zoosystema

2024 • 46 • 4

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Yaser AMIR AFZALI, Reza NADERLOO, Alireza KEIKHOSRAVI & Sebastian KLAUS

art. 46 (4) — Published on 20 February 2024
www.zoosystema.com

PUBLICATIONS SCIENTIFIQUES
MUSÉUM NAL HIST NATURELLE

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Extract from Figure 1, sampling localities of *Potamon persicum* Pretzmann, 1962 in Iran.

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Tél. : 33 (0)1 40 79 48 05 / Fax : 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / https://sciencepress.mnhn.fr

ISSN (imprimé / *print*) : 1280-9551/ ISSN (électronique / *electronic*) : 1638-9387

Geographic differentiation in the freshwater crab *Potamon persicum* Pretzmann, 1962 (Decapoda, Potamidae) in the Zagros Mountains: evidence from morphometry

Yaser AMIR AFZALI
Reza NADERLOO
School of Biology, College of Science, University of Tehran,
Enghelab Street, Tehran 1417935840 (Iran)
y.a.afzali@gmail.com
rnaderloo@ut.ac.ir (corresponding author)

Alireza KEIKHOSRAVI
Department of Biology, Hakim Sabzevari University,
Touhid Shahr District, Sabzevar 9617976487 (Iran)
a.keikhosravi@hsu.ac.ir

Sebastian KLAUS
Environmental Resources Management, ERM GmbH,
Neu-Isenburg Siemensstr. 9 · 63263 (Germany)
sebastian.klaus@erm.com

Submitted on 23 January 2023 | Accepted on 1 August 2023 | Published on 20 February 2024

urn:lsid:zoobank.org:pub:020933A2-5754-434F-9391-2A58CF26D7FD

Amir Afzali Y., Naderloo R., Keikhosravi A. & Klaus S. 2024. — Geographic differentiation in the freshwater crab *Potamon persicum* Pretzmann, 1962 (Decapoda, Potamidae) in the Zagros Mountains: evidence from morphometry. *Zoosystema* 46 (4): 77-93. https://doi.org/10.5252/zoosystema2024v46a4. http://zoosystema.com/46/4

ABSTRACT

The freshwater crab *Potamon persicum* Pretzmann, 1962 in Iran is distributed along the western Alborz Mountains, its range extending southeast through the whole Zagros Mountains. We expected a high geographic differentiation within *Potamon persicum* between the main drainage systems in the region (Khalij Fars-Oman, Markazi and Urmia basins). To test this hypothesis, we conducted conventional morphometric and geometric-morphometric analyses. Comparison of males and females between populations of three main drainage systems showed significant differences of eleven traits. We also detected significant sex-specific differences among the three main drainage systems. The results are supported by geometric-morphometric analysis of the carapace shape, as carapace shape varies between sex and populations of three main drainage systems. Based on both analyses, populations of Khalij Fars-Oman and Markazi basins are similar to each other. Furthermore, a higher differentiation was seen between populations from Markazi and Urmia basins. We hypothesize that the *P. persicum* geographic differentiation is a result of both isolation by topography and climate during the Pleistocene glacial periods.

KEY WORDS
Population variations, morphology, sexual dimorphism, maturity, freshwater crabs.

RÉSUMÉ
Différentiation géographique chez le crabe d'eau douce Potamon persicum *Pretzmann, 1962 (Decapoda, Potamidae) dans les monts Zagros ; données de la morphométrie.*
Le crabe d'eau douce *Potamon persicum* Pretzmann, 1962 en Iran est présent le long des monts Alborz occidentaux, son aire de répartition s'étendant vers le sud-est à l'ensemble des monts Zagros. Nous nous attendions à une forte différentiation géographique au sein de *Potamon persicum* entre les principaux systèmes de drainage de la région (bassins Khalij Fars-Oman, Markazi et Urmia). Pour tester cette hypothèse, nous avons effectué des analyses classiques de morphométrie et de morphométrie géométrique. La comparaison des mâles et des femelles entre les populations de trois principaux systèmes de drainage a montré des différences significatives pour onze caractères. Nous avons également détecté des différences significatives selon le sexe entre les trois principaux systèmes de drainage. Les résultats ont été corroborés par une analyse de morphométrie géométrique de la forme de la carapace, qui varie selon le sexe et entre les populations des trois principaux systèmes de drainage. D'après ces deux analyses, les populations des bassins de Khalij Fars-Oman et de Markazi sont similaires. En outre, une différentiation plus élevée a été observée entre les populations des bassins de Markazi et d'Ourmia. Nous émettons l'hypothèse que la différenciation géographique de *P. persicum* est le résultat à la fois de l'isolement par la topographie et du climat pendant les périodes glaciaires du Pléistocène.

MOTS CLÉS
Variations de population, morphologie, dimorphisme sexuel, maturité, crabes d'eau douce.

INTRODUCTION

Morphological analysis is useful to show adaptive differentiation, population dynamics, reproductive pattern, and are crucial to answer fundamental questions in evolutionary biology, as morphology is the outcome of a species evolutionary history (Hopkins & Thurman 2010; Herter *et al.* 2011; Lezcano *et al.* 2012; Yang *et al.* 2014; Amir Afzali *et al.* 2017). Morphometric analysis is frequently used in freshwater crabs to assess morphological variations. This includes variation between sexes, within and between population structure, as well as geographical differentiation (Silva & Paula 2008; Keikhosravi & Schubart 2013; Torres *et al.* 2014; Kalate *et al.* 2017; Parvizi *et al.* 2017). In brachyuran crabs, the growth rate of body parts (especially primary or secondary sexual characters), quickly changes with sexual maturity in relation to the body parts with steady growth rates. Therefore, the consideration of this kind of allometric growth is decisive for morphometric analyses. Only specimens that reach to the sexual maturity were used for morphometric analysis. Sexual size dimorphism is defined as the phenotypic differences in body dimensions and proportions between males and females (Glucksmann 1974). This phenomenon has also been documented in the family Potamidae Ortmann, 1896, for example *Potamon potamios* Olivier, 1804 (Gherardi & Micheli 2013), *Potamon elbursi* Pretzmann, 1962 (Kalate *et al.* 2017), and *Potamon ibericum* Bieberstein, 1809 (Parvizi *et al.* 2017), because there are differences between males and females (especially in abdomen and chela size), they are analysed separately.

The freshwater crab genus *Potamon* Savigny, 1816 is widely distributed from northern Africa through southern Europe, to the entire Middle East, extending to East and Southeast Asia (Yeo & Ng 2003, 2007; Jesse *et al.* 2011; Klaus *et al.* 2011, 2017; Cumberlidge *et al.* 2014). With currently 22 described species, it is one of the most speciose potamid genera (Keikhosravi & Schubart 2014; Ghanavi *et al.* 2023). Nine of 22 valid species of *Potamon* occur on the Iranian plateau. The most widely distributed species in Iran is *Potamon persicum* Pretzmann, 1962, which is found from the northwest of Iran along the western Alborz Mountains, extending southeast through the whole Zagros Mountains. Generally, *P. persicum* is distributed in eastern Turkey, northeastern Iraq, Armenia and Iran.

The taxonomic status of *P. persicum*, has been constantly discussed over the past half century. Pretzmann (1962, 1976) recognized four species/subspecies within the *P. persicum* complex: *Potamon persicum elbursi* Pretzmann, 1962, described from the Alborz Mountains; *Potamon armenicum* Pretzmann, 1962, described from Jerewan, Armenia; *Potamon magnum vangoelium* Pretzmann, 1976, described from the Lake Van, Turkey; and *Potamon persicum kermanshahi* Pretzmann, 1976, described from Kermanshah, Iran; but later, all species/subspecies were synonymized with *P. persicum* by Brandis *et al.* (2000). Keikhosravi & Schubart (2013) redescribed one of Pretzmann's subspecies (*P. persicum elbursi*) and elevated it to the species rank. They also described a new species, *Potamon ilam* Keikhosravi & Schubart, 2014, which has a limited distribution in the western part of the middle Zagros Mountains (Keikhosravi & Schubart 2014). Their preliminary genetic results also indicated divergence within populations of *P. persicum*. The high diversity of *P. persicum* in the Zagros Mountains is reflected by several studies on other animal taxa, e.g., freshwater fishes (Frisch 2006; Esmaeili *et al.* 2016), reptiles (Gholamifard 2013) and insects (Yakovlev 2015; Safaei-Mahroo *et al.* 2015). Similarly, the Zagros Mountains region is considered as a separate floristic province within the Irano-Anatolian hotspot due to its extremely high rate of endemism (Noroozi *et al.* 2007; Heydari *et al.* 2013; Abrari Vajari *et al.* 2014; Parvizi *et al.* 2016).

The Irano-Anatolian biodiversity hotspot mainly covers the high elevations of central and eastern Turkey, Armenia, northeastern Iraq and Iran. Iran contains 54% of the surface area of the hotspot. Five 'biodiversity hotspots-within-hotspots' were identified for Iran (i.e., Zagros, Azerbaijan, Alborz, Central Alborz and Kopet Dagh-Khorasan; Noroozi *et al.* 2018). In these mountainous ranges, a high degree of endemism is associated with heterogeneity of the environment and complexity of the topography (percentage of endemism directly increases along the elevational gradient). High topographic complexity probably causes high habitat diversity and thus a large number of local niche spaces. This is thought to foster adaptation to different niches (i.e., ecological speciation) as well as creating local refugia for species during climatic fluctuations and thus reducing extinction risks (Ashcroft *et al.* 2012; Darvish *et al.* 2012; Manafzadeh *et al.* 2016; Amir Afzali *et al.* 2018; Hashemzadeh Segherloo *et al.* 2018). Disjunct distributions, in particular caused by high elevations, further promote isolation and consequently allopatric speciation in the high mountains of the Irano-Turanian region during glacial times (Noroozi *et al.* 2018). Mountain uplift influences drainage patterns that act as bridges and barriers, and also affect atmospheric currents. The Zagros Orogenic Belt has been active until today (Agard *et al.* 2005; Gavillot *et al.* 2010) but an important phase of tectonic deformation happened in the Late Miocene and Early Pliocene (10-5 Ma), and raised the Iranian plateau, new arrangement of drainage patterns and mountain ranges (Homke *et al.* 2004; Agard *et al.* 2005; Mouthereau *et al.* 2007).

The Middle East has undergone an alteration of humid and dry periods over the last 6500 years, which led to lower or greater connectivity than currently for many mesic species (Schuster *et al.* 2006; Sun *et al.* 2021). There is evidence from paleoclimatic and phylogeographic modeling that have highlighted Zagros Mountains acting as glacial refugia for species of birds, reptiles, mammals and insects during past climatic oscillations (Eskandarzadeh *et al.* 2018). The Zagros Mountains were characterized by a cooler and more arid climate compared to the Holocene (Kehl 2009; Djamali *et al.* 2012). Repeated cycles of restriction and outward expansion during glacial and interglacial periods shaped the current distribution pattern of many animal species. Different selective pressures may affect species morphology and most cryptic species are a result of recent speciation so that distinct morphological traits have not yet evolved or become obvious (Ahmadzadeh *et al.* 2013).

Here, we hypothesize that *P. persicum* consists of morphologically distinct populations of separately evolving lineages, because the distribution range of this species in Iran includes three basins, seven sub-basins, five tectonic units, several glacial refugia and two hotspots-within-hotspots (Azerbaijan and Zagros), all with different topography, geology, drainage systems and climate conditions. Therefore, it is likely that past climate fluctuations, in line with unique topography of the region, had a significant impact on populations through genetic isolation and, consequently, the process of speciation in the Zagros Mountains. Therefore, although almost all species and subspecies of *Potamon persicum sensu lato* described by Pretzmann from the Zagros Mountains have been synonymized under the name *P. persicum*, based on recent genetic studies (Keikhosravi & Schubart 2013, 2014), we investigated the geographic differentiation of morphology within this freshwater crab that may have not been captured by mitochondrial genetic markers. This includes estimating the size at sexual maturity, describing sexual dimorphism, and consequently finding morphological distinctions among populations from different basins (Khalij Fars-Oman, Markazi and Urmia basins) and visualize the patterns of carapace shape by using geometric-morphometric methods.

MATERIAL AND METHODS

A total of 140 specimens were collected from 18 localities throughout three drainage systems (Fig. 1). The specimens included those collected in 2020 and 2022, as well as specimens deposited in the Zoological Museum of the University of Tehran (ZUTC) (Appendix 1).

Nineteen characters were measured and all measurements were taken twice with digital calipers to the nearest 0.01 mm; these were carapace length, carapace width, distance between anterolateral tubercles, distance between exorbital teeth, posterior carapace width, length of propodus of chela, height of propodus of chela, length of dactylus of chela, height of dactylus of chela, length of pollex of chela, height of pollex of chela, telson length, telson width, length of sixth pleonal somite, width of sixth pleonal somite, maximum pleonal width, merus length of third walking leg, merus width of third walking leg and body height; the mean measurements were used in the analysis (Fig. 2). Because the right chela is larger and dominant in this species, only right-handed individuals were included in the analysis of chelae. Only five males and five females were left-handed (7.1%).

Estimating size at sexual maturity was obtained using piecewise linear regressions. Carapace length (CL) was considered as an independent variable that has constant growth rate during ontogeny, while maximum pleonal width of females and chela length of males were considered as dependent variables (Somerton 1980; Corgos & Freire 2006; Silva *et al.* 2014; Williner *et al.* 2014; Parvizi *et al.* 2017). Piecewise linear regressions analysis between CL and each dependent variable were performed separately by R, package segmented (Muggeo 2008).

Morphological analysis was performed on the adults using SPSS 26.0. For standardisation and elimination of the size factor (making them independent of the size), all characteristics were divided by CL, then the data were transformed into a linear form by logarithm. Before performing analysis, traits alignment was examined by hierarchical clustering analysis and squared Euclidean distance. Data normality was tested by the Kolmogorov-Smirnov test. Discriminant Function Analysis (DFA) was performed on morphological traits to determine how much the specimens of each basin can be distinguished from each other based on the measured

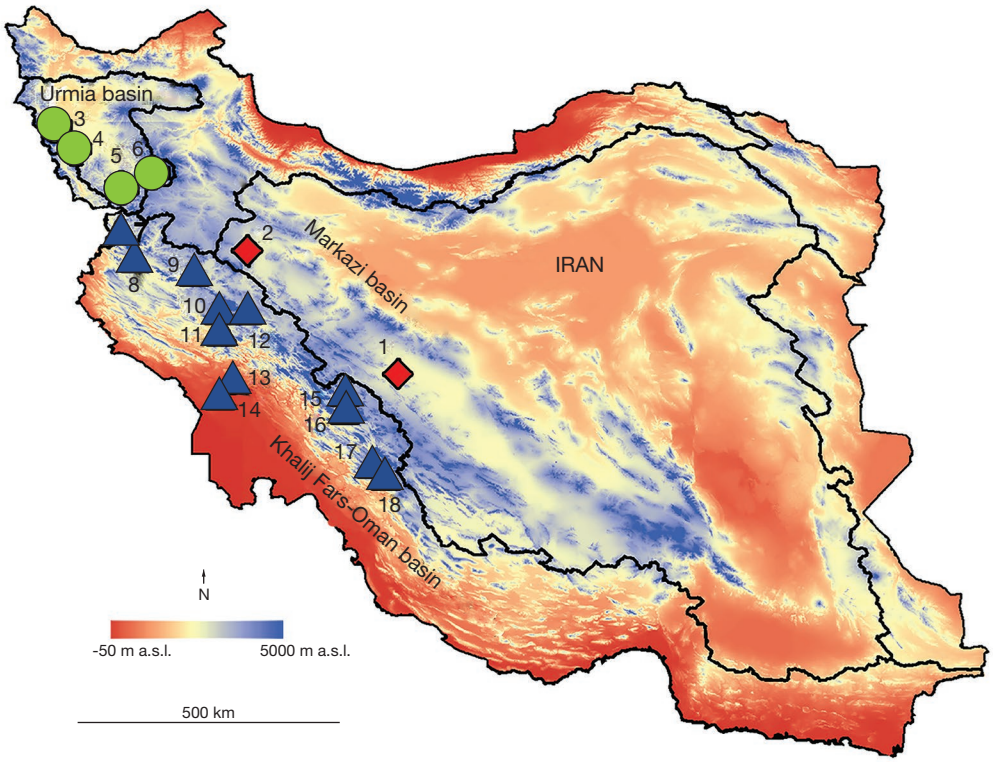

Fig. 1. — Sampling localities of *Potamon persicum* Pretzmann, 1962 in Iran. **Black lines** represent basins: ◆, Markazi basin; ●, Urmia basin; ▲, Khalij Fars-Oman basin. **Numbers in parentheses** represents number of males and females, respectively: **1**, Isfahan (6/1); **2**, Hamedan (11/7); **3**, Shahri Chay (8/6); **4**, Urmia (5/0); **5**, Saghez (5/4); **6**, Takab (4/2); **7**, Marivan (2/3); **8**, Paveh (2/3); **9**, Sahneh (1/0); **10**, Alashtar (1/1); **11**, Khoram Abad (7/1); **12**, Boroujerd (6/0); **13**, Dezful (2/1); **14**, Shush (3/5); **15**, Sureshjan (5/0); **16**, Jounaghan (8/9); **17**, Sisakht (1/0); **18**, Yasuj (12/8).

traits. This analysis was performed separately on males and females to identify any possible effects of gender differences. To determine the differences between the sexes, normally distributed variables were compared with Independent-Sample T Test while non-normally distributed variables were subjected to non-parametric Mann-Whitney U Test. To compare morphological traits among individuals of different populations and basins, normally distributed variables were compared with one-way ANOVA while non-normally distributed variables were subjected to Kruskal-Wallis Test.

For geometric-morphometric analysis, only adults (i.e., specimens that reached sexual maturity) were chosen to reduce the effect of allometry. Images were obtained from 54 males and 27 females with a digital camera (Canon PowerShot A10, 16 megapixels resolution) under fixed and stable conditions. Ten homologous landmarks were assigned on each specimen (Fig. 3). Due to the symmetry on the carapace, landmarks were only recorded on the left side of the carapace, to avoid duplication of homogenous landmarks and statistical problems (Zelditch *et al.* 2004; Grinang *et al.* 2019). The tpsUtil program was used to build tps files from images, landmarks were digitized using TpsDig2 2.22 (Rohlf 2015). Generalized procrustes analysis (GPA) was used to obtain consensus configuration, this analysis removing non-shape variation such as rotation, scale and orientation (Zelditch *et al.* 2004). We used MorphoJ 1.06d (Klingenberg 2011) and PAST 4.08 softwares (Hammer *et al.* 2001) to evaluate carapace shape variations. The carapace shape variations between males and females were investigated by principal component analysis (PCA). To test for shape differences among basins, a canonical variate analysis (CVA) was performed and pairwise comparison evaluated with discriminant function analyses (DFA). Finally, carapace shape variations between sexes and different populations were visualized by MorphoJ's Wireframe diagrams.

Abbreviations

ALTW	distance between anterolateral tubercles;
BH	body height;
CDH	height of dactylus of chela;
CDL	length of dactylus of chela;
CL	carapace length;
CPH	height of propodus of chela;
CPL	length of propodus of chela;
CW	carapace width;
ML	merus length of third walking leg;
MPW	maximum pleonal width;
MW	merus width of third walking leg;
OW	distance between exorbital teeth;
PCW	posterior carapace width;
PH	height of pollex of chela;
PL	length of pollex of chela;
Sixth ADL	length of sixth pleonal somite;
Sixth ADW	width of sixth pleonal somite;
TL	telson length;
TW	telson width.

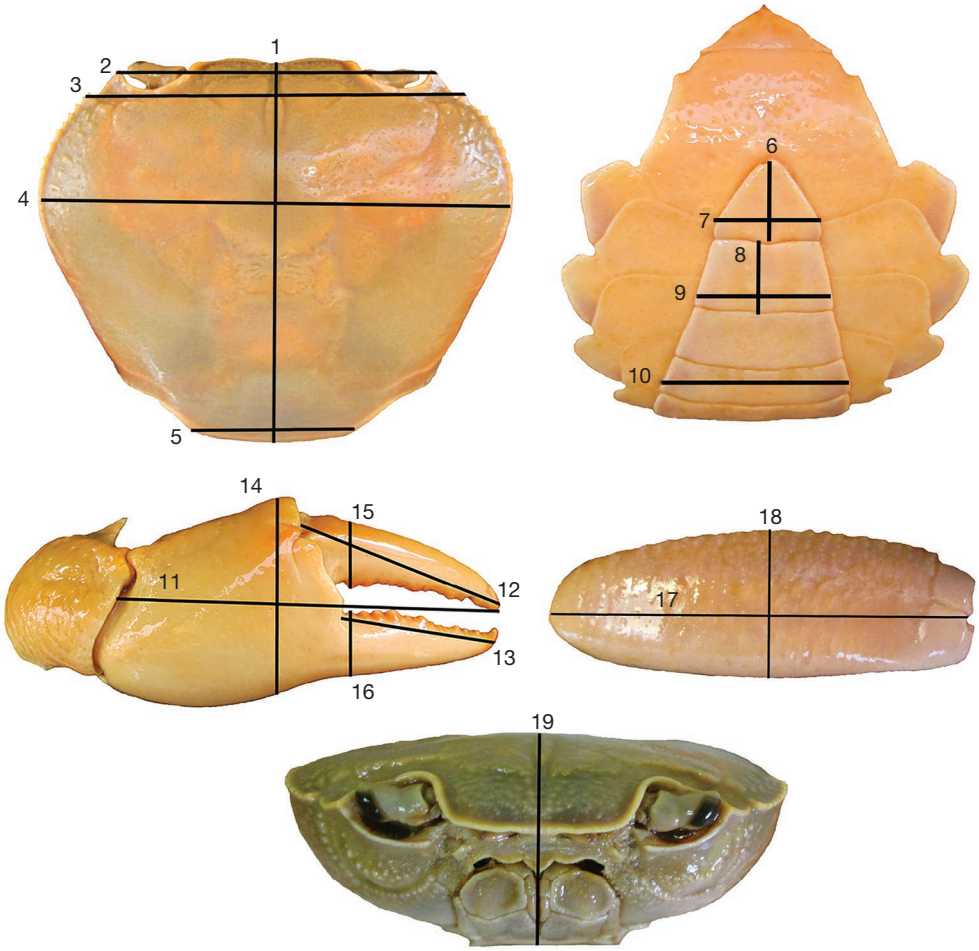

Fig. 2. — Morphological characters measured in *Potamon persicum* Pretzmann, 1962: **1**, carapace length; **2**, distance between exorbital teeth; **3**, distance between anterolateral tubercles; **4**, carapace width; **5**, posterior carapace width; **6**, telson length; **7**, telson width; **8**, length of sixth pleonal somite; **9**, width of sixth pleonal somite; **10**, maximum pleonal width; **11**, length of propodus of chela; **12**, length of dactylus of chela; **13**, length of pollex of chela; **14**, height of propodus of chela; **15**, height of dactylus of chela; **16**, height of pollex of chela; **17**, merus length of third walking leg; **18**, merus width of third walking leg; **19**, body height.

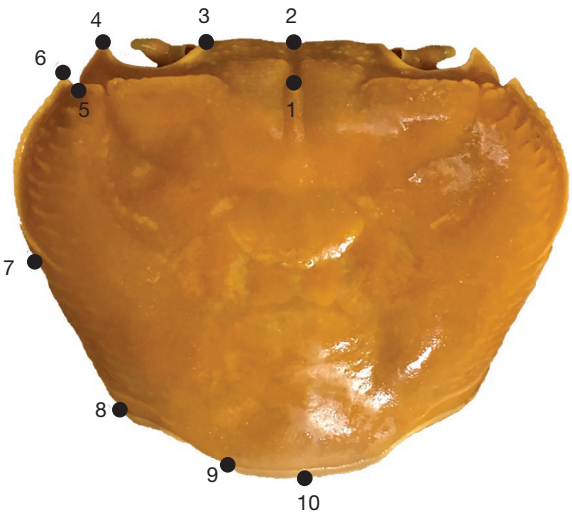

Fig. 3. — Landmarks on the left side of the carapace in *P. persicum* Pretzmann, 1962: **1**, the mesogastric lobe; **2**, the middle of the frontal margin; **3**, the anterolateral of the frontal margin; **4**, the tip of exorbital teeth; **5**, the angle between the exorbital and the first anterolateral teeth; **6**, the tip of the first anterolateral tubercle; **7**, the last anterolateral tubercle; **8**, the posterolateral margin; **9**, the posterolateral extreme; **10**, the middle of posterior margin.

RESULTS

A total number of 140 specimens were examined, of which 89 were male and 51 were female. Eighty-one specimens from Khalij Fars-Oman Basin (50 males, 31 females), 25 specimens from Markazi Basin (17 males, 8 females) and 34 specimens from Urmia Basin (22 males, 12 females). Mean carapace length in males was 36.79 mm (standard error SE = 1.24), the smallest crab measured was 17.09 mm and the largest one was 60.60 mm. In females, the mean carapace length was 33.14 mm (SE = 1.18), the smallest crab was 15.44 mm and the largest one was 49.85 mm. Based on breakpoint estimation from piecewise linear regression, sexual maturity in males was CL ≥ 30.58 mm and in females was CL ≥ 34.02 mm (Fig. 4). Hierarchical clustering analysis and squared Euclidean distance showed CW in males and females was in a separate cluster.

Morphometric analysis between sexes

Between males and females CL, PCW, CDL, PL, PH and BH were normally distributed and CW, OW, ALTW, CPL, CPH, CDH, TL, TW, Sixth ADL, Sixth ADW, MPW, ML and MW were non-normally distributed. Analysis showed that CL, PCW, CDL, PL, BH, TL, TW, Sixth ADL, Sixth ADW, MPW and ML had significant differences between sexes. DFA showed that 100% of males and females were correctly classified. Comparison of 19 morphometric characters showed male-biased sexual size dimorphism, also reflected by the carapace dimensions (Fig. 5).

Geometric-morphometric analysis between sexes

Principal component analysis revealed separation with partial overlap of the carapace shape between male and female crabs. The first ten PCA axes explained more than 96.00% of the total shape variation, with the first principal component explaining 29.53% and the second principal component explaining 23.76% of the total variance (Fig. 6).

Results of PCA were supported by both CVA and DFA. Discriminant Function Analysis based on geometric-morphometrics between males and females showed that 77.80% of sexes were correctly classified, seven of females classified as male and 11 of males classified as female. Hotelling's T^2 (DFA) indicated statistical evidence of differences in the carapace shape between males and females. CVA showed the procrustes distance of carapace between sexes is 0.0234, which in turn provides further evidence for difference between sexes (Table 1).

Morphometric analysis among populations

Among males from three basins PCW, CPL, CDL, PL, CDH, PH, TL, Sixth ADL, Sixth ADW, MPW and BH were normally distributed, and CW, OW, ALTW, CPH, TW, ML and MW were non-normally distributed. Analysis showed that CW, OW, PCW, Sixth ADL, MPW, and BH had significant differences between males from populations of three basins. DFA showed that 87.80% of males were correctly classified (Fig. 7; Table 2). Between males from Khalij Fars-Oman Basin and Markazi Basin only BH was significantly different, whereas between males from Khalij Fars-Oman Basin and Urmia Basin Sixth ADW, MPW and CW, and between males from Markazi Basin and Urmia Basin BH, MPW, PCW, CW and ALTW had significant differences.

Among females from three basins CL, PCW, CDL, PL, TW, Sixth ADL, Sixth ADW and BH were normally distributed, and CW, OW, ALTW, CPL, CPH, CDH, PH, TL, MPW, ML and MW were non-normally distributed. Analysis showed that CW, PCW, OW and ALTW had significant differences between females from populations of three basins. DFA showed 100% of females were correctly classified (Fig. 7; Table 2). Between females from Khalij Fars-Oman Basin and Markazi Basin PCW and ALTW had significant differences, while between females from Khalij Fars-Oman Basin and Urmia Basin CW, OW and ALTW, and between females from Markazi Basin and Urmia Basin CW, PCW, OW and PL had significant differences.

Geometric-morphometric analysis among populations

Populations from different basins were distinctly separated from each other based on carapace geometry. In males, DFA showed differences between Khalij Fars-Oman Basin and Markazi Basin, but there is no difference between Urmia and Markazi basins and also between Khalij Fars-Oman Basin and Urmia Basin (Fig. 8; Table 3). The first ten PCA axes explained more than 96.00% of the total shape varia-

Table 1. — Discriminant function analysis based on geometric-morphometrics between males and females of *Potamon persicum* Pretzmann, 1962. Abbreviation and symbols: **P**, significance; (*) for p ≤ 0.05, (**) for p ≤ 0.01, (***) for p≤ 0.001.

Canonical Variate Analysis		**Discriminant Function Analysis**	
Procrustes distance	p-Value	Hotelling's T2	p-Value
0.0234	<.0001***	199.2619	<.0001***
Predicted Group Membership			
Sex	Male	Female	Total
Male	77.6%	23.4%	100%
Female	20.6%	79.4%	100%
Wilks' lambda			
Wilks' lambda	Chi-square	df	p-Value
0.605	35.478	17	0.005**

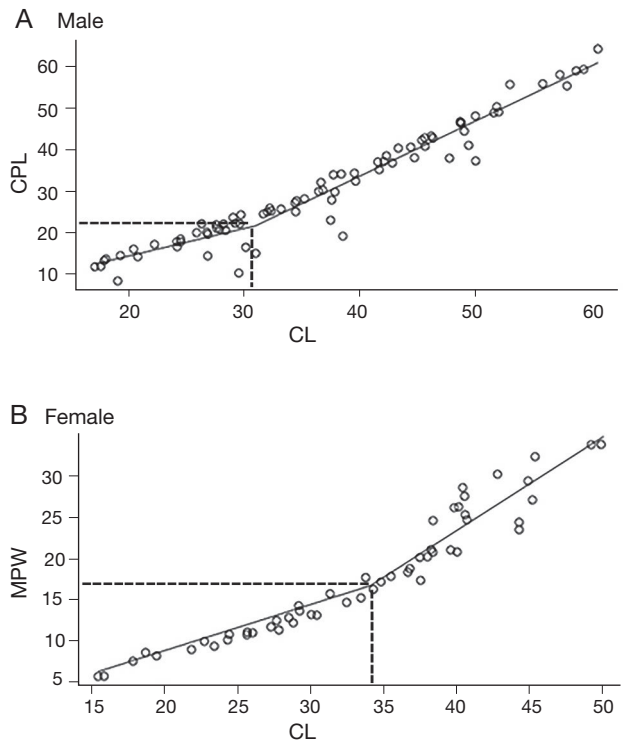

FIG. 4. — Piecewise linear regression showing breakpoint estimation at the onset of sexual maturity in males (**A**) and females (**B**) of *Potamon persicum* Pretzmann, 1962. Abbreviations: **CL**, carapace length; **CPL**, length of propodus of chela; **MPW**, maximum pleonal width.

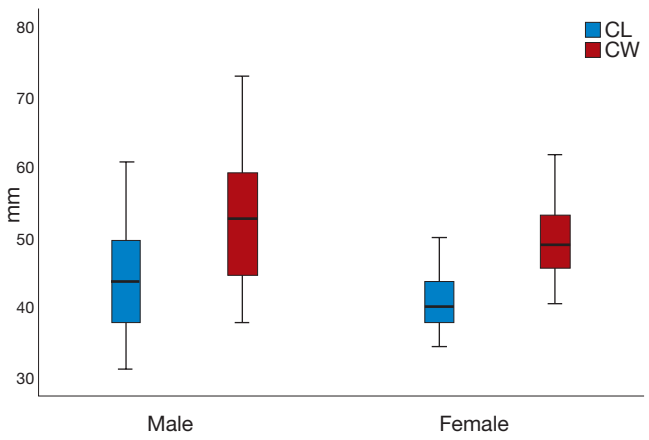

FIG. 5. — Box plot of sexual size dimorphism of carapace length and width between males and females of *Potamon persicum* Pretzmann, 1962. Abbreviations: **CL**, carapace length; **CPL**, length of propodus of chela.

TABLE 2. — Predicted group membership of *Potamon persicum* Pretzmann, 1962 from three basins.

Sex	Basin	Markazi	Urmia	Khalij Fars-Oman	Total
Male	Markazi	100%	0	0	100%
	Urmia	7.1%	92.9%	0	100%
	Khalij Fars-Oman	12%	8%	80%	100%
Female	Markazi	100%	0	0	100%
	Urmia	0	100%	0	100%
	Khalij Fars-Oman	0	0	100%	100%

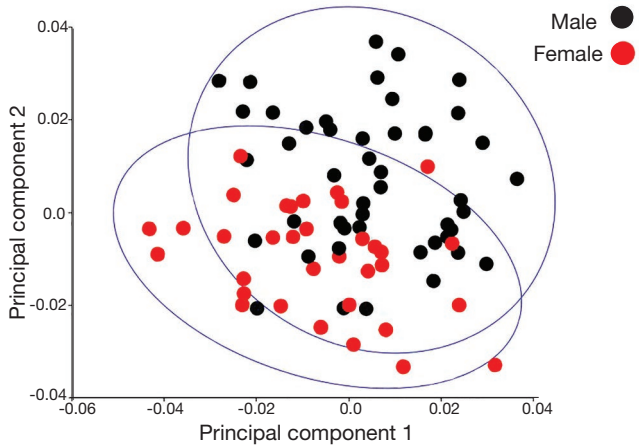

FIG. 6. — Principal component analysis on carapace procrustes residuals between males and females of *Potamon persicum* Pretzmann, 1962.

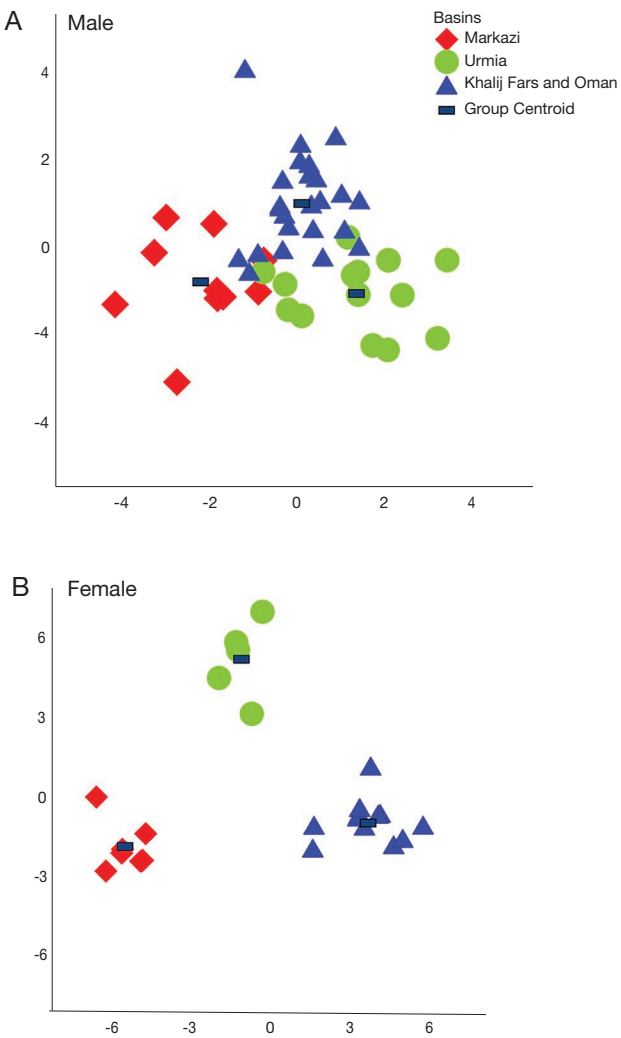

FIG. 7. — Discriminant function analysis of *Potamon persicum* Pretzmann, 1962 among three basins based on morphological characters of males (**A**) and females (**B**).

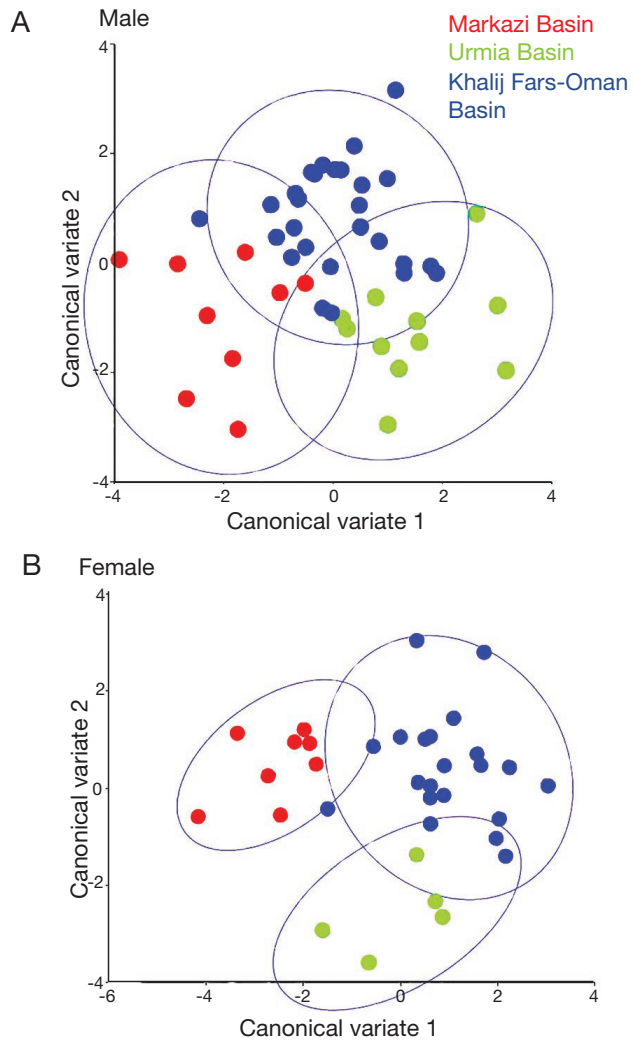

Fig. 8. — Scatter plot of canonical variant analysis on carapace procrustes residuals of *Potamon persicum* Pretzmann, 1962 males (**A**) and females (**B**) among three basins.

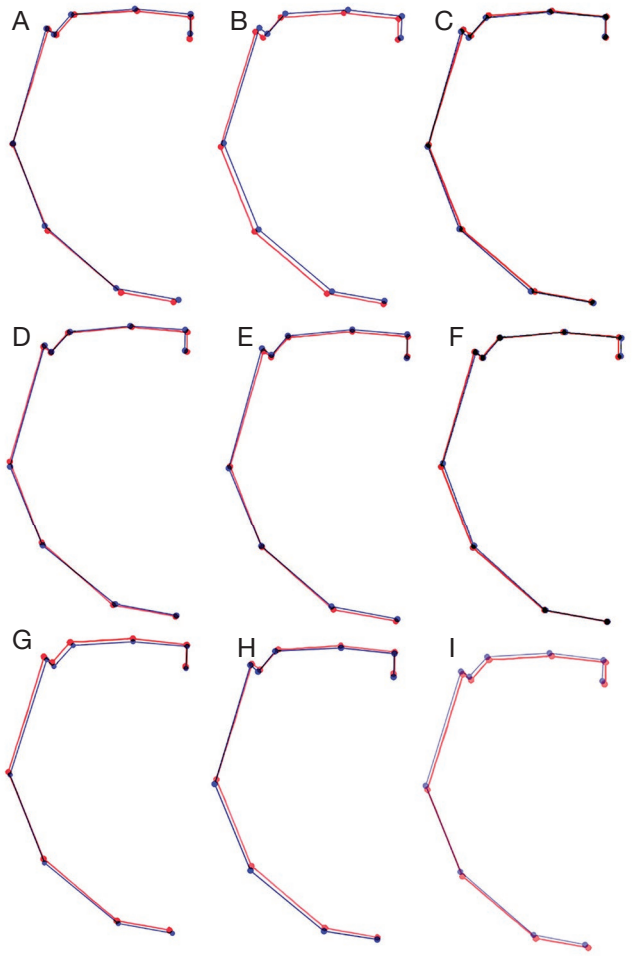

Fig. 9. — Wireframe graphs depicting shape changes of target shape from consensus: **A**, all males, **red**; all females, **blue**; **B**, all males, **blue**; all specimens, **red**; **C**, all female, **blue**; all specimens, **red**; **D**, Markazi basin females, **blue**; all females, **red**; **E**, Urmia basin females, **blue**; all females, **red**; **F**, Khalij Fars-Oman basin females, **blue**; all females, **red**; **G**, Markazi basin males, **blue**; all males, **red**; **H**, Urmia basin males, **blue**; all males, **red**; **I**, Khalij Fars-Oman basin males, **blue**; all males, **red**.

tion, with the first principal component explaining 30.87% and the second principal component explaining 25.68% of the total variance. In females, DFA showed differences between Khalij Fars-Oman Basin and Markazi Basin, but there was no difference between Urmia Basin and Markazi Basin and also between Khalij Fars-Oman Basin and Urmia Basin (Fig. 8; Table 3). The first ten PCA axes explained more than 96.00% of the total shape variation, with the first principal component explaining 38.43% and the second principal component explaining 16.57% of the total variance. In males, distances between the mesogastric lobe and the midpoint of the frontal margin, the last anterolateral tubercle and the posterolateral extreme were greater than those in females. In females, however, distances between the posterolateral extreme and the midpoint of the posterior margin were greater than those in males. The front half of the male carapace was bigger and the posterior half was smaller than all specimen consensus wireframe, but the female carapace was almost similar to all specimen consensus wireframe except for the distance between the posterolateral margin and the posterolateral extreme. In females of Markazi Basin, the middle of the frontal margin and in females of Urmia Basin, the middle of posterior margin were more internal than all female consensus wireframe. But in females of Khalij Fars-Oman Basin, the mesogastric lobe and the middle of the frontal margin were more external than all female consensus wireframe. In males of Markazi Basin, the middle of the frontal margin, the anterolateral of the frontal margin, the tip of the exorbital teeth, the angle between the exorbital and the first anterolateral teeth, and the tip of the first anterolateral tubercle were internal and the posterolateral margin, the posterolateral extreme, and the middle of the posterior margin were more external than all male consensus wireframe. In males of Urmia Basin, the distance between the mesogastric lobe and the middle of the frontal margin is more than all male consensus wireframe, and the last anterolateral tubercle, the posterolateral margin,

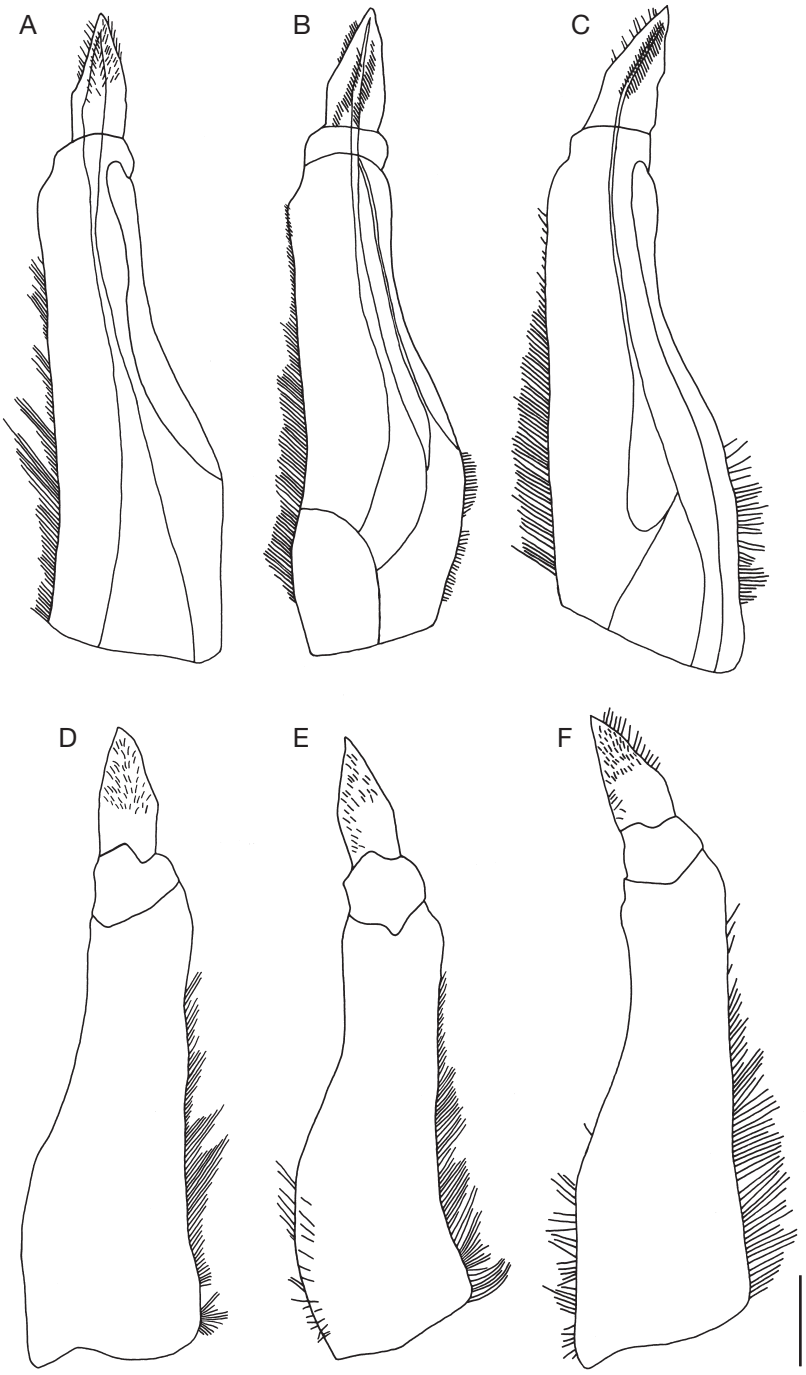

Fig. 10. — Male first gonopod (**G1**) morphology of *Potamon persicum* Pretzmann, 1962: **A**-**C** ventral view; **D**-**F**, dorsal view; **A**, **D**, Markazi basin; **B**, **E**, Urmia basin; **C**, **F**, Khalij Fars-Oman basin. Scale bar: 1 mm.

the posterolateral extreme, and the middle of the posterior margin, were more external than male consensus wireframe. In males of Khalij Fars-Oman Basin, the mesogastric lobe, the posterolateral extreme, and the middle of the posterior margin, are internal and the middle of the frontal margin, the anterolateral of the frontal margin, the tip of the exorbital teeth, the angle between the exorbital and the first anterolateral teeth, the tip of the first anterolateral tubercle and the last anterolateral tubercle were more external than male consensus wireframe. Based on geometric-morphometrics and traditional morphometry, Khalij Fars-Oman Basin males had bigger carapace length and width, the posterior

Table 3. — DFA & CVA results of *Potamon persicum* Pretzmann, 1962 between different basins: **P**, significance; (*) for p ≤ 0.05, (**) for p ≤ 0.01, (***) for p≤ 0.001.

		DFA			CVA	
Sex	**Basin**	**Procrustes distance**	**Hotelling's T^2**	**p-value**	**Mahalanobis distances among groups**	**p-value**
Male	Khalij Fars-Oman and Markazi	0.01087785	65.3211	0.04*	2.7985	<.0001***
	Urmia and Markazi	0.01551338	521.9625	0.09	3.5230	<.0001***
	Khalij Fars-Oman and Urmia	0.01189189	57.6531	0.06	2.4923	<.0001***
Female	Khalij Fars-Oman and Markazi	0.02559679	105.3395	0.03*	3.5599	<.0001***
	Urmia and Markazi	0.01823892	139.0300	0.63	3.9446	0.0002***
	Khalij Fars-Oman and Urmia	0.02210427	56.0779	0.35	3.1858	0.0001***

half of the carapace of Urmia Basin males was bigger and the front half of the carapace of Markazi Basin males was smaller than in the other males. Markazi Basin females had bigger carapace length and width, Urmia Basin females have smaller carapace length and Khalij Fars-Oman Basin females had bigger posterior carapace width than in the other females (Fig. 9).

Morphology of the male first gonopod

The results of carapace geometry were bolstered by qualitative differences in male first gonopod (G1) morphology. Each basin had its own pattern, with the lateral margin of the terminal article in males from the Markazi and Khalij Fars-Oman basin being nearly straight in contrast to the males from the Urmia Basin with margins bent inward. The flexible zone is well developed and the subterminal part of the G1 is semi-stout in males of Markazi and Urmia basins, while that of males inin the Khalij Fars-Oman Basin was stout and covered by long setae (Fig. 10).

DISCUSSION

Sexual dimorphism

Size at sexual maturity in brachyuran crabs can be estimated by comparing constant relative growth of body size with the sudden growth of emerging secondary sexual characteristics (Hartnoll 2015; Parvizi *et al.* 2017). There is no consistent pattern among brachyuran crabs about size on sexual maturity. In the mangrove root crab *Goniopsis cruentata* Latreille, 1803, males become sexually mature at a smaller size than females (Lira & Calado 2013), but in stone crabs of the genus *Menippe* De Haan, 1833, males have larger body sizes when reaching sexual maturity (Gerhart & Bert 2008). Several studies have even estimated the different pattern of sexual maturity in the *Potamon* species. In *P. potamios*, males reach sexual maturity at CL 35 mm, whereas the size for females ranges between 28-35 mm of CL (Gherardi & Micheli 2013). In *P. elbursi*, females have onset of maturity in smaller size (CL 31.62 mm) than males (CL 35.48 mm), (Kalate *et al.* 2017). The same pattern is seen in *P. ibericum*, where the maturity onset for females is CL 20.02, while it is CL 23.9 mm for males (Parvizi *et al.* 2017). The sexual maturity size may change under different bio-ecological conditions, even in populations of the same species (Hartnoll 1988). For instance, in a study on *Potamon fluviatile* Herbst, 1785 in Italy, in Latium, males reach maturity at smaller sizes than females (Scalici *et al.* 2010), whereas another study in Tuscany mentioned the same size of maturity in both sexes at CL 35 mm (Micheli *et al.* 1990). In *P. persicum*, females reach sexual maturity at bigger size than males (males at CL 30.58 mm and females at CL 34.02 mm), whereas mean carapace length of males were generally bigger than that in females. Before sexual maturity, the mean carapace length of females was 25.81 mm and in male was 24.84 mm but after sexual maturity, mean carapace length of females was 40.47 mm and in males was 43.88 mm. Before sexual maturity, females expend most of their energy on growth to mature earlier and be able to reproduce; after sexual maturity, females spend most of their energy for reproduction but because of sexual selection and competition for mates and resources, males expend more energy on growth (Micheli *et al.* 1990; Kobayashi & Archdale 2020; Quiñones-Llópiz *et al.* 2021). For these reasons, females before puberty and males after puberty had bigger mean carapace length. Males were bigger than females, except in the pleonal characters (TL, TW, Sixth ADL, Sixth ADW and MPW), also, geometric-morphometric analyses were able to separate the sexes with some overlap (Figs 5; 6); posterior carapace width appeared to be more enlarged for the females and this resulted from a positive correlation between fecundity and female abdomen size (Wickman *et al.* 1989; Adams & Funk 1997).

Geographical differentiation

Our specimens were collected from different basins, sub-basins, elevation (70-2500 m) and tectonic units, where climate conditions and amounts of annual precipitation are different. Average annual precipitation in Urmia Basin, Khalij Fars-Oman Basin and Markazi Basin is 301, 139 and 327 mm, respectively. In the northwest (Urmia Basin), winters are cold with heavy snowfall and subfreezing temperatures during the months of December and January. Relatively mild temperatures are in spring and fall, while summers are dry and hot. To the west (North of Khalij Fars-Oman Basin), the Zagros higher mountain valleys experience lower temperatures, severe winters with below zero average daily temperatures and heavy snowfall during winters but the summers are hot and dry. In the south (Khalij Fars-Oman

Basin), winters are mild with an average temperature of 18°C, and the summers are very hot, having average daily temperatures in June and July exceeding 41°C. Markazi Basin is arid, with less than 200 mm of rainfall and average summer temperatures 39°C (Delju *et al.* 2012; Vaheddoost & Aksoy 2016; Hosseini-Moghari *et al.* 2018). Analysis showed Khalij Fars-Oman Basin populations and Markazi Basin populations are similar to each other. Actually Khalij Fars-Oman and Markazi basins are located side by side, their drainage systems originate from the central Zagros Mountains and they share climatic conditions. Also, both of them belong to the Zagros hot-spot. They share more geology and historical events. It is likely that Markazi Basin populations originated from the central and south-west refugia in the Zagros Mountains. After the last glacial period, the populations, first spread from the central and southwest refugia into the Khalij Fars-Oman Basin then spread into the Markazi Basin from there. Rajaei *et al.* (2013) studied Quaternary refugia in southwestern Iran based on two sympatric moth species (*Gnopharmia colchidaria* and *G. kasrunensis*), and stated that the presence of a wide refugial area in southwest and southeast of Zagros Mountains can be expected. Consequently, this region could well have served as the source population for the detected postglacial expansion events. On the other hand, Markazi Basin populations and Urmia Basin populations show more differences, which may be due to high degree of isolation and differences in terms of ecology, climatic conditions and topography. Urmia Basin populations belong to the Azerbaijan hot-spot. Zagros and Azerbaijan Mountains act as a barrier between Urmia and Markazi basins. Probably their populations originated from different refugia, Urmia Basin populations likely were due to postglacial expansion from the northwest Zagros refugia but Markazi Basin population originated from the central and southwest Zagros refugia. Malekoutian *et al.* (2020) studied multiple Pleistocene glacial refugia for the Yellow-spotted mountain newt, *Neurergus derjugini* Nesterov, 1916, in the mid-Zagros range in Iran and Iraq; they concluded that the presence of geographically structured clades in north, center, and south sections of the species range (42 highland streams of Zagros Mountain range in western Iran and eastern Iraq) signify the disjunct populations that have emerged in three different refugia. One refugium was located in the Urmia Basin and the others in the south of Urmia Basin and west of the Zagros Mountains. Although the recent orogenic activity had a great influence on current biodiversity in the region, recent glacial fluctuations were also a potential reason for such inter and intraspecific variability (Keikhosravi & Schubart 2014). Ahmadzadeh *et al.* (2013) studied the distribution pattern of *Iranolacerta* lizards in the Zagros Mountains and concluded that no recent geological events explain the results and that speciation was likely due to climate fluctuations. Gholami *et al.* (2014) and Esmaeili *et al.* (2016) stated that the tooth-carp species in inland waters may have risen with the post-Pliocene uplift of the Zagros Mountains, therefore their speciation was closely linked to vicariance events. Teimori *et al.* (2012) studied geographical differentiation of *Aphanius dispar* Rüppel, 1829 from southern Iran; they recognized three distinct taxonomic units and stated that these groups resulted from geographical isolation due to orogeny events.

CONCLUSION

Probably morphological differences between basins based on carapace shape and body size is reflected by genetic differentiation. We think that such differences were the consequence of isolation and habitat fragmentation resulting from geological events and glacial periods. We showed that populations of the freshwater crabs in the Zagros region referred to *P. persicum* have a strong morphological variation and this is most likely due to recent orogenic activity and several glacial refugia within the Zagros mountains. The active geology of Iran, resulting from collisions of the Arabian with the Iranian plate during the Late Miocene (10-5 Ma), Pliocene (5-1.8 Ma) and Pleistocene (1.8 million-10000 years ago), has led to rapid isolation of areas and changing hydrological networks (Allen *et al.* 2004; Hatzfeld *et al.* 2010). The presence of several refugia in the northwest, central, southwest and southeast of the Zagros Mountains can be predicted, and these regions could well have sequentially served as the source populations for postglacial expansion events (Rajaei *et al.* 2013; Malekoutian *et al.* 2020; Ghane-Ameleh *et al.* 2021). These provided excellent conditions for the speciation of freshwater organisms in southern and western Iran (Zagros Mountains), similar to the recorded speciation of reptiles (Rastegar-Pouyani & Nilson 2002; Hrbek *et al.* 2006; Teimori *et al.* 2012). Therefore, ecological and geographical speciation are more likely in such regions with unique conditions. We suggest molecular studies to investigate the cryptic lineages and study of interspecific and intraspecific diversity to clarify taxonomic status of *P. persicum sensu lato*.

Acknowledgements
We would like to express our appreciation to Nima Hashemian, Hasan Salehi and specially to Mehrdad Rezaei for field work and collecting specimens. Special thanks go to Mostafa Thiam for helping with the French translation and Arash Raisbahrami for helping with the R analysis. We also thank Samaneh Pazoki and Neda Fahimi for their technical help in the molecular lab. We greatly appreciated the invaluable comments of Darren C. J. Yeo, Jose Christopher E. Mendoza and Vincent Debat that highly improved the initial manuscript.

Authors' contributions
R. N. and A. K. designed the study and sampled the specimens, Y. A. A. performed the statistical analyses and wrote the manuscript. All authors read and approved the final manuscript.

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Submitted on 23 January 2023;
accepted on 1 August 2023;
published on 20 February 2024.

APPENDIX

Appendix 1. — *Potamon persicum* Pretzmann, 1962 measurements. Abbreviations: see Material and methods.

CL	CW	OW	ALTW	PCW	CPL	CDL	PL	CPH	CDH	PH	TL	TW	sixth ADL	sixth ADW	MPW	ML	MW	BH	Sex	Locality	Voucher	Latitude	Longitude
32.34	38.21	27.26	32.45	16.01	25.1	14.61	11.56	10.45	3.88	3.68	4.67	5.93	4.18	7.88	12.22	20.74	7.62	18.15	1	Isfahan	1081	32.603446°	51.570074°
26.77	32.24	22.66	27.12	12.91	19.98	11.08	8.94	8.62	2.93	2.53	3.83	5.08	3.52	6.02	10.34	17.07	6.55	15.51	1	Isfahan	1081	32.603446°	51.570074°
24.18	2818	21.15	24.76	11.33	17.71	9.91	8.43	7.32	2.44	2.45	3.91	4.76	3.37	5.65	9.55	16.14	5.93	13.3	1	Isfahan	1081	32.603446°	51.570074°
39.64	46.73	32.26	38.08	17.57	32.32	18.21	13.98	14.71	5.28	4.83	5.75	7.31	5.02	9.27	14.6	24.86	9.71	22.45	1	Isfahan	1040	32.638835°	51.587535°
52.01	62.13	41.2	49.32	22.25	48.97	28.08	23.56	20.97	7.52	7.16	6.49	9.25	6.49	12.4	18.45	33.66	12.03	30.04	1	Isfahan	1040	32.638835°	51.587535°
44.73	53.26	36.66	43.42	19.37	37.95	22.2	17.9	16.55	6.27	5.85	6.32	8.59	6.04	11.23	16.46	27.6	10.11	24.89	1	Isfahan	1081	32.603446°	51.570074°
49.17	59.57	46.87	39.22	22.93	38.12	22.8	17.98	15.05	4.85	4.75	1084	24.33	13.22	32.78	33.81	29.68	10.3	32.73	2	Isfahan	1040	32.603446°	51.570074°
38.54	45.11	30.91	36.6	16.07	19.05	11.5	8.59	8.66	3.02	2.84	5.88	7.34	5.18	9.13	14.82	24.73	8.86	20.8	1	Hamedan	1021	34.840861°	48.503567°
29.24	34.38	24.23	29.15	13.32	22.14	12.27	9.85	9.6	3.48	3.24	4.64	6.02	4.25	6.99	11.27	18.6	7.01	16.14	1	Hamedan	1021	34.840861°	48.503567°
24.5	28.83	21.33	25.08	11.82	18.35	10.18	8.39	7.9	2.72	2.52	3.9	5.13	3.75	5.64	9.66	15.94	5.95	13.55	1	Hamedan	1021	34.840861°	48.503567°
22.25	26.84	19.49	22.64	10.79	17.05	9.72	7.43	7.12	2.7	2.32	3.49	4.46	3.63	5.31	8.85	13.94	5.43	12.4	1	Hamedan	1021	34.840861°	48.503567°
19.3	22.99	17.32	20.04	9.32	14.37	8.46	6.97	6.03	2.23	2	3.04	3.73	2.73	4.7	7.87	12.43	4.53	10.5	1	Hamedan	1021	34.840861°	48.503567°
51.6	61.61	38.89	47.11	21.25	48.79	27.97	23.47	21.56	8.05	7.89	7.21	9.31	6.31	12.37	18.48	33.1	11.39	28.54	1	Hamedan	1021	34.840861°	48.503567°
42.08	50.89	33.62	39.96	15.5	37.07	21.4	17.93	14.82	5.11	5.39	5.89	7.75	4.99	10.21	15.94	27.46	9.74	24	1	Hamedan	POT1400	34.840280°	48.497244°
42.82	50.14	34.59	41.19	16.01	36.7	20.6	16.36	16.26	5.95	5.54	5.96	7.82	5.73	10.06	15.79	27.69	10.21	25.45	1	Hamedan	POT1400	34.840280°	48.497244°
41.68	49.44	33.82	40.14	16.2	35.07	20.01	16.01	15.08	5.61	5.44	5.78	7.46	5.67	9.76	15.28	20.15	6.65	23.09	1	Hamedan	POT1400	34.840280°	48.497244°
48.79	58.06	39.42	47.47	17.45	46.37	26.88	22.27	19.16	6.77	6.86	6.77	8.65	5.98	11.33	17.43	33.06	9.89	28.87	1	Hamedan	POT1400	34.840280°	48.497244°
29.62	34.76	24.41	29.28	11.43	22.02	12.1	9.78	9.24	3.27	3.21	4.05	5.26	3.65	6.44	10.85	–	–	16.68	1	Hamedan	POT1400	34.840280°	48.497244°
35.47	61.68	29.19	33.98	14.64	28.63	16.57	13.32	12.42	4.8	4.52	6.85	12.92	6.75	17.03	17.81	21.6	7.87	20.03	2	Hamedan	POT1400	34.840280°	48.497244°
34.27	40.37	28.31	32.86	15.48	27.94	15.2	12.63	12.09	4.67	3.84	6.65	11.78	6.38	14.79	16.23	21.12	7.95	19.81	2	Hamedan	1021	34.840861°	48.503567°
49.85	60.4	39.12	47.25	22.33	50.2	27.34	21.46	23.73	8.63	7.97	11.68	23.5	13.38	32.73	33.84	30.51	10.58	31.66	2	Hamedan	1021	34.840861°	48.503567°
44.24	51.89	34.39	40.74	18.3	38.39	21.64	17.3	17.08	6.16	5.87	8.72	17.6	9.2	23.79	24.39	26.86	9.44	26.25	2	Hamedan	POT1400	34.840280°	48.497244°
26.13	56.12	35.86	43.37	19.5	43.05	24.02	18.48	20.8	6.98	6.54	10.31	21.29	12.66	29.54	30.91	28.31	9.67	28.52	2	Hamedan	POT1400	34.840280°	48.497244°
38.34	45.82	31.07	36.65	16	32.42	18.12	14.54	14.64	5.66	5.04	7.73	14.8	7.93	20.06	20.75	23.35	8.62	21.34	2	Hamedan	POT1400	34.840280°	48.497244°
39.56	46.81	31.6	37.54	16.66	34.17	19.43	14.99	14.31	5.25	4.91	7.81	15.49	8.45	20.5	21.01	25.63	8.65	23.13	2	Hamedan	POT1400	34.840280°	48.497244°
45.65	54.75	37.45	44.28	21.35	40.72	23.25	17.77	17.57	7.24	6.31	6.4	8.34	6.11	11.61	17.57	30.78	10.01	23.85	1	Shahri Chay	POT1013	37.532401°	45.077643°
34.53	42.05	29.59	34.38	16.23	27.6	14.94	11.77	12.46	4.47	4.26	5.22	6.83	4.73	8.51	13.21	23.21	8.58	17.85	1	Shahri Chay	POT1013	37.532401°	45.077643°
26.33	34.43	23.95	28.74	13.49	22.03	11.71	9.32	9.18	3.44	3.14	3.59	4.97	4.23	7.3	11.55	18.81	6.98	13.9	1	Shahri Chay	POT1013	37.532401°	45.077643°
18.04	22.01	16.52	19.52	8.47	13.56	7.3	5.88	5.51	2.11	2.03	2.7	3.26	281	4.71	7.61	12.58	4.51	8.89	1	Shahri Chay	POT1013	37.532401°	45.077643°
20.8	26.14	19.32	21.9	9.56	14.08	6.99	6	6.27	2.36	2.14	3.13	3.98	2.96	5.85	8.76	–	–	9.6	1	Shahri Chay	POT1013	37.532401°	45.077643°
20.44	25.82	19.13	21.78	9.8	15.93	8.42	6.61	6.76	2.46	2.37	3.11	3.78	2.99	4.91	8.03	–	–	10.36	1	Shahri Chay	POT1013	37.532401°	45.077643°
18.96	23.51	17.54	19.77	8.78	–	–	–	–	–	–	3.04	3.74	2.68	4.59	7.32	13.67	4.68	9.29	1	Shahri Chay	POT1013	37.532401°	45.077643°
17.88	22.06	16.34	18.93	9.27	13.13	7.03	6.35	5.38	1.95	1.98	3.03	3.77	2.54	4.23	7.12	–	–	8.76	1	Shahri Chay	POT1013	37.532401°	45.077643°
18.69	24.02	17.8	20.22	9.18	14.14	7.91	5.83	6.14	2.28	2.19	2.95	4.58	2.9	6.06	8.55	–	–	9.17	2	Shahri Chay	POT1013	37.532401°	45.077643°
27.65	35.36	25.16	29.07	14.21	–	–	–	–	–	–	4.55	7.45	4.95	10.05	12.43	18.87	7.02	14.33	2	Shahri Chay	POT1013	37.532401°	45.077643°
42.76	52.49	35.76	41.57	20.13	38.34.	21.19	15.16	19.07	6.82	6.06	10.13	21.46	12.04	30.1	30.22	26.58	9.15	25.21	2	Shahri Chay	POT1013	37.532401°	45.077643°
22.71	28.41	20.41	23.3	11.35	–	–	–	–	–	–	3.98	5.49	4.07	7.04	9.9	–	–	11.59	2	Shahri Chay	POT1013	37.532401°	45.077643°
24.41	30.52	21.86	25.53	11.99	18.73	9.8	8.08	8.16	3.03	2.78	4.1	6.13	3.98	8.4	10.74	16.8	5.23	12.13	2	Shahri Chay	POT1013	37.532401°	45.077643°
28.49	36.13	24.69	28.1	15.1	–	–	–	–	–	–	5.05	8.49	5.18	10.95	12.77	–	–	15.01	2	Shahri Chay	POT1013	37.532401°	45.077643°
44.41	53.23	36.37	43.31	19.5	40.51	25.54	17.36	16.83	6.95	5.75	6.03	7.78	5.68	10.01	16.36	29.66	9.94	22.31	1	Urmia	POT1089	37.623717°	44.950320°
38.4	45.9	31.6	37.11	16.7	34.02	18.19	13.95	14.69	5.5	5.21	5.18	6.82	4.95	9	14.83	25.59	8.82	19.81	1	Urmia	POT1089	37.623717°	44.950320°
43.33	53.18	36.59	43.29	18.85	40.27	22.83	17.94	17.39	7.01	5.79	6	7.95	5.71	10.39	16.08	28.01	9.76	23.09	1	Urmia	1089	37.616245°	44.959320°
37.72	45.62	31.62	37.28	15.72	33.86	18.71	14.42	14.7	5.34	5.22	5.56	7.31	4.83	9.16	14.23	23.17	7.16	20.57	1	Urmia	1089	37.616245°	44.959320°
50	61.31	40.81	47.68	20.5	48.05	27.8	22.83	20.62	7.36	7.05	6.95	9.11	6.14	12.07	17.73	35.49	11.39	28.7	1	Urmia	POT1089	37.623717°	44.950320°
52.99	66.32	41.69	50.41	24.11	55.63	32.33	26.86	22.23	7.85	7.45	7.7	10.12	6.63	12.74	19.3	37.21	10.18	28.48	1	Saghez	1001	36.221003°	46.257219°
34.39	43.28	34.82	28.81	15.42	27.1	15.52	11.57	11.49	4.22	3.85	5.06	6.02	4.49	7.92	13.67	21.24	7.86	19.81	1	Saghez	1001	36.221003°	46.257219°
29.72	38.69	31.09	26.71	13.07	24.21	13.07	10.68	9.66	3.47	3.2	4.36	4.94	4.27	7.13	12.17	20.24	7.28	16.65	1	Saghez	1001	36.221003°	46.257219°
32.22	41.5	33.29	28.1	14.63	25.8	13.35	11.12	10.14	3.71	3.34	4.55	5.48	4.12	7.75	12.79	20.94	7.63	17.49	1	Saghez	1001	36.221003°	46.257219°
29.04	36.96	30.48	25.07	12.46	23.56	13.52	9.68	9.75	3.55	3.32	3.68	5.19	4	6.74	11.21	–	–	16.29	1	Saghez	1065	36.227342°	46.264787°
37.45	48.77	37.74	31.33	16.66	31.83	18.5	13.83	13.41	5.15	4.36	7.06	14.84	8.02	19.46	20.11	23.52	8.21	21.29	2	Saghez	1001	36.221003°	46.257219°
38.22	47.04	37.25	31.41	16.45	31.73	17.85	13.09	14.62	5.16	4.71	7.48	15.19	8.16	20.14	21.08	23.35	8.77	22.49	2	Saghez	1001	36.221003°	46.257219°
34.79	43.96	35.49	29.81	16	27.63	15.2	11.06	12.3	4.36	3.9	6.39	12.18	7.11	16.04	17.15	22.35	8.54	18.55	2	Saghez	1001	36.221003°	46.257219°
15.85	19.74	17.3	15.37	7.9	10.81	6.06	5.28	4.45	1.33	1.36	2.55	3.18	2.38	4.54	5.67	9.22	3.09	8.72	2	Saghez	1001	36.221003°	46.257219°
37.85	47.74	38.73	32.2	16.05	29.7	17.13	14.61	12.24	4.11	4.04	5.19	6.81	4.99	8.82	14.12	23.12	8.47	21.3	1	Takab	1024	36.396567°	47.106629°
42.3	53.21	35.96	42.73	20.08	38.42	22	17.69	16.42	6.25	5.61	6.03	7.56	6.2	10.46	15.92	26.64	9.52	23.66	1	Takab	1024	36.396567°	47.106629°
39.54	48.67	33.58	40.31	17.88	34.24	18.89	15.18	14.59	5.21	4.9	5.73	7.61	5.32	9.75	15.63	25.06	9.19	21.61	1	Takab	1024	36.396567°	47.106629°
50.02	59.14	40.49	48.83	22.64	37.19	23.15	19.52	13.91	4.93	4.97	7.04	9.12	7.17	13.23	18.55	25.64	9.42	29.26	1	Takab	1024	36.396567°	47.106629°
45.33	56.3	36.74	45.22	22.54	40.75	22.73	17.43	19.01	7.37	6.34	10.55	22.55	12.04	31.96	32.36	27.24	9.32	25.94	2	Takab	1024	36.396567°	47.106629°

Appendix 1. — Continuation.

CL	CW	OW	ALTW	PCW	CPL	CDL	PL	CPH	CDH	PH	TL	TW	sixth ADL	sixth ADW	MPW	ML	MW	BH	Sex	Locality	Voucher	Latitude	Longitude
4038	51.97	39.97	33.89	19.5	33.45	19.68	13.5	15.02	5.2	4.65	8.9	20.22	9.89	27.66	28.6	25.52	8.05	24.54	2	Takab	1024	36.396567°	47.106629°
47.76	60.41	39.26	47.06	20.97	37.85	21.89	18.63	14.31	4.87	5.08	6.45	8.72	6.49	11.34	18.1	31.68	10.71	27.15	1	Marivan	1008	35.524445°	46.153038°
27.59	34.42	24.31	27.7	12.36	21.77	11.77	9.4	9.4	3.35	3.23	3.93	5.19	4.16	7.35	10.23	18.18	7.45	14.56	1	Marivan	1008	35.524445°	46.153038°
45.15	56.93	37	43.94	21.66	42.66	24.22	18.74	19.35	7.37	6.64	9.27	19.12	10.58	25.97	27.1	29.41	10.46	28.89	2	Marivan	1008	35.524445°	46.153038°
33.42	43.11	29.77	33.67	16.48	28.21	15.28	12.34	11.94	4.69	4.11	5.56	9.67	6.56	13.68	15.19	22.85	8.33	18.08	2	Marivan	1008	35.524445°	46.153038°
28.79	37.12	24.97	29.29	14	23.15	12.72	10.31	9.98	3.86	3.58	4.67	7.9	5.02	10.17	12.15	18.89	7.08	15.9	2	Marivan	1008	35.524445°	46.153038°
29.54	36.15	26	30.37	17.85	10.16	9.12	7.1	7.07	2.67	2.73	4.39	5.57	4.29	6.74	11.3	16.54	5.82	15.97	1	Paveh	1015	35.025414°	46.360254°
17.6	21.01	18.6	16.55	8.77	11.77	6.68	5.3	5.24	1.81	1.84	2.36	2.71	2.44	4.05	6.81	11.24	4.61	9.79	1	Paveh	1015	35.025414°	46.360254°
26.01	31.93	23.54	27.04	12.62	19.29	11.5	8.69	8.06	3.02	2.99	4.38	5.99	5.1	8.62	10.94	17.36	6.79	13.76	2	Paveh	1015	35.025414°	46.360254°
25.64	31.54	23.01	26.85	12.04	19.28	9.4	8.61	8.2	2.95	2.55	4.71	6.05	4.3	8.29	11.03	17.4	6.32	13.54	2	Paveh	1015	35.025414°	46.360254°
30.03	37.61	31.13	26.61	13.68	23.38	12.95	10.4	9.98	3.57	3.24	4.85	8.31	4.58	10.39	13.15	19.88	7.83	17.07	2	Paveh	1015	35.025414°	46.360254°
28.4	34.76	24.6	28.86	12.4	20.42	11.14	9.01	8.66	3.19	3.02	4.37	5.1	3.87	6.45	11.21	17.57	6.94	15.45	1	Sahneh	POT1055	34.474553°	47.686826°
57.92	70.88	55.95	45.91	22.17	55.28	32.03	25.99	25.04	8.54	8.42	8.21	9.81	7.36	13.33	20.93	37.04	12.71	33.63	1	Alashtar	1050	33.868885°	48.255835°
27.81	32.71	27.78	24.05	12.49	20.2	11.32	9.19	8.71	3.24	3.1	4.85	6.35	4.32	8.56	11.28	16.65	7.16	14.91	2	Alashtar	1050	33.868885°	48.255835°
27.61	32.07	24.24	27.64	13.22	20.94	12.5	9.76	8.46	2.89	2.88	4.14	4.94	3.72	6.11	9.71	16.66	7.18	15.25	1	Khoram Abad	1023	33.460444°	48.317946°
24.5	29.11	21.88	24.61	11.55	17.67	9.92	8.05	7.33	2.66	2.48	3.81	4.41	3.43	5.92	9.39	15.41	6.39	13.07	1	Khoram Abad	1023	33.460444°	48.317946°
58.72	69.83	45.96	54.95	23.61	58.92	34.39	28.2	25.39	9.22	8.53	8.61	11.21	6.86	13.5	21.32	38.56	11.84	31.8	1	Khoram Abad	1022	33.455181°	48.315841°
48.68	58.81	40.13	48.42	20.65	46.7	26.86	20.43	20.69	8.29	7.41	7.22	8.86	6.37	11.27	17.53	31.11	10.51	26.19	1	Khoram Abad	1022	33.455181°	48.315841°
51.85	62.85	42.83	51.04	22.59	50.26	28.99	22.63	22.49	7.92	7.11	8.01	10.23	6.35	12.82	19.1	35.51	11.01	28.58	1	Khoram Abad	1022	33.455181°	48.315841°
29.73	31.08	26.99	31.28	13.53	–	–	–	–	–	–	4.59	5.78	4.4	7.31	11.87	19.19	7.64	15.86	1	Khoram Abad	1022	33.455181°	48.315841°
26.85	32.71	24.8	28.73	12.55	14.28	8.31	7.54	5.45	2.15	2.06	4.28	5.44	3.91	5.91	10.52	18.2	6.72	14.59	1	Khoram Abad	1022	33.455181°	48.315841°
24.3	29.14	21.33	25.02	12.27	17.14	9.76	7.56	7.45	2.49	2.48	4.26	5.49	3.89	7.53	10.07	14.53	6.36	13	2	Khoram Abad	1023	33.460444°	48.317946°
55.91	67.48	43.79	52.53	24.56	–	–	–	–	–	–	7.68	9.69	6.92	12.46	19.76	–	–	30.54	1	Boroujerd	POT1029	33.882247°	48.775111°
37.48	44.49	30.35	35.95	17.81	22.9	13.48	10.39	10.09	3.46	3.56	5.57	7.32	5.04	9.3	14.73	23.48	9.41	20.52	1	Boroujerd	POT1029	33.882247°	48.775111°
26.86	32.24	22.89	26.17	12.67	19.47	10.65	8.75	8.86	3.05	3.02	4.17	5.03	3.82	6.48	10.54	16.42	6.73	14.42	1	Boroujerd	POT1029	33.882247°	48.775111°
19.44	24.04	17.74	20.67	10.17	–	–	–	–	–	–	3.53	4.1	2.94	5.19	8.14	–	–	10.26	1	Boroujerd	POT1029	33.882247°	48.775111°
17.83	21.36	16.25	18.46	8.38	13.22	6.79	6.54	5.48	1.75	1.85	–	–	–	–	7.49	–	–	9.16	1	Boroujerd	POT1029	33.882247°	48.775111°
17.09	20.21	15.77	17.79	9.38	11.67	6.42	5.36	4.7	1.58	1.62	2.83	3.25	2.65	4.03	7.01	–	–	8.94	1	Boroujerd	POT1029	33.882247°	48.775111°
30.14	36.34	26.44	31.29	14.21	16.37	6.22	4.12	8.95	3.13	3.03	4.14	5.23	4.03	7.41	11.8	20.88	7.42	16.43	1	Dezful	POT1061	32.408690°	48.418688°
43.42	52.17	36.29	42.64	18.45	–	–	–	–	–	–	–	–	5.41	10.27	15.92	28.2	10.21	23.74	1	Dezful	5362	32.409856°	48.424779°
33.74	39.36	29.18	32.99	15.58	20.45	12.8	9.77	7.99	3	2.8	6.27	12.57	7.18	16.8	17.67	21.56	7.97	19.46	2	Dezful	5362	32.409856°	48.424779°
48.69	58.58	40.38	47.39	22.02	46.35	26.83	22.51	20.29	7.72	7.42	6.91	9.41	6.19	12.24	17.85	35.51	10.4	26.68	1	Shush	6201	32.171499°	48.248614°
25.89	30.85	23.3	26.93	11.82	19.87	11.49	9.59	7.6	2.75	2.69	3.8	4.59	4.17	5.99	10.19	16.95	5.96	13.7	1	Shush	6201	32.171499°	48.248614°
15.44	18.2	14.71	16.9	7.8	11.08	6.26	5.28	4.01	1.03	1.15	2.3	2.54	2.37	3.92	5.64	8.62	2.42	7.73	1	Shush	6201	32.171499°	48.248614°
40.1	47.84	34.17	40.21	18.58	30.45	17.67	14.74	11.01	3.83	4.11	8.44	18.69	10.17	25.35	26.25	26.2	7.33	24.07	2	Shush	6201	32.171499°	48.248614°
40.67	48.46	34.59	40.01	20.46	33.69	18.4	14.63	14.71	5.39	4.95	9.21	18.46	10.32	24.32	24.69	26.28	8.79	23.84	2	Shush	6201	32.171499°	48.248614°
40.51	48.77	33.19	39.3	19.13	22.57	13.7	11.36	7.95	3.13	3.02	9.09	19.43	10.31	26.73	27.55	20.36	5.31	23.5	2	Shush	6201	32.171499°	48.248614°
29.16	34.89	25.76	29.32	14.45	21.82	11.41	8.95	9.9	3.64	3.25	5.58	10.15	5.9	13.51	14.24	–	–	15.56	2	Shush	6201	32.171499°	48.248614°
29.23	35.63	26.21	29.76	14.18	22.52	12.26	9.9	3.69	3.32	5.31	9.26	5.96	6.01	12.95	13.6	17.87	6.03	15.55	2	Shush	6201	32.171499°	48.248614°
49.04	57.73	37.77	45.65	22.55	44.37	26.32	21.62	19.93	8.03	6.89	6.9	8.88	5.86	11.35	17.77	29.02	8.98	28.71	1	Sureshjan	1070	32.322732°	50.670007°
57.31	70.17	43.23	52.74	23.46	58.01	34.51	27.84	25.51	9.18	8.39	7.85	10.16	6.29	13.32	19.64	38.06	13.08	32.08	1	Sureshjan	1018	32.323504°	50.671682°
59.37	71.35	44.4	54.04	23.9	59.27	35.84	27.97	26.46	9.94	9.46	7.85	10.44	6.87	13.71	20.38	–	–	33.41	1	Sureshjan	1018	32.323504°	50.671682°
60.6	73.05	45	55.67	26.03	64.18	38.77	38.87	27.26	9.79	9.37	8.36	10.22	7.08	13.23	20.06	41.57	13.94	34.52	1	Sureshjan	1053	32.322761°	50.671464°
55.83	67.37	42.09	51.67	23.99	55.81	32.57	26.97	24.43	9.08	7.95	7.81	9.61	6.63	12.67	19.34	34.02	11.78	29.63	1	Sureshjan	1018	32.323504°	50.671682°
36.8	44.11	31.16	36.82	17.25	30.16	17.52	13.53	13.09	4.75	4.35	5.48	7.14	4.88	8.8	13.64	22.51	8.78	21.11	1	Jounaghan	1019	32.124771°	50.678743°
33.19	39.77	27.24	32.61	15.82	25.59	15.03	11.43	11.01	4.06	3.46	5.06	6.07	4.42	7.74	11.91	20.94	8.36	17.42	1	Jounaghan	1019	32.124771°	50.678743°
34.46	40.89	28.74	34.54	15.45	24.94	14.89	12.06	9.59	3.19	3.17	4.97	6.49	5.11	8.43	12.67	21.89	8.04	18.48	1	Jounaghan	1019	32.124771°	50.678743°
28.21	32.96	24.28	28.46	13.67	21.96	12.02	8.72	9.83	3.6	3.13	4.19	4.83	3.88	6	10.27	17.89	7.09	15.14	1	Jounaghan	1019	32.124771°	50.678743°
31.66	37.59	27.26	32.42	14.84	24.39	13.49	10.62	10.75	3.6	3.46	4.52	5.61	4.24	7.49	11.74	20.25	7.81	16.45	1	Jounaghan	1019	32.124771°	50.678743°
27.87	32.99	24.39	28.23	14.54	20.76	11.91	9.41	8.43	2.91	2.9	2.26	4.95	4.14	6.63	10.8	17.62	7.13	15.24	1	Jounaghan	1019	32.124771°	50.678743°
26.9	31.61	23.26	27.04	13.21	–	–	–	–	–	–	4.24	4.8	3.91	6.71	9.82	16.21	6.33	13.79	1	Jounaghan	1019	32.124771°	50.678743°
24.21	29.6	21.82	25.3	12.79	16.48	9.98	8.26	6.37	2.29	2.19	4.2	4.51	4.28	5.49	9.01	15.39	6.38	12.66	1	Jounaghan	1019	32.124771°	50.678743°
40	48.28	32.99	39.15	18.76	33.95	19.19	14.04	16.14	5.93	4.61	7.27	15.1	8.24	19.72	20.78	24.7	9.52	22.57	2	Jounaghan	1019	32.124771°	50.678743°
36.76	44.18	30.04	36.15	17.56	29.6	16.15	12.44	13.66	4.84	4.29	6.9	13.74	7.46	17.98	18.75	23.26	8.9	21.06	2	Jounaghan	1019	32.124771°	50.678743°
44.85	53.95	36.06	42.17	21.18	41.46	23.37	17.62	19.93	6.91	6.35	9.28	20.88	11.31	27.42	29.41	28.12	9.61	27.37	2	Jounaghan	1019	32.124771°	50.678743°
36.63	43.25	29.99	35.87	17.04	28.66	15.27	12.12	13.44	5	4.22	6.66	13.44	7.38	17.74	18.31	22.7	8.83	21.19	2	Jounaghan	1019	32.124771°	50.678743°
37.97	45.25	31.78	37.42	18.62	31.79	17.24	13.52	14.1	5.25	4.5	7.11	14.72	8.37	19.46	20.18	23.76	9	21.35	2	Jounaghan	1019	32.124771°	50.678743°

Appendix 1. — Continuation.

CL	CW	OW	ALTW	PCW	CPL	CDL	PL	CPH	CDH	PH	TL	TW	sixth ADL	sixth ADW	MPW	ML	MW	BH	Sex	Locality	Voucher	Latitude	Longitude
38.35	45.42	32.15	37.81	17.98	33.03	18.82	14.2	15.69	5.81	4.76	8	17.68	9.73	23.83	24.59	23.34	8.45	23.59	2	Jounaghan	1019	32.124771°	50.678743°
37.5	45.46	31.17	37.22	18.55	29.51	16.76	12.49	14.41	5.55	4.61	6.74	12.9	7.39	16.59	17.32	23.1	8.83	21.54	2	Jounaghan	1019	32.124771°	50.678743°
25.62	31.35	2308	26.53	12.89	19.71	10.92	8.72	8.04	2.95	2.71	4.36	5.81	3.96	7.85	10.7	12.69	4.33	14.41	2	Jounaghan	1019	32.124771°	50.678743°
2183	26.74	19.6	23.2	11.59	14.79	8.93	7.57	5.27	2.08	1.94	3.73	4.75	3.93	6.51	8.9	13.41	5.45	11.51	2	Jounaghan	1019	32.124771°	50.678743°
49.42	49.27	40.7	49.17	20.54	40.95	24.45	20.73	15.37	5.37	5.4	7.17	9.14	6.42	11.51	17.44	–	–	26.4	1	Sisakht	POT1062	30.860954°	51.464501°
37.57	45.92	31.92	38.18	16.68	27.76	16.6	13.08	11.32	3.8	3.65	5.32	7.05	4.96	8.9	13.89	24.95	9.06	20.01	1	Yasuj	POT1028	30.690764°	51.556197°
32.01	38.6	27.13	32.28	14.52	24.89	13.05	10.24	10.62	3.96	3.51	4.84	5.84	4.44	7.44	11.97	21.86	8.16	16.91	1	Yasuj	POT1028	30.690764°	51.556197°
36.45	43.74	31.07	36.76	16.29	29.84	16.6	13.58	13.05	4.97	4.33	5.35	7.11	5.35	8.78	13.79	20.49	7.17	18.94	1	Yasuj	POT1028	30.690764°	51.556197°
19.07	23.53	17.53	20.8	9.18	8.25	5.46	4.18	2.86	1.22	1.13	2.94	3.83	2.84	4.73	7.27	12.03	4.48	9.94	1	Yasuj	POT1028	30.690764°	51.556197°
36.64	44.12	30.83	36.44	15.55	32.01	17.72	14.37	13.62	5.45	4.67	5.1	7.36	4.95	8.61	13.52	24.79	8.81	19.44	1	Yasuj	POT1028	30.690764°	51.556197°
31	37.68	26.61	31.46	12.88	14.91	–	7.86	5.47	2.23	2.25	4.42	5.66	4.4	6.49	11.1	20.5	7.52	16.16	1	Yasuj	POT1028	30.690764°	51.556197°
46.33	56.13	38.74	46.44	18.38	42.69	25.02	19.48	18.51	7.21	6.42	6.25	7.81	6.14	10.68	16.19	25.56	8.42	25.14	1	Yasuj	POT1028	30.690764°	51.556197°
45.37	55.04	36.76	44.07	18.79	42.2	24.11	19.43	18.24	7.53	6.35	6.46	8.3	6.12	10.56	16.1	31.34	10.49	23.82	1	Yasuj	POT1028	30.690764°	51.556197°
46.19	55.48	37.27	44.08	20.75	43.2	24.68	19.89	17.27	6.37	5.72	6.59	3.11	5.62	10.3	16.44	30.97	9.82	24.53	1	Yasuj	POT1028	30.690764°	51.556197°
41.56	50.22	34.07	40.23	17.41	36.96	19.48	16.55	15.34	6.23	5.25	6.19	7.45	5.61	9.79	14.75	28.79	9.91	21.81	1	Yasuj	POT1028	30.690764°	51.556197°
35.22	42.37	29.39	35.09	15.19	28.06	15.34	11.51	12.11	4.59	4.13	5.27	6.2	4.91	8.06	13.45	24	8.63	19.05	1	Yasuj	POT1028	30.690764°	51.556197°
45.62	55.89	37.54	46.68	20.13	42.76	25.12	20.33	18.44	6.73	6.07	6.26	8.42	5.98	10.73	16.23	32.21	10.3	24.41	1	Yasuj	POT1028	30.690764°	51.556197°
39.8	48.94	32.61	39.75	18.18	–	–	–	–	–	–	9.32	20.95	11.02	25.98	26.16	25.98	8.49	23.14	2	Yasuj	POT1028	30.690764°	51.556197°
44.24	53.38	36.02	42.65	19.88	38.02	21.13	16.31	17.3	6.44	5.75	5.09	14.19	6.96	22.92	23.48	23.31	3.85	24.48	2	Yasuj	POT1028	30.690764°	51.556197°
40.55	49.1	33.25	40.37	18.06	34.32	18.91	15.36	15.67	5.29	4.85	8.67	18.68	10.44	24.69	25.29	–	–	17.53	2	Yasuj	POT1028	30.690764°	51.556197°
27.26	32.65	24.07	28.03	12.52	20.54	9.84	8.79	8.65	3.18	2.9	4.6	7.84	4.64	9.32	11.65	18.45	6.54	13.77	2	Yasuj	POT1028	30.690764°	51.556197°
30.4	36.08	26.26	30.31	14.34	23.08	12.54	10.13	10.15	3.98	3.33	5.13	9.43	6.07	12	13.08	20.05	7.53	15.65	2	Yasuj	POT1028	30.690764°	51.556197°
32.44	39.53	28.3	33.74	14.88	25.44	13.9	10.84	11.14	4.32	3.68	5.97	10.4	5.99	13.79	14.63	17.3	6.62	17	2	Yasuj	POT1028	30.690764°	51.556197°
31.31	37.73	26.52	31.05	14.69	15.31	9.09	7.17	6.29	2.52	2.34	6.45	10.94	6.33	15.06	15.7	20.54	7.18	16.57	2	Yasuj	POT1028	30.690764°	51.556197°
23.39	26.93	19.94	23.46	10.71	15.74	9.72	6.86	7.02	2.53	2.24	4.04	5.4	4.18	6.9	9.31	15.17	5.44	11.6	2	Yasuj	POT1028	30.690764°	51.556197°