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Molecular phylogeny of *Tamarix* (Tamaricaceae) species from Iran based on ITS sequence data

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ABSTRACT

Tamarix L. with almost 54 species is the largest genus of the Tamaricaceae. This study was carried out on the species of Tamarix that growing in Iran. Internal transcribed spacer (ITS) sequences were obtained for 15 samples recognized by recent taxonomic treatments from Iran. In addition, we used 19 previously ITS sequences from Gen Bank to test the monophyly of Tamarix in Iran. Phylogenetic analysis were conducted using Bayesian inference. In this study we use DNA sequence data to identify species of Tamarix that growing in Iran, and to determine if the molecular data are congruent with the morphological distinctions that currently segregate taxa. We also test congruence of morphologically based sectional classifications and our molecular gene trees. The results indicate that Tamarix species from Iran constituted a monophyletic group. Data analysis indicates the three taxonomic sections based on morphology (Baum 1978) are not supported by the molecular analyses as well as the classification of species according to androecial disc morphology so not true but leaf morphology and number of floral parts are useful for the taxonomy of Tamarix species. To determine the evolution of Tamarix use of morphological characteristics coupled with molecular data will be most effective.

Keywords: Iran, *Tamarix*, phylogeny, ITS.

INTRODUCTION

Tamaricaceae are found in temperate and subtropical regions of Africa and Eurasia, salt and sand in the desert, steppe, coastal sands along the river [19]. This family consists of 5 genera *Hololachna* Ehrenb., *Myricaria* Desv., *Reaumuria* L., *Tamarix* L., *Myrtama* Ovcz. & Kinzik. and about 100 species [26].

Tamarix was first monographed by Willdenow (1816), who described 16 species [20]. Beginning with Decaisnc (1835) taxonomic relationships were, and continue to be, based mostly on the morphology of the small nectary or androecial disc in the center of the flower [17]. Bunge monographed the genus in 1852, identifying 51 species, and based much of his taxonomy on whether the racemes were produced on the previous year's woody branches (vernal) or on the current year's green branches (aestival) [1]. This character was considered diagnostically unreliable by Baum (1964), who later completed an exhaustive revision of the genus that has been complimented by Qaiser's (1983) work on the Pakistani species [4, 5, 23]. Baum (1978) considers that *Tamarix* has a major center of speciation in the Pakistan–Afghanistan–Iran–Turkmenistan–southern Kazakhstan–western China area and another in the eastern Mediterranean area [14].

Tamaricaceae usually were placed in the plant order Violales of the Dilleniidae (e.g., Cronquist, 1981) [2], but recent molecular sequence data analyses have altered the traditional ordinal placement of many plant families, and

Tamaricaceae are now included in the Caryophyllales (APG III, 2009) [10]. Taxonomy of genus Tamarix is very complex. According to Willdenow (1816), Desvaux (1824), Ehrenberg (1872), Bunge (1852) and Ahrendt (1926), 200 specific and intraspecific taxa are included in the genus *Tamarix* [20, 22, 6, 1, 12]. This number was reduced to 69 (54 species and 15 varieties) by Baum (1978) [13]. Among the genera of the Tamaricaceae, *Tamarix* is the largest with 55 species [25].

Table 1. Distribution of Tamarix species in Iran

Geographical abbreviations: C, enter Iran; S, southern Iran; SE, south-eastern Iran; N, northern Iran; NE, north-eastern Iran; NW, northwesternIran; E, eastern Iran; W, western Iran [5, 21].

Taxon	Distribution in Iran [5,21]		Section [5]	Major Features of morphological traits of Tamarix [5].
T.dioica Roxb. Ex Roth.	E, S, SE		TAMARIX	Leaf morphology: vaginate Androecial disc morphology: hololophic Number of floral parts: pentamerous
T.kermanensis Baum.	S, SE		-	Leaf morphology: vaginate Androecial disc morphology: synlophic Number of floral parts: pentamerous
T.stricta Boiss.	S, SE		POLYADENIA	
T.aphylla (L.) Karst.	C, S, SE		TAMARIX	Leaf morphology: vaginate Androecial disc morphology: hololophic Number of floral parts: pentamerous
T.ramosissima Ledeb.	N, NW, W, C, NE, E		TAMARIX	Leaf morphology: sessile with narrow base Androecial disc morphology: hololophic Number of floral parts: pentamerous
T.rosea Bge.	NW, C		OLIGADENIA	
T.arceuthoides Bge.	NW, W, SW, C, SE		TAMARIX	
T.indica Willd.	E, SE		TAMARIX	
T.korolkowii Regel & Schmalh.	W, NE, C		TAMARIX	
T.karakalensis Freyn.	N, C		TAMARIX	
T.aralensis Bge.	N, C, NE		TAMARIX	
T.smyrnensis	N, NW, W, C, NE, E		TAMARIX	
T.mascatensis Bge.	E, S, SE		TAMARIX	Leaf morphology: amplexicaul or sessile with narrow base Androecial disc morphology: synlophic Number of floral parts: pentamerous
T.serotina Bge, ex Boiss.	E		TAMARIX	
T.hispida Willd.	Var. hispida	C, E, S	TAMARIX	
	Var. karelinii	C, NE, SE		
T.dubia Bge.	C, SE		POLYADENIA	Leaf morphology: amplexicaul or sessile with narrow base Androecial disc morphology: paralophic Number of floral parts: pentamerous
T.kotschyi Bge.	N, C, E		OLIGADENIA	Leaf morphology: amplexicaul or sessile with narrow base Androecial disc morphology: synlophic to para-synlophic Number of floral parts: tetra-pentamerous
T.androssowii Litw.	N, C, NE, E		OLIGADENIA	
T.tetragyna Ehrenb.	Var. meyeri	NW, SW, C, NE, S	OLIGADENIA	Leaf morphology: amplexicaul or sessile with narrow base Androecial disc morphology: paralophic Number of floral parts: tetra-pentamerous
	Var. deserti	C, E		
T.octandra (M. B.) Bge.	NW		OLIGADENIA	Leaf morphology: amplexicaul or sessile with narrow base Androecial disc morphology: paralophic Number of floral parts: tetramerous
T.passerinoides Del. Ex Desv.	Var. passerinoides	NW, SW, C, NE, E, S, SE	POLYADENIA	Leaf morphology: amplexicaul or sessile with auriculate base Androecial disc morphology: undetermined disc (disc without lobes) Number of floral parts: pentamerous
	Var. macrocarpa	S, SE, NE		
T.aucheriana	S,W		POLYADENIA	
T.pycnocarpa	C		POLYADENIA	
T.leptopetala Bge.	SW, S, SE, C		OLIGADENIA	Leaf morphology: amplexicaul or sessile with narrow base Androecial disc morphology: hololophic sometimes synlophic Number of floral parts: pentamerous
T.szowitsiana Bge.	NW, C, NE, SE		OLIGADENIA	Leaf morphology: amplexicaul or sessile with narrow base Androecial disc morphology: synlophic or para-synlophic Number of floral parts: tetramerous

Tamarix plants are shrubs, semi-shrubs and tall trees that can grow up to 18 m in height. They are adaptable halophytic or xerophytic plants mostly with multiple stems and slender branches [16]. Young branches are reddish brown in colour, sometimes black with light-green coloured leaves. Leaves of *Tamarix* are taxonomically useful as their shape and attachment modes vary according to species, e.g. sessile vs. vaginate [5]. They are scale-like, about 3 mm in length and usually contain salt glands [10].

Table 2. List of taxa investigated in our analysis and herbaria where the vouchers are deposited
TARI= herbarium of Research Institute of Forests and Rangelands, IAUH= Islamic Azad University AvicenniaHerbarium

Species	Origin, voucher
T. octandra	Iran: Prov. West Azerbaijan; Urmia lake, 1330m, Assadi and Shirdelpour, (12011 TARI).
T. passerinoides var macrocarpa	Iran: Prov. Ghom; West of Namak lake, 950m, Assadi and Bazgosha, (56601 TARI).
T. korolkowii	Iran: Prov. Khorasan; 6km south of Sabzehvar, 1000m, Assadi and Massoumi, (55891 TARI).
T. arceuthoides	Iran: Prov. Golestan; Atrak river, 180m, Assadi and Massoumi, (55407a TARI).
T. hispida var karelinii	Iran: Prov. Isfahan; Zavareh, 992m , Arianmanesh. IAUH without herbariums number.
T. ramosissima	Iran: Prov. Isfahan; Varzaneh,1479m , Arianmanesh. IAUH without herbariums number.
T. tetragyna var meyeri	Iran: Prov. Isfahan; Isfahan,1578m , Arianmanesh. IAUH without herbariums number.
T. kotschyi	Iran: Prov. Ghom; Ghom,1029m , Arianmanesh. IAUH without herbariums number.
T. tetragyna var deserti	Iran: Prov. Isfahan; Varzaneh,1481m , Arianmanesh. IAUH without herbariums number.
T. androssowii	Iran: Prov. Isfahan; between Naein and Ardestan, 2062m , Arianmanesh. IAUH without herbariums number.
T. rosea	Iran: Prov. Yazd; between Bafgh and Ravar, 2200m, Assadi and Bazgosha, (56068 TARI).
T. karakalensis	Iran: Prov. Kerman; Bam, 1110m, Arianmanesh. IAUH without herbariums number.
T. aralensis	Iran: Prov. Isfahan; 20 km Meymeh to Delijan, 2113m , Arianmanesh. IAUH without herbariums number.
T. mascatensis	Iran: Prov. Fars; Kazeroon, Parishan lake, 1970m, Arianmanesh. IAUH without herbariums number.
T. aphylla	Iran: Prov. Isfahan; between Ardestan and Zavareh, 1089m , Arianmanesh. IAUH without herbariums number.

Table 3. List of Iranian* and non-Iranian taxa used in our analysis from GenBank with accession number

Species	Genbank accession numbers
Myricaria alopecuroides	KJ808603
T.amplexicaulis	HE602440
T.arborea	AF484780
T.canariensis	AF484808
T.chinensis	AF484776
T.dalmatica	AF484794
T.elongata	AF484777
T.gallica	AF484807
T.laxa	AF484756
T.nilotica	AF484749
T.parviflora	AF484810
T.usneoides	KM657172
*T.pycnocarpa**	AF484763
T.hohenackeri	AF484779
T.meyeri	AF484772
*T.korolkowii**	AF484795
*T.octandra**	AF484759
*T.aucheriana**	AF484762
*T.smyrnensis**	AF484773

Tamarix consists of many species, some of which are morphologically very similar. Most *Tamarix* species can not distinguished without flowers or fruit present [26]. Baum's (1978) and Crins' (1989) studies agree that some characters are useful for segregating certain species, such as gross leaf morphology (vaginate vs. sessile), number of floral parts, and certain aspects of androecial disc morphology [5, 26]. The value of other characters, such as petal shape, presence or absence of hairs on the raceme rachis, and whether the filament is inserted under or from the side of the androecial disc are debated [19]. The number of floral parts is sometimes constant but this parameter cannot be considered valid for any identification of specimens when it is not correlated with the position of flowers on the raceme, the reciprocal position of floral parts, the variability in their numbers, etc. The difficulties in the identification of *Tamarx* species are sometimes caused by inaccurate descriptions and by problems in analytical keys [13]. In Iran, 25 species of Tamarix are present [3, 4, 5, 9, 21, 24]. *Tamarix* species that distribution in different regions of Iran, showed in Table 1. The purpose in this study were to test the naturalness of *Tamarix* species classification that are present in Iran and to test the congruence of morphological and molecular data at sectional and species level.

MATERIALS AND METHODS

Specimen were collected in the field and dried in silica gel or preparation from herbaria in Iran (TARI, IAUH).Phylogenetic reconstruct were carried out in 19specimen of *Tamarix* presented from Iran. Tables 2 and 3 lists all taxa used in this study and summarizes sources, voucher specimen data and Gen Bank accession numbers. Total DNA was extracted using the DNeasy Plant Mini kit (Qiagen, Germany). We amplified the ITS region (ITS1-5.8S-ITS2) of the nuclear ribosomal DNA using primer combinations ITSTX4F and ITSTX4R primers: a forward

primer ITSTX4F annealing, 5'-ACT TGTTCACCGAAACACGG-3', and a reverse primer ITSTX4Rannealing, 5'-TAAGGCGCACGGCGTGATCC -3'. The PCR protocol for ITS region included: 30cycles of 2 min denaturation (95°C), 1 min annealing (55°C), and 2 min elongation (72° C), with two additional seconds elongation per cycle [19].

PHYLOGENETIC ANALYSIS

Phylogenetic reconstruct were carried out in 19specimen of *Tamarix* presented from Iran. In this study we used the ITS sequence of 18species of *Tamarix* from Gen Bank. List of Iranian and non-Iranian taxa used in our analysis with Gen Bank accession numbers showed in Table 3. We also used the ITS sequence of *Myricaria alopecuroides*, from Gen Bank as the out group[18].Matrices were analyzed with PAUP4.0b10, with the following options: heuristic search with 1,000 random-addition-sequence replicates; tree bisection-reconnection (TBR) branch swapping; "collapse zero length branches;" saving all most parsimonious trees. Character state changes were treated as equally weighted. No overlapping parsimony informative idols were coded as binary characters and added to the end of the data matrix. Relative clade support was estimated using 1,000 bootstrap, replicates in PAUP via "full heuristic" searches and simple taxon addition. The consistency index (CI) and retention index (RI) were used to assess the amount of homoplasy present in the data. The best-fitting substitution model (GTR+I+G) was determined under the Akaike Information Criterion (AIC) in Model selected [22]. BI was performed in MrBayes ver. 3.1.2 [24]. A 50% majority-rule consensus tree with Bayesian posterior probabilities (PPs) of clades was calculated after removing the first 10% generations as burn in.

RESULTS AND DISCUSSION

The data set of the ITS region included 503 characters, 43 of them potentially parsimony informative. Strict consensus phylogeny trees, with 189 steps was included consistency index (CI)=0.772 and retention index (RI)=0.802. Three major clades were identified which have been given the name of A, B and C. A little supported relationships between major clades were existed. Clade A included two species (*T.kotschyi* from Iran and *T.parviflora* non from Iran) of sect. Oligadenia (PP = 0.97; BS = 95%). Within the clade B, Fourteen major clades were identified. A little supported relationships between major clades were existed. Clade F included two species (*T.canariensis* and *T.galica*) of sect. Tamarix (PP = 1; BS = 95%). Two species not recognized in Iran. Clade G included two species (*T.aphylla* from Iran and *T.usneoides* non from Iran) of sect. Tamarix (PP = 0.92; BS = 97%). Clade H included one species (*T.rosea* from Iran) of sect. Oligadenia. Clade J included three species: *T.tetragyna* var.*meyeri* and *T.meyeri* from Iran (PP = 1; BS = 99%) belong to sect. Oligadenia and *T.arborea* non from Iran of section Tamarix. Clade L included two species (*T.korolkowii* from Iran and *T.dalmatica* non from Iran) of section Tamarix and Oligadenia respectively (PP = 0.97; BS = 95%). Clade N included one species (*T.passerinoides* from Iran) of section Polyadenia. Clade O included one species (*T.korolkowii* from Iran) of section Tamarix. Clade P included one species (*T.karakalensis* from Iran) of section Tamarix. Clade Q included seven species: *T.ramosissima*, *T.hispida* var.*karelinii*, *T.arceuthoides*, *T.aralensis*, *T.androsowii* from Iran and *T.nilotica* non from Iran (PP = 0.55; BS = 64%). *T.mascatensis* from Iran is sister to other species in clade Q. *T.androsowii* belong to sect. Oligadenia and other species belong to section Tamarix. Clade R included three species: *T.smyrnensis* from Iran and *T.hohenackeri* and *T.chinensis* non from Iran (PP = 0.99; BS = 76%). Relationship between *T.hohenackeri* and *T.chinensis* was supported by BI (PP = 0.97; BS = 56%). *T. smyrnensis* and *T.hohenackeri* belong to sect. Tamarix and *T.chinensis* belong to section Oligadenia. Clade T included five species (BS = 52%). Clade V included two species (*T.octandra* and *T.tetragina* var.*deserti* from Iran) of sect. Oligadenia (PP = 0.94; BS = 76%). Clade W included three species (*T.octandra* from Iran and *T.laxa* and *T.elongata* non from Iran) of section Oligadenia. Clade U included three species (*T.pycnocarpa* and *T.aucheriana* from Iran and *T.amplexicaulis* non from Iran) of section polyadenia. Relationship between *T.pycnocarpa* and *T.aucheriana* was supported by BI (PP = 0.9; BS = 74%). *T.amplexicaulis* is sister to other species in clade U. Best support was occurred in clade J between *T.tetragyna* var.*meyeri* and *T.meyeri* from Iran (PP = 1; BS = 99%), in clade F between *T.canariensis* and *T.galica* non from Iran (PP = 1; BS = 95%), in clade A between *T.kotschyi* from Iran and *T.parviflora* non from Iran (PP = 0.97; BS = 95%) and in clade G between *T.aphylla* from Iran and *T.usneoides* non from Iran (PP = 0.92; BS = 97%).

All species of clade A and clade T belonge to section Oligadenia with at least vernal racemes 5-12 mm broad, or 3-5 mm and then flowers tetrandrous, petals of various lenghts, 4-5 of the 4-9 stamens antesepalous and disc with nectariferous lobes. All species of clade D, *T.arborea* in clade J, *T.korolkowii* in clade L, all species of clade M except *T.passerinoides* and *T.androsowii* and in clade R, *T.hohenackeri* and *T. smyrnensis* belong to section Tamarix with racemes 3-5 mm broad or in dioecious trees 5-7 mm broad, petals 1-2.25 mm long, stamens usually 5 (antesepalous) and disc various. All species of clade U and *T.passerinoides* belong to section Polyadenia with racemes 6-10 (-15) mm broad, petals various lengths, stamens 6-15 (mostly 10), of these 5 antesepalous and with slightly longer filaments and disc with no nectariferous lobes [5].

In this study we provide the first phylogenetic analysis about *Tamarix* from Iran. At first the monophyly of *Tamarix* on the 26 species exponent the three sections of Baum's classification, proposed by Gaskin and Barbara (2003) [19]. This analysis include 19 species of *Tamarix* from Iran and 13 species of non Iranian *Tamarix* . In this ITS phylogeny study, according to our obtained data the genus *Tamarix* in Iran was determined as a monophyletic group (fig. 1).

Congruence of morphological and molecular data at Sectional Level.
The three taxonomic sections based on morphology (Baum 1978) are not supported by the molecular analyses. For example, in clade R, *T.smyrnensis*, *T.hohenackeri* (belong to section Tamarix) and *T.chinensis* (belong to section Oligadenia), as well as, in clades R, Q, J and L, species belong to different sections are found together. Thus, the morphological characters used to define the sections of *Tamarix* should be reevaluated.

Data analysis indicates that the classification of *Tamarix* species according androecial disc morphology so not true, but leaf morphology and number of floral parts that have been considered are useful for the taxonomy of *Tamarix* species. For example in clade G, containing *Tamarix aphylla* is well supported (PP = 0.92; BS = 97%) and includes another vaginate leaved species, *T. usneoides* as well as in more clades, species with identical number of floral parts are found together (for example in clades U, R, M and D, all species have pentamerous flowers and in clade W, all species have tetramerous flowers) but in clade Q, *T.ramosissima*, *T.arceuthoides*, *T.nilotica* and *T.aralensis* all have hololophic androecial disc with *T.hispida* and *T.androssowii* that have synlophic androecial disc are found together.

Identification of species
T. aralensis and *T. ramosissima* can be identified by their sessile leaves, pentamerous flowers and hololophic androecial discs (see Tab. 1) . *T.aralensis* is distinguished from *T. ramosissima* by its caducous petals at the time of seed maturation (Baum 1967) [4]. Crins (1989) claims that their morphology is similar, and that it is difficult to recognize these two taxa as different species[14]. In this cladogram, molecular evidence support *T. ramosissima* and *T.aralensis* are distinct species.

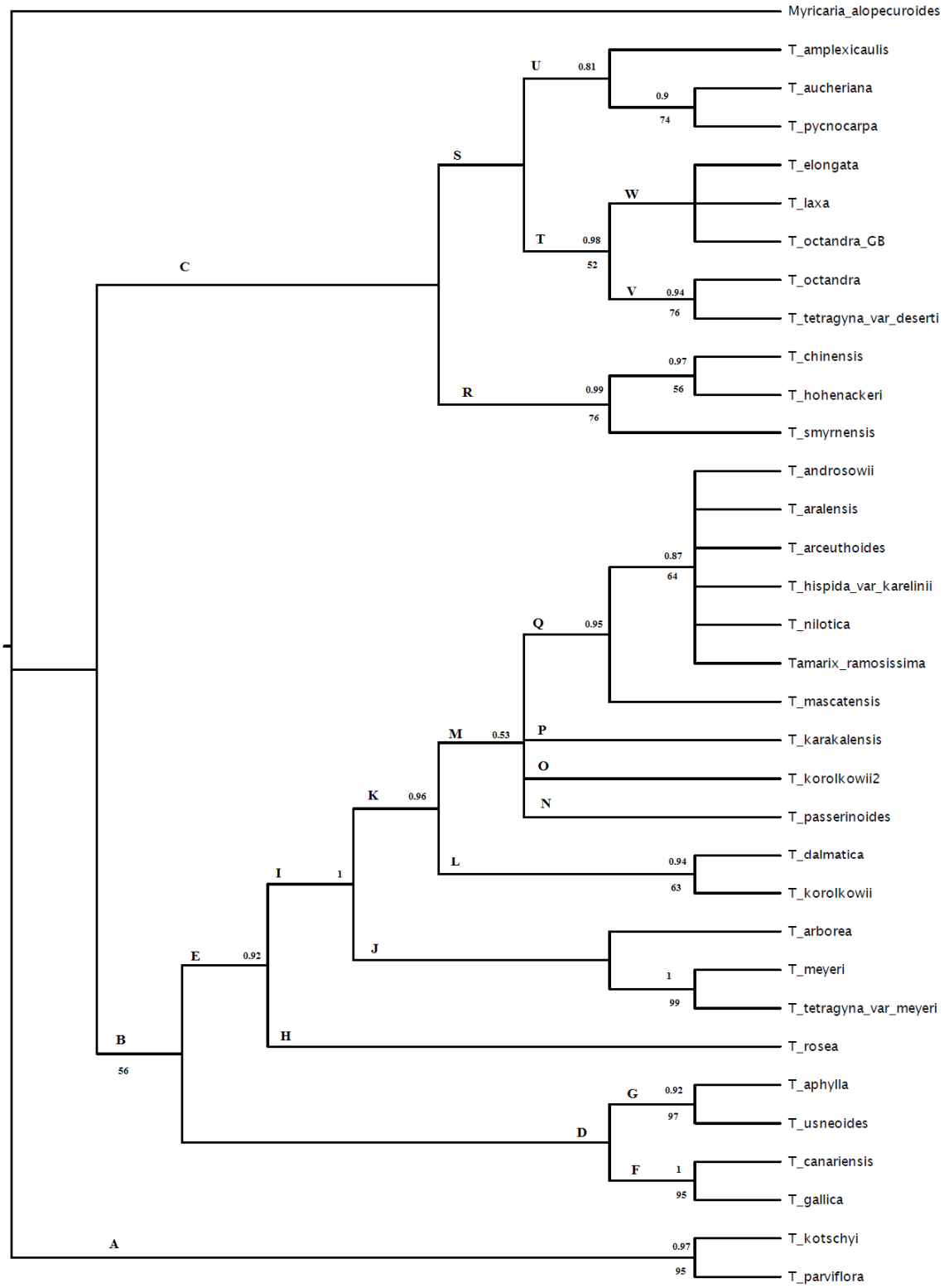
Based on morphological characteristics, it is difficult to distinguish the two species *T.arceuthoides* and *T.korolkowii*. In *T.arceuthoides*, raceme is no dense and flowers are placed at a distance, in addition in the observed sample , the flower color is red but in *T.korolkowii*, raceme is dense and in the observed sample, the flower color is white. Assadi (1987) said, further research may prove one of two species [21]. In according to our research, they have located in different clades and have distinct DNA sequences.

Two species *T.hohenackeri* and *T.smyrnensis* are known synonymous by Baum (1978) but Qaser (1983) knows *T.hohenackeri* independent of *T.smyrnensis*, also in Flora of Iran, both species *T. ramosissima* and *T.smyrnensis* are known synonymous by Assadi (1987). The major difference in the literature as to the separation of the two species is in the shape of petals [21]. In *T.smyrnensis*, petals are ovate to suborbicular, strongle keeled especially in their lower part but in *T. ramosissima*, petals are obovate and not keeled [4]. In according to this study, *T.smyrnensis* and *T.hohenackeri* located in clade R and *T.ramosissima* located in clade Q. The results revealed that three species with little morphological difference have distinct DNA sequences and synonym of *T.ramosissima* and *T.smyrnensis*, as well as synonym of *T.hohenackeri* and *T.smyrnensis* is not confirmed.

Based on morphological characteristics, *T. kotschyi* and *T. androssowii* are very similar and it is difficult to distinguish the two species. In *T. androssowii*, Bracts shorter than the pedicels and inflorescence is no dense or semi-dense. Assadi (1987) said, further research may prove one of two species [21]. In this study, they have located in different clades and have distinct DNA sequences.

Two species *T.meyeri* and *T. tetragyna* are known as distinct species by Baum (1978) [5] but Assadi (1987), for *T. tetragyna*, has identified two varieties: var.*meyeri* and var. *deserti* [21]. In this cladogram, both varieties are distinct from each other as well as *T.meyeri* and *T. tetragyna var meyeri* with high bootstrap support (99%) were put together thus, the specific status of *T.meyeri* is accepted in contrary to some authors who considered this as *T.tetragyna* var.*meyeri*.

Fig. 1 Phylogenetic relationships of 33 samples of *Tamarix*(19 species of *Tamarix* from Iran)based on ITS sequence data *Numbers above branches are Bayesian posterior probabilities. Numbers below branches are percentage bootstrap values*



CONCLUSION

The results indicate that *Tamarix* species from Iran constituted a monophyletic group. Despite the existence of a fairly recent monograph of the genus (Baum, 1978) *Tamarix* remains an exceedingly complex genus. Most species can not be identified without flowers and intermediate states exist for several morphological characters (and can even vary on a single individual or from season to season). Finally, DNA sequence data are in part incongruent with

morphological distinctions currently used to segregate taxa. Data analysis indicates that the classification of species according androecial disc morphology so not true, but leaf morphology and number of floral parts that have been considered are useful for the taxonomy of *Tamarix* species. In conclusion, this analysis reveals that morphology within *Tamarix* does not always correlate with DNA sequence data. Baum's (1978) sectional classification of the genus is not statistically similar to DNA sequence data, and future subgeneric classification of *Tamarix* must include molecular data.

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