control programs (Milbrath et al., 2003).

The taxonomic and morphological complexity of this genus makes the correct identification of the invasive species remarkably difficult. In America, the morphological differentiation among closely similar species, such as *Tamarix ramosissima* Ledeb. and *Tamarix chinensis* Lour., has become notably problematic, due to their resemblance and also because of the frequent presence of hybrid forms, not previously reported in their native areas (Baum, 1967; Gaskin and Schaal, 2003; Gaskin and Kazmer, 2009).

In Mexico, *Tamarix* species were introduced through the United States and also due to commercial plantations (Glenn and Nagler, 2005). However, there are scarce publications focused on the genus *Tamarix* in Mexico. For the time being, five different species have been reported: *Tamarix ramosissima* Ledeb. (*Tamarix pentandra* Pall.), *Tamarix chinensis* Lour., *Tamarix parviflora* DC., *Tamarix gallica* L. and *Tamarix aphylla* (L.) Karst. (Villaseñor et al., 2002; Chambers and Hawkins, 2004; Rebman, 2007). *T. ramosissima* and *T. chinensis* are widely distributed in the western United States, with populations in all of the bordering states with Mexico. In the Mexican territory, these species are abundant in the Lower Colorado, Sonora and Chihuahua deserts, reaching Guaymas (Sonora) and the southern part of the Baja California peninsula (Zamora-Arroyo et al., 2001; Chambers and Hawkins, 2004; Glenn and Nagler, 2005; Rebman, 2007). In the case of *Tamarix parviflora,* it has been reported from California of the United States (Gaskin and Schaal, 2003), and some Mexican locations of Baja California and Baja California Sur (Anonymous, 2011). Populations of *T. gallica* have been mainly stated along the United

States coast of the Gulf of Mexico (Gaskin and Schaal, 2003). There are some records of *T. gallica* for Mexico (Villaseñor et al., 2002), whose reference vouchers could not be reviewed for this study. Finally, *T. aphylla* shows a similar distribution to those of *T. ramosissima* and *T. chinensis* (Glenn and Nagler, 2005). Nevertheless, the distribution of this species in Mexico may be larger since other populations have been also identified in Baja California (pers. obs.) and in other southern locations such as "El Tule", near Oaxaca.

Field investigations and herbarium revisions carried out in Mexico identified samples that do not correspond to any of the formerly mentioned *Tamarix* taxa. Hence, a new record for the Mexican flora is given here.

MATERIALS AND METHODS

Plant material was collected in Baja California during the spring of 2010, and it is conserved at the herbarium ABH (University of Alicante, Spain). For the species identification and morphological characterization, different monographs of the genus *Tamarix* were consulted (Baum, 1978; Zohary, 1987; Yang and Gaskin, 2007). In addition, herbarium vouchers from BCMEX, G, K, MA, MO, PRC, PR, VAL and W (Thiers, 2011) were also examined. The abbreviations of author names follow those proposed by Brummitt and Powell (1992), amended by the IPNI (2012). Plant images were taken using Pentax K200D reflex digital camera with Pentax D FA Macro 100mm F2.8 WR.

RESULTS AND DISCUSSION

The species *Tamarix hohenackeri* is reported from Mexico for the first time, on the basis of plant material collected beside the San Salvador river (Ensenada, Baja California) (Fig. 1, Annex). This *Tamarix* population grows along both sides of the river, forming a long belt. Besides, herbaria reference works allowed us to find a voucher from Colorado (United States) in the Missouri herbarium (MO04808092), which also corresponds to *T. hohenackeri* (Annex). Therefore, this voucher, originally identified as *T. parviflora*, may represent the first record of the species for the American continent.

The following description of *Tamarix hohenackeri* is based on the observations of the herbarium material observed.

Fig. 1. Image of a specimen of *T. hohenackeri* from Mexico. A. general view of the herbarium voucher (ABH57398); B. detail of inflorescence; 1. apical bracts; 2. fasciculate racemes; 3. basal bracts.

Tamarix hohenackeri Bunge, Tentamen, p. 44 (1852).

Tree, up to 5 m tall, entirely glabrous. Leaves ovate-triangular to lanceolate, acute, with a decurrent narrow base, sometimes slightly auriculate, 1.5-3.0 mm long. Inflorescences composed mostly of fasciculate arranged racemes, placed in spike-like panicles (not branched). Racemes 3.0-8.0(11.0) cm long, (5.0)5.5-6.0 mm wide, on short peduncles (3.0-10.0 mm long), naked or with a few bracts; rachis glabrous. Bracts of the racemes 1.5-3.0 mm long; lowermost bracts oblong and obtuse, wider and shorter than the narrowly triangular and acute uppermost bracts; bract length sub-equaling pedicel length at the lower part of the racemes to sub-equaling or slightly exceeding calyx length at the apex of the inflorescences. Pedicels 0.5-1.75(3.0) mm long, usually longer in the lower part of the racemes, occasionally with 1-3 small secondary bracts. Sepals 5 (rarely 4), ovate, usually acute, with narrow hyaline margin, 1.0-1.3(1.5) mm long, 0.6-0.8 mm wide. Petals 5, white or yellowish to pink, persistent, ovate-oblong to oblong, or widely elliptic, slightly emarginated, sometimes slightly keeled, 1.8-2.75 mm long, 1.0-2.0 mm wide. Stamens 5 (rarely 6), inserted between the lobes of the nectariferous disc; additional filaments inserted on the lobes. Anthers mostly not apiculate. Ovary always with 3 styles. Fruit 3-4 mm long.

The taxonomic placement of *T. hohenackeri* is not totally resolved, because this species was considered by Baum (1978) as a synonym of *T. smyrnensis* Bunge. This taxonomical treatment is especially relevant, since his monograph is a world-wide reference for the genus *Tamarix*. However, both taxa were originally described as two independent species (Bunge, 1852). Other authors as Yang and Gaskin (2007) and certain Asian botanists (e.g. N. Lachashvili, in sched. (W2008-21042); Belolipov and Haydarov, in sched. (MO6047301)] have also recognized *T. hohenackeri* as a species independent from *T. smyrnensis*. According to our data, there are enough morphological differences supporting the idea that the synonymization of *T. hohenackeri* into *T. smyrnensis* might not be fully appropriate. These morphological differences have not been only based on bibliographical data (Bunge, 1852; Yang and Gaskin, 2007), but also on the detailed study of herbarium vouchers of *T. hohenackeri* and *T. smyrnensis*, including the type material of both species (see Annex). The main vegetative and reproductive morphological differences between *T. hohenackeri* and *T. smyrnensis* are shown in Table 1. The most useful character to discriminate among these species corresponds to the fasciculate placement of racemes and their size, although the size and shape of bracts, sepals and petals are also essential for their accurate identification.

Table 1. Morphological comparison between *T. hohenackeri* and *T. smyrnensis*.

	T. hohenackeri Bunge	*T. smyrnensis* Bunge
Raceme disposition	in spike-shaped panicles, solitary or fasciculate. Racemes pedunculate and laxly flowered	in panicles compound at their base. Racemes sessile and densely flowered
Raceme length (mm)	30.0-80.0	8.5-25.0
Bract shape	short oblong (at lower part of racemes) to narrowly triangular (at upper part of racemes)	narrow triangular-lanceolate, acute
Bract length (mm)	1.5-3.0	1.0-2.0(3.0)
Bract-flower ratio	equaling pedicel (at lower part of racemes), almost equaling or slightly exceeding calyx (at the upper part of racemes)	almost equaling or slightly exceeding calyx (at lower part of the racemes)
Pedicel length (mm)	0.5-1.75(3.0)	subsessile (≤ 0.5)
Sepal length (mm)	1.0-1.3(1.5)	0.7-1.0
Sepal shape	ovate, acute, with hyaline margin	ovate-lanceolate, acute, with hyaline margin
Petal size: length x width (mm)	1.8-2.75 x 1.0-2.0	1.2-1.9 x 1.2-1.6
Petal shape	ovate-oblong to oblong, sometimes elliptic, slightly emarginated. Sometimes slightly keeled	suborbicular-elliptic, variable from slightly ovate to slightly obovate, with the lower half clearly carinate-gibose

The native distribution area of *Tamarix hohenackeri* extends, at least, from the eastern Black Sea to Mongolia, central Asia and south-western Asia (Yang and Gaskin, 2007). There it is in contact with two closely related species, *T. ramosissima* and *T. austromongolica* Nakai. It is highly probable that *T. hohenackeri* was introduced in North America by the 19th or early 20th century for ornamental purposes, but was confused or intermixed with other similar ornamental species such as *T. ramosissima.* The distribution area of *T. hohenackeri* in North America could be wider than expected, since some additional vouchers of *T. hohenackeri* from the United States and Mexico could be misidentified as other species, such as *T. chinensis*, *T. ramosissima* and even *T. parviflora*.

With this new record, and including the previously available data (Zamora-Arroyo et al., 2001; Villaseñor et al., 2002; Glenn and Nagler, 2005), six *Tamarix* species are part of the aloctonous flora of Mexico: *Tamarix aphylla, T. gallica, T.*

parviflora, T. hohenackeri, T. ramosissima and *T. chinensis,* as well as the hybrids between the two latter species. Among them, *T. aphylla*, *T. hohenackeri*, *T. ramosissima* and *T. chinensis* were newly collected during the fieldwork conducted in April 2010, from different locations of Baja California (see Annex).

Below, a dichotomous key is presented for the six species of *Tamarix* reported for Mexico. The main morphological features are focused on leaf shape and insertion, raceme length and its disposition, bract shape, relative bract length, number, shape and size of the perianth sections and the site of insertion of the staminal filaments on the nectariferous disc.

Dichotomous key for the identification of *Tamarix* species in Mexico

1 Leaves vaginate .... *T. aphylla*
1 Leaves sessile with a narrow base, sometimes slightly auriculate at their lower half but never vaginate 2
2 Flowers tetramerous .... *T. parviflora*
2 Flowers pentamerous 3
3 Staminal filaments arising from the apex of the nectariferous disc lobes .... *T. gallica*
3 Staminal filaments arising between the nectariferous disc lobes 4
4 Inflorescences with both solitary and fasciculate racemes (groups from 2 to 4) .... *T. hohenackeri*
4 Inflorescences with racemes always solitary 5
5 Racemes 5-7 mm wide. Bracts equal or slightly longer than the pedicel. Pedicels as long as sepals, at least the lowermost pedicels of the raceme .... *T. chinensis*
5 Racemes 3-5 mm wide. Bracts equal or slightly longer than the calyx. Pedicel length always shorter than that of the sepals ... *T. ramosissima*

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LITERATURE CITED

Anonymous. 2005. Program for biological control of saltcedar (*Tamarix* spp.) in thirteen States. Environmental Assessment. Animal and Plant Health Inspection Service, United States Department of Agriculture, Western Region. Fort Collins, USA. 56 pp.

Anonymous. 2011. *Tamarix parviflora*, IEB 116120, 2 registers, CIBNOR-HCIB 11988, 2 registers. Unidad de Coordinación de Global Biodiversity Information Facility. Madrid, Spain. http://data.gbif.org/species/2874706/ accessed on 13-6-2011.

Baum, B. 1967. Introduced and naturalized tamarisks in the United States and Canada. Baileya 15: 19-25.

Baum, B. 1978. The genus *Tamarix*. Israel Academy of Sciences and Humanities. Jerusalem, Israel. 209 pp.

Brummitt, R. K. and C. E. Powell. 1992. Authors of plant names. Royal Botanic Gardens. Kew, UK. 732 pp.

Bunge, A. 1852. Tentamen generis *Tamaricum* species accuratius definiendi. Dorpati, Estonia. 83 pp.

Chambers, N. and T. O. Hawkins. 2004. Plantas invasoras del desierto sonorense: una guía de campo. Sonoran Institute, Environmental Education Exchange y National Birds and Wildlife Foundation. Tucson, USA. 60 pp.

Csurhes, S. 2008. Pest plant risk assessment: Athel pine *Tamarix* spp. The State of Queensland, Department of Primary Industries and Fisheries. Brisbane, Australia. 10 pp.

Di Tomaso, J. 1998. Impact, biology and ecology of saltcedar (*Tamarix* sp.) in southwestern United States. Weed Technol. 12: 326-336.

Gaskin, J. F. and D. J. Kazmer. 2009. Introgression between invasive saltcedars (*Tamarix chinensis* and *T. ramosissima*) in USA. Biol. Invasions 11: 1121-1130.

Gaskin, J. F. and B. Schaal. 2003. Molecular phylogenetic investigation of U.S. invasive *Tamarix*. Syst. Bot. 28(1): 86-95.

Glenn, E. P. and P. L. Nagler. 2005. Comparative ecophysiology of *Tamarix ramosissima* and native trees in western U.S. riparian zones. J. Arid Environ. 61: 419-446.

Linnaeus, C. 1753. Species plantarum, exhibentes plantas rite cognitas, ad genera relatas, cum differentiis specificis, nominibus trivialibus, synonymis selectis, locis natalibus, secundum sistema sexuale digestas. Vol. I. Holmiae Impensis Laurentii. Salvii. Stockholm, Sweden. 560 pp.

Melgarejo, P. 2000. Tratado de fruticultura para zonas áridas y semiáridas. Vol. 1. Ed. Mundi-Prensa. Madrid, Spain. 382 pp.

Milbrath, L. R., C. J. DeLoach and A. E. Knutson. 2003. Initial results of biological control of saltcedar (*Tamarix* spp.) in the United States. Proceedings of the Symposium, Saltcedar and Water Resources in the West. Texas Cooperative Extension. San Angelo, USA. 135-141.

Natale, E. S., J. F. Gaskin, S. M. Zalba, M. Ceballos and H. E. Reinoso. 2008. Especies del género *Tamarix* (Tamaricaceae) invadiendo ambientes naturales en Argentina. Bol. Soc. Arg. Bot. 43(1-2): 137-145.

Prince, W. and Sons. 1837. Annual catalogue of trees and plants cultivated at the Linnean Botanic Garden and Nurseries. New York, USA. pp. 2-4, 50.

Rebman, J. P. (comp.). 2007. The flora of Cedros Island, Mexico. San Diego Natural History Museum, Biodiversity Research Center of the Californias Botany. San Diego, USA. www.bajaflora.org/Floras/CedrosIsland.htm (accessed 10-6-2011).

Sisneros, D. 1990. Vegetation management study: Lower Colorado River. Appendix II: Herbicide Analysis. USDI Bureau of Reclamation, Report. Denver, USA. 56 pp.

Stromberg, J. 1998. Dynamics of Fremont cottonwood (*Populus fremontii*) and saltcedar (*Tamarix chinensis*) populations along the San Pedro River, Arizona. J. Arid Environ. 40: 133-155.

The International Plant Names Index. 2012. Published on the Internet http://www.ipni.org (accessed 3-XII-2012).

Thiers, B. 2011. continuously updated. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/ih/

Velasco, J. 2008. Manual para la restauración de riberas en la cuenca del río Segura. Confederación Hidrográfica del Segura. San Vicente del Raspeig, Spain. 227 pp.

Villaseñor, J. L., J. Rzedowski and F. J. Espinosa. 2002. In: Espinosa, F. J. Malezas introducidas en México. Universidad Nacional Autónoma de México, Centro de Investigaciones en Ecosistemas. Informe final SNIB-CONABIO proyecto No. U024. Morelia, México. 25 pp. http://www.conabio.gob.mx/institucion/proyectos/resultados/InfU024.pdf (accessed 3-XII-2012).

Warner Harper, W. 1903. Andorra hand-book of trees and shrubs. Andorra Nurseries. Philadelphia, USA. pp. 5, 98.

Yang, Q. and J. Gaskin. 2007. *Tamarix*. In: Zhengyi, W. and P. H. Raven (eds.). Flora of China 13: Science Press, Beijing and Missouri Botanical Garden Press. St. Louis, USA. pp. 59-65.

Zamora-Arroyo, F., P. L. Nagler, M. Briggs, D. Radtke, H. Rodriguez, J. García, C. Valdés, A. Huete and E. P. Glenn. 2001. Regeneration of native trees in response to flood releases from the United States into the delta of the Colorado River, Mexico. J. Arid Environ. 49(1): 49-64.

Zohary, M. 1987. *Tamarix* L. Flora Palestina 2: 350-362.

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ANNEX

Selected material:

T. aphylla. MEXICO. Baja California: Mexicali, Laguna Salada, junto a carr. Tecate - Mexicali, 11SPS177042 (32º34'8,4" N-115º44'46,1" W), 0 m, 18-4-2010, Leg. J.L. Villar, M.A. Alonso, A. Juan (ABH55929); Oaxaca: El Tule, 14QQP5286 (17º2'53,7" N-96º38'1,6" W), 1560 m, 20-4-2010, Leg. A. Juan (ABH56707); Sonora: Región del Pinacate, rancho entre dunas cercanas a la estación de ferrocarril Gustavo Sotelo, 16-9-1980. Leg. M. Equihua, J. López-Portillo, E, Ezcurra, Det. R.S. Felger (BCMEX005453).

T. chinensis. MEXICO. Baja California: Ensenada, carr. Ensenada - Maniadero, 11RNR350143 (31º45'49,2" N-116º37'49,4" W), 100 m, 15-4-2010, Leg. J.L. Villar, M.A. Alonso (ABH57396); Ensenada, carr. Ensenada - Maniadero, 11RNR350143 (31º45'49,2" N-116º37'49,4" W), 100 m, 15-4-2010, Leg. J.L. Villar, M.A. Alonso (ABH57397); Ensenada, Estero Beach, carr. Ensenada - La Bufadora, 11RNR355088 (31º42'50,5" N-116º37'31,2" W), 0 m, 15-4-2010, Leg. J.L. Villar, M.A. Alonso (ABH57461); La Angostura, 11RNQ6475 (31º24'28,3" N-116º19'36,2" W), 172 m, 24-4-2010, Leg. J.L. Villar, M.A. Alonso (ABH55928).

T. hohenackeri. ARMENIA. Syunik province, SSE Sisian, Between Darbas and Ltsen, 14-6-2007, Leg. M. Oganesian, Ter-Voskanyan, E. Vitek, Det. J.L. Villar (W2010-02963). REPUBLIC OF GEORGIA. Ad rivulos pr. Helenendorf, 1838, Hohenacker (W1889-880289, W0227453, PRC452707, 452708, G-Boiss, isolectotypes); Prope pag. Karajazy, 21-5-1908, Leg. Koenig (W1940-22731, W1954-4398); Lagodechi Reserve, 41º44'25" N 45º13'35" E, 15-6-1995, Leg. J. Gaskin (MO5568882, *ut T. smyrnensis*); East Georgia, Iori Table land, Vashlovani reserve, 25-5-2002, Leg. K. Ishagashvili, N. Lachashvili (W2009-06712, *ut T. smyrnensis*); East Georgia, Dedoplistskaro district, Iori plateau, Lekistskali gorge, ca. 41º12'36" N, 46º32'31" E, 14-3-2006, Leg. Nikoloz Lachashvili (W2008-21042). IRAN. South 7 km west of Dahst along Qez-qaleh valley, 18-5-1995, Leg. H. Akhani (W1999-07675, *ut T. ramosissima*). MEXICO. Baja California: Ensenada, Maniadero, Río San Salvador, 11R587235243, 803 m. 16-4-2010, Leg. J.L. Villar, M.A. Alonso, A. Juan (ABH57398). UNITED STATES OF AMERICA. Colorado: Mesa County, along frontage road to Interstate 70, at exit to DeBeque, 39°19'24” N, 108°12'00” W, 4919 ft, 2-6-2005, Leg. Robert M. King, Robert M. Garvey (MO04808092, *ut T. parviflora*). UZBEKISTAN: Tashkent, Bekabaddistrict, 40º31.82' N-69º5.00' E, Leg. Igor Belolipov, Hislat Haydarov (MO6047301).

T. ramosissima. MEXICO: Baja California: Playas de San Felipe, 11RQQ010508 (31º10'26,4" N-114º53'27,3" W), 0 m, 16-4-2010, Leg. J.L. Villar, M.A. Alonso (ABH57459); Mexicali, Laguna Salada, junto a carr. Tecate - Mexicali, 11SPS177042 (32º34'8,4" N-115º44'46,1" W), 0 m, 18-4-2010, Leg. J.L. Villar, M.A. Alonso, A. Juan (ABH57462); Isla Ángel de la Guarda, East side of island, in middle of narrow dry arroyo, 29º27'579" N-113º24'830" W, 85 feet, 3-2006, Leg. P. García (BCMEX0013719); Mexicali, Lower Rio Colorado valley, 32º13'48.4" N-115º02'55.8" W, 10 m, 17-3-2006, Leg. Richard S. Felger, K, Reichhard, E. Soto-Montoya (BCMEX013156); Ensenada, Ctra Ensenada - San Felipe, 31º10' N-115º19' W, 21-7-1980, Leg. A. Díaz (BCMEX0010101, *ut T. pentandra*); La

Annex. Continuation.

Bocana, 31º33' N-116º10' W, 30-9-1982, Leg. Ortiz, Arroyo, Mora (BCMEX005512, *ut T. pentandra*); Ensenada, Arroyo, zona adentrada a la presa, 31º53' N-116º35' W, 15-6-1980, Leg. Gálvez, López, Héctor, Det. Gálvez (BCMEX000166, *ut T. pentandra*); Ensenada, Agua Viva, carr. Ojos Negros, 31º54' N-116º26' W, 3-7-1981, Leg. V.M. Preciado (BCMEX000119, *ut T. pentandra*); Ensenada, 31º53' N-116º40' W, 21-7-1980, Leg. L. Heredia (BCMEX000037, *ut T. pentandra*); Isla Cedros, Casa de Piedra del Gran Cañón, 28º10' N-115º15' W, 50 m, 27-12-1986, Leg. Hugo Cota (BCMEX003223, *ut T. pentandra*); South of Santa Catarina, near coast south of Punta Canoas and Puerto Mujeres, Cañon Lázaro, 29º24'69" N-115º02'22" W, 20-150 m, 17-4-1997, Leg. J. Rebman, J. Merzbacher, T. Demeré (BCMEX009904); Along the Ensenada to Tecate highway, about 28.5.miles north of Ensenada, near Predio Belen, North of Guadalupe, along cold water stream, 32º11' N-116º29' W, 500 m, Leg. R.F. Thorne, W. Wisura, W. Steinmetz (BCMEX001393); Sonora: Hermosillo, La Victoria, 29º06'49.219" N-110º52'17.786" W, 310 m, 25-5-1996, Leg. R. Palafox, Det. O.J. Soto (BCMEX003545, *ut T. pentandra*).

T. smyrnensis. CYPRUS. Cap Arnaouk, près polis, Leg. M. Haradjian (MO1621122); Ad alveos prope litora maris in viciniis Kuklia Amathus et aliis locis, 5-1862, Leg. Kotschy (W, G-Boiss). GREECE. Rhodes. Bords des torrents près Salakos, 31-5-1870, Leg. Bourgeau (W1889-150434, G-Boiss); Ad ripas Penes prope Larissam, 2-8-1882, Leg. Heldreich (G); Etolias-Akaranias, Mesolongui, coast by the salt works, c. 5 km NW of Mesolongi, clayey marsh, 9-6-1997, Leg. Nielsen (G). TURKEY. In arenosis humidis Smyrnae, april-majo 1827, Leg. Fleischer (W1889-320298, PRC452718, PRC452719, PRC452720 isotypes); Smyrne, Leg. Monbret (W1889-223513); Marais d´eau saumatre situès entre la Papeterie et la mer, près de Smyrne, 1854, Leg. Balansa (MO5475118, W1889-81992, W1889-80859); C4 Icel. 12 km S Mut, 200 m, 6-6-1966, Leg. F. Sorger (W1990-07003); Pamukkale E C2 Denizli, 400 m, 28-6-1967, Leg. F. Sorger (W1990-06983); Gök Pinar. B6 Sivas, 1600 m, 9-9-1977, Leg. F. Sorger (W1990-06992); 4 km S Uluabat, Damm A2 Bursa, 27-6-1977, Leg. F. Sorger (W1990-06989).

Artículo 6

Villar J. L., Alonso M. A., Vicente A., Juan A. & Crespo M. B. 2014. The genus *Tamarix* (*Tamaricaceae*) in Crete (Greece). *Willdenowia* 44: 321-326.

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The genus *Tamarix* (*Tamaricaceae*) in Crete (Greece)

Abstract

Villar J. L., Alonso M. A., Vicente A., Juan A. & Crespo M. B.: The genus *Tamarix* (*Tamaricaceae*) in Crete (Greece). – Willdenowia 44: 321–326. 2014. – Version of record first published online on 30 October 2014 ahead of inclusion in December 2014 issue; ISSN 1868-6397; © 2014 BGBM Berlin-Dahlem.

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A report on the genus *Tamarix* (*Tamaricaceae*) in Crete is provided. The previously recorded taxa are compared with new collections made on the island and with vouchers found at different herbaria. Three species were fully confirmed: *T. nilotica* and *T. parviflora*, collected in the field, and *T. smyrnensis*, found only in herbarium vouchers. The other previously reported taxa, *T. dalmatica*, *T. hampeana*, *T. pallasii* and *T. tetrandra* were not found; *T. dalmatica* was erroneously reported, the record of *T. hampeana* represents a fourth species but its identity requires further study, records of *T. pallasii* are probably misidentifications of *T. nilotica* and/or *T. smyrnensis*, and the record of *T. tetrandra* probably refers to *T. parviflora*. The presence of *T. nilotica* is documented, confirming that it has been historically overlooked and mistaken for *T. smyrnensis*. A morphological comparison between *T. nilotica* and *T. smyrnensis* is provided in order to avoid further confusion and misidentifications. A dichotomous key for the *Tamarix* species reported in Crete is provided.

Additional key words: distribution, Aegean Islands, taxonomy, Mediterranean flora

Introduction

The taxonomy of the genus *Tamarix* L. (*Tamaricaceae*) is notoriously complex (Bunge 1852; Zohary 1972; Baum 1978). It is thought to contain between 54 and 90 species (Zohary 1972; Baum 1978; Yang & Gaskin 2007), although about 200 taxa, including species, subspecies, varieties and forms, have been described since Linnaeus (1753) named the genus. According to Baum (1978: 178–179), *Tamarix* shows two main speciation centres, one in the Indo-Turanian region and the other in the Middle East. From there, the genus migrated south and west towards Africa and Europe, and also north and east to the cold deserts and the Pacific coast of Asia (Baum 1978).

The island of Crete is located in the Aegean Sea, 97 km from continental Greece, 179 km from continental Turkey and 287 km from the NE coast of Libya. *Tamarix* is widely distributed in Crete, particularly along the coastline, in ravines and in the lower courses of rivers. Seven species have been reported until now: *T. dalmatica* B. R. Baum, *T. hampeana* Boiss. & Heldr., *T. nilotica* (Ehrenb.) Bunge, *T. pallasii* Desv., *T. parviflora* DC., *T. smyrnensis* Bunge and *T. tetrandra* Pall. ex M. Bieb.

The first report of the genus *Tamarix* in Crete was *T. cretica* Bunge, which was described (Bunge 1852: 33) from plants collected by Sieber at "Armiro". However, *T. cretica* was soon synonymized to *T. parviflora* (Boissier 1867: 769), a synonymization that is now widely accepted (Baum 1968: 1978). *Tamarix pallasii* was reported by Boissier (1867: 773) and, based on material determined by Boissier, Raulin (1869: 419). In the first printed version of his monograph of the genus, Baum (1966: 122)

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only reported the presence of *T. parviflora* in Crete. However, two years later, in his Flora europaea account, Baum (1968: 293) added *T. dalmatica* and *T. smyrnensis*. Due to the lack of records, the occurrence of *T. dalmatica* was rejected by Greuter (1974: 139), who was followed by Dimopoulos & al. (2013: 143) and by most other publications. It should be noted that the correct identification of *T. dalmatica* has been regarded as troublesome in the W Mediterranean region (Villar & al. 2012: 254). There also exists a record of *T. hampeana* in the Chania region (Turland 2010, determined by B. R. Baum). Recently, Dimopoulos & al. (2013: 143) have cited *T. nilotica* and *T. tetrandra* as occurring in Crete. The *T. tetrandra* record probably follows Zieliński's (1994: 34) treatment of *T. parviflora* as a synonym of *T. tetrandra*. Jahn & al. (2014: 295) questioned this record and called for further revision. In the present study, we have still considered both species as separate. Among all records, *T. parviflora* and *T. smyrnensis* were thought to be by far the most abundant species in Crete (cf. Fielding & Turland 2005: 414).

During two field trips to Crete, in July and October of 2009, a number of *Tamarix* specimens were collected throughout the island, but some did not match with any of the previously reported taxa. The aim of this study was to clarify the identity of those specimens, and to provide a tool to easily identify the species present on the island.

Material and methods

The 22 specimens collected during the fieldwork were prepared, databased and stored at the Herbarium of the University of Alicante (ABH), Spain. Moreover, several international herbaria were visited or consulted (B, G, K, MA, MO, MPU, P, PR, PRC, VAL and W; herbarium codes according to Thiers, 2008+). About 180 vouchers, belonging to the reported species in Crete, were studied in order to properly clarify the identity of the specimens collected. Different taxonomic studies and dichotomous keys were also consulted to obtain accurate identifications (Bunge 1852; Baum 1968; 1978; Zohary 1972; Villar & al. 2014). The main studied material of the species found in Crete is listed in the Appendix. Detailed images were obtained using a binocular motorized microscope (Olympus SZX16) with adapted digital camera.

Results

After a detailed morphological study of the 22 collected specimens, twelve were identified as *Tamarix nilotica*, seven as *T. parviflora*, and three remained unclear, although their scarce remaining floral features suggested some resemblance to *T. africana* Poir. At the different herbaria visited, the following species were recognized among those vouchers collected in Crete: *T. nilotica* (as *T. pallasii* and *T. smyrnensis*), *T. parviflora*, and *T. smyrnensis* (as *T. pallasii*). The first record of *T. parviflora* (as *T. cretica*) corresponds to Sieber's collection at "Armiro", which is the type material of *T. cretica*. The oldest, and the only, herbarium vouchers of *T. smyrnensis* we found from Crete belong to the collection *Raulin 618* from 1845 (G! and P!), first identified as *T. pallasii* (probably by Boissier) and as *T. smyrnensis* by Bunge, respectively. On the other hand, the oldest *T. nilotica* specimens we found from Crete are *Greuter* collections from 1966 (G! and W!), which were identified as *T. pallasii* and stored as *T. smyrnensis.*

Among all samples and records, the presence of *Tamarix nilotica* was only reported recently (Dimopoulos & al. 2013: 143), but no explicit reference to any voucher was made. According to Strid (pers. comm. 2014), the entry in Dimopoulos & al. (2013) is based on the following specimen: Greece, Kriti, Nomos of Lasithi, Eparchia of Mirabello: peninsula of Spinalonga, 35°16'N, 25°45'E, 1 Aug 1973, *Stamatiadou 17391* (ATH); conf. J. Zieliński. Actually, according to our observations, it is widely distributed in Crete. It is easily found growing wild on coastal salt marshes (e.g. Aposelemis, Kouremenos bay), as well as planted in most of the coastal villages and towns (eg. Paleochora, Tris Ekklisies). Among the species reported from Crete, the most similar to *T. nilotica* is clearly *T. smyrnensis.* These two species show similarities in their general morphology and they resemble each other in their general aspect. They both produce racemes of equivalent size, arranged on terminal compound panicles. In addition, they are both pentamerous-flowered species with white or whitish petals, and are both also pentandrous, with the staminal filaments inserted between the nectariferous disk lobes. However, there are some notable differential characters (Fig. 1), which are to be observed to avoid confusion. The leaves (Fig. 1D & E) of *T. nilotica* are broad at their base, ampexicaul or subamplexicaul in their lower half, with deep and numerous salt glands on their surface, whereas *T. smyrnensis* presents lanceolate leaves with a narrow and decurrent base, notably less glandular (Fig. 1A & B). These differences are maintained throughout the complete leaf development, from young to old stages. The sepals of *T. nilotica* show some morphological variation through the natural distribution area of the species. Nevertheless, the specimens growing in Crete seem to be quite stable in presenting ovate-orbicular, obtuse-tipped sepals, whereas *T. smyrnensis* shows ovate to lanceolate, acute-tipped sepals. *Tamarix nilotica* shows elliptic petals, deciduous at the fruiting stage, whereas *T. smyrnensis* has broadly elliptic to ovate petals, characteristically gibbous keeled, or at least with a rougher and coloured central part, persistent after anthesis. Finally, the phenology of both species differs notably: *T. nilotica* flowers essentially at late summer and autumn, whereas *T. smyrnensis* has its main flowering period in late winter and spring. Although *Tamarix* species are able to show secondary flowering periods, they tend to be weaker and

Fig. 1. A–C: *Tamarix smyrnensis* – A: older leaves; B: recent leaves; C: petals. – D–F: *Tamarix nilotica* – D: older leaves; E: recent leaves; F: petals. – Scale bars = 1 mm. – A & B: *Yaprak 2007-011* (ANK); C: *J. Kashefi* (MO); D & F: *Villar & Vicente* (ABH54325); E: *Villar & Vicente* (ABH54323).

less coordinated with the surrounding individuals than the main flowering periods.

Discussion

The previously reported geographic distributions of both taxa could have played a key role in the identification of *T. nilotica* specimens as *T. smyrnensis*. According to Baum (1966; 1978), *T. nilotica* is native to Lebanon, Israel, Egypt, Sudan, Somalia and Kenya. *Tamarix smyrnensis* is supposed to be distributed in Romania, Bulgaria, Greece, Turkey, Cyprus, Syria, Lebanon, Israel, Russia, Georgia, Turkmenistan, Iraq, Iran and Afghanistan (Baum 1966, 1978). However, the most eastern localities of *T. smyrnensis* may correspond to *T. hohenackeri* Bunge, which we do not recognize as a synonym of *T. smyrnensis* (Villar & al. 2014). Therefore, we consider that the main distribution area for *T. smyrnensis* is found in the Turkish and Greek continental coasts, making its presence in Crete easily predictable.

Below we briefly discuss the presence of each of the previously reported taxa.

Tamarix dalmatica B. R. Baum, Monogr. Rev. Gen. Tamarix: 100, 180. 1966.

No specimen of *Tamarix dalmatica* was found in the field or in the herbaria visited. Baum (1968) made no mention of a precise location or a concrete voucher and no other occurrence has been reported since then. In addition, Greuter (1974: 139) and Dimopoulos & al. (2013: 298) considered this species as erroneously reported from Crete. Accordingly, the presence of *T. dalmatica* has to be discarded.

Tamarix hampeana Boiss. & Heldr. in Boiss., Diagn. Pl. Orient., ser. 1, 10: 8. 1849.

We examined the sample on which the record of *Tamarix hampeana* (Turland 2010) was based (*Turland 1778 & Bareka*), and it corresponds with our three samples collected at the same location (see Appendix), which we found difficult to identify, although they showed some resemblance to *T. africana*. However the morphology of these specimens shows certain peculiarities, and detailed studies are being undertaken in order to better clarify their taxonomic identity.

Tamarix nilotica (Ehrenb.) Bunge, Tent. Gen. Tamar.: 54. 1852 ≡ *T. gallica* var. *nilotica* Ehrenb. in Linnaea 2: 269. 1827.
? *Tamarix pallasii* auct. non Desv.

The previous data suggest that *Tamarix nilotica* has been overlooked and confused with *T. smyrnensis*. The existence of the collection *Raulin 618* confirms the presence in Crete of *T. smyrnensis*, and suggests that both species coexist there. The reported presence of *T. smyrnensis* is likely to have led to the misidentification of *T. nilotica*, due to the general resemblance of these species to each other.

It remains doubtful whether *Tamarix nilotica* can be considered native or introduced to Crete, although some trees show big, wide trunks suggesting that their presence in the island goes further back than Greuter's 1966 collection. As can be seen in the Appendix, *T. nilotica* is also present in the East Aegean islands (Samos, Patmos, Rhodes), and it is also reported for two other regions of Greece, the Ionian Islands and the West Aegean Islands (Dimopoulos & al. 2013: 143). Therefore, further research would be needed to date its previously known distribution, or to clarify if its natural populations extend more than expected towards S Anatolia and the Aegean coasts.

Tamarix pallasii Desv. in Ann. Sci. Nat. (Paris) 4: 349. 1825.

Boissier's *Tamarix pallasii* could correspond to *T. smyrnensis*, as could many of the varieties of *T. pallasii* described by Bunge (1852; Baum 1978: 44). Indeed, the oldest Cretan specimens of *T. smyrnensis* – and *T. nilotica* – were initially identified as *T. pallasii.* This indicates that the presence of *T. pallasii* in Crete is doubtful, and that the name has probably been applied to specimens of *T. nilotica* and/or *T. smyrnensis.*

Tamarix parviflora DC., Prodr. 3: 97. 1828.
= *Tamarix cretica* Bunge, Tent. Gen. Tamar.: 33. 1852.
? *Tamarix tetrandra* auct. non Pall. ex M. Bieb.

Beyond any doubt, *Tamarix parviflora* is abundantly present in Crete, *T. cretica* being accepted as a synonym.

Tamarix smyrnensis Bunge, Tent. Gen. Tamar.: 53. 1852.
? *Tamarix pallasii* auct. non Desv.

The presence of *Tamarix smyrnensis* in Crete is confirmed. However, it seems clear that its abundance has been overestimated, as *T. nilotica* specimens were commonly identified as *T. smyrnensis*. Nonetheless, having conducted the fieldwork in July and October, we cannot be sure of the real abundance of *T. smyrnensis.* Spring surveys would be needed in order to clarify if it is widely distributed or just sporadic, as the only specimens found are those belonging to the collection *Raulin 618*.

Tamarix tetrandra Pall. ex M. Bieb, Fl. Taur.-Caucas. 1: 247. 1808.

The recent record of *Tamarix tetrandra* (Dimopoulos & al., 2013: 143) probably arises from Zieliński's (1994: 34) treatment of *T. parviflora* as a synonym of *T. tetrandra.* However, this synonymization still needs further research to be fully clarified, and for the time being we consider the two species as separate.

Identification key for Cretan *Tamarix*

The key below includes all four species of *Tamarix* that we recognize as present in Crete. The identity of the population recorded as *T. hampeana* still needs clarification.

1. Racemes broader than 6 mm . . . . **T. sp.** (*T. "hampeana"*)
– Racemes usually narrower than 5 mm **2**
2. Flowers with 4 sepals, 4 petals and 4 stamens . . . . ***T. parviflora***
– Flowers with 5 sepals, 5 petals and 5 stamens **3**
3. Leaves with a narrow and decurrent base; petals gibbous keeled, whitish with a yellowish brown central part . . . . ***T. smyrnensis***
– Leaves with a broad base, sub-amplexicaul to amplexicaul; petals elliptic and flat, white . . . . ***T. nilotica***

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References

Baum B. 1966: Monographic revision of the genus *Tamarix*. Final research report for the USDA. – Jerusalem: Department of Botany, Hebrew University.

Baum B. 1968: *Tamarix* L. – Pp. 292–294 in: Tutin T. G., Heywood V. H., Burges N. A., Moore D. M., Valentine D. H., Walters S. M. & Webb D. A. (ed.), Flora europaea **2.** – Cambridge: University Press.

Baum B. 1978: The genus *Tamarix*. – Jerusalem: Israel Academy of Sciences and Humanities.

Boissier E. 1867: Flora orientalis **1.** – Basileae, Genevae: H. Georg.

Bunge A. 1852: Tentamen generis Tamaricum species accuratius definiendi. – Dorpati: J. C. Schuenmanni et C. Mattieseni.

Candolle A. P. de 1828: Prodromus systematis naturalis regni vegetabilis **3.** – Parisiis: Treuttel et Würtz.

Dimopoulos P., Raus Th., Bergmeier E., Constantinidis Th., Iatrou G., Kokkini S., Strid A. & Tzanoudakis D. 2013: Vascular plants of Greece: an annotated checklist. – Berlin: Botanic Garden and Botanical Museum Berlin-Dahlem; Athens: Hellenic Botanical Society. [Englera **31**].

Fielding J. & Turland N. [Mathew B. (ed.)] 2005: Flowers of Crete. – Kew: Royal Botanic Gardens.

Greuter W. 1974: Floristic report on the Cretan area. – Mem. Soc. Brot. **24:** 131–171.

Jahn R., Raus Th. & Strid A. 2014: *Tamarix tetrandra*. – In: Raab-Straube E. von & Raus Th. (ed.), Euro+Med-Checklist Notulae 3. – Willdenowia **44:** 287–299.

Linnaeus C. 1753: Species plantarum **1.** – Holmiae: Laurentii Salvii.

Raulin V. 1869: Livre IV. Botanique. – Pp. 693–974 in: Description physique de l'île de Crète **2.** – Paris: Arthus Bertrand.

Thiers B. 2008+ [continuously updated]: Index herbariorum: a global directory of public herbaria and associated staff. – New York Botanical Garden: published at http://sweetgum.nybg.org/ih/ [accessed 29 Jul 2014].

Turland N. 2010: *Tamarix hampeana* Boiss. & Heldr. – Pp. 198–199 in: Greuter W. & Raus Th. (ed.), Med-Checklist Notulae 29. – Willdenowia **40:** 189–204.

Villar J. L., Alonso M. A., Juan A. & Crespo M. B. 2012: Does *Tamarix dalmatica* (*Tamaricaceae*) occur in Spain? – Anales Jard. Bot. Madrid **69:** 253–258.

Villar J. L., Juan A. & Alonso M. A. 2014: *Tamarix hohenackeri* Bunge, a new record for the flora of Mexico. – Acta Bot. Mex. **106:** 117–128.

Yang Q. E. & Gaskin J. 2007: *Tamarix* Linnaeus. – Pp. 59–65 in: Wu Z. Y., Raven P. H. & Hong D. Y. (ed.), Flora of China **13.** – Beijing: Science Press; St. Louis: Missouri Botanical Garden Press.

Zieliński J. 1994: *Tamarix* L. – Pp. 30–34 in: Browicz K. (ed.), Chorology of trees and shrubs in south-west Asia and adjacent regions **10.** – Ponzań: Bogucki Wydawnictwo Naukowe.

Zohary M. 1972: *Tamarix*. – Pp. 351–364 in: Zohary M. (ed.), Flora palaestina **2.** – Jerusalem: Israel Academy of Sciences and Humanities.

Appendix: Herbarium specimens examined

***Tamarix* sp.** (*T. "hampeana"*)

Greece: Crete, Hania, Georgioupoli, river mouth, 35S KV 508171 [35°22'00"N, 24°15'28"E], 12 Jul 2009, *Alonso, Vicente & Villar T2CR* (ABH54194); Crete, Hania, Georgioupoli, river mouth, 35S KV 512172 [35°22'04"N, 24°15'42"E], 12 Jul 2009, *Alonso, Vicente & Villar T3CR* (ABH54196); Crete, Hania, Georgioupoli, 35S KV 516163 [35°21'34"N, 24°15'59"E], 12 Jul 2009, *Alonso, Vicente & Villar T4CR* (ABH54195); Crete, Nomos Chanion, Eparchia Apokorounou, Georgioupoli beach, by river mouth at E edge of village, 35°21'34.3"N, 24°15'59.6"E, 28 Mar 2009, *Turland 1778 & Bareka* (MO6207620).

Tamarix nilotica

Egypt: in Aegypto, 1829, *Savi* (W1889-65784 as *T. senegalensis*); Aegypt. sup., *Kotschy 1002* (W); Prov. Fayum et in insul. Nili, 1820–1826, *Ehrenberg* (K000242697); Ismailia, Qantra road, 28 Sep 1928, *A. Abdel Aty & M. Mokhtar* (MO5814872); Sinai, Straße von St. Katharina Richtung Dahab & Nuweibaa, c. 2 km N Gebel Barari, 1230 m, 24 Feb 2003, *Eberl & Kaiser* (W2007-25493, W2007-25494).

Greece: Crete, Hania, Paleochora, 34S GE438 016 [35°13'40"N, 23°40'43"E], 14 Oct 2009, *Villar & Vicente* (ABH54319, ABH54320); Crete, [Chania], Chora Sfakion, ad viam prope portum, ut videtur culta, 9 Oct 1966, *Greuter 7695* (W1967-18626); Crete, Heraklion, Tris Ekklisies, 35S LU298 694 [34°57'10"N, 25°08'09"E], 12 Oct 2009, *Villar & Vicente* (ABH54318); Crete, [Iraklio], Pedias, ad litus maris prope Chani Kokini, ab Iraklio 10 km, in depressis salsuginosis hyeme inundatis, solo argilloso, 1 Nov 1966, *Greuter 7854* (G as *T. smyrnensis*); Crete, Heraklion, Aposelemis, 35S LV481 113 [35°20'00"N, 25°19'43"E], 9 Oct 2009, *Villar & Vicente* (ABH54314); Crete, Heraklion, prox. Dermatos, 35S LU477 724 [34°58'57"N, 25°19'53"E], 11 Oct 2009, *Villar & Vicente* (ABH54323); Crete, Heraklion, prox. Dermatos, 35S LU485 729 [34°59'14"N, 25°20'24"E], 11 Oct 2009, *Villar & Vicente* (ABH54326); Crete, Heraklion, prox. Arvi, 35S LU587 732 [34°59'29"N, 25°27'06"E], 11 Oct 2009, *Villar & Vicente* (ABH54325); Crete, Heraklion, prox. Arvi, 35S LU664 729 [34°59'23"N, 25°32'10"E], 11 Oct 2009, *Villar & Vicente* (ABH54322); Crete, Lasithi, Kalo Nero, 35S MU134 756 [35°01'09"N, 26°03'02"E], 10 Oct 2009, *Villar & Vicente* (ABH54317); Crete, Lasithi, Perivolakia, 35S MU140 785 [35°02'43"N, 26°03'25"E], 314 m, 10 Oct 2009, *Villar & Vicente* (ABH54327); Crete, Lasithi, Kouremenos Bay, 35S MU334 962 [35°12'23"N, 26°16'05"E], 10 Oct 2009, *Villar & Vicente* (ABH54315); Crete, Lasithi, Xerokambos, 35S MU308 793 [35°03'14"N, 26°14'28"E], 10 Oct 2009, *Villar & Vicente* (ABH54316); Samos, 18 Sep 1978, *K. H. Rechinger* (W2001-05521); Dodecanesa, Patmos, Strand östlich von Skala, 10–30 m, 10 Oct 1999, *H. Förther* (W2006-23819, W2002-13392); Rhodes, Lalisou, 36°25'15"N, 28°11'16"E, 20 Oct 2011, *Izquierdo* (ABH70539).

Israel: env. of Dead Sea, near Her Sedom, moist saline soil, 18 Dec 1938, *M. Zohary & T. Rayss* (W1960-1876).

Lebanon: prope Saïda, Oct, *Gaillardot 543b* (W); Jarezia and de Saïda, 10 Oct, *Gaillardot* (W); Antour de Saïda, haies des jardins, 14 Oct 1842, *I. Blanche 64* (W1889-96596).

Palestine: Kalia, wadi on the plain, 5 Dec 1942, *P. H. Davis* (W1961-10509).

Tamarix parviflora

Greece: Crete, Armiro [Almyro], *Sieber* (type collection for *T. cretica*: G-BOIS unnumbered, MO3728838, P05171492, PR616956, PRC452710, PRC452711, PRC452712, PRC452713, W0031736, W0031737, W0031738); Crete, Hania, Platanias estuary, 34S GE 562 360 [35°32'04"N, 23°49'32"E], 12 Jul 2009, *Villar, Vicente & Alonso* (ABH54202); Crete, Distr. Apokorono, ad flumen Kilaris prope Kalyves, Mar 1904, *Dörfler 5264* (W1911-5630); Crete, Rethimnon, prox. Sises, 35S KV 863 213 [35°24'43"N, 24°38'47"E], 14 Jul 2009, *Villar*, *Vicente & Alonso* (ABH54201); Crete, Heraklion, Geropotamou estuary, 35S KU 944 836 [35°04'27"N, 24°44'42"E], 13 Jul 2009, *Villar*, *Vicente & Alonso* (ABH54200); Crete, Heraklion, Geropotamou estuary, 35S KU 957 800 [35°02'31"N, 24°45'36"E], 13 Jul 2009, *Villar*, *Vicente & Alonso* (ABH54198); Crete, Heraklion, Aposelemis, 35S LV 481 114 [35°20'03"N, 25°19'43"E], 10 Jul 2009, *Villar & Vicente* (ABH54199); Crete, Heraklion, prox. Aposelemis, 35S LV 487 103 [35°19'28"N, 25°20'07"E], 11 m, 14 Jul 2009, *Villar, Vicente & Alonso* (ABH54197); Crete, Heraklion, prox. Dermatos, 35S LU 476 726 [34°59'04"N, 25°19'49"E], 11 Oct 2009, *Villar & Vicente* (ABH54321).

Turkey: Constantinople, 1822, *Castagne* (holotype of *T. parviflora*: G-DC 3-97-14).

Tamarix smyrnensis

Cyprus: Cap Arnauti, près Polis, *M. Haradjian* (MO1621122); ad alveos prope litora maris in viciniis Kuklia, Amathus et aliis locis, May 1862, *Kotschy 572* (W1889-342770, W1889-342771, G-BOIS); in humid. pr. Kythraea, 2 Jun 1880, *Sintenis & Rigo* (PR as *T. pallasii*).

Greece: Larissa in Thessalia, Aug 1889, *Formanek* (PR); ad ripas Penes pr. Larissam, 2 Aug 1882, *Heldreich* (G); Etolias-Akaranias, Mesolongi, coast by the salt works, c. 5 km NW of Mesolongi, clayey marsh, 9 Jun 1997, *Nielsen 12171* (G as *T. parviflora*); Elis in paludosis maritimis Lintri, 3 Jun 1899, *Heldreich* (G); S Greece, NE Peloponnisos, Nafplion, 37°35'19"N, 22°47'44"E, 23 May 2003, *J. Kashefi* (MO); Crete, maritimus prope Khania, Jun 1845, *Raulin 618* (G-BOIS, P-L04034468 pro parte); Rhodes, bords des torrents près Salakos, 31 May 1870, *Bourgeau* (G-BOIS, PR as *T. gallica*, W1889-150434).

Macedonia: im Radovisna-Tal, 3–4 km N von Radovis, Bachlandschaft, 400–500 m, 11 Jul 1977, *F. Krendl* (W1994-01524).

Turkey: Smyrne, *Monbret* (W1889-223513); Smyrnae, in arenosis humidis, Apr–May 1827, *Fleischer* (P-L04034468 pro parte, PR376105, PRC452718, PRC452719, PRC452720, W1889-320298); marais d'eau saumâtre situés entre la Papeterie et la mer, près de Smyrne, 12 Apr 1854, *B. Balansa* (MO5475118, W1889-81992, W1889-80859); Lydia, in humidis ad ruinas Ephesi, 1 Jun 1906, *Bornmüller 9202* (W1908-678); A2 Bursa, 4 km S Uluabat, Damm, 27 Jun 1977, *F. Sorger* (W1990-06989); C2 Denizli, Pamukkale E, 400 m, 28 Jun 1967, *F. Sorger* (W1990-06983); Antalya, from Antalya to Akseki, beside the river, under the Karpuzçay bridge, 15 m, 17 May 2007, *Yaprak 2007-011* (ANK); C4 İçel, 12 km S Mut, 200 m, 6 Jun 1966, *F. Sorger* (W1990-07003); Cilicia, Mersina, bords du Guzel-Déré, à l'ouest de Mersina, 2 Apr 1855, *B. Balansa* (W1889-76155); B6 Sivas, Divriği, 2 km SO Sincan, 1600 m, 30 Jun 1970, *F. Sorger* (W1990-06991); N Muş, rechtes Murat Ufer, 1300 m, 20 Jun 1984, *F. Sorger* (W1990-06990).

Sección III:

Aspectos taxonómico-filogenéticos

Artículo 7

Villar J. L., Turland N., Juan A., Gaskin J. F., Alonso M. A. & Crespo M. B. 2015. *Tamarix minoa* (*Tamaricaceae*), a new species from the island of Crete (Greece) based on morphological and plastid molecular sequence data. *Willdenowia* 45 (2): 161-172.

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Tamarix minoa (*Tamaricaceae*), a new species from the island of Crete (Greece) based on morphological and plastid molecular sequence data

Abstract

Villar J. L., Turland N. J., Juan A., Gaskin J. F., Alonso M. A. & Crespo M. B.: *Tamarix minoa* (*Tamaricaceae*), a new species from the island of Crete (Greece) based on morphological and plastid molecular sequence data. – Willdenowia 45: 161–172. 2015. – Version of record first published online on 17 June 2015 ahead of inclusion in August 2015 issue; ISSN 1868-6397; © 2015 BGBM Berlin.

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Tamarix minoa is described from material collected on the S Aegean island of Crete (Kriti), Greece. A morphological comparison with the species considered to be closest, *T. africana* and *T. hampeana*, is provided. An original illustration showing the main morphological characters of the new species is also given, as are photographs of the new species in its habitat. The isolated phylogenetic position of *T. minoa* is shown to be strongly supported by plastid molecular sequence data (*trnS-trnG*, *trnQ-rps16* and *ndhF-rpl32*), thus warranting its recognition at specific rank.

Additional key words: Mediterranean flora, Aegean flora, molecular phylogeny, taxonomy, *Tamarix africana*, *Tamarix hampeana*

Introduction

The recent revision of the genus *Tamarix* in Crete (Villar & al. 2014) confirmed the presence of at least four species on that island: *T. hampeana* Boiss. & Heldr., *T. nilotica* (Ehrenb.) Bunge, *T. parviflora* DC. and *T. smyrnensis* Bunge. Among these, the record of *T. hampeana* was considered to be controversial and its identity was left in need of further clarification. It was difficult to obtain a precise identification of the specimens initially assigned to *T. hampeana* (Turland 2010; Villar & al. 2014). In fact, the different taxonomic works consulted (Boissier 1849, 1867; Bunge 1852; Baum 1968, 1978) did not lead to satisfactory results in respect to the morphology of the studied specimens or their identity with *T. hampeana* or any other described taxa. The specimen MO6207620 (herbarium codes according to Thiers 2015+) was first identified as *T. africana* Poir. However, on B. Baum's advice, it was finally identified and reported as *T. hampeana* (Turland 2010; Villar & al. 2014). On the other hand, the specimens ABH54194, ABH54195 and ABH54196 (see Appendix) were first identified as *T. tetragyna* Ehrenb., due to the high proportion of tetramerous and pentamerous flowers present in the late-season racemes. Nevertheless, after examining several herbarium specimens of *T. tetragyna*, its morphological features showed clear dif-

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ferences from the Cretan specimens and, therefore, that identification was proven to be clearly erroneous. These specimens were finally assigned, with reservations, to *T. hampeana* (Villar & al. 2014).

On account of the doubts held about the taxonomic identity of these specimens from Crete, a deeper morphological study was conducted. In addition, a preliminary phylogeny, based on three plastid DNA regions (intergenic spacers *trnS-trnG*, *ndhF-rpl32* and *trnQ-rps16*), was conducted to identify which of the existing taxa could be genetically closest to the controversial Cretan samples.

The combination of morphological and molecular evidence allows the description of a new species, *Tamarix minoa*, apparently endemic to Crete. The morphological features of the new species, as well as its taxonomic relationships, are described below.

Material and methods

The material on which this study is focused was collected at Georgioupoli, on the N coast of W Crete. The precise locations for all samples are not more than 1 km apart, so they can be considered to belong to a single population. The specimens collected by Turland and Bareka are kept at UPA, with duplicates at B and MO; the ones collected by Villar, Alonso and Vicente are conserved at ABH.

In order to clarify the morphological identity of the Cretan specimens, over 120 herbarium specimens of the morphologically closest taxa (*Tamarix africana* and *T. hampeana*) were studied, including type material (Villar & al. 2015) kept at G, K, MA and P. Moreover, different European and American herbaria (ABH, B, G, MO, MPU, P, PR, PRC, VAL and W) (Thiers 2015+) were visited in order to obtain a wider view of the morphological characterization of the whole genus. In addition, field collections were made around the W Mediterranean region, where *T. africana* is mainly distributed, as well as around the coasts of continental Greece, where *T. hampeana* is widespread. Those field collections are kept at ABH. Detailed observations and morphological measurements of vegetative and flower parameters were undertaken according to Villar & al. (2012). The main floras and taxonomic works dealing with *Tamarix* in the Mediterranean region were consulted (Candolle 1828; Boissier 1849, 1867; Bunge 1852; Baum 1966, 1968, 1978).

A total of 23 samples of *Tamarix*, belonging to 10 species from 11 countries, were used for the molecular analyses (Table 1). *Reaumuria alternifolia* (Labill.) Britten, *Myricaria bracteata* Royle and *Myrtama elegans* (Royle) Ovcz. & Kinzik., all belonging to *Tamaricaceae*, were also included as the outgroup. Regarding *Tamarix* samples, in addition to three of the Cretan samples, we included the vaginate-leaved *T. aphylla* (L.) H. Karst. and *T. usneoides* E. Mey. ex Bunge; the generic type species *T. gallica* L.; species occurring geographically nearby (*T. dalmatica* B. R. Baum and *T. parviflora*); and those species once thought to match with the Cretan samples (Villar & al. 2014): *T. africana*, *T. hampeana* and *T. tetragyna* (along with its close relative *T. boveana* Bunge). All the studied samples are kept at the herbaria ABH or MO, with the exception of the outgroup samples corresponding to *R. alternifolia* and *M. bracteata*, which belong to John F. Gaskin, kept at the USDA ARS at Sidney (MT, U.S.A.), soon to be deposited at MO (Table 1).

Genomic DNA was extracted from silica-gel-dried leaf material (Chase & Hill 1991), following a modified 2xCTAB method (Doyle & Doyle 1987). Total DNA is kept at the ABH-DNA bank. The species-level phylogeny is based on three plastid intergenic spacers (*trnS-trnG*, *trnQ-rps16* and *ndhF-rpl32*), which were amplified using the primers described in Hamilton (1999) and Shaw & al. (2007). The amplifications were performed in a reaction volume of 25 µl containing 22.5 µl ABGene 1.1× Master Mix 2.5 mM $MgCl_2$ (Thermo Scientific Waltham, MA, U.S.A.), 0.5 µl of 0.4% 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 regions was an initial denaturation of 94°C for 2 min, followed by 35 cycles at 94°C (1 min 15 sec), 55°C (1 min 30 sec) and 72°C (2 min); and a final elongation at 72°C for 10 min. PCR products were purified using Ultraclean® PCR Clean-Up Kit (MOBIO, Carlsbad, CA, U.S.A.) micro-columns, following the instructions provided by the manufacturer. Both strands were sequenced with the same primers for each region and for all samples at Macrogen Inc. Korea (www.macrogen.com).

Complementary strands were assembled using Sequencher 4.1 (Gene Codes Corp., Ann Arbor, MI, U.S.A.). The three plastid regions were aligned automatically by ClustalW, conducted in MEGA 5.05 (Tamura & al. 2011). Minor manual corrections were made to obtain the final alignments, and the three regions were joined in a single matrix. Maximum parsimony analyses (MP) and Bayesian analyses were performed on the plastid dataset.

MP 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 commented options. MP support was assessed by 1000 bootstrap replicates, TBR branch swapping, simple addition sequence and MULTREES on, keeping 10 trees per replicate (Salamin & al. 2003). 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.

A Bayesian Inference (BI) analysis was conducted using MrBayes v.3.1.2 (Huelsenbeck & Ronquist 2001;

Table 1. Materials used in the molecular analysis.

Label on Fig. 3	**Taxon**	**Origin**	**Voucher**	**GenBank ref. *trnS-trnG***	**GenBank ref. *trnQ-rps16***	**GenBank ref. *ndhF-rpl32***
R. alternifolia	*Reaumuria alternifolia* (Labill.) Britten	Iran	*Gaskin 919**	KP244371	KP244397	KP244423
M. bracteata	*Myricaria bracteata* Royle	Kazakhstan	*Gaskin 1148**	KP244372	KP244398	KP244424
M. elegans	*Myrtama elegans* (Royle) Ovcz. & Kinzik.	China	MO5799414	KP244373	KP244399	KP244425
T. aphylla TA1Mo	*Tamarix aphylla* (L.) H. Karst.	Morocco	ABH54280	KP244374	KP244400	KP244426
T. aphylla TACD	*Tamarix aphylla* (L.) H. Karst.	Italy (Sardinia)	ABH54422	KP244375	KP244401	KP244427
T. usneoides T1NMB	*Tamarix usneoides* E. Mey.	Namibia	ABH58684	KP244376	KP244402	KP244428
T. usneoides TSA7	*Tamarix usneoides* E. Mey.	South Africa	ABH58683	KP244377	KP244403	KP244429
T. africana T13Mo	*Tamarix africana* Poir.	Morocco	ABH54205	KP244378	KP244404	KP244430
T. africana T2V	*Tamarix africana* Poir.	Spain	ABH55366	KP244379	KP244405	KP244431
T. minoa T2CR	*Tamarix minoa* J. L. Villar & al.	Greece (Crete)	ABH54194	KP244382	KP244408	KP244434
T. minoa T4CR	*Tamarix minoa* J. L. Villar & al.	Greece (Crete)	ABH54195	KP244383	KP244409	KP244435
T. minoa NT	*Tamarix minoa* J. L. Villar & al.	Greece (Crete)	MO6207620	KP244384	KP244410	KP244436
T. tetragyna W07-28	*Tamarix tetragyna* Ehrenb.	Egypt	W2007-25728	KP244385	KP244411	KP244437
T. boveana T7AG	*Tamarix boveana* Bunge	Algeria	ABH56326	KP244387	KP244413	KP244439
T. boveana T18Mo	*Tamarix boveana* Bunge	Morocco	ABH54183	KP244388	KP244414	KP244440
T. boveana Tb2Eb	*Tamarix boveana* Bunge	Spain	ABH54330	KP244389	KP244415	KP244441
T. gallica TC1Eb	*Tamarix gallica* L.	Spain	ABH54331	KP244396	KP244422	KP244448
T. gallica T2Fr	*Tamarix gallica* L.	France	ABH57865	KP244395	KP244421	KP244447
T. tetragyna W07-48	*Tamarix tetragyna* Ehrenb.	Egypt	W2007-14048	KP244386	KP244412	KP244438
T. parviflora T8CR	*Tamarix parviflora* DC.	Greece (Crete)	ABH54197	KP244393	KP244419	KP244445
T. parviflora TCR10	*Tamarix parviflora* DC.	Greece (Crete)	ABH54321	KP244394	KP244420	KP244446
T. hampeana T6GRE	*Tamarix hampeana* Boiss. & Heldr.	Greece (Epirus)	ABH59025	KP244390	KP244416	KP244442
T. hampeana T72GRE	*Tamarix hampeana* Boiss. & Heldr.	Greece (Central)	ABH59877	KP244391	KP244417	KP244443
T. hampeana T3MNE	*Tamarix hampeana* Boiss. & Heldr.	Montenegro	ABH57891	KP244392	KP244418	KP244444
T. dalmatica T1ALB	*Tamarix dalmatica* B. R. Baum	Albania	ABH57830	KP244380	KP244406	KP244432
T. dalmatica T6MNE	*Tamarix dalmatica* B. R. Baum	Montenegro	ABH57844	KP244381	KP244407	KP244433

* Vouchers soon to be deposited at MO.

Ronquist & Huelsenbeck 2003). The most accurate evolutionary model required for Bayesian estimation was selected using the AIC (Akaike Information Criterion) (Posada & Crandall 1998; Posada & Buckley 2004), conducted in JMODELTEST 2.1.5 (Darriba & al. 2012). Two simultaneous and independent analyses were performed. For each analysis, the Markov and Monte Carlo chains were run for 2×10^6 generations and sampled every 100 generations. The chains became stationary and the average standard deviation of the split frequencies stabilized in 250 000 generations. Thus the first 250 trees were excluded ("burn-in") and the remaining trees were used to compile a posterior probability (PP) distribution using a 50% majority-rule consensus.

Results and Discussion

Tamarix minoa J. L. Villar, Turland, Juan, Gaskin, M. A. Alonso & M. B. Crespo, **sp. nov.** – Fig. 1 & 2.
Holotype: Greece, Crete, Nomos Chanion, Eparchia Apokoronou, Georgioupoli beach, by river mouth at E edge of village, 35°21'34.3"N, 24°15'59.6"E, 0 m, sandy river bank on beach with springs emerging beneath the *Tamarix* trees, 28 Mar 2009, *N. J. Turland 1778 & P. Bareka* (UPA-Herb. Phitos & Kamari; isotypes: B, MO6207620).
– *Tamarix hampeana* sensu Turland in Willdenowia 40: 198. 2010, non Boiss. & Heldr. 1849.

Diagnosis — Species distincta primo aspectu ad *Tamaricem africanam* Poir. aemulans et cum *T. hampeana* Boiss. & Heldr. plerumque confusa, sed eis singulari characterum combinatio valde diversa et multo differt; racemis vernalis e ramorum vetustiorum productis aliquando junioribus hornotinis ramulis alternantibus; bracteis lineari-oblongis, concavis, subpatulis, calyces paulo superantibus; floribus plerumque pentameris, sed ad postremum tempum florendi cum aliis tetrameris floribus simul commixtis; sepalis acutis, marginibus denticulatis; petalis oblongo-obovatis vel obovatis, concavis vel leviter carinatis; antheris mucronatis.

Description — *Shrubs* or low shrubby *trees*, up to 5 m tall. *Bark* reddish brown to dark burgundy. *Leaves* green to glaucous green, lanceolate, (1–)1.5–2.5(–3.5) mm long, surface slightly papillose, bearing salt glands, more evident and abundant in older leaves, base narrow, slightly decurrent, broader and auriculate in leaves remaining from previous year, apex acuminate, slightly incurved. *Racemes* loosely arranged on previous year's branchlets, sometimes alternating with new-leaved twigs (Fig. 2B), 2.5–4.5(–6) cm long, 6–7.5 mm wide. *Peduncle* 3–5 mm long, with 4–8 scarious bracts grouped at base, sometimes showing 2–3 mm of naked rachis before first floral bract; *rachis* lacking papillae on all studied specimens. *Bracts* patent, yellowish brown, linear-oblong, narrowing at apex, concave, (2–)2.5–3.5(–4.5) mm long, usually slightly surpassing calyx, sometimes not reaching it, base narrow, slightly decurrent, sometimes showing 2 small auricles, margin sparsely papillose-ciliate, apex obtuse to acute, slightly incurved. *Pedicels* 0.5–0.75 mm long, always shorter than sepals. *Calyx* of 5 sepals (sometimes 4, very rarely 6)*. *Sepals* green, ovate-triangular, 1.5–2 mm long, 1–1.2 mm wide, 2 outer ones slightly larger than 3 inner ones, margin broadly membranous, markedly denticulate, apex acute; pentamerous calyx sepals almost alike; tetramerous* calyx outer sepals sometimes with a marked central nerve and apex apiculate, inner sepals evidently smaller and apex obtuse. *Corolla* of 5 petals (sometimes 4, very rarely 6)*. *Petals* deciduous at fruit maturity, white, oblong-obovate to obovate, concave to keeled, recurved at late anthesis, 2.8–3.2 mm long, 1–1.5 mm wide, margin sometimes irregular, base sometimes cuneate, not unguiculate. *Staminal disk* dark brown, 5-lobed (rarely 4-lobed, exceptionally 6-lobed)*; *lobes* antesepalous, broadly ovate, apex somewhat progressively narrowed into filaments; *filaments* white, 1.5–2 mm long; *anthers* pale yellow to light pink, 0.8–1 mm long, 0.5–0.6 mm wide, apex mucronate. *Gynoecium* of 3 styles and 3 carpels, (rarely 4)*; *styles* nearly 0.6 mm long.
* More common in late-season racemes.

Phenology — Flowering mainly in March and April, though some late-season racemes may extend the flowering period until the end of May.

Distribution and biogeography — At present, *Tamarix minoa* is known only from the type locality at Georgioupoli on the N coast of W Crete in the S Aegean region, Greece. Further exploration in the field and examination of herbarium material are needed to clarify if its distribution is confined to Crete or if it extends to other territories. According to Rivas-Martínez & al. (2004), the type locality of *T. minoa* is located in the Cretan Subprovince, which belongs to the Graeco-Aegean Province, Eastern Mediterranean Subregion and Mediterranean Region. The biogeographical unit Cretan Subprovince matches the "Cretan area" ("Cr") of *Flora europaea* (Tutin & al. 1964–1980) and the Euro+Med PlantBase (Euro+Med 2006+) as well as the floristic region "Kriti+Karpathos" ("KK") of *Flora hellenica* (Strid & Tan 1997, 2002) and the recent checklist of Greek vascular plants (Dimopoulos & al. 2013).

Ecology — Growing on sandy river banks close to the sea, with springs of percolating (fresh or brackish?) groundwater emerging beneath the *Tamarix* trees, exposed to inundation by seawater during storms (Fig. 2A).

Etymology — The epithet *minoa* makes reference to the Minoan civilization, which existed in Crete in the Bronze Age between 3500–2500 BCE and c. 1100 BCE. The term "Minoan" itself is derived from Minos (Μίνως), a mythical king of Crete.

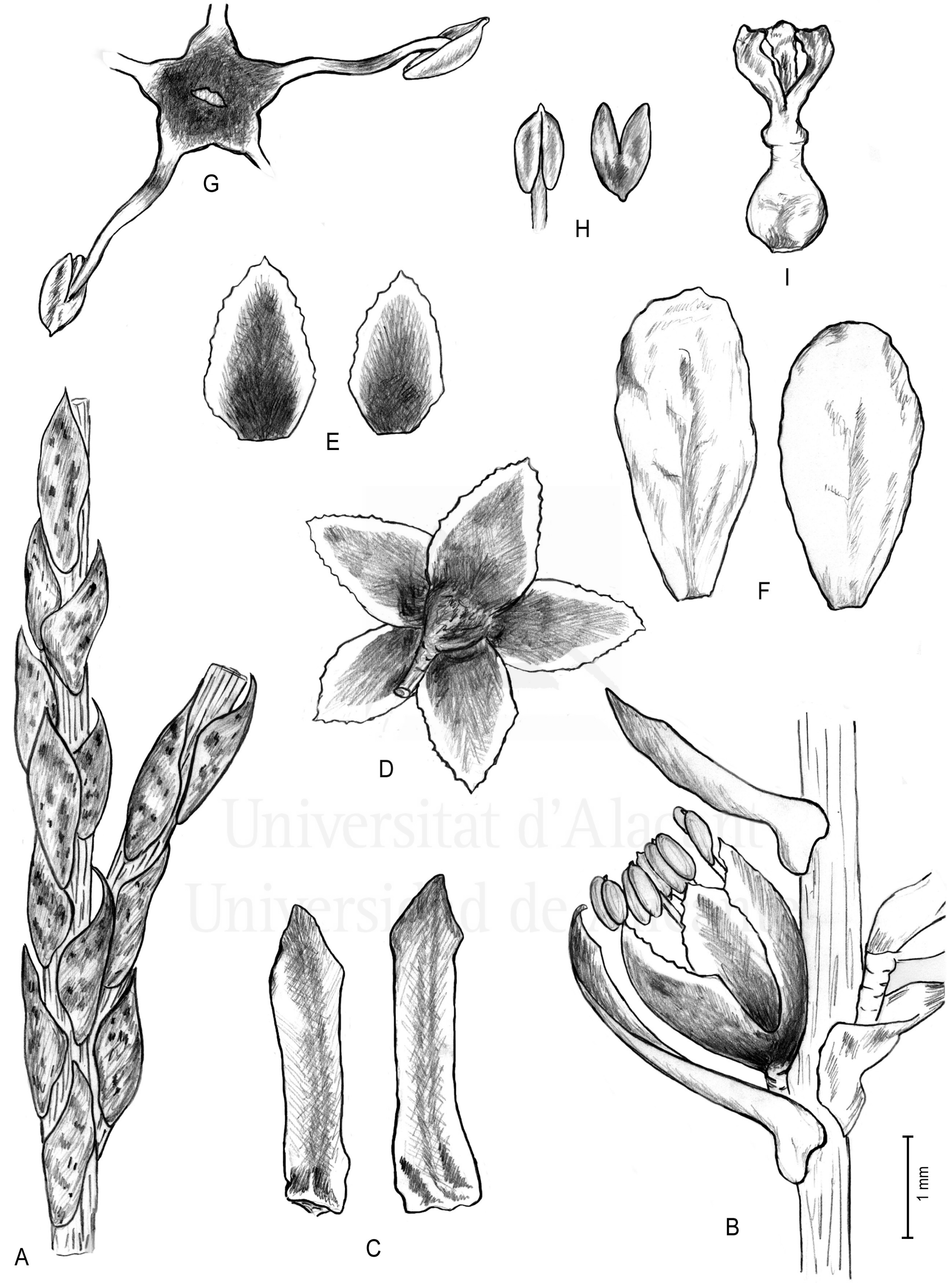

Fig. 1. *Tamarix minoa* – A: young branchlet with leaves; B: portion of branchlet with bracts and flower (petals removed); C: bracts, adaxial (left) and abaxial (right) surfaces; D: flower, basal view, showing pedicel and calyx; E: sepals, abaxial surface, outer sepal (left), inner sepal (right); F: petals, adaxial surface; G: staminal disk, apical view with filaments and anthers; H: anthers, lateral views, with distal part of filament (left), with apex at bottom (right); I: gynoecium, lateral view. – Drawn by María García Rivas from the isotype MO6207620.

Fig. 2. *Tamarix minoa* – A: tree growing on sandy ground beside river (left), springs emerging beneath tree, sea in distance; B: flowering branchlets. – Type locality, 28 Mar 2009, photographs by N. J. Turland.

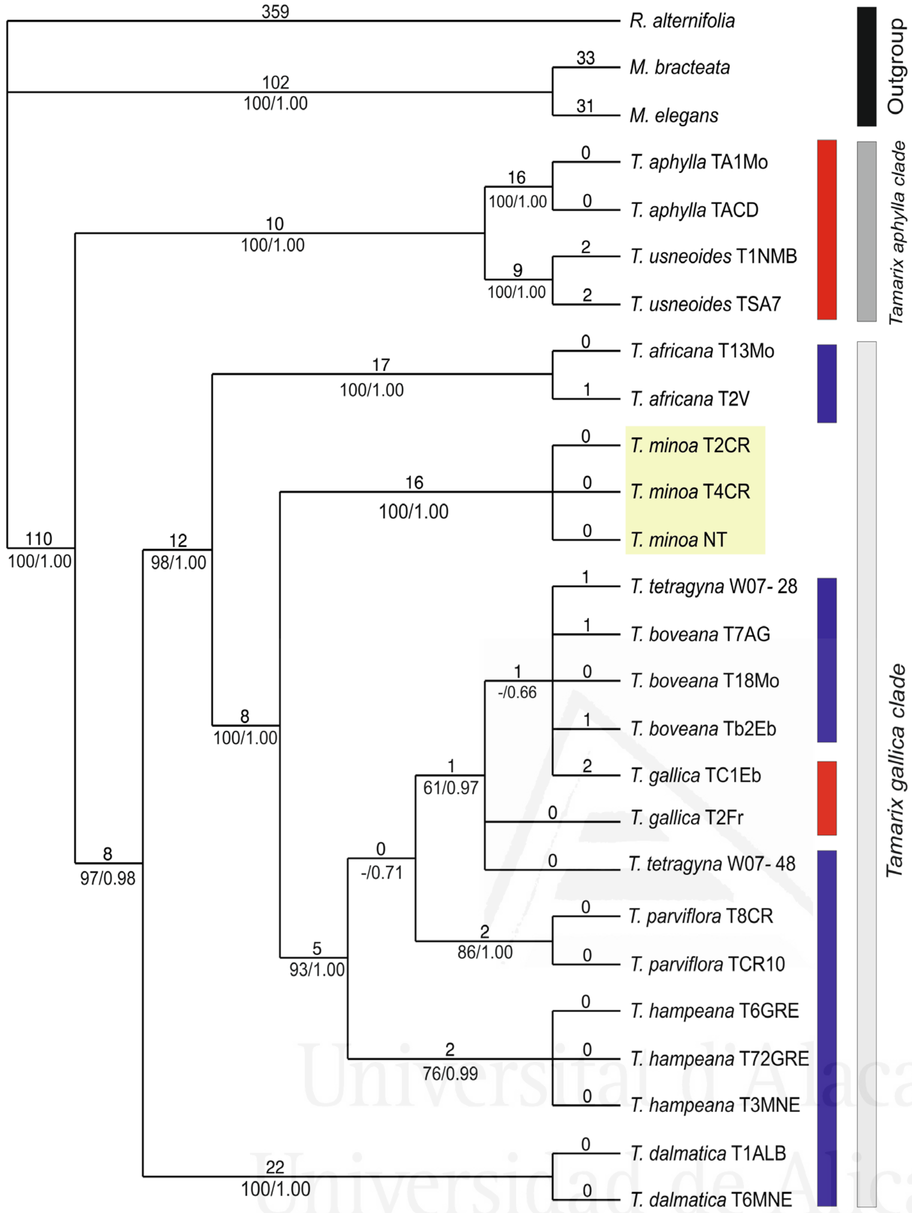

Fig. 3. One of the six most parsimonious trees obtained (774 steps, CI 0.935, RI 0.916). Branch lengths for parsimony analysis are shown above branches. Bootstrap values (BS) > 50% and Bayesian posterior probability (PP) > 0.90 are shown below branches (BS/PP). The outer vertical bars represent the outgroup and the two first split clades in *Tamarix*. The inner vertical bars represent the sections accepted by Baum (1978).

Additional specimens seen (paratypes) — Greece, Crete, Chania, Georgioupoli, river mouth, 30S KV 508171 [35°22'00"N, 24°15'28"E], 12 Jul 2009, *Alonso*, *Vicente & Villar T2CR* (ABH54194); ibid., 30S KV 512172 [35°22'04"N, 24°15'42"E], 12 Jul 2009, *Alonso*, *Vicente & Villar T3CR* (ABH54196); Georgioupoli, 30S KV 516163 [35°21'34"N, 24°15'59"E], 12 Jul 2009, *Alonso*, *Vicente & Villar T4CR* (ABH54195).

Remarks — According to our observations, *Tamarix minoa* is mostly a pentamerous-flowered species, with 5 sepals, 5 petals, 5 stamens and 3 styles. A few rare flowers, though, can be found to be tetramerous or hexamerous in some of the floral whorls, more frequently on late flowering racemes. Often tetramery or hexamery does not affect all whorls at the same time. Most of the examined flowers with a tetramerous calyx had a pentamerous staminal disk. Most of the hexamerous staminal disks were found in pentamerous flowers in relation to sepals and petals. In a few cases, tetramery of sepals was related to hexamery of petals (or vice-versa). No special pattern was found in the occurrence of a 4-styled/-valved gynoecium.

Molecular results and phylogenetic relations

The aligned and combined plastid dataset resulted in a 3105-base-pair (bp) matrix. The *trnS-trnG* region contributed 989 bp, *trnQ-rps16* 1147 bp and *ndhF-rpl32* 969 bp. Among the total number of nucleotides, 296 (9.53 %) were potentially parsimony-informative. Both Bayesian and MP analyses yielded trees with the same topology. One of the six most parsimonious trees, obtained with 774 steps (CI of 0.935; RI of 0.916), is shown in Fig. 3.

According to our data (Fig. 3), the monophyly of *Tamarix* was strongly supported (BS 100 %, PP 1.00), and two highly supported clades were fully resolved, corresponding to two different groups here named the *T. aphylla* clade (BS 100 %, PP 1.00) and the *T. gallica* clade (BS 97 %, PP 0.98). Within the *T. gallica* clade, *T. minoa* formed an independent and strongly supported clade (BS 100 %, PP 1.00). Its phylogenetic position is well resolved, being a sister group of a large clade (BS 93%, PP 1.00) that includes *T. hampeana* (BS 76 %, PP 0.99), *T. parviflora* (BS 86 %, PP 1.00) and a third clade formed by *T. boveana*, *T. gallica* and *T. tetragyna* (BS 61%, PP 0.97). The phylogenetic relationships within this third clade are not adequately resolved. Consequently the phylogenetic position of these three species appeared collapsed. Finally, *T. africana* and *T. dalmatica* are placed in the outermost positions of this

T. gallica clade, as independent branches (BS 100%, PP 1.00, for both taxa).

The current work is not intended to offer a complete phylogeny of the genus *Tamarix*, since many species were not sequenced for this study and, specifically, no specimens characterized by amplexicaul leaves (e.g. *T. passerinoides* Delile ex Desv., *T. pycnocarpa* DC.) were included. Further phylogenetic studies are needed in order to obtain a better overview of the whole genus, including a larger number of samples and species. Nonetheless, and as Gaskin & Schaal (2003) already pointed out, the sections of *Tamarix* accepted by Baum (1978) do not correspond to monophyletic groups in this preliminary molecular study. In Fig. 3, *T. gallica* (*T.* sect. *Tamarix*, *T.* ser. *Gallicae* B. R. Baum) is included in a large group of species belonging to *T.* sect. *Oligadenia* (Ehrenb.) B. R. Baum, and separated from *T. aphylla* and *T. usneoides* (*T.* sect. *Tamarix*, *T.* ser. *Vaginantes* (Bunge) Bunge). Moreover, *T. parviflora* (*T.* sect. *Oligadenia*, *T.* ser. *Arbusculae* B. R. Baum) shares the same clade with *T. tetragyna* and *T. boveana* (*T.* sect. *Oligadenia*, *T.* ser. *Anisandrae* Bunge), as well as with *T. gallica. Tamarix africana*, the closest species morphologically to *T. minoa*, is included in *T.* sect. *Oligadenia*, *T.* ser. *Anisandrae*. These results suggest that a reanalysis of sections and series should be undertaken. Consequently, we prefer not to classify the new species *T. minoa* in any of the existing sections.

Morphological comparisons

Despite the taxonomic complexity of the genus, and the diffuse borders between similar species, we can highlight some morphological features to separate *Tamarix minoa* from the morphologically close *T. africana*, as well as from its previous identification of *T. hampeana* (Table 2).

Leaves — Leaves are similar between *Tamarix minoa* and *T. africana*, though those of *T. africana* tend to show a broader auriculate base. In both species the longer leaves rarely reach 3.5 mm. The leaves of *T. hampeana* are narrower, and it is common to find some longer ones (4–7 mm) at the base of the first young twigs of the year.

Racemes — *Tamarix hampeana* racemes are among the larger ones in the genus (usually 4–10 cm long × 7–12 mm wide), some reaching up to 16 cm long × 14 mm wide. The racemes of *T. minoa* and *T. africana*, are smaller (usually less than 5 cm long × 8 mm wide), although the smallest *T. hampeana* racemes can overlap in size with *T. africana* and *T. minoa*. However, those of *T. minoa* show the peculiarity of frequently alternating with new leafy twigs.

Bracts — The bract size of the three species falls into a similar range. However, the bracts of *Tamarix minoa* are patent, linear-oblong, only narrowing at the apex, with a narrow slightly decurrent base sometimes with two small auricles. On the other hand, the bracts of *T. africana* are triangular-oblong, always narrowing progressively toward the apex, with a narrow decurrent base sometimes calcarate with two small auricles that can even be slightly decurrent. The bracts of *T. hampeana* can be ovate-oblong, oblong or narrowly triangular; they are so variable that they are not very reliable for comparison with the other two species.

Pedicels — The pedicels of *Tamarix hampeana* (usually 1–4 mm long) are frequently longer than the sepals and significantly larger than those of *T. africana* and *T. minoa* (in both species subsessile to 0.75 mm long).

Calyx — *Tamarix africana* and *T. minoa* show essentially a pentamerous calyx, although both species can show exceptions. Tetramerous calyces are more common in *T. minoa* than in *T. africana*. *Tamarix hampeana* shows flowers with normally 4 or 5 sepals, but sometimes 6 or 7 or even 8 or 9. This variability makes it difficult to identify *T. hampeana* as tetramerous or pentamerous. The sepals of *T. minoa* look similar, the two outer ones are slightly larger than the three inner ones, all are clearly denticulate at the margin and most are acute at the apex. The two outer sepals of *T. africana* tend to be narrower and usually show a marked central nerve, and all sepals usually have a subentire margin and obtuse apex. The two outer sepals of *T. hampeana* tend to be narrower and sometimes show a marked central nerve, and all sepals have a subentire margin and acute to obtuse apex.

Corolla — *Tamarix africana* and *T. minoa* are essentially pentamerous, with rare exceptions. In *T. hampeana*, the number of petals is as variable as the number of sepals (4–6(–9)). The petals of *T. hampeana* tend to be elliptic-oblong, whereas those of *T. minoa* are oblong-obovate to obovate and concave to keeled, and those of *T. africana* tend to be broadly ovate and flat (in the typical variety) to oblong-unguiculate. In a single flower, for all three species, all petals are the same size.

Staminal disk — The configuration of the disk is very similar in *Tamarix minoa* and *T. africana*, both showing disks with the filaments rising progressively from the apex of disk lobes. They are also quite stable in showing 5 stamens, rarely 6, exceptionally 7 or 8 (Villar & al. 2012). On the other hand, the filaments of *T. hampeana* rise abruptly from the apex of the disk lobes. Moreover, *T. hampeana* shows an extremely high variability in the staminal disk features: disks with 4 or 5 staminal filaments are not always easy to find, whereas disks with 6–8(–10) well-developed stamens are common.

Anthers — Only the anthers of *Tamarix minoa* are clearly mucronate. Those of *T. africana* and *T. hampeana* are not, although submucronate anthers can sometimes be found.

Table 2. Some key morphological features for distinguishing among *Tamarix minoa* and the related *T. africana* and *T. hampeana*.

	Tamarix minoa	***Tamarix africana***	***Tamarix hampeana***
Raceme disposition	loosely arranged on previous year's branchlets, sometimes alternating with new leafy twigs	loosely arranged on previous year's branchlets	loosely arranged on previous year's branchlets and branches
Raceme size [mm]	25–45(–60) × 6–7.5	20–50(–80) × 5–8(–9)	(30–)40–100(–160) × (6–)7–12(–14)
Pedicel length [mm]	0.5–0.75	< 0.75(–1)	1–4
Sepal shape	ovate, margin denticulate, apex acute; 2 outer sepals slightly larger than inner ones	ovate, margin subentire, apex obtuse; 2 outer sepals slightly narrower than inner ones	ovate, margin subentire, apex acute to obtuse; 2 outer sepals slightly narrower than inner ones
Number of sepals	(4 or)5(or 6)	5(or 6)	4 or 5(–9)
Number of stamens	(4 or)5(or 6)	5(or 6(–8))	4–7(–10)
Anthers mucronate	yes (markedly)	no (rarely minutely)	no (rarely minutely)

According to the molecular and morphological results obtained, we can conclude that *Tamarix minoa* is indeed an independent species well separated from any other taxa of *Tamarix.* The closest species with respect to morphology is *T. africana.* However, *T. minoa* can be separated from *T. africana* by the linear-oblong concave bracts, acute and denticulate sepals, concave-keeled petals and apiculate anthers. Our phylogenetic results have pointed out the well-supported, isolated position of the studied samples, clearly separated from the morphological close taxa *T. africana* and *T. hampeana*, as well as from geographically close taxa such as *T. dalmatica* and *T. parviflora*. Regarding morphology, the correct identification of *Tamarix* collections is known as a troublesome matter, and *T. africana* is one of the most widely distributed and morphologically variable species in the Mediterranean region. Taking these points into consideration, we would recommend being careful with future records of apparent *T. minoa* from outside the Aegean region, in order to avoid mistaken identifications, as happened with *T. dalmatica* in the Iberian Peninsula (Villar & al. 2012).

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References

Baum B. 1966: Monographic revision of the genus *Tamarix*. Final research report for the USDA. – Jerusalem: Department of Botany, Hebrew University.

Baum B. 1968: *Tamarix* L. – Pp. 292–294 in: Tutin T. G., Heywood V. H., Burges N. A., Moore D. M., Valentine D. H., Walters S. M. & Webb D. A. (ed.), Flora europaea **2.** – Cambridge: University Press.

Baum B. 1978: The genus *Tamarix*. – Jerusalem: Israel Academy of Sciences and Humanities.

Boissier E. 1849: Diagnoses plantarum orientalium novarum, ser. 1, **10.** – Paris: M. Ducloux et cons.

Boissier E. 1867: Flora orientalis **1.** – Basileae, Genevae: H. Georg.

Bunge A. 1852: Tentamen generis *Tamaricum* species accuratius definiendi. – Dorpati: J. C. Schuenmanni et C. Mattieseni.

Candolle A. P. de 1828: Prodromus systematis naturalis regni vegetabilis **3.** – Parisiis: Treuttel et Würtz.

Chase M. W. & Hill H. G. 1991: Silica gel: an ideal material for field preservation of leaf samples for DNA studies. – Taxon **40:** 215–220.

Darriba D., Taboada G. L., Doallo R. & Posada D. 2012: jModelTest 2: more models, new heuristics and parallel computing. – Nature Methods **9:** 772.

Dimopoulos P., Raus Th., Bergmeier E., Constantinidis Th., Iatrou G., Kokkini S., Strid A. & Tzanoudakis D. 2013: Vascular plants of Greece: An annotated checklist. – Berlin: Botanischer Garten und Botanisches Museum Berlin-Dahlem; Athens: Hellenic Botanical Society. – Englera **31.**

Doyle J. J. & Doyle J. L. 1987: A rapid DNA isolation procedure for small quantities of fresh leaf tissue. – Phytochem. Bull. **19:** 11–15.

Euro+Med 2006+ [continuously updated]: Euro+Med PlantBase – the information resource for Euro-Mediterranean plant diversity. – Published at http://ww2.bgbm.org/EuroPlusMed/ [accessed 29 Jan 2015].

Gaskin J. F. & Schaal B. 2003: Molecular phylogenetic investigation of U.S. invasive *Tamarix*. – Syst. Bot. **28:** 86–95.

Hamilton M. 1999: Four primer pairs for the amplification of chloroplast intergenic regions with intraspecific variation. – Molec. Ecol. **8:** 521–523.

Huelsenbeck J. P. & Ronquist F. 2001: MRBAYES: Bayesian inference of phylogenetic trees. – Bioinformatics **17:** 754–755.

Posada D. & Buckley T. R. 2004: Model selection and model averaging in phylogenetics: advantages for the AIC and Bayesian approaches over Likelihood ratio tests. – Syst. Biol. **53:** 793–808.

Posada D. & Crandall K. A. 1998: Modeltest: testing the model of DNA substitution. – Bioinformatics **14:** 817–818.

Rivas-Martínez S., Penas A. & Díaz T. E. 2004: Biogeographic Map of Europe. – León: Cartographic Service, University of León: published at http://www.globalbioclimatics.org

Ronquist F. & Huelsenbeck J. P. 2003: Bayesian phylogenetic inference under mixed models. – Bioinformatics **19:** 1572–1574.

Salamin N., Chase M. W., Hodkinson T. R. & Savolainen V. 2003: Assessing internal support with large phylogenetic DNA matrices. – Molec. Phylogen. Evol. **27:** 528–539.

Shaw J., Lickey E. B., Schilling E. E. & Small R. L. 2007: Comparison of whole chloroplast genome sequences to choose noncoding regions for phylogenetic studies in angiosperms: The tortoise and the hare III. – Amer. J. Bot. **94:** 275–288.

Strid A. & Tan K. (ed.) 1997; 2002: Flora hellenica **1; 2.** – Königstein: Koeltz Scientific Books; Ruggell: A. R. G. Gantner Verlag.

Swofford D. L. 2002: PAUP, version 4.0b10 for Macintosh. – Sunderland, MA: Sinauer Associates.

Tamura K., Peterson D., Peterson N., Steccher G., Nei M. & Kumar S. 2011: MEGA5: molecular evolutionary genetic analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. – Molec. Biol. Evol. **28:** 2731–2739.

Thiers B. 2015+ [continuously updated]: Index herbariorum: a global directory of public herbaria and associated staff. – New York Botanical Garden: published at http://sweetgum.nybg.org/ih/ [accessed 29 Jan 2015].

Turland N. 2010: *Tamarix hampeana* Boiss. & Heldr. – Pp. 198–199 in: Greuter W. & Raus Th. (ed.), Med-Checklist Notulae **29.** – Willdenowia **40:** 189–204.

Tutin T. G., Heywood V. H., Burges N. A., Moore D. M., Valentine D. H., Walters S. M. & Webb D. A. (ed.) 1964–1980: Flora europaea **1–5.** – Cambridge: University Press.

Villar J. L., Alonso M. A., Juan A. & Crespo M. B. 2012: Does *Tamarix dalmatica* (*Tamaricaceae*) occur in Spain? – Anales Jard. Bot. Madrid **69:** 253–258.

Villar J. L., Alonso M. A., Juan A. & Crespo M. B. 2015: Remarks on typification of nineteen names in *Tamarix* (*Tamaricaceae*). – Nordic J. Bot. [early view: 1–10; DOI: http://dx.doi.org/10.1111/njb.00740].

Villar J. L., Alonso M. A., Vicente A., Juan A. & Crespo M. B. 2014: The genus *Tamarix* (*Tamaricaceae*) in Crete (Greece). – Willdenowia **44:** 321–326.

Appendix: *Tamarix africana* and *T. hampeana*, specimens examined

Tamarix africana (for more specimens see Villar & al. 2012)

Algeria: “Cote de Barbarie”, *Poiret* (lectotype of *Tamarix africana*, P-LA, P00287249); “*T. africana* (n.), 5. andr. 3.g. ex Numidia”, *Poiret* (syntype of *T. africana*, Herb. Poiret in Herb. Moquin-Tandon, P00166702). — Morocco: Taza-Al Hoceima, Tizi Ouasli, road R505 from Tizi Ouasli to Aknoul, 30S VD 2545 [34°44'39"N, 03°49'09"W], 1252 m, 30 Apr 2013, *Crespo, Alonso, Vicente & Villar T53MO & T54MO* (ABH69534, ABH69535); Meknes, Khenifra, From Azrou to Khenifra, Oum Rabii sources, 30S TB 748608 [33°03'44"N, 05°24'43"W], 1223 m, 1 May 2013, *Crespo, Alonso, Vicente & Villar T55MO & T56MO* (ABH69594, ABH69593); Casablanca, Mohammedia, Oued Mefifik, below the bridge of N1 road, 29S PT 548298 [33°41'48"N,07°19'47"W], 5 m, 3 May 2013, *Crespo, Alonso, Vicente & Villar T57MO & T59MO* (ABH69591, ABH69589). — Spain: Valencia, Cullera, Cap de Cullera, 30S YJ 397414 [39°11'19"N, 00°13'28"W], 4 m, 10 May 2012, *Vicente & Villar* (ABH67412, ABH67410); Almería, Vera, between Coto de Vera and Puerto Rey, 30S XG 0418 [37°12'09"N, 01°49'41"W], 4 m, 14 May 2012, *Alonso, Vicente & Villar T26AL* (ABH67465); Almería, Pulpí, beside the sea, 30S XG1639 [37°23'25"N, 01°41'22"W], 11 m, 15 May 2012, *Alonso, Vicente & Villar T35AL* (ABH69653); Almería, Pulpí, Pilar de Jaravía, 30S XG 1639 [37°19'33"N, 00°57'25"W], 84 m, 15 May 2012, *Alonso, Vicente & Villar T39AL & T42AL* (ABH69649, ABH69646); Alicante, Albatera, on the way to Rambla Salada, 30S XH 8133 [38°13'36"N, 00°55'55"W], 230 m, 18 Mar 2013, *Villar T127A, Agulló, Vicente, Quinto & Marchant* (ABH648456); Alicante, Mutxamel, Río Monnegre, Next to Riopark, 30S XH 2157 [38°27'11"N, 01°36'47"W], 105 m, 17 Apr 2013, *Moreno, Terrones & Villar* (ABH69576, ABH69568, ABH69574, ABH69564).

Tamarix hampeana

Albania: Lushnje, beside the road to Durres, 34T CL 704007 [40°38'49"N, 19°28'05"E], 7 m, 26 Apr 2011, *Martínez & Villar T4ALB* (ABH58162); Lushnje, Babujne, beside the road, 34T CL 810268 [40°53'02"N, 19°35'15"E], 9 m, 26 Apr 2011, *Martínez & Villar T5ALB* (ABH58161). — Greece: Phalère, au bord des fosses, 14 Apr 1844, *Heldreich 64* (lectotype of *Tamarix hampeana* G-BOIS G00330259); Phalareus, 1841, *Spruner*, (syntype of *T. hampeana* G-BOIS G00330260); Attica, 1842, *Spruner* (syntype of *T. hampeana* G00380106); Attica, Phalareus, 1844, *Spruner* (syntype of *T. hampeana* G00380107); Phalareus, *Spruner* (syntype of *T. hampeana* G00380108); Astros ad mare, Apr 1842, *Boissier* (syntype of *T. hampeana* G-BOIS G00330258); ad Phalerum, 1844, *Heldreich* (syntype of *T. hampeana* P06618760); Grèce Phalere, 1846, *Heldreich* (syntype of *T. hampeana* P05144597); in maritimis ad Phalerum, Apr 1844, de *Heldreich* (syntypes of *T. hampeana* G00380104, G00380104_a, G00380105, K000641864, P06618759); Attica, Apr 1844, de *Heldreich* (syntype of *T. hampeana* P06618441); Attica: in subpaludosis et ad ripas in halipedo Phaleri, 8 Apr 1847, "De Heldreich Herbarium Graecum Normale", *Heldreich* (syntype of *T. hampeana* MA78790); Attica, Phaleri, 3 Apr 1890, *Heldreich* (G); Attica ad Phalerum, 3 May 1854, *Heldreich* (PR); ad Cephissi ostia, Phalaerum, May 1856, *Heldreich* (G); Attica, in subpaludosis et ad ripas in halipedo Phaleri, 5 Apr 1893, *Heldreich 927* (G, 2 vouchers); Phaleres, Jun 1852, *W. Barbey* (G); ad Phalaerum, Jun 1852, *Heldreich* (G); in maritimis ad Phaleri, 18/30 Apr 1852, *Orphanides 318* (G); in maritimis Phaleri Atticae, 30 Mar 1852, *Orphanides* (PR); Regio aegaea orientalis, Insula Hios, ad litus orientale inter coenobium Panajia Mirtidhiotissa Mersinidhiou et pagum Virsi Passa, ad margines viae, forsan culta, 16 Apr 1976, 50 m, *Greuter* (G); Thessaloniki, in arenosis maritimis, Apr 1909, *Dimonie* (G, 2 vouchers; PR, a complex voucher with 3 *T. parviflora* and 1 *T. hampeana* branches); Zakynthos, oppidi et ad Kryonero, 28 May 1926, *Bornmüller* (G, 2 vouchers), Samos, in limosis ad ruinam templi Herae, prope Colonna, 12 Apr 1934, *K. H. Rechinger & F. Rechinger 4002* (G); Phanarion prope Porto Lagos, in arenosis maritimis, *Rechinger 22419* (G, as *T. tetrandra*); Kastades, Corfú, an der Strasse nach Gasturi in der Nähe des Hyllaeischen Hafens, 22 Apr 1896, *Baenitz* (PR); Epiro, Igoumenitsa, coastal salt marshes north-west of Igoumenitsa, 34S DJ 331738 [39°30'40"N, 20°13'19"E], 1 m, 17 Apr 2011, *Martínez & Villar T3GRE* (ABH59028); *ibid*, 34S DJ 330737 [39°30'39"N, 20°13'15"E], 5 m, 17 Apr 2011, *Martínez & Villar T4GRE* (ABH59027); *ibid*, 34S DJ 315746 [39°31'06"N, 20°12'13"E], 0 m, 17 Apr 2011, *Martínez & Villar T5GRE* (ABH59026); *ibid*, 34S DJ 311754 [39°31'32"N, 20°11'57"E], 1 m, 17 Apr 2011, *Martínez & Villar T6GRE* (ABH59025); Epiro, Ammoudia, Acherondas river delta, *Tamarix* grove between Mesopotamo and Ammoudia, 34S DJ 565436 [39°14'26"N, 20°29'46"E], 0 m, 17 Apr 2011, *Martínez & Villar T7GRE* (ABH59040); *ibid*, 34S DJ 5743 [39°14'15"N, 20°30'19"E], 0 m, 17 Apr 2011, *Martínez & Villar T8GRE & T9GRE* (ABH59039, ABH59038); *ibid*, 34S DJ 559428 [39°14'01"N, 20°29'21"E], 0 m, 17 Apr 2011, *Martínez & Villar T10GRE* (ABH59037); Epiro, Koronisia, beside the sea, 34S DJ 884231 [39°03'27"N, 20°51'57"E], 2 m, 17 Apr 2011, *Martínez & Villar T11GRE* (ABH59036); Epiro, Strongyli, *Tamarix* grove on coastal marsh, 34S DJ 840312 [39°07'48"N, 20°48'57"E], 17 Apr 2011, *Martínez & Villar T12GRE* (ABH59031); Epiro, road Strongyli-Petra, *Tamarix* grove on coastal marsh, 34S DJ 838334 [39°08'59"N, 20°48'45"E], 17 Apr 2011, *Martínez & Villar T13GRE* (ABH59032); Western Greece, Paleros, 34S DH 897919 [38°46'35"N, 20°52'56"E], 25 m, 18 Apr 2011, *Martínez & Villar T16GRE* (ABH59857); Western Greece, road from Astakos to Messolonghi, 34S EH 137610 [38°29'52"N, 21°09'29"E], 0 m, 18 Apr 2011, *Martínez & Villar T17GRE* (ABH59858); Western Greece, Aitoniko, degraded coastal *Tamarix* grove, 34S EH 303537 [38°25'54"N, 21°20'53"E], 0 m, 18 Apr 2011, *Martínez & Villar T18GRE* (ABH59859); Western Greece, Messolonghi, 34S EH 367484 [38°23'00"N, 21°25'14"E], 0 m, 18 Apr 2011, *Martínez & Villar T19GRE & T20GRE* (ABH59861, ABH59860); *ibid*, 34S EH 366485 [38°23'02"N, 21°25'11"E], 0 m, 18 Apr 2011, *Martínez & Villar T21GRE* (ABH59862); Western Greece, Kounoupelli, salt marsh beside the sea, 34S EH 307171 [38°06'06"N, 21°21'02"E], 0 m, 18 Apr 2011, *Martínez & Villar T25GRE, T26GRE & T27GRE* (ABH59863, ABH59864, ABH59865); Peloponnisos, Marathopoli, south of the town, 34S EG 5160012 [37°03'21"N, 21°34'52"E], 20 m, 19 Apr 2011, *Martínez & Villar T32GRE* (ABH58545); Peloponnisos, salt marsh close to Pylos, 34S EF 588897 [36°57'08"N, 21°39'40"E], 0 m, 19 Apr 2011, *Martínez & Villar T33GRE* (ABH58544); Peloponnisos, Itilo beach, 34S FF 241617 [36°41'34"N, 22°23'21"E], 0 m, 20 Apr 2011, *Martínez & Villar T35GRE* (ABH58622); Peloponnisos, Valtaki, *Tamarix* grove between Agios Konstantinos and Valtaki, 34S FF 4172 [36°47'21"N, 22°34'54"E], 0 m, 20 Apr 2011, *Martínez & Villar T36GRE & T37GRE* (ABH58623, ABH58624); Peloponnisos, Agios Andreas, Karakouvni, 34S FG 564356 [37°21'14"N, 22°46'00"E], 8 m, 20 Apr 2011, *Martínez & Villar T39GRE* (ABH58625); Peloponnisos, Agios Andreas beach, salt marsh, 34S FG 571387 [37°22'56"N, 22°46'28"E], 0 m, 20 Apr 2011, *Martínez & Villar T41GRE* (ABH58621); Peloponnisos, Agia Anastasia, big salt marsh near Astros, 34S FG 555391 [37°23'08"N, 22°45'26"E], 0 m, 20 Apr 2011, *Martínez & Villar T42GRE* (ABH58620); Peloponnisos, Drepano, coastal *Tamarix* grove close to Drepano, 34S FG 741541 [37°31'04"N, 22°58'13"E], 0 m, 21 Apr 2011, *Martínez & Villar T44GRE* (ABH59002); Peloponnisos, Almyri, small grove in the mouth of a ravine, 34S FG 771903 [37°50'37"N, 23°00'48"E], 0 m, 21 Apr 2011, *Martínez & Villar T49GRE* (ABH58999); Attica, Glyfada, between Glyfada and Vouliagmeni, 34S GG 430914 [37°50'17"N, 23°45'44"E], 5 m, 22 Apr 2011, *Martínez & Villar T52GRE* (ABH59049); Attica, Saronida, 34S GG 522877 [37°48'07"N, 23°51'56"E], 3 m, 22 Apr 2011, *Martínez & Villar T55GRE* (ABH59016); Attica, Lavriou, degraded coastal *Tamarix* grove, 35S KB 403788 [37°43'11"N, 24°03'15"E], 9 m, 22 Apr 2011, *Martínez & Villar T61GRE* (ABH59051); Central Greece, Dilesi, beside the sea, 34S GH 378467 [38°20'14"N, 23°43'16"E], 6 m, 22 Apr 2011, *Martínez & Villar T65GRE* (ABH59021); Central Greece, Neo Thronio, *Tamarix* grove 200 m south of Camping Venezuela, 34S FH 494986 [38°49'27"N, 22°43'18"E], 9 m, 23 Apr 2011, *Martínez & Villar T66GRE, T67GRE, T68GRE, T69GRE & T70GRE* (ABH59875, ABH59871, ABH59872, ABH59873, ABH59874); Central Greece, Neo Thronio, 1 km north of Camping Venezuela, 34S FH 478997 [38°50'03"N, 22°42'12"E], 6 m, 23 Apr 2011, *Martínez & Villar T72GRE* (ABH59877); Central Greece, Anthili, in a river floodplain, 34S FJ 302025 [38°51'44"N, 22°30'05"E], 12 m, 23 Apr 2011, *Martínez & Villar T75GRE* (ABH59866); Thessalia, Nees Pagases, small grove close to Volos, 34S FJ 664551 [39°19'46"N, 22°55'52"E], 0 m, 23 Apr 2011, *Martínez & Villar T77GRE* (ABH59870); Central Macedonia, Limenas, degraded *Tamarix* grove, 34T FK 334498 [40°11'18"N, 22°34'2"E], 23 Apr 2011, *Martínez & Villar T78GRE & T79GRE* (ABH59868, ABH59869); Central Macedonia, Methoni, Aliakmona river delta, 34T FK 364833 [40°29'22"N, 22°36'34"E], 8 m, 24 Apr 2011, *Martínez & Villar T81GRE* (ABH59867). — MONTENEGRO: Ulcinj, Sveti Nikola, *Tamarix* grove in the Bojana river mouth, in the northern branch of the river, close to the Albanian border, 34T CM 632367 [41°52'16"N, 19°21'09"E], 27 Apr 2011, *Martínez & Villar T2MNE, T3MNE, T4MNE & T5MNE* (ABH57893, ABH57891, ABH57890, ABH57892). — TURKEY: Marais sales situés sur les bords de la route conduisant de Smyrne à Vorula, à 2 lieues environ à l'est de cette première ville, 29 May 1854, *Balansa 130* (type of *T. hampeana* var. *smyrnea* G-BOIS; G, 2 vouchers); "Constantinopla", 1845, *Noë* (G-BOIS, ut *T. parviflora*); Golfe de Smyrne, Echelle de Papa, 24 Apr 1854, *Balansa 133* (type of *T. hampeana* var. *composita*, G); Aydın, Söke, B. Menderes Agli, Avlon merlii, denis kendri, 10 Apr 1976, *Uslu 4173* (G); Trockenes Bachbett, Aydın, Samsun Daği bei Güzelçlami, 8 Apr 1990, *Nydegger* (G440247).

Anexo:

Artículos no publicados

Artículo 8

Villar J. L., Juan A., Alonso M. A., Gaskin J. F. & Crespo M. B. 2015. Preliminary phylogeny of the genus *Tamarix* (Tamaricaceae) with a focus on the Mediterranean taxa.

Preliminary phylogeny of the genus *Tamarix* (Tamaricaceae), with a focus on the Mediterranean taxa.

J. L. Villar, M. A. Alonso, A. Juan, J. F. Gaskin & M. B. Crespo.

Abstract

The genus *Tamarix* is one of the most taxonomically complex among the angiosperms, and previous classification attempts have had both strengths and weaknesses. Here we present the most complete phylogenetic work conducted on the genus to date. This includes a nuclear DNA phylogenetic tree, based on ITS and a plastidial DNA phylogeny, based on three intergenic spacers (*trnS-trnG, ndhF-rpl32* and *trnQ-rps16*). In total, both phylogenetic approaches included more than 70 samples from 36 species and 27 countries. Two smaller trees, based only on one plastidial marker, were also included. The first, based on *trnS-trnG*, was used to increase the number of studied species with strong amplexicaul leaves and twice the number of stamens than sepals. The second, based on *ndhF-rpl32,* was used to check the separation between *T. tetrandra* and *T. parviflora*. In combination, these trees produced interesting results. The contradiction between the infrageneric classification and the molecular results is confirmed once again. A reticulate evolution is inferred from the trees, allowing characters such as vaginate leaves to appear at different stages along the evolutionary pathway 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 considered to be *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 unresolved, and additional studies will be needed further refine the complex taxonomy of *Tamarix.*

Introduction

Tamarix L. (Tamaricaceae Link) comprises tall shrubs or trees of up to 5-6 m height, although some species as *T. aphylla* (L.) Karst. may reach heights of close to 20 m under favorable conditions. The *Tamarix* species have green, light brown, reddish brown, dark brown or black branches. The *leaves* are deciduous, marcescent or perennial, presenting diverse shapes that usually fall into three categories: vaginate, surrounding the twigs all along the limb, or pseudo-vaginate, with a visible scar along the contact of both leaf sides; amplexicaul, deltoid shaped, thick and broader than longer, embracing more than half the twig or even clasping or scale-like, or triangular lanceolate, only the lower half amplexicaul; scale-like, lanceolate, with slightly decurrent narrow base or wide auriculate base, not embracing more than half of the twig. Intermediate forms can also be found. The *inflorescences* are formed by pedunculate racemes arranged in diverse structures: solitary, fasciculate, in simple panicles or in compound panicles. Some species may show variation in raceme arrangements at different flowering periods over the year (Baum 1978, Yang & Gaskin 2007). The *raceme peduncles* vary from naked to densely covered with bracts. *Bracts* can be up to 8 mm long, usually one per flower, although accessory bracts are present in certain species (Villar & al. 2012). The *sepals* 4-5 (9), 0.5-4 mm long, show diverse shapes from triangular-lanceolate to widely orbicular. The *petals* 4-5 (9), 1-4 (8) mm long, present diverse shapes, and 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 in 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 instead. The *gynoecium* is usually formed of three carpels, sometimes four, exceptionally five or more. The *styles* are free, clavate or club shaped, equal in number to the carpels. The *fruits* are dry capsules, dehiscent by 3 (4) valves open at maturity, 3-15 mm long. 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.

Tamarix species are native to Africa and Eurasia, inhabiting mainly desertic, sub-desertic or arid zones, but also in freshwater riparian habitats in temperate or subtropical regions (Qaiser 1981, Zohary 1987). It is widespread in the Mediterranean, Irano-Turanian and Indian regions, where the highest number of species, and the two main diversity centers (East Mediterranean and Indo-Turanian, sensu Baum 1978), are found (Baum 1978, 1990, Villar & al. 2014a). From those two centers, *Tamarix* has reached the Eurasian parts of the Circumboreal region, as well as the Indochinean, Eastern Asiatic, Saharo-Arabian, Sudano-Zambezian, Karoo-Namib and Macaronesian regions (names according to Takhtajan 1986) (Baum 1978).

Secondarily, some species (e.g. *T. aphylla, T. ramosissima* Ledeb.) have been naturalized in Oceania (Csurhes 2008) and America, where they were introduced as ornamentals in the 19th century (Prince & sons nursery catalogue 1837, Warner Harper 1903). In the last decades, many works have dealt with the invasive potential of *Tamarix,* particularly in North America, where it has been considered as the second worst plant invasion in the U.S.A. (Baum 1967, Di Tomaso 1998, Stromberg 1998, Gaskin & Schaal 2003, Villar & al. 2014a).

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), Desvaux (1824), Marshall Bieberstein (1808), Ledebour (1829, 1843), Candolle (1828), Webb & Berthelot (1840), Walpers (1843), Bunge (1833, 1851) or Boissier (1849, 1856, 1867), added new species to the genus, or dealt with its taxonomical classification in different geographic areas. Desvaux (1824) was the first to separate the genus *Myricaria* Desv. from *Tamarix.* Also in the 19th century, Willdenow (1812), Ehrenberg (1827), Bunge (1852) and Niedenzu (1895) monographed the genus *Tamarix* with the available information at that time, typically adding some new taxa or remarkable information about morphology, synonyms, or infrageneric divisions.

During the 20th century, the number of taxa continued to increase, particularly on account of local treatments (Freyn 1903, Maire 1931, 1935, 1938, Pau 1906, 1922, Sennen 1932, 1934). Afterwards, Gorschkova (1949) made a remarkable contribution on the Central-Asian species, translated into English by Shinners (1957). Baum (1966) published the last monograph dealing with the whole genus, later re-edited and published with minor modifications (Baum 1978). The monograph included almost every *Tamarix* name published, by that date, with specific and infraspecific ranks, accepting 54 species arranged in three sections and nine series. This work is still considered a key reference for the genus *Tamarix* worldwide, and has been the taxonomical base for most of the local and regional treatments of *Tamarix* (Pignatti 1982, Cirujano 1993, Salazar 2009, De Martis & al. 1984, 1986, Venturella & al. 2007), with certain exceptions (Qaiser 1981, Zieliński 1994, Yang & Gaskin 2007). However, recent molecular studies (Gaskin & Schaal 2003, Villar & al. 2015a) have demonstrated that some of the divisions proposed by Baum (1978) were unnecessary. Despite the numerous taxonomic revisions carried out in the last two centuries, *Tamarix* has been always considered a particularly difficult genus among the angiosperms (Bunge 1852, Baum 1978). Many groups of species are separated by small phenotypic differences, some of which may only be seasonally apparent, and therefore, accurate identification is very difficult (Villar & al. 2012, 2014b, 2015a). This has resulted in a highly unresolved taxonomy, with a large number of synonyms and combinations between more than 200 taxa, at specific and infraspecific ranks, that have been described to date (Villar & al. 2012a, 2015b). Therefore, no general consensus on the number of accepted species has been reached, with such different estimations as the 54 accepted by Baum (1966, 1978) and the “about 90” suggested by Zohary (1987) or Yang and Gaskin (2007). Of course Baum (1966) could not check the validity of the 13 species (at least) that were described after the publication of his monograph (Baum 1968, Qaiser 1981, Liu 1979, Zhang & Liu 1988, Çakan & Zieliński 2004, Villar & al. 2015a).

Recently, some molecular techniques have been used to deal with the taxonomy of *Tamarix.* However, most of these efforts have been 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 & al. 2015). Recently, plastid phylogenetic data were also used to identify new species of *Tamarix* (Villar & al. 2015a). Some of the aforementioned works have already shown important preliminary results, for example that the series and sections proposed by Baum (1978) would not correspond to natural groups (Gaskin & Schaal 2003, Villar & al. 2015a). However, these studies are incomplete without the integration of most of the species of the genus. In this study, we examined representatives covering all sections of *Tamarix* to disentangle the phylogenetic history of this genus using nuclear and plastid DNA regions, with special focus on the Mediterranean area.

This represents one of the most complete molecular phylogeneis of *Tamarix* conducted so far. The main aims of our study were to: (1) establish a phylogeny of *Tamarix* in order to evaluate the correctness and utility of present classification systems, (2) detect the weakest points in the taxonomy of the genus, as a tool to point out possible future research lines, (3) assess the value of the morphological characters used in classification and systematics of *Tamarix*.

Materials and methods

Taxon sampling. A total of 40 species were sampled, representing most of the higher taxonomic units above species level that have been proposed in the Tamaricaceae to date. Our samples also represented most of the geographical range of the family (Table 1). 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, 2008+), which were properly marked on the herbarium sheets by the respective curators. Newly collected field specimens are kept at ABH, MO and the John F. Gaskin personal herbarium (MT, U.S.A.) (Table 1).

To assure their taxonomic identity, all of the sequenced specimens have been directly examined by the authors. Many studies dealing with the taxonomy of *Tamarix* were consulted (Linné 1753, Poiret 1789, Loureiro 1790, Pallas 1789, Willdenow 1816, Desvaux 1824, Ehrenberg 1827, Ledebour 1829, 1843, Candolle 1828, Boissier 1849, 1867, Bunge 1851, 1852, Niedenzu 1895, Gorschkova 1949, Baum 1966, 1968, 1978, Qaiser 1981, Zohary 1987, Zieliński 1994, Cirujano 1993, Yang & Gaskin 2007, Salazar & Quesada 2009, Villar & al. 2012, 2014a, 2014b, 2014c, 2014d, 2015a, 2015b, Samadi & al. 2013), including original descriptions, treatments in local floras and taxonomic papers. Moreover, herbaria material from ABH, BCMEX, BM, G, HUAL, JAEN, K, MA, MO, MPU, P, PR, PRC VAL and W were also consulted (over 2500 specimens), with special attention to type material. Outgroup specimens correspond to the species *Reaumuria alternifolia* (Labill.) Britten, *Myricaria bracteata* Royle and *Myrtama elegans* (Royle) Ovcz. & Linzik., all of which belong to Tamaricaceae*.*

Table 1. Materials used in the molecular analyses *(only in small single region trees)

Label on Figures	Taxon	Origin	Voucher	*trnS-trnG*	*trnQ-rps16*	*ndhF-rpl32*	ITS
Myricaria bracteata	*Myricaria bracteata* Royle	Kazajstan	*Gaskin 1148*	X	X	X	X
Myrtama elegans	*Myrtama elegans* (Royle) Ovcz. & Kinzik.	China	MO5799414	X	X	X	X
Reaumuria alternifolia	*Reaumuria alternifolia* (Labill.) Britten	Iran	*Gaskin 919*	X	X	X	X
T. africana T13Mo	*Tamarix africana* Poir.	Morocco	ABH54205	X	X	X	X
T. africana T17CRO	*Tamarix africana* Poir.	Croatia	ABH57846	X	X	X	X
T. africana T1Ge	*Tamarix africana* Poir.	Spain	ABH55078	X	X	X	X
T. africana T2To	*Tamarix africana* Poir.	Spain	ABH55362	X	X	X	X
T. africana T2V	*Tamarix africana* Poir.	Spain	ABH55366	X	X	X	X
T. africana T30CD	*Tamarix africana* Poir.	Sardinia (Italy)	ABH54439	X	X	X	X
T. amplexicaulis T24AG	*Tamarix amplexicaulis* Ehrenb.	Algeria	ABH70685	X	X	X	X
T. amplexicaulis T25AG	*Tamarix amplexicaulis* Ehrenb.	Algeria	ABH70686	X	X	X	X
T. amplexicaulis T26AG	*Tamarix amplexicaulis* Ehrenb.	Algeria	ABH70687	X	X	X	X
T. amplexicaulis T27AG	*Tamarix amplexicaulis* Ehrenb.	Algeria	ABH70688	X	X	X	X
T. androssowii JG871	*Tamarix androssowii* Litv.	Iran	MO5568887	X	X	X	-
T. androssowii W08-98	*Tamarix androssowii* Litv.	Armenia	W2008-05598	X	X	X	X
T. aphylla TA1Mo	*Tamarix aphylla* (L.) H. Karst	Morocco	ABH54280	X	X	X	X
T. aphylla TACD	*Tamarix aphylla* (L.) H. Karst	Sardinia (Italy)	ABH54422	X	X	X	X
T. arabica P359	*Tamarix arabica Bunge*	Yemen	P05113359	-	-	-	X
T. arabica P360	*Tamarix arabica Bunge*	Yemen	P05113360	-	-	-	X
T. arborea W06-39	*Tamarix arborea* (Sieber ex Ehrenb.) Bunge	Egypt	W2006-12039	X	X	X	X
T. arborea W06-41	*Tamarix arborea* (Sieber ex Ehrenb.) Bunge	Egypt	W2006-12041	-	-	-	X
T. arceuthoides JG825	*Tamarix arceuthoides* Bunge	Iran	MO5568891	X	X	X	X
T. arceuthoides JG846	*Tamarix arceuthoides* Bunge	Iran	MO5568908	-	-	-	X
T. aucheriana JG850	*Tamarix aucheriana* (Decne. ex Walp.) B.R. Baum	Iran	MO5568836	X*	-	-	-
T. austromongolica JG10163	*Tamarix austromongolica* Nakai	China	*Gaskin 10163*	X	X	X	X

Label on Figures	**Taxon**	**Origin**	**Voucher**	*trnS-trnG*	*trnQ-rps16*	*ndhF-rpl32*	ITS
T. boveana T18Mo	*Tamarix boveana* Bunge	Morocco	ABH54183	X	X	X	X
T. boveana T2Gr	*Tamarix boveana* Bunge	Spain	ABH55339	X	X	X	X
T. boveana T7AG	*Tamarix boveana* Bunge	Algeria	ABH56326	X	X	X	X
T. boveana Tb2Eb	*Tamarix boveana* Bunge	Spain	ABH54330	X	X	X	X
T. canariensis Gara	*Tamarix canariensis* Willd.	Tenerife (Spain)	ABH53701	X	X	X	-
T. canariensis Gui	*Tamarix canariensis* Willd.	Tenerife (Spain)	ABH53707	X	X	X	-
T. canariensis TGC1	*Tamarix canariensis* Willd.	Gran Canaria (Spain)	ABH69605	X	X	X	X
T. canariensis TGC8	*Tamarix canariensis* Willd.	Gran Canaria (Spain)	ABH69599	X	X	X	X
T. chinensis JG202	*Tamarix chinensis* Lour.	South Korea	*Gaskin 202*	X	X	X	X
T. dalmatica T1ALB	*Tamarix dalmatica* B.R. Baum	Albania	ABH57830	X	X	X	X
T. dalmatica T6MNE	*Tamarix dalmatica* B.R. Baum	Montenegro	ABH57844	X	X	X	X
T. elongata JG10176	*Tamarix elongata* Ledeb.	China	*Gaskin 10176*	X	X	X	X
T. gallica T23Ken	*Tamarix gallica* L.	Morocco	ABH69587	X	X	X	X
T. gallica T2Fr	*Tamarix gallica* L.	France	ABH57865	X	X	X	X
T. gallica TC1Eb	*Tamarix gallica* L.	Spain	ABH54331	X	X	X	X
T. gansuensis JG10171	*Tamarix gansuensis* H.Z. Zhang ex P.Y. Zhang & M.T. Liu	China	*Gaskin 10171*	X	X	X	X
T. gracilis JG10173	*Tamarix gracilis* Willd.	China	*Gaskin 10173*	X	X	X	X
T. hampeana T2MNE	*Tamarix hampeana* Boiss. & Heldr.	Montenegro	ABH57893	X	X	X	X
T. hampeana T3MNE	*Tamarix hampeana* Boiss. & Heldr.	Montenegro	ABH57891	X	X	X	X
T. hampeana T6GRE	*Tamarix hampeana* Boiss. & Heldr.	Greece	ABH59025	X	X	X	X
T. hampeana T72GRE	*Tamarix hampeana* Boiss. & Heldr.	Greece	ABH59877	X	X	X	X
T. hispida lvl	*Tamarix hispida* Willd.	Kazajstan	MO sn	X	X	X	X
T. hispida JG10164	*Tamarix hispida* Willd.	China	*Gaskin 10164*	X	X	X	X
T. hohenackeri JG828	*Tamarix hohenackeri* Bunge	Iran	MO5568893	X	X	X	-
T. hohenackeri W08-42	*Tamarix hohenackeri* Bunge	Georgia	W2008-21042	X	X	X	-

Label on Figures	**Taxon**	**Origin**	**Voucher**	*trnS-trnG*	*trnQ-rps16*	*ndhF-rpl32*	ITS
T. indica W67-10	*Tamarix indica* Willd.	Pakistan	W1967-1110	X	X	X	X
T. karelinii JG10161	*Tamarix karelinii* Bunge	China	*Gaskin 10161*	X	X	X	X
T. karelinii JG144	*Tamarix karelinii* Bunge	China	*Gaskin 144*	X	X	X	-
T. kermanensis W83-21	*Tamarix kermanensis* B.R. Baum	Iran	W1983-09221	X	X	X	X
T. komarovii JG1059	*Tamarix komarovii* Gorschk.	Turkmenistan	*Gaskin 1059*	X*	-	-	-
T. laxa G-russ	*Tamarix laxa Willd.*	Russia	G sn	-	-	-	X
T. leptostachya lvl	*Tamarix leptostachya* Bunge	Kazajstan	MO sn	X	X	X	X
T. leptostachya JG1158	*Tamarix leptostachya* Bunge	Kazajstan	*Gaskin 1158*	X	X	X	X
T. leptostachya JG10177	*Tamarix leptostachya* Bunge	China	*Gaskin 10177*	X	X	X	X
T. macrocarpa W07-67	*Tamarix macrocarpa* Ehrenb. ex Bunge	Egypt	W2007-14067	X	X	X	X
T. minoa NT	*Tamarix minoa* J.L. Villar & al.	Crete (Greece)	MO6207620	X	X	X	X
T. minoa T2CR	*Tamarix minoa* J.L. Villar & al.	Crete (Greece)	ABH54194	X	X	X	X
T. minoa T4CR	*Tamarix minoa* J.L. Villar & al.	Crete (Greece)	ABH54195	X	X	X	X
T. nilotica TCR14	*Tamarix nilotica* (Ehrenb.) Bunge	Crete (Greece)	ABH54320	X	X	X	X
T. nilotica TCR5	*Tamarix nilotica* (Ehrenb.) Bunge	Crete (Greece)	ABH54317	X	X	X	X
T. nilotica W07-05	*Tamarix nilotica* (Ehrenb.) Bunge	Egypt	W2007-25805	X	X	X	-
T. nilotica W07-26	*Tamarix nilotica* (Ehrenb.) Bunge	Egypt	W2007-25726	X	X	X	-
T. octandra lvl	*Tamarix octandra* Bunge	Kazajstan	MO sn	X	X	X	X
T. octandra JG189	*Tamarix octandra* Bunge	Russia	MO04992086	-	-	-	X
T. octandra MO-07	*Tamarix octandra* Bunge	Russia	MO05044107	X	X	X	-
T. parviflora T8CR	*Tamarix parviflora* DC.	Crete (Greece)	ABH54197	X	X	X	X
T. parviflora TCR10	*Tamarix parviflora* DC.	Crete (Greece)	ABH54321	X	X	X	X
T. pycnocarpa JG1100	*Tamarix pycnocarpa* DC.	Turkmenistan	*Gaskin 1100*	X*	-	-	-
T. ramosissima W09-43	*Tamarix ramosissima* Ledeb.	Argentina	W2009-19143	X	X	X	X
T. senegalensis K242	*Tamarix senegalensis* DC.	Senegal	K-DNA-38242	-	-	-	X

Label on Figures	**Taxon**	**Origin**	**Voucher**	*trnS-trnG*	*trnQ-rps16*	*ndhF-rpl32*	ITS
T. senegalensis P240	*Tamarix senegalensis* DC.	Senegal	P05113240	X	X	X	X
T. smyrnensis JG4690	*Tamarix smyrnensis* Bunge	Turkey	Mo sn	X	X	X	X
T. smyrnensis JG4691	*Tamarix smyrnensis* Bunge	Turkey	MO sn	-	-	-	X
T. smyrnensis W03-43	*Tamarix smyrnensis* Bunge	Armenia	W2003-14043	X	X	X	X
T. taklamakanensis JG10172	*Tamarix taklamakanensis* M.T. Liu	China	*Gaskin 10172*	X	X	X	X
T. tetragyna W07-28	*Tamarix tetragyna* Ehrenb.	Egypt	W2007-25728	X	X	X	X
T. tetragyna W07-48	*Tamarix tetragyna* Ehrenb.	Egypt	W2007-14048	X	X	X	X
T. tetrandra G-Beli	*Tamarix tetrandra* Pall. ex M.Bieb.	Ukraine	G sn	-	-	X*	-
T. usneoides T1NMB	*Tamarix usneoides* E. Mey.	Namibia	ABH58684	X	X	X	X
T. usneoides TSA7	*Tamarix usneoides* E. Mey.	South Africa	ABH58683	X	X	X	X

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, U.S.A.) 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 & al. 2007)*, trnS-trnG* (Hamilton 1999) and *ndhF-rpl32* (Shaw & al. 2007). The nuclear ITS (Internal Transcribed Spacer) region was amplified for 69 *Tamarix* specimens using the primers ITS4 and ITS5 (White & al. 1990). Due to amplification problems, the amplified samples for plastid and nuclear DNA are not identical. In addition, two detailed phylogenies based on single plastidial regions were conducted to get a clearer insight into two specific topics that could not be resolved in the main phylogenetic trees due to amplification problems with some of the samples. The first one, 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. Therefore, 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, based on *ndhF-rpl32,* included 11 *Tamarix* specimens and aimed to deal with the relationship between the species *T. parviflora* DC. and *T. tetrandra* Pall. ex M. Bieb., whose taxonomic identities have been considered either as mere synonyms or as independent taxa, (e.g. Baum 1978, Zieliński 1994, Dimopoulos & al. 2013, Villar & al. 2014b). Other than *T. tetrandra* and *T. parviflora, T. aphylla* and *T. africana* Poir. would represent external groups as reflected in the large cpDNA 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.* Other accessions initially included in trees previous to this final version (*T. boveana* Bunge*, T. tetragyna* Ehrenb.*, T. elongata* Ledeb.) were finally removed, as they made no contribution to the *T. tetrandra-T. parviflora* issue and may have proved a distraction..

For all regions, PCR amplifications were performed in a reaction volume of 25 µl, containing 22.5 µl ABGene 1.1x Master Mix, 2.5 mM $MgCl_2$ (Thermo Scientific Waltham, MA, U.S.A.), 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 for 2 min, followed by 35 cycles of 94°C (1'15"), 55°C (1'30"), and 72°C (2'), with a final elongation at 72°C for 10 min. The profile used for ITS was an initial denaturation of 94ºC (2') followed by 30 cycles of 94ºC (1'), 53ºC (1') and 72ºC (1'), with a final elongation at 72ºC for 5 min. PCR products were purified using Ultraclean® PCR Clean-Up Kit (MOBIO, Carlsbad, CA, U.S.A.) mini-columns, following the manufacturer's indications. Both strands were sequenced with the same primers for each region, and for all samples, at the Macrogen Europe Laboratory (www.macrogen.com).

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.

Sequencher 4.1 (Gene Codes Corp., Ann Arbor, MI, U.S.A.) was used to assemble the complementary strands. Each matrix was aligned using ClustalW, conducted in MEGA 5.05 (Tamura & al. 2011). Minor manual corrections were made to get the final alignments. Maximum parsimony analyses (MP) and Bayesian analyses were performed on the combined plastidial and nuclear matrixes, as well as on the smaller single cpDNA region matrixes. In the case of the large nDNA and cpDNA 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 & al. 2003). Given the long branches observed in the basal groups of cpDNA analyses, we suspect that this affinity could be the result of a long-branch attraction artefact. To evaluate this possibility, we followed the strategy described by Bergsten (2005), by re-running MP analyses (data not shown). In all MP analyses, gaps were treated as missing, thus avoiding long-branch attraction artefacts that were especially notable in the cpDNA phylogeny.

In the case of the two smaller 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 & al. 2012). The most accurate evolutionary models required for Bayesian estimation were selected for every plastidial and nuclear DNA matrixes. In the case of the plastid combined matrix, models were selected individually for each of the three regions included. Model selection was undertaken by using the AICc (Akaike Information Criterion) (Posada & Crandall 1998, Posada & Buckley 2004), in JMODELTEST 2.1.5 (Darriba & al. 2012). Model parameters were included in MrBayes presets before running each of the analyses. In the case of the combined plastidial DNA matrix, different model parameters were included for the matrix fragments corresponding to each cpDNA region. Two simultaneous and independent analyses were performed for each analysis. For the combined plastid matrix, the Markov Chain Monte Carlo chains (MCMC) were run for 10×10^6 generations and sampled every 1000 generations. For the nuclear matrix, the MCMC chains were run for 5×10^6 generations and sampled every 500 generations. For the small cpDNA matrixes, the MCMC chains were run for 2×10^6 generations and sampled every 200 generations. For all the analyses, 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 as weakly supported, 0.86-0.95 PP moderately supported and 0.96-1.0 PP strongly supported.

Topological incongruence. A congruence ILD test was performed in PAUP v. 4.0b10 (Swofford 2002), using heuristic search options, between the cpDNA and nDNA datasets, resulting in significant differences (p=0.01). 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.

Results

The ILD test comparing nuclear and plastid datasets indicated significant incongruence (p=0.01). Therefore, independent phylogenetic analyses were performed for ITS and combined plastid datasets. While the topologies of nuclear and plastid phylogenies are significantly incongruent, *Tamarix* was resolved as robustly monophyletic in all trees, and the previously proposed sections and series (based on morphology) do not correspond to monophyletic groups (Figures 1 and 2). Detailed alignment and sequence information for the analysed regions, and tree statistics from the phylogenetic analyses are described in Table 2.

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)
	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 analyses	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	Each region its model	TPM1uf+G	GTR+G

nDNA phylogeny

MP and Bayesian analyses produced trees with similar topologies (Figure 1). The *Tamarix* accessions were arranged in four well-supported monophyletic clusters (Clades A, B, C and D). The phylogenetic relationships among them are not adequately resolved, and their phylogenetic position appeared to be collapsed or weakly supported by MP or BI.

The Clade A includes two vaginate-leaved species, *T. aphylla* and *T. usneoides* E. Mey., which are strongly supported (BS 100/PP 1.00). The Clade B groups the species *T. minoa* J.L. Villar & al. and *T. dalmatica* B.R. Baum (BS 100/PP 1.00), although their phylogenetic relationships appear collapsed. Similarly, the Clade C is highly supported (BS 98/PP 1.00), including *T. canariensis* Willd. and *T. africana.* These species do not form two independent monophyletic clades, since *T. canariensis* appears totally embedded among *T. africana* accessions. The remaining *Tamarix* species are grouped in Clade D (BS 81/PP 0.84), whose basal phylogenetic relationships appear mostly unresolved. The species *T. hispida* Willd. conforms to a monophyletic clade (BS 93/PP 0.99; subgroup D1) and the position of *T. karelinii* Bunge is not supported (D2). The subgroup D3 comprises all the accessions of *T. amplexicaulis* Ehrenb. (BS 64/PP 0.98), as *T. macrocarpa* Ehrenb. ex Bunge (BS 84/PP 0.99) and *T. aucheriana* (BS 61/PP 0.96) sister branches, respectively. This clade is well characterised by the presence of strongly amplexicaul leaves and twice the number of stamens than sepals. The largest subgroup D4 is highly supported by BI (PP 0.97), but not by MP (BS 52). Most of the internal phylogenetic relationships also appear unresolved. The best supported cluster by both phylogenetic analyses corresponds to *T. boveana* - *T. gallica* L. - *T. tetragyna* clade (BS 98/PP 1.00), but their phylogenetic positions are totally collapsed. Another well-supported clade (BS 89/PP 1.00) includes all of the studied accessions of *T. smyrnesis* Bunge as a clear monophyletic group (BS 67/PP 1.00), together with *T. chinensis* Lour., *T. austromongolica* Nakai, *T. ramossisima* and *T. taklamakanensis* M.T. Liu, whose phylogenetic position appears unresolved.

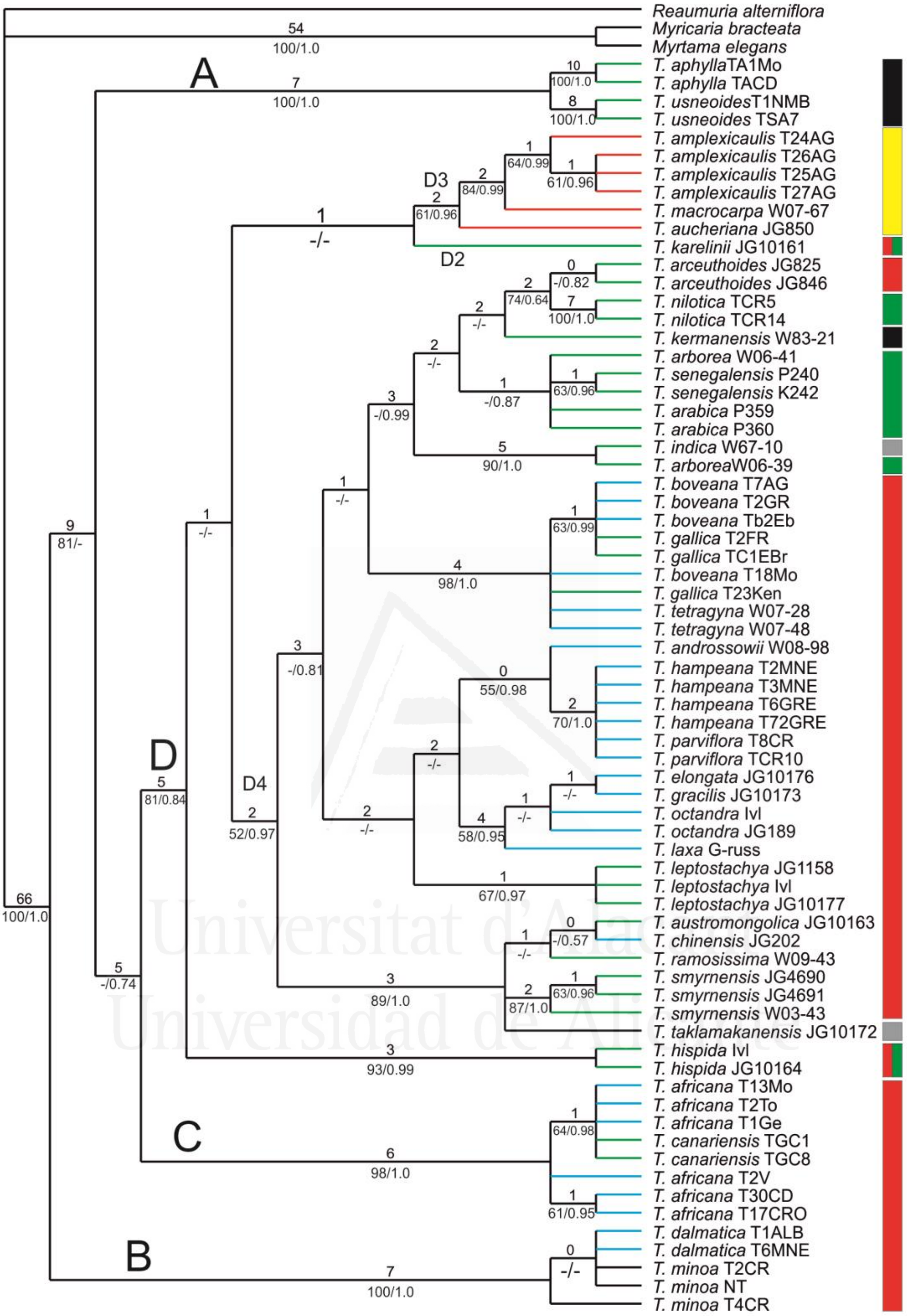

Figure 1. One of the 10 most-parsimonious trees obtained in the second MP heuristic search, based on the ITS matrix. Steps are shown above branches. Maximum parsimony bootstrap support (BS) and Bayesian posterior probability (PP) are shown below branches (BS/PP). Colored branch tips refer to Baum's sections (1978): — *T.* section *Tamarix,* — *T.* section *Oligadenia,* — *T.* section *Polyadenia,* — no section assigned. Vertical bars refer to leaf shape: 🟥 sessile with narrow base; 🟩 triangular-lanceolate with amplexicaul base; 🟨 full amplexicaul; ▨ pseudo-vaginate; ⬛ vaginate.

The Bayesian analysis highly supported a large clade (PP 0.99), where the accessions of *T. arceuthoides* Bunge, *T. nilotica* (Ehrenb.) Bunge and *T. senegalensis* DC. form monophyletic supported clusters, 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 0.67). The species *T. leptostachya* Bunge groups in a monophyletic cluster (BS 67/PP 0.97). The species *T. androssowii*, *T. hampeana* and *T. parviflora* group in another cluster (PP 0.85). The phylogenetic relationships between *T. hampeana* and *T. parviflora* are unresolved (BS 70/PP 1.00), whereas *T. androssowii* is an external sister group (BS 55/PP 0.98). Finally, the species *T. elongata*, *T. gracilis* Willd., *T. octandra* and *T. laxa* Willd. were clustered together (BS 58/PP 0.95), although their phylogenetic relationships were totally collapsed.

cpDNA phylogeny

Bayesian and MP analyses displayed similar topologies (Figure 2). In this case, the *Tamarix* accessions were arranged in five well-supported clusters (Clades 1, 2, 3, 4 and 5).

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

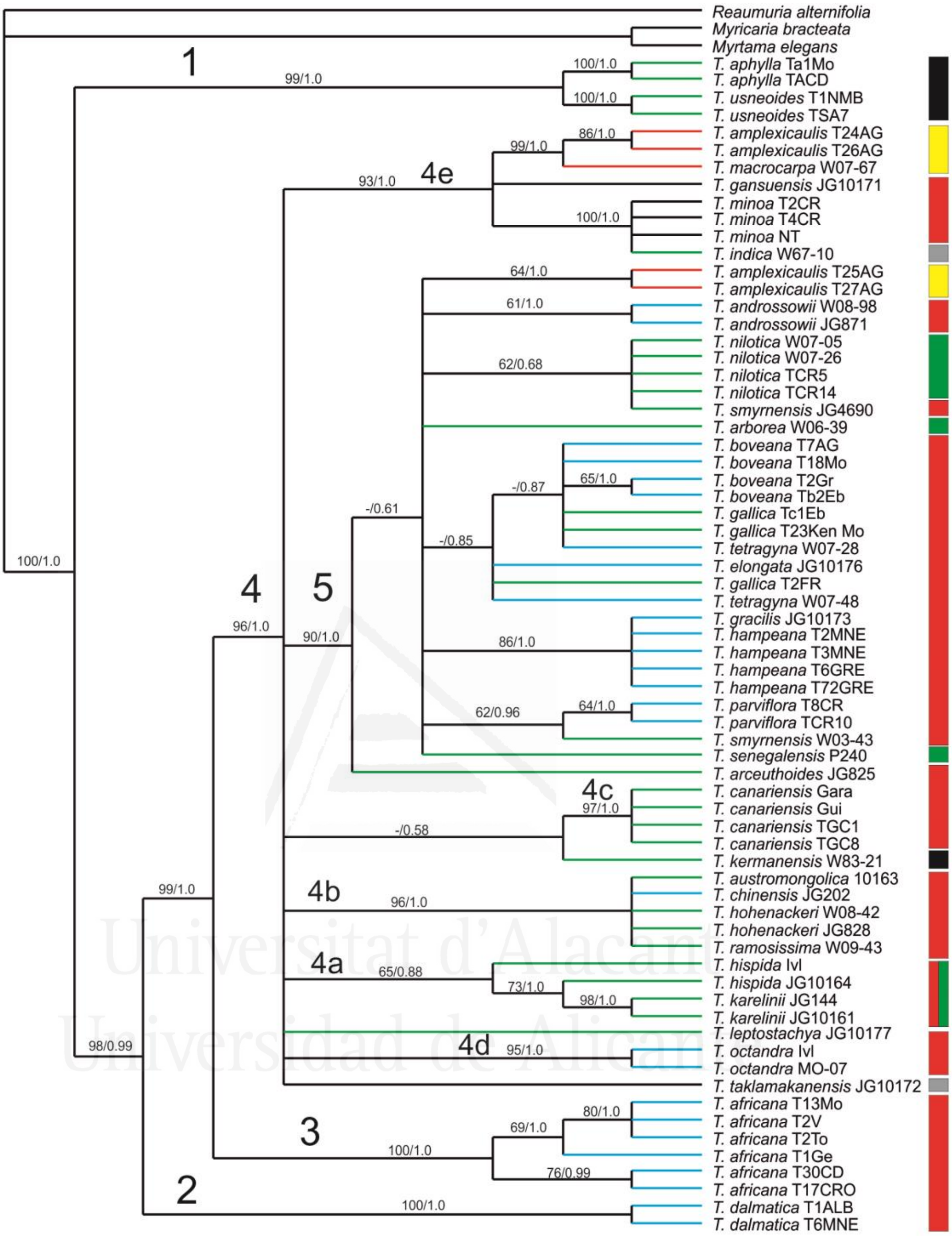

Figure 2. Strict consensus tree obtained from the 10 MP trees obtained in the second heuristic search, based on the combined plastid matrix. Maximum parsimony bootstrap support (BS) and Bayesian posterior probability (PP) are shown above branches (BS/PP). Colored branch tips refer to Baum's sections (1978): — *T.* section *Tamarix,* — *T.* section *Oligadenia,* — *T.* section *Polyadenia,* — no section assigned. Vertical bars refer to leaf shape: 🟥 sessile with narrow base; 🟩 triangular-lanceolate with amplexicaul base; 🟨 full amplexicaul; ▨ pseudo-vaginate; ⬛ vaginate.

The Clade 4 includes all of the remaining *Tamarix* species (BS 96/PP 1.00), whose basal phylogenetic relationships appear totally unresolved, though several clades show a strong support. The species *T. hispida* and *T. karelinii* group together in subclade 4a (BS 65/PP 0.88), where the *T. karelinii* accessions form a monophyletic group (BS 98/PP 1.00), and the accessions of *T. hispida* are sister branches. The 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 totally unresolved. Subclade 4c gives a strong support (BS 97/PP 1.00) to the accessions of *T. canariensis,* as is also 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 is formed by *T. macrocarpa* and two of the four studied accessions 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 unresolved; 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 appear to be collapsed.

Due to its inclusion within Clade 4, the large and well-supported Clade 5 (BS 90/PP 1.00) has been named independently given the considerable number of accessions included in it. Within Clade 5, the phylogenetic relationships among the obtained groups and branches appear collapsed. The clade with the strongest MP and PP support is formed by *T. hampeana* and *T. gracilis* (BS 86/PP 1.00), 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 the studied accessions of *T. nilotica* and one of the two *T. smyrnensis* accessions are clustered together but with a very weak support (BS 62/PP 0.68). The single accessions of *T. arceuthoides, T. senegalensis* and *T. arborea* appear as independent branches, respectively. Finally, the largest clade is only weakly supported by PP (0.85), including all of the analysed accessions of *T. boveana, T. elongata, T. gallica* and *T. tetragyna.* It is remarkable that none of these species have clustered as independent monophyletic groups, and their relationships are totally collapsed.

Detailed cpDNA phylogenies

The small tree shown in Figure 3, enlarges the group of species characterized by wide amplexicaul leaves and twice the number of stamens than sepals, with the addition of three species that could not be included in the main cpDNA phylogeny: *T.*

aucheriana, T. komarovii and *T. pycnocarpa. T. aphylla* samples group in a strongly supported clade (BS 100/PP 1.00) external to any other *Tamarix* samples included, which group in a large clade (BS 99/PP 1.00). All three new samples group in a clade together with *T. amplexicaulis* and *T. macrocarpa* (BS 73/PP 0.97). Moreover, inside this clade *T. aucheriana, T. pycnocarpa, T. komarowii* and *T. macrocarpa* 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 Figure 2, 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.

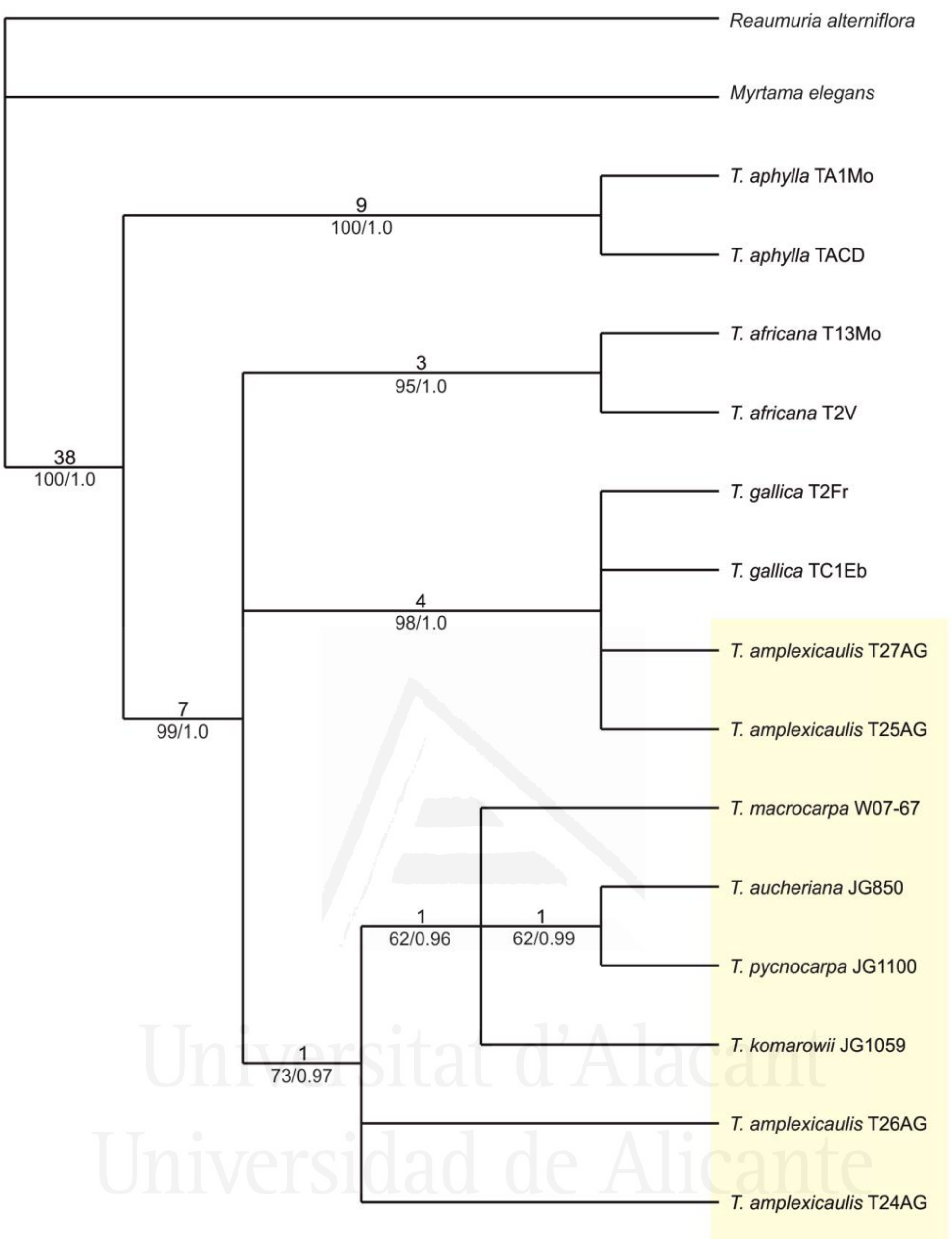

Figure 3. One of the three most parsimonious trees obtained in the MP heuristic search, based on the *trnS-G* plastidial region. Amplexicaul leaved species are included inside the yellow square. Steps are represented above branches. Maximum parsimony bootstrap support (BS) and Bayesian posterior probability (PP) are shown below branches (BS/PP).

The tree shown in Figure 4, 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). *T. tetrandra* appears as a sister branch of all the remaining accessions, although this separation is not well supported (BS not supported/PP 0.70). However, *T. parviflora* accessions form an independent clade with strong PP support (0.99), although weakly supported by MP (BS 63). Therefore, *T. parviflora* and *T. tetrandra* do not tend to cluster together.

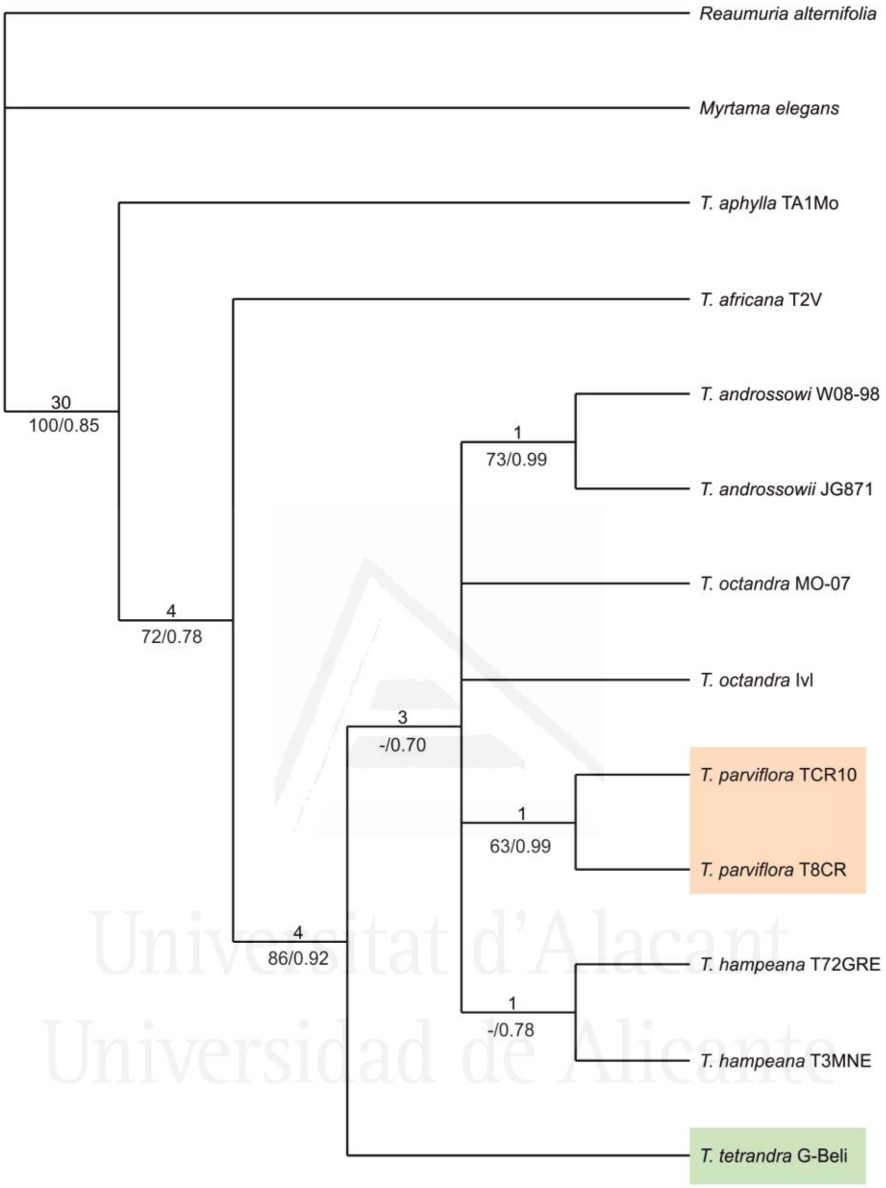

Figure 4. One of the 19 most parsimonious trees obtained in the MP heuristic search, based on the *ndhF-rpl32* plastidial region. Focused in the differentiation between *T. tetrandra* (green square) and *T. parviflora* (light orange square). Steps are represented above branches. Maximum parsimony bootstrap support (BS) and Bayesian posterior probability (PP) are shown below branches (BS/PP).

Discussion

This work represents the most complete molecular phylogenetic study of the genus *Tamarix*, 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) and Villar & al. (2015a), based on partial molecular phylogenies.

The most-recent taxonomical classification of *Tamarix* species in sections and series (Baum 1978) proved to be unnatural according to the nuclear and plastid data presented here (Figures 1 and 2), which was initially highlighted by the studies mentioned above. Our phylogenetic data revealed many examples in which morphological features did not always correspond to monophyletic clades and even closely-related groups. Among others, the sections that are characterised by vaginate leaves and even quite similar species such as *T. canariensis* or *T. gallica* did not form monophyletic clades, as we have explained 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.) would have likely appeared in *Tamarix* at different stages of its evolution. This hypothesis would be supported by, for example, the clear separation of *T. kermanensis* 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. Nevertheless, specific studies will be reqiured to identify those pleisomorphic morphological characters in this genus.

In addition, incongruence has been observed among the gene trees, as in most of the phylogenetic studies that investigated multiple markers (e.g. Doyle & al. 2003). Gene tree incongruence is mainly caused by different 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 & al. 2012). Although detailed analyses are necessary, Whitfield and Lockhart (2007) suggested that where different molecular markers indicate that the same branches are short or obtained low support, this could be used as an indication of rapid radiation. This might have been favored by a reticulate evolution with introgression processes that may still happen through hybridization. Current hybridization processes in *Tamarix* have frequently been reported (Rusanov 1949, Gaskin & Schaal 2003, Gaskin & Kazmer 2009), even between extremely different species (Gaskin & Shafroth 2005, Samadi & al. 2013, Mayonde & al. 2015). These findings are notably supported by the differences found between the nDNA and cpDNA phylogenies. Some of the incongruent position of certain species might be explained by this process.

Vaginate leaved species

As previously confirmed by Gaskin and Schaal (2003), both cpDNA and nDNA phylogenies show a strong relationship between *T. aphylla* and *T. usneoides,* placed in external clades. This is expected, due to similarities in their morphology, e.g. vaginate leaves, 5 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 was pointed out in its description (Baum 1968). Surprisingly, although *T. kermanensis,* shares these morphologic features, it is not placed phylogenetically close to *T. aphylla* and *T. usneoides* in either the nDNA or cpDNA analyses. However, our data are only based on one accession and more *T. kermanensis* specimens would be needed to confirm its phylogenetic placement within the genus. Indeed, Samadi & al. (2013) experienced some difficulties for the morphological identification of *T. kermanensis*, as they reported a notable morphological variability based on the two studied accessions, which also show different chromosome counts (triploidy and tetraploidy) from two accessions. It would also be interesting to study the phylogenetic relationships of *T. aphylla* and *T. usneoides* with the other fully vaginate-leaved species, *T. angolensis* and *T. dioica,* which could not be included in this study. *T. dioica* and *T. usneoides* are the only dioecious species in *Tamarix* (Baum 1978), but they inhabit geographical distinct areas. *T. usneoides* is restricted to the South-West of Africa, while *T. dioica* is mainly distributed in Iran, Afghanistan, Pakistan and India (Baum 1978, Qaiser 1981). The former, alongside *T. angolensis* are the only *Tamarix* species native to Southwestern Africa. However, *T. angolensis* is monoecious, like *T. aphylla* (Baum 1978). A deeper study of the phylogenetic relationships among *T. aphylla, T. angolensis, T. dioica* and *T. usneoides* would help to understand wether the dioecious *T. dioica* and *T. usneoides* share a common origin or wether this particular feature has appeared independently in both species.

The amplexicaul leaved and duplicated stamens group

According to our results, we have found a monophyletic group of species characterized by broad amplexicaul leaves and twice the number of stamens than sepals, though some species can show a few less (*T. macrocarpa*) or more stamens (*T. pycnocarpa*) (Baum 1978). The studied species have also shown a similar phylogenetic behaviour based on plastid data, being a monophyletic group, except for two samples of *T. amplexicaulis* (Figures 2 and 3). These particular two accessions jumped to a different clade in the cpDNA phylogeny (see Clade 5, Figure 2), and appear more closely-related to other species of the genus that have totally different leaf and androecium characters (e.g. *T. nilotica*, *T. gallica*, *T. hampeana*, among others). We found no clear explanation for this split. All four *T. amplexicaulis* samples are from nearby localities and all have the same morphological features. The fact that the two split specimens group together with high PP support (0.99) in Figure 2, gives no indication of possible hybridization, as supported by the fact that ITS chromatograms showed no double signal at key positions.

The taxonomy of this group is still in need of further investigation. The morphological separation between *T. pycnocarpa* and *T. aucheriana* is quite doubtful, as the morphological differences reported by Baum (1978) regarding the androecium and sepals and petals features, might be considered as phenotypic variation. Recently, Samadi & al. (2013) have suggested them to be conspecific, being *T. pycnocarpa* the prioritary name. This taxonomic suggestion would be supported by our morphological observations of type materials as well as with our phylogenetic plastid results (Figure 3). Other authors (Gorschkova 1949, Zieliński 1994) even regarded *T. aucheriana, T. pycnocarpa* and *T. macrocarpa* as synonyms of *T. passerinoides*; the latter taxon has not been adequately sequenced here. These taxonomical considerations would reflect a broad morphological interpretation of this group. Therefore, new nuclear and plastid phylogenetic data should be obtained, and more accessions of the aforementioned taxa should be added, to investigate the phylogenetic relationships among these taxa within the genus together with a detailed morphological study. In addition, the presence of hybrid specimens has been reported within this group, as *T. pycnocarpa* x *T. androssowii* by Samadi & al. (2013), and even, Rusanov (1949) and Gorschkova (1949) already wrote about the possible hybrid origin of the species *T. komarovii* between *T. passerinoides* and *T. ramosissima.* As mentioned previously, further studies are needed to elucidate the morphological and phylogenetic relationships within this group, and, hence, to clarify the taxonomical treatment of these taxa.

Mediterranean Tamarix species and related groups

We have found a strong relationship between the Eastern Mediterranean species *T. dalmatica* and *T. minoa* in the nDNA phylogeny (Clade B, Figure 1), both as monophyletic groups. These species show a general resemblance when observed in the wild, as they are trees of the same size and their racemes are similar in colour and size. Moreover, both species show a certain tendency to have tetramerous and pentamerous flowers intermixed (Baum 1978, Villar & al. 2012, Villar & al. 2015a). However, *T. dalmatica* is generally tetramerous, sometimes developing some pentamerous flowers (Villar & al. 2012), whereas *T. minoa* is pentamerous and sometimes develops tetramerous flowers (Villar & al. 2015a). Conversely, the cpDNA phylogeny splits both species into distinct well-supported clades. Hence, *T. dalmatica* is a monophyletic group with an external phylogenetic position (Clade 2, Figure 2) similar to the nuclear phylogeny. However, *T. minoa* appears as an independent monophyletic group together with the unexpected species *T. indica* inside subclade 4e (Figure 2), which is closer related to the *T. amplexicaulis* and *T. macrocarpa* cluster. 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 & al. 2005, Kim & al. 2008, Soltis & Soltis 2009, Cires & al. 2013). Our current phylogenetic evidence suggests that *T. minoa* might have an 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 in most of its length. Nevertheless, Baum (1966, 1978) reported a higher plasticity in leaf shape. According to Samadi & 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 Qaiser´s close related species (Qaiser 1981, Samadi & al. 2013) were considered as synonyms of *T. indica*, the natural distribution of *T. indica* would extend from India, Bangladesh, Sri-Lanka, Pakistan and Afghanistan (Baum 1966, 1978) to Southwestern Iran (Samadi & al. 2013). A further detailed phylogenetic study including more accessions of *T. indica* and its close relatives would give more resolution about their phylogenetic positions related to the genus, especially to *T. minoa.*

The monophyletic group composed of the three Mediterranean species (*T. boveana*, *T. gallica* and *T. tetragyna*) was recognised clearly by both the nuclear and plastid data, although the Asian *T. elongata* is also included based on the plastid analyses (see Figure 2). The species *T. boveana*, *T. tetragyna* and also *T. elongata* share long and wide racemes, long oblong bracts, large sized tetramerous flowers, and stamens that are generally equal in number to sepals (Ehrenberg 1827, Bunge 1852, Baum 1978). *T. 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 & al. 2012). On the other hand *T. tetragyna* is widespread in the Southeastern Mediterranean Basin, especially in Egypt (Ehrenberg 1827, Bunge 1852, Baum 1978). The distribution of *T. elongata* extends from the Eastern shores of the Caspian Sea to the North-East, 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 the Western Mediterranean countries and the Southern coast of Great Britain. The unexpected phylogenetic relation between *T. gallica* and the other 3 mentioned species is not adequately resolved according to our present DNA data, although their identification is clearly supported by independent morphological and geographical data. The lack of phylogenetic resolution would support the use of other types of molecular markers, for example AFLP or microsatellites, which might clarify their genetic relationships and to clarify their taxonomic identification, as has been reported recently for other complex genera (e.g. Duminil & al. 2012, Prebble & al. 2012, Andrés-Sánchez & al. 2015). Focusing on the plastid phylogenetic position of *T. elongata*, additional samples of the species *T. brachystachys* Bunge or *T. meyeri* Boiss. (sometimes considered as a variety of *T. tetragyna*), which are morphologically close to *T. boveana, T. elongata* and *T. tetragyna* (see Villar & al. 2015b), should be included in future phylogenetic analyses to better understand their relationships.

In the case of *T. parviflora*, this species has been considered as a possible synonym of *T. tetrandra* (Zieliński 1994, Dimopoulos & al. 2013, Villar & al. 2014b), although they were also commonly treated as distinct taxa (Baum 1966, 1978, Qaiser 1981, Zohary 1987, Cirujano 1993, Salazar & Quesada 2009). However, their well separated phylogenetic position based on our preliminary plastid phylogeny would support their taxonomic independence. According to our observations, there are certain morphological features that can be used to separate both species. Petals tend to be longer and wider in *T. tetrandra* (up to 2.75 x 1.25 mm), when compared with those of

T. parviflora (up to 2.5 x 1.1 mm). Sepals have the same tendency, extending up to 1.5 x 1.2 mm in *T. tetrandra* and up to 1.25 x 0.9 mm in *T. parviflora.* Therefore, according to the data presented here, these two taxa might be considered taxonomically independent, supporting the interpretation of Baum (1966, 1978), among others. Nevertheless, specimens of *T. tetrandra* should also be included in the nuclear phylogeny to check their phylogenetic position in relation to *T. parviflora* and to other Mediterranean taxa. The phylogenetic and morphological study of more specimens of both species would be required to support a final conclusion on the taxonomic identity of these two species.

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 cluster totally collapsed 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 & al. 2015a). These two species appeared as a sister clade to *T. androssowii*, the latter species is distributed in central Asia, with its westernmost localities in the Caucasus (Baum 1978). These phylogenetic relationships should be investigated in future studies, adding more samples of *T. androssowii*, to test this close relationship, which is not maintained by plastid data. Conversely, *T. parviflora* and *T. hampeana* appeared in different clades and related to other species in the cpDNA phylogeny. On one hand, the phylogenetic identity of *T. parviflora* is supported in a clade that includes one of the *T. smyrnensis* accessions as an external branch. The placement of *T. smyrnensis* will be discussed below, alongside its morphologically close species (*T. ramosissima, T. hohenackeri, T. chinensis* and *T. austromongolica*)*.* On the other hand, *T. hampeana* groups together with *T. gracilis* (Figure 2)*,* whose known distribution extends from both Russian shores of the Caspian Sea to Northern China and Mongolia, with a westernmost locality in central Anatolia (Baum 1978, Yang and Gaskin 2007). More *T. gracilis* specimens would be needed to confirm this close phylogenetic relation. However, certain morphological features as defined in Baum (1978) or Yang & Gaskin (2007) for *T. gracilis*, such as long pedicels and instability in respect to the number of petals and sepals, resemble to the concept of *T. hampeana* (Villar & al. 2014b, Villar & al. 2015a). Hence, a close relation between *T. gracilis* and *T. hampeana* would seem appropriate.

The case of T. canariensis and T. gallica

The phylogenetic separation existing between *T. canariensis* and *T. gallica,* shown in both cpDNA and nDNA phylogenies, is a remarkable result. These two species have been commonly reported to be morphologically very close to one another, with a widely overlapping distribution (Baum 1966, 1968, 1978, Pignatti 1982, Cirujano 1993, Salazar & Quesada 2009). The main morphological differences set by Baum (1966, 1978) were: (i) a glabrous inflorescence rachis in *T. gallica* compared with an usually papillose rachis in *T. canariensis*; (ii) bracts narrowly triangular, acuminate, not exceeding the calyx vs. bracts linear-triangular, long acuminate to subulate, almost equaling 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, all of these characters have been found to be rather variably mixed after studying a large number of European and North African specimens. In fact, we have observed all degrees of variation within single specimens throughout the flowering period in the Iberian Peninsula (in prep.). In the first bloom (early May in the South-East of the Iberian Peninsula), the specimens show a more similar morphology 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 assumed to belong to *T. canariensis*, with a strongly papillose rachis, triangular-linear subulate bracts, frequently exceeding the calyx, and denticulate margined sepals. Some herbarium vouchers reflecting this seasonal morphological plasticity are kept at ABH (e.g. ABH 59957, ABH 59955, ABH 59956 and ABH 59958). 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 molecular results would initially suggest that *T. canariensis* would probably be restricted to the Canary Islands, whereas *T. gallica* would show a wider geographical distribution along the Mediterranean and Atlantic territories. 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 & 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 analyzed *T. gallica* samples. This would mean that all European and North African records of *T. canariensis* might in fact belong to *T. gallica,* including a large number of synonyms usually assigned to *T. canariensis* (Baum 1966, 1978). In addition, and similarly to *T.*

minoa, the different phylogenetic relationships of *T. canariensis* accessions within the genus might be related to a possible hybrid origin, with the *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 still required, because the studied *T. canariensis* materials (from the Canary Islands) show no clear morphological differences with the widespread *T. gallica.* If no morphological features were found, we would have to deal with the concept of cryptic species (Bickford & al. 2007), which would add another degree of complication to an already difficult genus.

Species with triangular-lanceolate leaves, amplexicaul in their lower half

The morphological relationships between the following group of species, *T. arabica*, *T. arborea* and *T. nilotica* remains unclear. These three species are notably similar in respect to 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 x 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 rather complicated. 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 & al. 2015b). The main morphological feature to distinguish between both species corresponds to 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 & al. 2015b), it seems clear that there is introgression and that intermediate steps exist between the morphotypes represented by *T. arborea* and *T. nilotica* in the Southeastern Mediterranean Region. The morphotype of *T. nilotica* seems to be more stable in the populations recently reported from some Greek islands (cf. Dimopoulos & al. 2013, Villar & al. 2014b), where *T. arborea* has not been reported. Moreover, Zohary (1987) included *T. arabica* and *T. arborea* in the synonymy of *T. nilotica.* Our phylogenetic results would support the existence of these complex relationships. Although nuclear data would group them in an unresolved monophyletic clade, together with other *Tamarix* species (e.g. *T. arceuthoides*, *T. indica*), only the accessions of *T. senegalensis* and *T. nilotica* would form monophyletic groups. Despite the scarce number of sequenced accessions, *T. nilotica*, *T. senegalensis* and *T. arborea* would correspond to independent monophyletic branches, and similar to nuclear data, none of their phylogenetic relationships is resolved. Our nuclear and plastid phylogenetic data unfortunately did not provide clear resolution about the relationships among them. More detailed studies are needed to clarify the taxonomy of this group.

Asian species

According to our plastid data, the species *T. hispida* and *T. karelinii* appeared to be a monophyletic group, although their positions based on the nuclear data were unresolved. In fact, *T. karelinii* has been considered a variety of *T. hispida* (Baum 1966, 1978, Villar & 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 x 1 mm) and medium to long and thin racemes (up to 15 cm x 5 mm). However, they differ in the dense hairy indument 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 North-East, 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 cpDNA phylogenies would provide some support to the authors that interpreted *T. karelinii* as an independent taxon 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) would suggest the existence of hybridization processes. Nevertheless, further detailed morphological and phylogenetic studies are needed to clarify their taxonomical identity.

Tamarix leptostachya is shown as an independent clade or branch for both obtained phylogenies. From a morphological point of view, this taxon is notably characterized by long and thin racemes (up to 15 cm and 3-4 mm, respectively) and generally herbaceous bracts, being typically distributed around central Asia, from the North-West of Iran towards East, reaching Mongolia, China and the North of India (see Baum 1978, Qaiser 1981, Yang & Gaskin 2007). Nonetheless, the collapsed phylogenetic position does not provide any data about the evolutionary relationships with other *Tamarix* species.

The monophyletic clade of *T. arceuthoides* showed weak support in the nDNA phylogeny, and its relationships with other species remained unresolved in both nDNA and cpDNA phylogeny. This species is mainly characterised by its sessile narrow-based leaves (sometimes slightly auriculate), small pentamerous flowered racemes (usually less than 5 cm x 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 Iraq in the West and Pakistan in the South-East (Baum 1978, Qaiser 1981). However, species showing strong morphological similarities with *T. arceuthoides*, such as *T. korolkowii, T. aralensis* or *T. karakalensis*, could not be included in this study. Recently, the three latter species were indeed included as part of a broad concept of *T. arceuthoides* by Samadi & al. (2013). The inclusion of specimens of the three mentioned species would be needed to support or reject the hypothesis that they are synonyms of *T. arceuthoides.*

Tamarix octandra is well characterized by long and wide racemes (up to 12 x 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 than sepals (Bunge 1852, Gorschkova 1949, Baum 1966, 1978, Zieliński 1993). Its distribution is restricted to the Caucasus and nearby areas between the Black and the Caspian Seas, with known localities in Iran, Azerbaijan, Armenia Turkey and Russia, and a westernmost spot in Crimea (Gorschkova 1949, Schiman-Czeika 1964, Baum 1966, 1978, Zieliński 1993). This species was only monophyletic based on the cpDNA phylogeny, and its nuclear and plastid phylogenetic relationships are unresolved in relation to most of the other *Tamarix* species. As mentioned for other studied *Tamarix* species, the position of *T. octandra* should be confirmed by the addition of more samples plus additional specimens of other Asian species such as *T. gracilis T. elongata* and *T. laxa*, which might be closely related according to our preliminary nDNA phylogeny.

Finally, some more species with certain morphological relation to *T. androssowii* (see comments on *T. hampeana* and *T. parviflora*), such as *T. polystachya* Ledeb., *T. litwinowii* Gorschk. and *T. laxa* would be 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 did not group together with *T. androssowii*. Moreover, Samadi & 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 “small flowered tetramerous species”, and to test wether the proposed hypothesis of Samadi & al. (2013) would be confirmed.

Asian and Mediterranean species with petals persistent after anthesis

The following group of species is formed by the sessile-leaved taxa with 5 stamens, inserted between the nectariferous disc lobes, and petals persistent after anthesis. This group includes *T. austromongolica, T. chinensis, T. hohenackeri, T. ramosissima* and *T. smyrnensis,* which is 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 monophyletic clade, completed by *T. taklamakanensis*, whose morphology is notably different (Yang & Gaskin 2007). All the studied specimens of *T. smyrnensis* appear well resolved in a small sister clade to the other relatives. However, the phylogenetic relationships are not resolved within this particular group. Similarly, most of the other species of this morphological group, *T. austromongolica, T. chinensis, T. hohenackeri* and *T. ramosissima*, clustered together in the cpDNA phylogeny, but *T. smyrnensis* are 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 here studied are rather complex, which might be supported by the lack of resolution in both phylogenies. 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 the hybrids between both species have been widely reported (Gaskin & Schaal 2003, Gaskin & Kazmer 2009). Moreover, the natural distributions of *T. ramosissima, T. austromongolica* and *T. chinensis* form a continuous geographical area, from the Middle East and the Caucasus to the Pacific coasts of Asia towards its Central Steppes (see Gorschkova 1949, Baum 1978, Yang & Gaskin 2007). The morphological limits of these three taxa may therefore be quite diffuse (Baum 1978, Yang & Gaskin 2007). In addition, the phylogenetic position of *T. hohenackeri* should be studied properly in further studies, as samples of this species were excluded from nDNA phylogeny because they showed clear double signals in the key positions in which *T. smyrnensis* shows differences with *T. austromongolica, T. ramosissima* and *T. chinensis*. This result might be interpreted as a signal of 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 also studied in detail. One of the *T. smyrnensis* specimens groups into a weakly supported clade alongside *T. nilotica* accessions, while the other sample groups in a monophyletic clade as a sister branch to *T. parviflora.* More specimens from other geographical areas of *T. smyrnensis* should be included in the cpDNA phylogeny to check if the species would show the observed tendency, or conversely would reveal a close relationship to morphologically-related taxa. Therefore, further detailed studies would be needed to clarify the morphological and phylogenetic relationships among the Asian and Mediterranean species characterised by petal persistence after anthesis.

References

Andrés-Sánchez, S., Gutiérrez-Larruscain, D., Rico, E. & Martínez-Ortega, M. M. 2015. Overlooked singularity and tiny plants: the *Filago desertorum* clade (Gnaphalieae, Asteraceae). *Botanical Journal of the Linnean Society* 179: 742-754.

Albadalejo, R. G., Fuertes Aguilar, J., Aparicio, A. & Nieto Feliner, G. 2005. Contrasting nuclear-plastidial phylogenetic patterns in the recently diverged Iberian *Phlomis crinita* and *P. lychnitis* lineages (Lamiaceae). *Taxon* 54:987-997.

Baum, B. R. 1966. *Monographic Revision of the genus Tamarix*. Final research report for the USDA. Department of Botany, Hebrew University, Jerusalem, 193 pp.

Baum, B. R. 1967. Introduced and naturalized tamarisks in the United States and Canada. *Baileya* 15: 19-25.

Baum, B. R. 1968. A new species of *Tamarix* from South-Eastern Iran. *Oesterreichische Botanische Zeitschrift* 114:379-382.

Baum, B. R. 1978. *The genus Tamarix.* Israel Academy of Sciences and Humanities. Jerusalem. 209 pp.

Baum, B. R. 1990. *Tamarix* L. In: Tutin, T. G., Heywood, V.H., Burges, N. A., Moore, D. M., Valentine, D. H., Walters, S. M. & Webb, D. A. (eds.). *Flora Europaea* 2. Cambridge University Press. 292-294.

Bergsten, J. 2005. A review of long-branch attraction. *Cladistics* 21: 163-193.

Bieberstein, M. 1808. *Flora Taurico-Caucasica* 1. Krakovia. 246-248.

Blanco-Pastor, J. L., Vargas, P. & Pfeil, B.E. 2012. Coalescent Simulations Reveal Hybridization and Incomplete Lineage Sorting in Mediterranean Linaria. *PLoS ONE* 7(6): e39089. doi:10.1371/journal.pone.0039089.

Bunge, A. 1833. Enumeratio Plantarum quas in China Boreali collegit Dr. Al. Bunge. *Mémoires présentés à l'Académie Impériale des Sciences de St.-Pétersbourg par Divers Savants et lus dans ses assemblées* 2: 75-147.

Bunge, A. 1851. Alexandri Lehmann reliquiae botanicae. *Mémoires présentés à l'Académie Impériale des Sciences de St.-Pétersbourg par Divers Savants et lus dans ses assemblées* 7: 290-296.

Bunge, A. 1852. *Tentamen Generis Tamaricum Species Accuratius Definiendi*. J.C. Schuenmanni & C. Mattieseni. Dorpati. 84 pp.

Boissier, E. 1849. *Diagnoses Plantarum Orientalium Novarum*, ser. 1, 10. M. Ducloux et Cons. Paris.

Boissier, E. 1856. *Diagnoses Plantarum Orientalium Novarum*, ser. 2, 2. M. Apud B. Herrmann. Leipzig.

Boissier, E. 1867. *Flora orientalis* 1. H. Georg. Gèneve. 763-779.

Bickford, D., Lohman, D. J., Shodi, S. N., Ng, P. K. L., Meier, R., Winkler, K., Ingram, K. K. & Das, I. 2007. Cryptic species as a window to diversity and conservation. *Trends in Ecology and Evolution* 22: 148-155.

Çakan, H. & Zieliński, J. 2004. *Tamarix duezlenlii* (Tamaricaceae) – a species new to science from southern Turkey. *Acta Societatis Botanicorum Poloniae* 73 : 53-55.

Candolle, A. P. 1828. *Prodromus Systematis Naturalis Regni Vegetabilis* 3. Treuttel & Würtz. Paris. 95-98.

Cires, E., Baltisberger, M., Cuesta, C., Vargas, P. & Fernández Prieto, J. E. 2013. Allopolyploid origin of the Balkan endemic *Ranunculus wettsteinii* (Ranunculaceae) inferred from nuclear and plastid DNA sequences. *Organisms Diversity & Evolution* 14: 1-10.

Cirujano, S. 1993. *Tamarix* L. In: Castroviejo, S. & al. (eds.). *Flora Iberica* 3. Real Jardín Botánico, CSIC. Madrid. 437-443.

Csurhes, S. 2008. *Pest plant risk assessment: Athel pine Tamarix spp*. The State of Queensland. Department of Primary Industries and Fisheries. Brisbane. Australia. 10 pp.

Darriba, D., Taboada, G. L., Doallo, R. & Posada, D. 2012. jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 9: 772.

De Martis, B., Loi, M. C. & Polo, M. B. 1984. Il genere *Tamarix* L. (Tamaricaceae) in Sardegna*. Webbia* 37(2): 211-235.

De Martis, B., Loi, M. C. & Polo, M. B. 1986. Contribution to a better understanding of the genus *Tamarix* in Portugal. *Candollea* 41: 293-298.

Desvaux, M. 1824. Sur la nouvelle famille de plantes fondée sur le genere *Tamarix*. *Annales des Sciences Naturelles. Botanique. Paris.* 4: 344-350.

Dimopoulos, P., Raus, Th., Bergmeier, E., Constantinidis, Th., Iatrou, G., Kokkini, S., Strid, A. & Tzanoudakis, D. 2013: Vascular plants of Greece: An annotated checklist. Berlin: Botanischer Garten und Botanisches Museum Berlin-Dahlem; Athens: Hellenic Botanical Society. *Englera* 31. 372 pp.

Di Tomaso, J. 1998. Impact, biology and ecology of saltcedar (*Tamarix sp.*) in southwestern United States. *Weed Technology* 12: 326-336.

Doyle, J. J. & Doyle, J. L. 1987. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochemical Bulletin* 19: 11-15.

Doyle, J. J., Doyle, J. L., Rauscher, J. T. & Brown, A. H. D. 2003. Diploid and polyploid reticulate evolution throughout the history of the perennial soybeans (Glycine subgenus Glycine). *New Phytologist* 161: 121-132.

Duminil, J., Kenfack, D., Viscosi, V., Grumiau, L. & Hardy, O. J. 2012. Testing species delimitation in sympatric species: the case of an African tropical tree, *Carapa* spp. (Meliaceae). *Molecular Phylogenetics and Evolution* 62: 275–285.

Ehrenberg, C. G. 1827. Über die Manna-Tamariske nebst allgemeinen Bemerkungen über die Tamariscineen. *Linnaea* 2: 241-344.

Freyn, J. 1903. Plantae ex Asia Media. *Bulletin de l´Herbier Boissier*, sér. 2, 3: 1058-1068.

Gaskin, J. F. & Schaal, B. 2003. Molecular phylogenetic investigation of U.S. invasive *Tamarix*. *Systematic Botany* 28 (1): 86–95.

Gaskin, J. F. & Shafroth, P. B. 2005. Hybridization of *T. ramosissima* and *T. chinensis* (saltcedars) with *T. aphylla* (athel) (Tamaricaceae) in the Southwestern USA determined from DNA sequence data. *Madroño* 52: 1-10.

Gaskin, J. F. & Kazmer, D. J. 2009. Introgression between Invasive Saltcedars (*Tamarix chinensis* and *T. ramosissima*) in the USA. *Biological Invasions* 11: 1121-1130.

Gorschkova, S. G. 1949. Tamaricaceae. In: Komarov, V. L. (ed.). *Flora URSS* 15. Moscow-Lenningrad. 290-327.

Hamilton, M. 1999. Four primer pairs for the amplification of chloroplast intergenic regions with intraspecific variation. *Molecular Ecology* 8: 521-523.

Kim, S.-C., Mejías, J. A. & Lubinsky, P. 2008. Molecular confirmation of the hybrid origin of the critically endangered western Mediterranean endemic *Sonchus pustulatus* (Asteraceae: Sonchinae). *Journal of Plant Research 121* (4): 357-364.

Ledebour, C. F. 1829. *Flora Altaica* 1. G. Reimeri. Berlin. 421-426.

Ledebour, C. F. 1843. *Flora rossica, sive enumeratio plantarum in totius imperii Rossici provinciis Europaeis, Asiaticis, et Americanis hucusque observatarum* 2 (4). E. Schweizerbart, Stuttgart. 130-138.

Linnaeus, C. 1753. *Species plantarum* 1. Holmiae. Laurentii Salvii. 560 pp.

Liu, M. T. 1979. A new species of *Tamarix* from Xinjiang. *Acta Phytotaxonomica Sinica* 17 (3): 120-121.

Loureiro, J. 1790. Flora Cochinchinensis. *Actas da Academia Real Das Scientias*. Lisbon. 182-183.

Maire, R. 1931. Contribution à l'étude de la Flore de l'Afrique du Nord 17(1). *Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord* 22: 34-36.

Maire, R. 1935. Contribution à l'étude de la Flore de l'Afrique du Nord 23. *Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord* 26: 192-195.

Maire, R. 1938. Contribution à l'étude de la Flore de l'Afrique du Nord 26. *Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord* 29: 410.

Mayonde, S. G., Cron, G. V., Gaskin, J. F. & Byrne, M. J. 2015. Evidence of *Tamarix* hybrids in South Africa, as inferred by nuclear ITS and plastid *trnS-trnG* DNA sequences. *South African Journal of Botany* 96: 122-131.

Niedenzu, F. 1895. In: Engler, A. & Prantl, K. (eds.). *Die natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigeren Arten* 3 (6). Leipzig. 289-297.

Pallas, P. S. 1789. *Flora rossica, seu stirpium Imperii Rossici per Europam et Asiam indigenarum descriptiones et icones* 1 (2). E Typographia imperiali J.J. Weitbrecht. Petropoli. 72-73.

Pau, C. 1906. Synopsis formarum novarum hispanicarum cum synonimin nonnullis accedentibus. *Bulletin de l’Académie Internationale de Géographie Botanique* 206: 73-77.

Pau, C. 1922. Nueva contribución al estudio de la flora de Granada. *Memòries del Museu de Ciències Naturals de Barcelona*. *Sèrie Botànica* 1 (1): 74 pp.

Pignatti, S. 1982. *Flora d’Italia* 2. Edagricole. Bologna. 133-134.

Poiret, J. 1789. *Voyage en Barbarie* 2. J. B. F Née de la Rochelle. Paris. 139.

Posada, D. & Buckley, T. R. 2004. Model selection and model averaging in phylogenetics: advantages for the AIC and Bayesian approaches over Likelihood ratio tests. *Systematic Biology* 53: 793-808.

Posada, D. & Crandall, K. A. 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* 14: 817-818.

Prebble, J. M., Meudt, H. M. & Garnock-Jones, P. J. 2012. Phylogenetic relationships and species delimitation of New Zealand bluebells (*Wahlenbergia*, Campanulaceae) based on analyses of AFLP data. *New Zealand Journal of Botany* 50: 365-378.

Prince, W. & Sons. 1837. *Annual catalogue of trees and plants cultivated at the Linnean Botanic Garden and Nurseries*. New York. USA. 2-4 and 50.

Qaiser, M. 1981. The genus *Tamarix* Linn. (Tamaricaceae) in *Pakistan. Pakistan Journal of Botany* 13: 107-158.

Ronquist, F., Teslenko, M., Van Der Mark, P., Ayres, D. I., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M. A. & Huelsenbeck, J. P. 2012. MrBayes 3.2: Efficient Bayesian Phylogenetic Inference and Model Choice across a Large Model Space. *Systematic Biology* 61: 1-4.

Rusanov, F. N. 1949. *Sredniyeaziatskie Tamariksi*. Tashkent.

Samadi, N., Ghaffari, S. M. & Akhani, H. 2013. Meiotic behaviour, karyotype analyses and pollen viability in species of *Tamarix* (*Tamaricaceae*). *Willdenowia* 43: 195-203.

Salamin. N., Chase, M. W., Hodkinson, T. R. & Savolainen, V. 2003. Assessing internal support with large phylogenetic DNA matrices. *Molecular Phylogenetics and Evolution* 27: 528–539.

Salazar, C. & Quesada, J. 2009. *Tamarix* L. In: Blanca, G. & al. (eds.). *Flora vascular de Andalucía Oriental* 2. Consejería de Medio Ambiente. Junta de Andalucía. Sevilla. 190-193.

Schiman-Czeika, H. 1964. In: Rechinger, K. H. (ed.). *Flora Iranica* 4. Akademische Druck. Graz. 17 pp.

Sennen, F. 1932. Brèves diagnoses des formes nouvelles parues dans nos exsiccata “Plantes d’Espagne-F. Sennen”. *Butlletí de la Institució Catalana d’Història Natural* 32: 90.

Sennen, F. & Mauricio, F. 1934. *Catálogo de Flora del Rif oriental*. La Ibérica. Melilla. 42-43.

Shaw, J., Lickey, E. B., Schilling, E. E. & Small, R. L. 2007: Comparison of whole chloroplast genome sequences to choose noncoding regions for phylogenetic studies in angiosperms: The tortoise and the hare III. *American Journal of Botany* 94: 275-288.

Shinners, L. H. 1957. Salt cedars (*Tamarix*, Tamaricaceae) of the Soviet Union by S. G. Gorschkova. *The Southwestern Naturalist* 2 (2-3): 48-73.

Soltis, P. S., Soltis, D. E. 2009. The role of hybridization in plant speciation. *Annual Review of Plant Biology* 60: 561-588.

Stromberg, J. 1998. Dynamics of Fremont cottonwood (*Populus fremontii*) and saltcedar (*Tamarix chinensis*) populations along the San Pedro River, Arizona. *Journal of Arid Environments* 40: 133-155.

Swofford, D. L. 2002. *PAUP, version 4.0b10 for Macintosh*. Sunderland. MA. Sinauer Associates.

Takhtajan, A. 1986. *Floristic regions of the world*. University of California Press. Berkeley-Los Angeles-London. 522 pp.

Tamura, K., Peterson, D., Peterson, N., Steccher, G., Nei, M. & Kumar, S. 2011. MEGA5: molecular evolutionary genetic analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution* 28: 2731-2739.

Terzoli, S., Abbruzense, G., Beritognolo, I., Sabatti, M., Valentini, R. & Kuzminsky, E. 2014. Genetic characterization of a Tamarix spp. germoplasm collection in Italy. *Botany* 92 (5): 360-369.

Thiers, B. 2008+ [continuously updated]. *Index herbariorum: a global directory of public herbaria and associated staff*. New York Botanical Garden: published at http://sweetgum.nybg.org/ih

Venturella, G., Baum, B. R. & Mandracchia, G. 2007. The genus *Tamarix* (Tamaricaceae) in Sicily: first contribution. *Flora Mediterranea* 17: 25-46.

Villar, J. L., Alonso, M. A., Juan, A. & Crespo, M. B. 2012. Does *Tamarix dalmatica* (Tamaricaceae) occur in Spain? *Anales del Jardín Botánico de Madrid* 69: 253-258.

Villar, J. L., Juan, A. & Alonso, M. A. 2014a. *Tamarix hohenackeri* Bunge, a new record for the flora of Mexico. *Acta Botánica Mexicana* 106: 117-128.

Villar, J. L., Alonso, M. A., Vicente, A., Juan, A. & Crespo, M. B. 2014b. The genus *Tamarix* (*Tamaricaceae*) in Crete (Greece). *Willdenowia* 44: 321-326.

Villar, J. L., Juan, A., Alonso, M. A. & Crespo, M. B. 2014c. Type specimens of *Tamarix* (Tamaricaceae) described by Josef Franz Freyn in 1903. *Phytotaxa* 173 (3): 289-292.

Villar, J. L., Alonso, M. A., Juan, A., Gaskin, J. F., & Crespo, M. B. 2014d. Proposal to conserve the name *Tamarix ramosissima* against *T. pentandra* (*Tamaricaceae*). *Taxon* 63 (5): 1140-1141.

Villar, J. L., Turland, N. J., Juan, A., Gaskin, J. F., Alonso, M. A. & Crespo, M. B. 2015a. *Tamarix minoa* (*Tamaricaceae*), a new species from the island of Crete (Greece) based on morphological and plastid molecular sequence data. *Willdenowia* 45: 161-172.

Villar, J. L., Alonso, M. A., Juan, A. & Crespo, M. B. 2015b. Remarks on typification of nineteen names in *Tamarix* (Tamaricaceae). *Nordic Journal of Botany* 33: 591-600.

Walpers, G. G. 1843. *Repertorium Botanices Systematicae* 2. Leipzig. 114-117.

Warner Harper, W. 1903. *Andorra hand-book of trees and shrubs*. Philadelphia, USA. 5, 98.

Webb, P. B. & Berthelot, S. 1840. Historie naturelle des Iles Canaries 3 (2). *Phytographia canariensis*, Sect. 1. Paris. 170-172.

Whitfield, J. B. & Lockhart, P. J. 2007. Deciphering ancient rapid radiations. *Trends in Ecology and Evolution* 22: 258-265.

White, T. J., Burns, T. D., Lee, S. & Taylor, J. W. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis, M., Gelfand, D., Sninsky, J. & White, T. (eds.). *PCR protocols: a guide to methods and applications*. Academic Press. San Diego. CA. 315-322.

Willdenow, C. L. 1816. Beschreibung der Gattung Tamarix. *Abh. Königl. Akad. Wiss. Berlin 1812-1813*. 76-86.

Yang, Q. & Gaskin, J. F. 2007. *Tamarix.* In: Zhengyi, W. & Raven, P. H. (eds.). *Flora of China* 13. Science Press; Miss. Bot. Gard. Press. 59-65.

Zhang, P. Y. & Liu, M. T. 1988. Zuo liu shu si xin zhong. *Acta Botanica Boreali-Occidentalia Sinica* 8 (4): 259-264.

Zieliński, J. 1993. *Tamarix octandra* (Tamaricaceae) - a species new to Turkey. The Karaca Arboretum Magazine 2 (1): 7-10.

Zieliński, J. 1994. *Tamarix* L. In: Browicz, K. (ed.). *Chorology of trees and shrubs in south-west Asia and adjacent regions* 10**.** Bogucki Wydawnictwo Naukowe. Ponzań. 30-34.

Zohary, M. 1987. *Tamarix* L. In: Zohary, M. (ed.). *Flora Palaestina* 2. Reprint (first released in 1972). *Israel Academy of Sciences and Humanities*. 350-362.