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ECOMORPHOLOGY OF TORTOISES (*Testudo graeca* COMPLEX) FROM THE ARAKS RIVER VALLEY

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We described the high diversity of morphotypes of spur-thighed tortoises (the *Testudo graeca* complex) that inhabit the Araks River Valley. The habitat conditions of tortoises was highly correlated with their external morphology, where the variety of environmental conditions along the Araks River Valley affects the morphological plasticity of tortoises. We speculate that the diversity of external morphology of tortoises might have been promoted by admixed gene expression combined with a high environmental flexibility of the shell in different habitat conditions, as well as by geographical isolation of *T. graeca* in fragmented areas of distribution in the Ararat Valley.

Keywords: habitat differences; variability; shell morphology; spur-thighed tortoises.

INTRODUCTION

Spur-thighed tortoises (the *Testudo graeca* complex) are widely distributed from Southwest Asia to the Mediterranean, and the Middle East. These medium-sized terrestrial tortoises have a complex nomenclatural history. As many as 16 distinct subspecies have been described in the *Testudo graeca* complex (for a review see Guyot-Jackson, 2004; Rhodin et al., 2017). Molecular studies discounted the amount of species-level diversity, and instead proposed different nomenclatural arrangements. Parham et al. (2006) recommended a conservative approach of one species, *T. graeca*, while Fritz et al. (2007, 2009) used six mitochondrial clades as subspecies of *T. graeca*. Türkozan et al. (2010) showed that only a few mitochondrial clades corresponded to morphometric differences within Turkey. Such discordance between genetic and morphological data sets complicated the nomenclature of *Testudo graeca* complex. Mashkaryan et al. (2013) used 10 polymorphic microsatellite loci and sequences of the mitochondrial cytochrome b gene of tortoises from 26 sites in Armenia, Georgia, Iran, and Nagorno Karabakh Republic (NKR) to describe an intergradation zone among lineages corresponding to *T. g. armeniaca* Chkhikvadze et Bakradze, 1991, *T. g. ibera* Pallas, 1814 and *T. g. buxtoni* Boulenger, 1921 in the Araks River Valley.

Range-wide studies of *T. graeca* showed some populations in region of the Araks River Valley are of particular interest as they are the most distinct form of *Testudo graeca* (Parham et al., 2006; Fritz et al., 2007; Türkozan et al., 2010; Mashkaryan et al., 2013). The Araks River Valley is an area characterized by high biodiversity and by the presence of many endemic species (Darevsky, 1957; Chkhikvadze and Bakradze, 1991; Tuniyev, 1996; Arakelyan et al., 2011) and it is one of the most important biodiversity hotspots of Asia (Darevsky, 1957, Chkhikvadze and Bakradze, 1991). The continental and arid climate of the Araks River Valley support many suitable habitats for the spur-thighed tortoise that include desert, semidesert, dry-steppe, steppe, and subtropical light forest (Arakelyan and Parham, 2008; Arakelyan et al., 2011). The high mountain ranges (<1500 m) and large rivers are considered primary geographical barriers for the tortoises in Transcaucasia (Arakelyan and Parham, 2008). Unlike all other populations, some of the *T. graeca* from the Araks River Valley have very flat shells with rigid, hingeless, ventral armor (plastron). These features

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are considered specializations for deep burrowing (Chkhikvadze and Bakradze, 1991; Parham et al., 2006; Fritz et al., 2007; Arakelyan et al., 2008). This morphology characterizes the subspecies *Testudo graeca armeniaca* sensu Chkhikvadze and Bakradze (1991) (type locality: Meghri, Syunik Province, Armenia borderland region with Iran). Chkhikvadze and Bakradze (1991) and Pieh et al. (2002) suggest that all *T. graeca* of the Araks River Valley should be assigned to the flat-shelled "*T. g. armeniaca*" based on a locality further up the Araks River in Turkey (Aralık village, foothill of Ararat Mt., Turkey). However, Arakelyan et al. (2008) and Arakelyan and Parham (2008) complicate this assertion by showing that the morphology of *T. graeca* from different parts along the Araks River Valley can be quite variable. For example, the *T. graeca* populations that inhabit the Araks River Valley from side of northern Iran also have a high-domed shell (Rezazadeh et al., 2014).

The objectives of our study were to 1) study morphological variation among tortoises from different habitats along the Araks River Valley in Armenia, Turkey, Iran and Nagorno Karabakh, and 2) combine data on the morphology and habitats of tortoises.

MATERIAL AND METHODS

We measured tortoises over a ten-year period from 2002 – 2011 in Armenia, NKR, Turkey, and Iran (Table 1, Fig. 1). All tortoises were measured and photographed in field and then released to the same location.

We recognized three areas according to the distribution pattern of samples of *T. graeca* in the Araks River Valley (Fig. 1); "Area 1" is the temperate arid Ararat Plain and foothills of mountains in Turkey (points T1 – T3 on Fig. 1) and southwestern Armenia (points A1 – A5); "Area 2" is the subtropical semi-arid plain in southern Armenia (point A6), NKR (N1, N2) and northern Iran (I1 – I6); "Area 3" is the thermally moderate, humid mountains in NKR (N3). Area 1 includes the Ararat mountain plateau with a flat landscape of stony semi-desert covered by dry dwarf shrub vegetation and volca-

TABLE 1. Number of Captured *T. graeca* from Araks River Valley.

Code	Locality	Lat.	Long.	Alt	Sex	*N*
A1	Armenia, Armavir Province, Vanand village	40°06′ N	43°49′ E	1040	female	10
					male	9
A2	Armenia, Ararat Province, Urtsadzor village	39°54′ N	44°49′ E	1120	female	13
					male	5
A3	Armenia, vicinity of Yerevan city	40°10′ N	44°29′ E	1000	female	2
A4	Armenia, Ararat Province, Gorovan village	40°09′ N	44°02′ E	886	female	1
					male	1
A5	Armenia, Kotayk Province, Garni village	40°06′ N	44°42′ E	930	female	2
					male	1
A6	Armenia, Syunik Province, Meghri city	38°54′ N	46°15′ E	740	male	4
N1	NKR, Kashatagh Province, Tcobi village	39°00′ N	46°40′ E	350	female	20
					male	4
N2	NKR, Kashatagh Province, Lusavan village	39°18′ N	47°01′ E	270	female	5
					male	7
N3	NKR, Hadrut Province, vicinity of Aknakhbyur village	39°33′ N	47°05′ E	684	female	2
					male	3
I1	Iran, West Azarbaijan Province, Marand city	38°47′ N	45°33′ E	1380	female	3
					male	1
I2	Iran, Eastern Azarbaijan Province, Khodafarin	39°23′ N	47°41′ E	1400	female	3
I3	Iran, Eastern Azarbaijan Province, Ahar	39°08′ N	47°12′ E	1120	female	1
I4	Iran, Western Azarbaijan Province, Khoy	38°56′ N	45°32′ E		female	1
I5	Iran, Eastern Azarbaijan Province, near border with NKR, Ahar	39°10′ N	47°06′ E	1360	female	3
I6	Iran, Eastern Azarbaijan Province, Kalibar	38°58′ N	46°48′ E	1620	female	1
T1	Turkey, Aralık Province, near Nakhichevan border	39°47′ N	44°35′ E	809	female	1
T2	Turkey, Aralık Province, vicinity Aralik city	39°53′ N	44°29′ E	828	female	10
					male	15
T3	Turkey, Iğdir Province, Melekli village	39°54′ N	44°55′ E	800	female	1

nic highlands with steppe and meadow-steppe habitats mixed with wetlands. The friable soil is the gray mosaic semi-desert type suitable for burrowing by tortoises. Area 2 has complex habitats including hilly and foothill landscapes with *Botriochloa* and *Stipa* steppes, dry shrublands (shibliak), dwarf shrub (phrygana) vegetation, semi-deserts and middle mountain beech forests alternating with hornbeam-oak forests and secondary grassland. The vegetation cover is a diverse assemblage of plants. The main soil type is chestnut-carbonate with deficient drainage, which is convenient for digging animals. In Area 3 the landscape is mountain steppe. Grasslands dominate the foothills and mid-mountain areas. The tops of the hills and the mountain are mostly forested with oak, hornbeam, linden, ash, birch, and other trees. The brown forest soil structure, with significant humus and massive fibrous root structure of grass, complicates the process of burrowing by tortoises.

We measured 53 morphometric characteristics on each captured tortoise according to scheme of Türkozan et al. (2003, 2010). For statistic analyses we used the following 37 characters: SCL, straight carapace length from the outermost projection of the cervical scale to the outermost projection of the posteriors marginals; PL, plastron length from the outermost projection of the gulars to the posterior end of the anals; CW, median carapace width, straight-line measurement at the middle of the carapace; MCW, maximum carapace width; CH, carapace height, the vertical measurement between the most dorsal point of the carapace and the most ventral point of the plastron; LB, bridge length between axillary and inguinal scales; MGSL, maximum (not midline) gular scale length; MGSW, maximum (combined left plus right) gular scale width; CHSW, maximum humeral scale width; CPSW, maximum pectoral scale width; CAbSW, maximum abdominal scale width; CFSW, maximum femoral scale width; CSAW, maximum anal scale width; GSL, length of suture between gulars; HSL, length of suture between humerals; PSL, length of suture between pectorals; AbSL, length of suture between abdominals; FSL, length of suture between femorals; ASL, length of suture between anals; NL, length of nuchal scale; NW, the width of nuchal scale; VW1 – 5, maximum width of first till fifth vertebral scale; VL1 – 5, maximum median length of first till fifth vertebral scale; DSW, maximum dorsal width of supracaudal scale; VSW, maximum ventral width of supracaudal; SL, maximum median length of supracaudal length; CL1 – 4, first till fourth pleural scale along length as the minimum straight line distance between the anteriormost and posteriormost contact points with adjacent marginal scales. In addition to the measurements above, we recorded weight, sex, and color pattern.

We performed statistical analyses using STATISTICA 7.0 software. We compared differences among sex only in populations of NKR (10 males and 21 females) and Turkey (15 males and 12 females) because of a sufficient number of both sexes in these samples. Juveniles (<15 cm SCL) were excluded from all analyses. Because

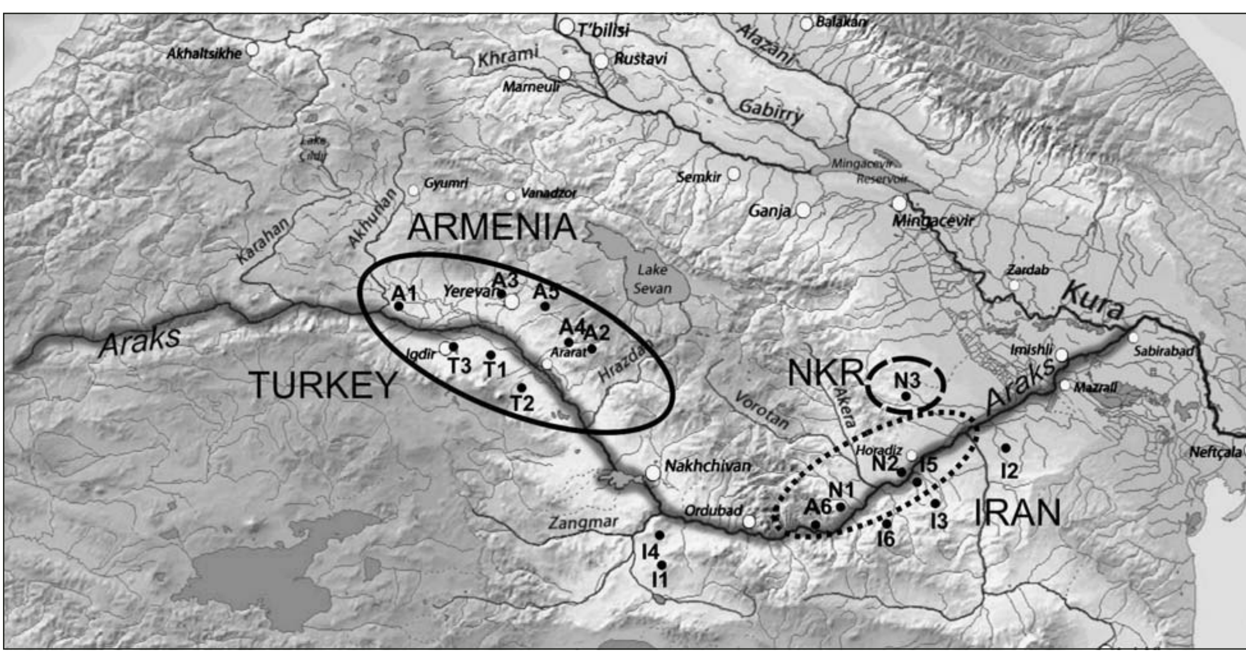

Fig. 1. Sampling localities. See Table 1 for abbreviations of localities.

TABLE 2. Comparison of Area 1 and Area 2

Variable	Mean "Area 1"	Mean "Area 2"	*t*-value	*p*
Pl/SCL	0.904	0.885	1.416	0.164
CW/SCL	0.766	0.755	0.966	0.339
MCW/SCL	0.776	0.769	0.603	0.549
CH/SCL	**0.484**	**0.510**	**–2.664**	**0.011**
LB/SCL	0.466	0.458	1.046	0.301
MGSL/SCL	**0.179**	**0.159**	**5.362**	**0.000**
MGSW/SCL	0.159	0.167	–1.260	0.214
CHSW/SCL	0.500	0.472	2.986	0.005
CPSW/SCL	0.690	0.684	0.458	0.649
CAbSW/SCL	0.727	0.708	1.750	0.087
CFSW/SCL	0.494	0.493	0.034	0.973
CSAW/SCL	0.353	0.372	–2.487	0.017
GSL/SCL	**0.155**	**0.138**	**3.967**	**0.000**
HSL/SCL	0.107	0.122	–2.137	0.038
PSL/SCL	0.061	0.066	–1.419	0.163
AbSL/SCL	0.312	0.308	0.526	0.601
FSL/SCL	0.103	0.096	1.081	0.285
ASL/SCL	0.150	0.153	–0.418	0.678
NL/SCL	0.078	0.077	0.256	0.799
NW/SCL	0.032	0.036	–1.493	0.142
VW1/SCL	**0.227**	**0.249**	**–3.409**	**0.001**
VW2/SCL	**0.242**	**0.271**	**–5.031**	**0.000**
VW3/SCL	**0.282**	**0.300**	**–2.925**	**0.005**
VW4/SCL	**0.258**	**0.271**	**–2.800**	**0.007**
VW5/SCL	0.323	0.325	–0.298	0.767
VL1/SCL	0.203	0.206	–0.465	0.644
VL2/SCL	0.190	0.195	–1.283	0.206
VL3/SCL	0.180	0.185	–1.140	0.260
VL4/SCL	0.194	0.202	–1.913	0.062
VL5/SCL	0.227	0.230	–0.530	0.598
DSW/SCL	0.189	0.181	1.086	0.283
VSW/SCL	0.294	0.278	1.681	0.099
SL/SCL	0.144	0.150	–1.307	0.198
CL1/SCL	0.295	0.289	0.919	0.363
CL2/SCL	0.225	0.219	1.378	0.175
CL3/SCL	0.214	0.208	1.340	0.187
CL4/SCL	**0.173**	**0.197**	**–5.237**	**0.000**

Note. Student's *t*-test statistically important differences in bold, for abbreviations, see the *Materials and Methods*.

of the rarity of tortoises in southern Armenia, Iran, and NKR populations as well as scarcity of males in samples, we made our comparative analyses among populations based on only morphology of females. We performed ANOVA on measurements standardized for straight carapace length (SCL) to verify a sexual dimorphism and determine morphological variability between localities. We used the Scheffé's post hoc tests to determine the significance of differences between groups. We performed Principal Component Analyses (PCA) with 37 morphometric characters of raw data for visualization of dispersion of tortoises from all examined samples to reveal the main characters of their morphology. The significance level for all tests was set at $P < 0.05$.

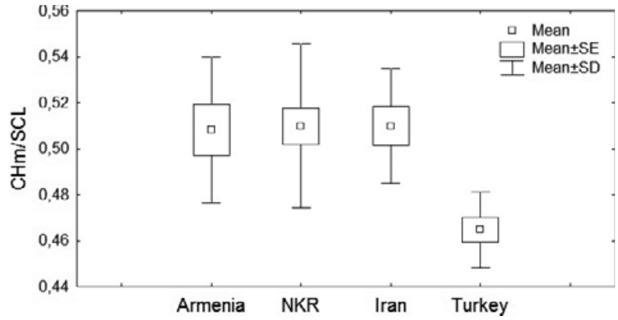

Fig. 2. The comparison of the maximal carapace height (CHm) standardized for straight carapace length (SCL) of tortoises from different countries.

RESULTS

The shell morphology of tortoises from different mountain ranges along the Araks River Valley displayed significant differences in external morphology. Tortoises from Turkey and Armenia in Area 1 have low-domed carapaces, which is one of the main morphological diagnostic character of "*armeniaca*." Furthermore, plastral measurements such as GSL, HSWC, ASWC, GSL, HSL and carapacial measurements of VW1, VW2, VW3, VW4, and CL4 varied between Area 1 and Area 2 (Table 2). Tortoises from Turkey have the lowest domed shell (Fig. 2). The shells of most tortoises from the Ararat Plain were heavily worn, probably due to a burrowing lifestyle. The PCA showed clear morphological separation of Area1 from Area 2 (Fig. 3). The main characteristics of shells of tortoises from four different populations is presented in Table 3.

The shells of tortoises from NKR and Iran populations in Area 2 have variable carapace heights and mixed external morphology (Figs. 2, 3). In the northern bank of the river in Armenia and NKR (sites A6, N1, N2), we found a few typical-looking "*armeniaca*" individuals with low-domed shells together with individuals with high-domed shells and kinetic plastron that look like "*ibera*" and "*buxtoni*," as well as many intermediate forms. Among Iranian samples only one specimen showed some similarity with "*armeniaca*" according morphological characteristics of shell, however the largest carapace length (SCL = 270 mm) and high domed shell put this individual out of range of this form and ex-

TABLE 3. The Mean (± standard deviation) of Morphological Characteristics of Shells of Adult Females of *T. graeca* from Four Populations

Variability	Armenia, Armavir Province (*N* = 10)	Armenia, Ararat Province (*N* = 12)	NKR, Kashatagh Province (*N* = 19)	Turkey, Aralık Province (*N* = 10)
Carapace length	189.0 ± 38.68	186.0 ± 38.38	166.6 ± 46.56	187.4 ± 17.86
Plastron length/Median	170.9 ± 32.71	160.2 ± 29.20	146.6 ± 40.43	171.8 ± 15.09
Carapace width/Median	156.8 ± 6.62	146.2 ± 27.72	125.1 ± 29.71	142.6 ± 10.79
Carapace width	160.3 ± 4.58	159.4 ± 10.93	127.0 ± 32.95	143.3 ± 10.99
Carapace height	94.4 ± 16.52	90.4 ± 15.44	83.8 ± 19.17	87.6 ± 7.42
Length of bridge	89.9 ± 18.15	85.4 ± 17.80	78.4 ± 21.98	87.8 ± 7.50
Gular scute length	32.7 ± 7.48	31.6 ± 7.81	25.8 ± 6.79	34.7 ± 3.27
Gular scute width	32.4 ± 6.50	30.3 ± 6.13	26.5 ± 5.87	28.7 ± 3.22
Humeral scute width	94.5 ± 19.21	89.4 ± 16.45	79.3 ± 19.97	95.2 ± 6.87
Pectoral scute width	131.1 ± 26.25	130.7 ± 25.57	113.0 ± 27.85	131.5 ± 10.25
Abnominalscute width	136.1 ± 26.43	136.1 ± 26.71	118.0 ± 28.85	137.5 ± 9.30
Femoral scute width	95.8 ± 19.79	91.1 ± 17.85	83.7 ± 23.81	90.8 ± 6.42
Anal scute width	69.5 ± 15.29	68.6 ± 13.77	61.2 ± 18.66	64.0 ± 6.08
Gular suture length	29.7 ± 7.34	28.4 ± 7.49	22.7 ± 6.39	29.0 ± 2.40
Humeral suture length	23.1 ± 7.17	23.3 ± 7.64	19.8 ± 6.35	17.5 ± 2.20
Pectoral suture length	11.7 ± 2.40	11.2 ± 1.84	11.4 ± 3.05	12.1 ± 1.95
Abdominal suture length	58.6 ± 13.53	54.8 ± 10.22	52.7 ± 15.05	59.8 ± 6.65
Femoral suture length	21.1 ± 5.10	17.7 ± 3.72	17.6 ± 5.50	18.4 ± 3.55
Anal suture length	26.9 ± 6.70	29.4 ± 7.12	25.8 ± 7.96	28.7 ± 3.42
Nuchal scute length	14.2 ± 3.01	15.5 ± 2.64	13.1 ± 3.48	15.5 ± 1.25
Nuchal scute width	7.0 ± 2.64	5.5 ± 0.91	6.1 ± 2.30	5.9 ± 0.98
Vertebral width — First	45.4 ± 8.27	40.2 ± 5.88	40.9 ± 8.99	41.0 ± 1.80
Vertebral width — Second	45.4 ± 8.78	44.0 ± 6.74	44.6 ± 10.23	45.4 ± 3.25
Vertebral width — Third	53.5 ± 10.90	52.0 ± 9.17	49.8 ± 11.82	53.1 ± 4.42
Vertebral width — Fourth	48.9 ± 9.74	49.9 ± 10.92	45.2 ± 11.25	48.2 ± 3.94
Vertebral width — Fifth	64.2 ± 15.17	59.4 ± 10.84	53.0 ± 14.53	58.8 ± 5.16
Vertebral length — First	39.4 ± 8.15	35.9 ± 6.02	33.9 ± 7.86	37.7 ± 3.10
Vertebral length — Second	36.1 ± 7.85	34.3 ± 6.69	33.4 ± 9.13	35.8 ± 3.44
Vertebral length — Third	34.2 ± 7.90	32.5 ± 6.55	30.8 ± 7.90	33.7 ± 3.28
Vertebral length — Fourth	36.2 ± 7.80	35.6 ± 6.67	33.7 ± 8.09	37.3 ± 4.13
Vertebral length — Fifth	44.4 ± 10.11	42.5 ± 10.34	37.7 ± 12.37	40.6 ± 4.25
Dorsal supracaudalis width	36.1 ± 9.11	35.4 ± 8.60	30.0 ± 8.37	35.3 ± 3.46
Ventral supracaudalis width	57.4 ± 13.14	49.9 ± 14.60	47.5 ± 12.37	55.6 ± 4.55
Median supracaudalis length	27.5 ± 7.10	27.9 ± 6.66	24.1 ± 6.12	25.9 ± 3.34
Costal length — First	56.4 ± 11.44	54.3 ± 10.06	47.1 ± 11.70	56.4 ± 5.13
Costal length — Second	41.1 ± 9.10	40.8 ± 8.26	37.1 ± 9.46	44.1 ± 3.11
Costal length — Third	40.8 ± 9.77	39.4 ± 8.08	35.6 ± 9.76	40.5 ± 4.41
Costal length — Fourth	32.9 ± 7.23	35.1 ± 7.19	33.4 ± 9.61	31.6 ± 4.55

cluded from the analysis of this study. The shells of tortoises from Area 2 had higher CH (test-test, $P < 0.05$), shorter GSL ($t = -5.36$; $P > 0.001$), narrower HSWC ($t = 2.99$ $P < 0.01$), wider ASWC ($t = -2.49$ $P < 0.05$), longer HSL ($t = -2.13$ $P < 0.05$), wider VW1 ($t = -3.41$ $P < 0.01$), VW2 ($t = 5.03$ $P < 0.001$), VW3 ($t = -2.93$ $P < 0.01$), VW4 ($t = -2.80$ p.01) and shorter CL4 ($t = -5.24$ $P < 0.001$). In comparison to Area 1, the carapace coloration has more distinct color patterns and vary from only dark-brown colors to gray without tan patches. The head coloration of Armenian and Turkish tortoises (Area 1 and Area 2) is uniform dark gray color with large scales while five tortoises from Iran (Area 2) had yellowish color of head with small scales.

In Area 3, we have found only high-domed tortoises that have the external morphology of "*ibera*," with typical coloration of the carapace and head. The carapaces were dark colors without traces of abrasions of shell.

The largest tortoise among our samples was a female (SCL = 270 mm) from West Azarbaijan Province of Iran (Area 2), while the maximum length of carapace for "armeniaca" in Turkey was 220 mm according to data of

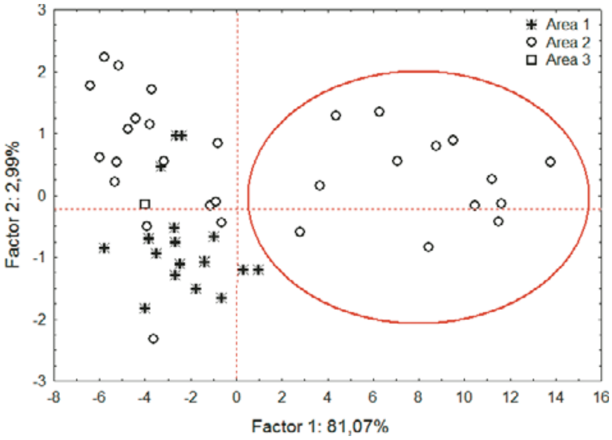

Fig. 3. Principal component analysis plots of morphological data for *T. graeca* females from main areas of distribution of tortoises along the Araks River Valley. Note that none of Area 1 samples remained in Area 2, while Area 2 samples remained in the circle of Area 1.

Turkozan et al. (2010). The numbers of largest tortoises that have SCL more than 220 mm were 5 out of 11 (45%) from Iran, 4 of 69 (6%) from Ararat Valley in Armenia, and 4 of 45 (9%) from NKR.

A plot of PCA (Fig. 3) shows the morphological differences between shells of female individuals from Area1 (Armenia and Turkey) and Area 2 (NKR and Iran). The first axis explained81.07% of the total variation and positively loaded with linear dimensions of median and maximum carapace width (CW and MCW), length of bridge (LB), and abdominal scute width (CAbSW), while the second axis accounted only for 2.99% and positively loaded with humeral suture length (HSL) and nuchal scute width (NW).

Sexual dimorphism is well documented for *T. graeca* (Carretero et al., 2005; Turkozan et al., 2003; Turkozan et al., 2010; Willemsen and Hailey, 2003, Fritz et al., 2008), including "*armeniaca*" form (Pieh et al., 2002). Females from different sites of our samples generally exceed males in carapace length (2-way ANOVA, site $F_2 = 4.09$, $P < 0.05$; sex $F_1 = 0.42$, $P = 0.52$; site*sex $F_1 = 0.66$, $P = 0.52$), with exception of one population in NKR. The comparison between sexes in our samples for populations from NKR and Turkey shows that females have larger PL, LB, AbCL, ASL, VL3 and smaller CL2, SL (curved in males) than males (ANOVA, Scheffé's post hoc tests, $P < 0.05$). Furthermore, females from Turkey have smaller MGSL, VW4, VW5, VL5, and VSW than males, whereas NKR populations had larger GSL and CL3 in males and a larger PSL in females.

DISCUSSION

Mountain ranges and rivers fragment the distribution of *T. graeca* within the Araks River Valley. In Armenia, the southern populations of *T. graeca* in the Araks River Valley are separated by high mountain ranges from northern populations in the Kura River Valley. The confluence of the Araks and Kura Rivers in NKR form a corridor for the integration of the two forms, where extensive gene flow (Mashkaryan et al., 2013) and phenotypic plasticity (Fritz et al., 2007) generates a diversity of external morphologies. The paleogeographic and tectonic evolution of the Kura – Araks River Basin plays important role in determining the distribution of different forms (species, subspecies or forms) of *Testudo* (Fritz et al., 2007; Popov et al., 2006; Chkhikvadze et al., 2013). There is no doubt that in the past, the valleys of the Kura and Araks Rivers were migration routes for different species of flora and fauna, penetrating in the Transcaucasia from the south (Darevsky, 1956). In particular, many species of Iranian and Eastern Mediterranean reptiles spread along the Kura River, and penetrated northern Armenia (independent from the Araks River corridor). Thus, the Kura River Valley population of tortoises referred to "*ibera*" mt clade sensu Parham et al. (2006) have gaps in its range that are most probably the result of glacial extinction (Fritz et al., 2007). The "*armeniaca*" form probably penetrated the Araks River Valley from southern territories in the Late Miocene, when the Araks River was connected with the Euphrates and Tigris River drainages (Starobogatov, 1975; Chkhikvadze, 1991; Vasilyan and Carnevale, 2013). The "*armeniaca*" form met "*ibera*" and "*buxtoni*" in the Kura – Araks lowland, where currently hybridization events are creating genetic diversity (Mashkaryan et al., 2013), which is confirmed by our morphological analyses.

Comparisons of the shell parameters, with genetic data from the same individuals, confirm several phylogeographic units. Thus, the Ararat Plain tortoises have flat shells and other morphological characters corresponding to description of subspecies *T. g. armeniaca* presented by Chkhikvadze and Bakradze (1991) as well as the *armeniaca* mt clade of Parham et al. (2006) and the Caucasian AFLP group (Mikulîcek et al., 2013). Northwestern Iran is occupied by the *T. g. buxtoni* morphotype that corresponds to the *buxtoni* mt clade of Parham et al. (2006) and includes the same Caucasian AFLP group. Tortoises from the northern part of Armenia and NKR are close to *T. g. ibera* morphotype where occur the *ibera* mt clade of Parham et al. (2006) and Balkans-Middle eastern AFLP group (Mikulîcek et al., 2013). The pattern of shells of tortoises from area in southern part of Armenia and NKR are complex and consists of high diversity of morphotypes and intermediate forms. Our findings agree with data reported for admixed *armeniaca*, *buxtoni*, and *ibera* mt types, as well as a high degree of admixture of microsatellite loci (Mashakaryan et al., 2013) from this area. The results of morphological and genetic analyses have shown the existence of a contact zone and extensive gene flow between different forms in the southern part of NKR and Armenia.

Analyses of external morphology of tortoises revealed significant differences in the external morphology of *T. graeca* from "Armavir," "Ararat," "Aralik" populations. Moreover, our study confirms the previous explanations for the phenotypes of tortoises in the Caucasus Region and confirms their ecological adaptation and plasticity (Parham et al., 2006; Fritz et al., 2007; Arakelyan et al., 2008). The divergence between environments along the Araks River Valley generates different morphotypes of tortoises. According to Claude et al. (2003), environment acts mostly on shell height and on the architecture of costal plates. Thus, in Area 1 we have found the flat-shelled "*armeniaca*" morphotype of tortoises highly specialized to deep burrowing. In this area, represented by semi-desert and dry steppe, the distribution of tortoises is fragmented and restricted by altitude and the friability type of soil. In contrast, only the high-domed "*ibera*" forms were found in open sites of mountain forests edge, on slopes with grass and bushes on mountain steppes in the vicinity of Aknakhbyur village in NKR in Area 3. In Area 2, the morphotypes of tortoises are most diverse, where flat-shelled animals occur alongside specimens with domed shells together with many intermediate forms. The landscapes in this area represent patches of different habitats. In arid semi-desert zones with xerophytic vegetation and soil favorable for burrowing (in vicinity of Lusavan village in NKR) there are tortoises with low-domed shells, while in zones of dry mountain steppe covered with scarce bushes and grassy vegetation (in vicinity Tcobi village in NKR) *T. graeca* displays intermediate as well as high-domed types of shells.

Because of the low density of populations of tortoises in all sites of the Araks River Valley, the organization of conservation measures should be a priority. The Araks River Valley is characterized by intensive development of the region and drastic anthropogenic transformation of natural biodiversity. An accurate understanding of the Evolutionarily Significant Units in this taxon is also important for guiding conservation strategies of *T. graeca*, which is listed as "Critical Endangered" in the IUCN Red List of Threatened Animals and Red Data Book of Armenia. Consequently, a better understanding of the Araks River Valley tortoises has the dual benefit of informing species delineations within the *T. graeca* complex, but also informing regional conservation efforts.

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