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An integrated taxonomic approach, using geometric morphometric methods, reveals the cryptic diversity of *Parhyale darvishi* Momtazi & Maghsoudlou, 2016 (Crustacea: Amphipoda: Hyalidae)

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ABSTRACT

In recent years, morphological analyses and molecular methods have been increasingly used to describe new species of amphipods. Geometric morphometric methods are recognized as part of an integrated approach in taxonomy and are a cost-effective way to identify species, but its application is rare in Amphipoda. Taxonomically, the shape of gnathopods is important in the family Hyalidae, and species could be identified based on changes in these anatomical parts. Previously, *Parhyale darvishi* Momtazi & Maghsoudlou, 2016, had been described as a very scattered amphipod on a wide range of northern coasts of the Persian Gulf and the Gulf of Oman. In the present study, a geometric morphometric method based on semilandmarks was used to investigate intraspecific gnathopod's shape changes of *P. darvishi* population in the Persian Gulf and the Gulf of Oman. Therefore, 180 semilandmarks were selected on the propodus of first and second gnathopods of 100 male and 50 female. Data were analysed using tps package software. The results of UPGMA clustering and relative warp analysis reveal cryptic diversity in *P. darvishi* and show the main morphometric variations between sexes and populations. The present results, clearly separated Bushehr population samples from other studied populations of *P. darvishi* with concave posterio-distal margin in propodus of first and second male gnathopods and subquadrate propodus of first female gnathopod. Surveying detailed morphology of Bushehr samples confirmed geometric morphometric results. Therefore, *Parhyale bushehri* **sp. nov.** was described and distinguished from similar species by revealed propodus shape variations of geometric morphometric analyses and also having setae on the outer ramous of first and second uropods, peduncle of third uropod and some mouthparts characters. Consequently, the results show the integrated approach (numerical variations and statistical analyses along with morphological analyses) in amphipod taxonomy could reveal cryptic diversity.

1. Introduction

Amphipoda is regarded as an orders of crustacean with more than 9000 species which inhabited in different niches. Also, they are used as bioindicator for ecological assessments (Thomas 1993; Maghsoudlou et al. 2020; Momtazi & Maghsoudlou 2022). Increasing taxonomic studies in recent decades lead to discovery of more new species of amphipods (Coleman 2015). Despite these efforts, Arfianti et al. (2018) mentioned that two thirds of order Amphipoda are yet to be described. Most of the taxonomic studies on amphipods are based on traditional methods i.e. taxonomic characters and their comparisons without using statistical methods. The use of molecular methods has also become popular in order to find cryptic diversity in amphipods. However, statistical methods are rarely used in spite of being practical in revealing morphological variations between populations. Few statistical approaches could be found in amphipod taxonomy including Wilhelm & Venarsky (2009), Audoglio et al. (1999), Henzler and Ingólfsson (2008), Nahavandi et al. (2011), and Medeiros & Weber (2016) studies.

Abbreviations: GO, Gulf of Oman; PG, Persian Gulf; GM, geometric morphometric.

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Table 1
The geographical coordination of studied stations and number of individuals in each station.

N	station	Abbreviation on map	Coordinates	Males	Females
1	Tiss (Chabahar Bay)	Tiss	25°21′25″N; 60° 36′17″E	10	10
2	Baghestan	Baq	27°09′01″N; 56°07′38″E	10	10
3	Qeshm Island	Qesh	26°56′3″N; 56°16′29″E	8	
4	Bandar Hasineh	Has	26°38′35″N; 54°22′01″E	10	
5	Bandar Charak	Char	26°42′53″N; 54°08′20″E	10	
6	Chiruyeh	Chir	26°42′42″N; 53°43′57″E	10	10
7	Kish Island	Kis	26°31′25″N; 54°02′51″E	10	
8	Abu Musa	Abu	25°52′07″N; 55°01′6″E	10	10
9	Chahpahn	Chah	28°20′53″N; 51°11′00″E	12	
10	Bushehr Port	Bush	28°59′51″N; 50°50′15″E	10	10

The geometric morphometrics (GM) have been known as a cost effective statistical method to find cryptic diversity across crustaceans (Karanovic et al. 2016). However its application in amphipod taxonomy is restricted to Riedlecker et al. (2009) and Curatolo et al. (2013) studies.

The Hyalidae family is mostly distributed across the intertidal zone. Three representative species of the genus *Parhyale* Stebbing, 1897 were already described from the western Indian Ocean including *Parhyale basrensis* Salman, 1986, *Parhyale piloi* Myers et al., 2017 and *Parhyale darvishi* Momtazi & Maghsoudlou, 2016. The last species widely distributed along 2250 Km coastline of the northern Persian Gulf (PG) and Gulf of Oman (GO) (Pak & Farajzadeh 2007) where high environmental fluctuations (i.e. salinity, temperature) are found (Barth & Khan 2008; Sheppard et al., 2010). No morphological variations were reported for *P. darvishi* so far. Consequently, the present study aims to find morphological variations in propodus of gnathopods of *P. darvishi* populations via geometric morphometrics methods. The findings led us to describe *Parhyale bushehri* **sp. nov**.

1.1. Materials and methods

Geometric morphometric method. Samples of *P. darvishi* were obtained from zoological collection of Iranian National institute for Oceanography and atmospheric science which were deposited in 96 percent ethanol. They comprised 150 adult specimens; 100 males and 50 females. The availability of material in museum collections did not allow us to gather data from population frequency and sex-matched samples. The geographic location of each populations and studied samples are given in Table 1 and Fig. 1.

The specimens were dissected; gnathopods were detached and positioned while submerging in glycerine. Pictures were taken by Nikon eclipse80i equipped with a digital camera (Nikon Ds-Fi). Z-stack pictures (Five to ten) were taken from gnathopods, due to captured picture under the microscope while focusing on different parts of the image. For stacking them together into one clearly focused image, CombineZP software was used (Hadley 2008).

Due to the scarcity of reliable homologous landmarks on gnathopods (4 landmarks), semilandmarks were determined by the curve-tracing method in the tpsDig software package (Rohlf 2010a). Semilandmarks are points evenly spaced on the outline delimited by two fixed points. First and second gnathopods (G1, G2) were digitized with two curves including; anterior curve with 80 semilandmarks, and posterior curve with 100 semilandmarks (Fig. 2. B, C). The posterior curve is started from the posterior joint of propodus-carpus and finished at the posterior joint of propodus-dactylus. The anterior curve is defined from the anterior joint of propodus-carpus to the anterior joint of propodus-dactylus.

Correlations between the Procrustes and tangent-shape distances were calculated using tpsSmall software version 1.20 (Rohlf 2003). The semilandmarks were entered into a generalized Procrustes analysis (GPA), and then they were slid along the outline curve until they have matched the positions of corresponding points in a reference configuration. In the context of geometric morphometrics, reference configuration is the average (consensus) configuration for a sample (Bookstein

Fig. 1. Localities of studied stations of *Parhyale darvishi* on the map and locality for alliance species; A. *P. basrensis*, B. *P. piloi*.

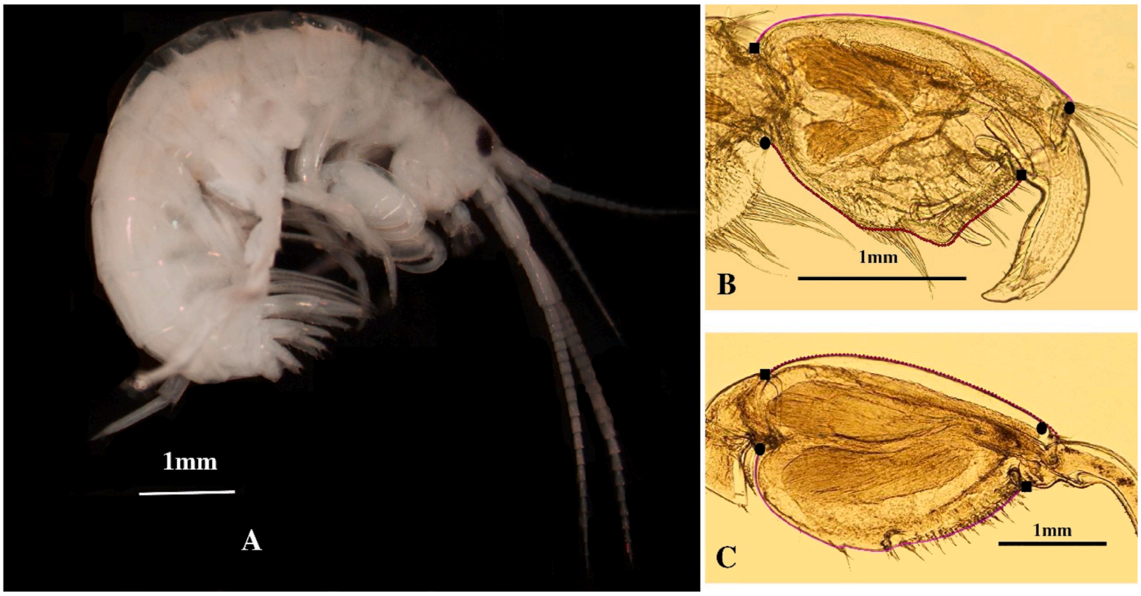

Fig. 2. The whole body of *Parhyale darvishi* (A), the number and positions of semilandmarks (starting landmark is remarked with circle and ending landmark with quadrate) B: first gnathopod with 100 semilandmarks for posterior curve and 80 semilandmarks for anterior curve, C: second gnathopod with 100 semilandmarks for posterior curve and 80 semilandmarks for anterior curve.

Table 2
Discriminate statistics for first gnathopod and second gnathopod.

Anatomical part	Variance for sexes%	Goodall's F-test F (F-value)	(P-value)
G1 propodus	92/52	4/165	000/0
G2 propodus p	8/34	62/76	000/0

1997). There are two mostly used criteria to slide semilandmarks along an outline; minimum bending energy (Bookstein et al. 2002) and perpendicular projection or minimum Procrustes distance (Sheets et al., 2004). Semilandmarks were superimposed and slided by using tpsRelw software package version 1.49 (Rohlf 2010b). This program provides sliding semilandmarks based on minimum bending energy. After computing a mean configuration and aligning the targets, the program moved the semilandmarks of each target to minimize the bending energy of the thin-plate spline, thus describing the deformation of the reference to that target (Zelditch et al. 2004).

Deformation grids were generated by using relative warps (RWs) as characters with the tpsRegr software program (Rohlf 2009) then calculated a multivariate regression analysis with the input RWs and x-y-shape coordinates of the semilandmarks. The software transforms the coordinate information to deformation grids related to the relative warp scores. The resulting mean deformation grids for better visualization were exaggerated by factor three.

Multivariate analysis of variance (MANOVA) and linear discriminant analysis (LDA) with leave-one-out cross-validation (Morrison 1967; Lachenbruch & Mickey 1968; Lesaffre and Albert, 1989) were performed to test significant differences between the populations and two sexes. To explore relative relationships between the individuals, an explorative clustering -Unweighted Pair-Group Method with Arithmetic means (UPGMA) was performed on relative warps.

Morphological study. Samples dissection were made in glycerol. Illustrations were made using the methods described in Coleman (2006). They were deposited on Iranian National Institute for Oceanography Collection (INIOC).

Abbreviations are: A, antenna; A.F, accessory flagellum; EP, epimeron; G, gnathopod; L.L, lower lip; MD, mandible; Mx, maxilla; Mxp, maxilliped; P, pereopod; PL, pleopod; T, telson; U, uropod; U.L, upper lip.

2. Results

Variation in shape space of the specimens was perfectly correlated with tangent space. This allows the use of the plane approximation in future statistical analyses and interpretation of results. Exploratory analyses, UPGMA clustering, and relative warp analysis showed the main morphometric variations associated with sexual dimorphism. The first relative warp of G1 and G2 separates two sexes and explains 68 and 45 percent of total shape variation respectively. The MANOVA indicated a significant difference for mean vectors between two sexes for all two anatomical features (Table .2). The same results were achieved in LDA with 100% correctly classified individuals based on sexes by G1 and G2 shapes. Because of sharp sexual dimorphism of the gnathopods shapes, split-sex samples were used in all further analyses.

Exploratory relative warp analysis of G1 configurations showed a clear separation between the Bushehr population and other populations in two sexes (Fig. 3). Relative warp analysis of female samples yielded higher resolution in the assessment of phenotypic divergence observed among the Bushehr coast populations than male samples. The same results of RW analysis were achieved on G2 (Fig. 4).

Results of cluster analysis also confirmed relative warp result and grouped samples of Bushehr population in one cluster, female samples showed more clear separation of Bushehr population than male samples (not shown).

Linear discriminant analysis correctly classified all specimens of Bushehr population into their true population based on five first relative warps of females' first gnathopod and second gnathopod configurations, the correct grouping of first and second gnathopod shapes in males was 90 percent.

Shape deformations between the Bushehr population and other samples have been shown in Fig. 5 for males and females separately. The deformation grid of the first male gnathopod shows that samples with less measure of first component have a subquadrate shape with acute margin in the palm section. While a higher value of the first component could be seen in the Bushehr population that is remarked with concave

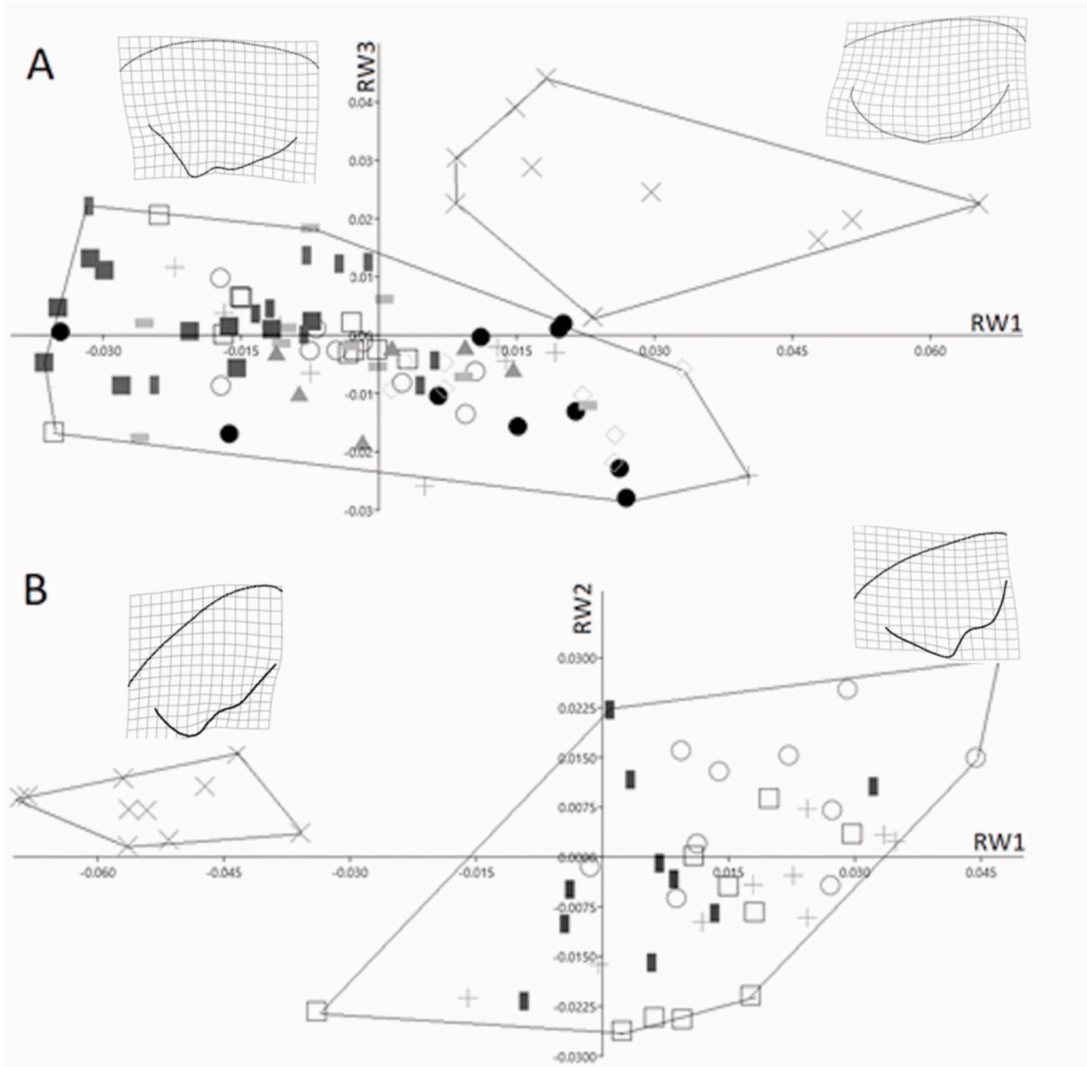

Fig. 3. Relative warp scattering G1 of *P. darvishi* populations (×), A: Male and B: Female samples. Symbols are ▌ Tiss, □ Baghestan, Qeshm Island, Bandar Hasineh, ● Bandar Charak, ◯ Chiruyeh, ■ Kish Island, + Abu Musa, Chahpahn, × Bushehr Port.

palm, posterior-proximal margin and faded defining angle of palm. Similarly, the first female gnathopod in the Bushehr population is clearly separated by subquadrate propodus with transverse palm; from subtriangular propodus with acute palm in other populations. The shape of propodus in the second male and female gnathopods reveals variations in *P. darvishi* as well. The female G2 of the Bushehr population is characterized by subquadrate propodus and straight palm margin; and male G2 with lacking proximal protuberance in the posterior margin of propodus.

3. Discussion

The representatives of the genus *Parhyale* Stebbing, 1897 from the western Indian Ocean are *P. basrensis* Salman, 1986 from Arvand River in the North western coast of the PG (Fig. 1. A), *P. darvishi* Momtazi & Maghsoudlou, 2016 from northern coasts of the PG and GO, and *P. piloi* Myers et al., 2017 from Indian coasts (Fig. 1. B). They are characterized with similar gnathopod shapes. The results of GM analysis in the present study revealed clear variations in studied populations of *P. darvishi*. The male and female gnathopod shapes of the western population of *P. darvishi* (Bushehr) were significantly different from other populations.

These variations could be either intraspecific or interspecific. The complementary morphological studies revealed additional differentiated characters, leading to description of a new species *P. bushehri* **sp. nov.** from the Bushehr port. The detailed description is as follows.

P. bushehri **sp. nov.**

(Figs. 5–7).

3.1. Types

Holotype male, 5.4 mm (INIOC 1–42S), Bushehr (28°59′51.01″N 50°50′15.31″E). Allotype female 7.5 mm, (INIOC 1–43S), same data as holotype.

3.2. Other material examined

9 males, 9 females (INIOC 1–44).

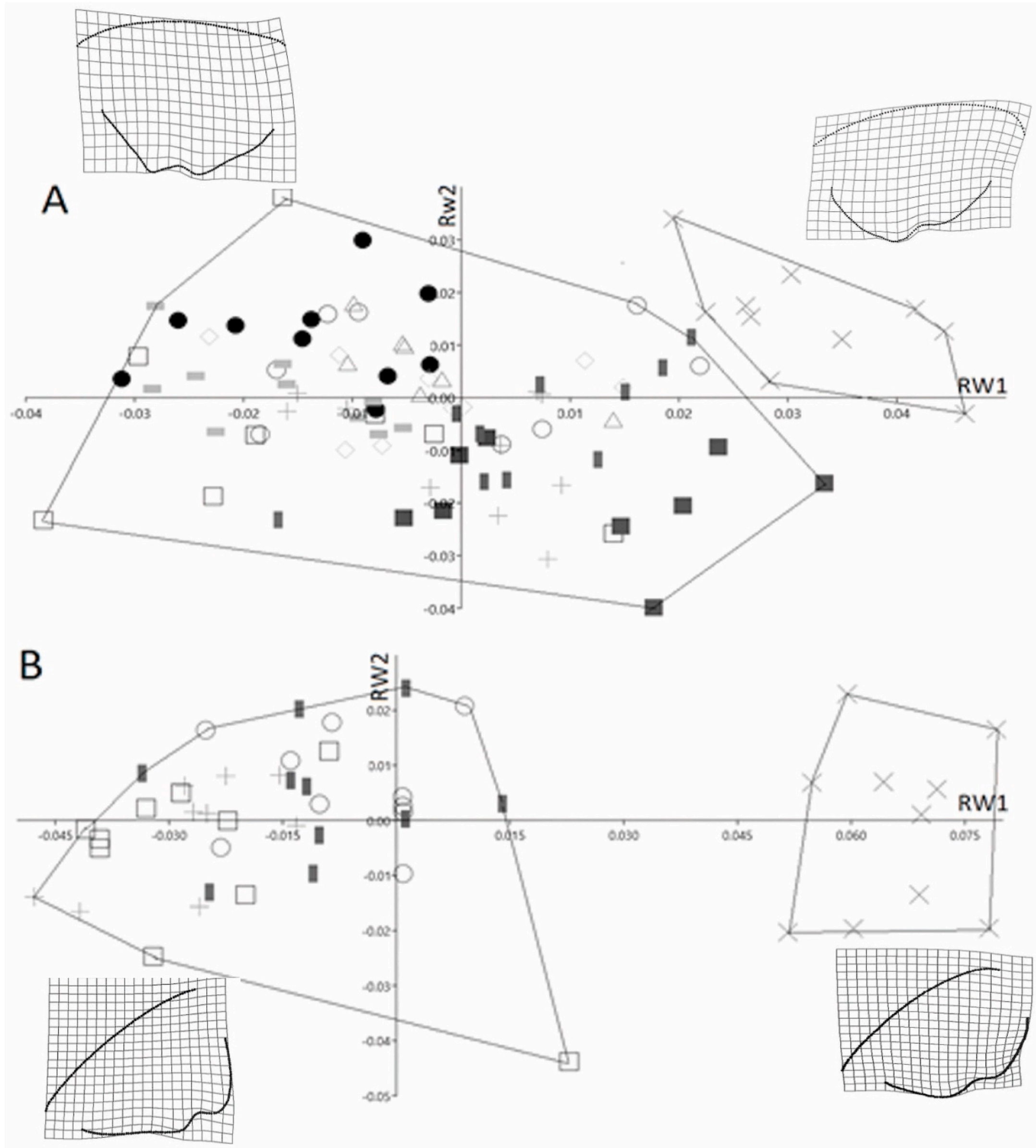

Fig. 4. Relative warp scattering G2 of *P. darvishi* populations (×), A: Male and B Female samples. Symbols are ▌Tiss, □ Baghestan, Qeshm Island, Bandar Hasineh, ● Bandar Charak, ◯ Chiruyeh, ■ Kish Island, + Abu Musa, Chahpahn, × Bushehr Port.

3.3. Type locality

Bushehr (28°59′51.01″N 50°50′15.31″E), Persian Gulf, Iran, high intertidal zone.

3.4. Etymology

The species name was referred to its type locality, Bushehr port in the Persian Gulf.

3.5. Description

Based on holotype, male, 5.4 mm, (INIOC 1–42S). Body without dorsal carina, eyes present, well developed, oval. Antenna 1 about half size of antenna 2, flagellum much longer than peduncle. Antenna 2 slightly greater than half of body length; flagellum about twice as long as the peduncle, 21 articles. Upper lip setose distally. Mandible left lacinia mobilis 5-dentate, bearing 4 accessory plumose setae; right mandible with molar bearing a plumose seta. Maxilla 1 palp one articulate, **shorter than base of outer lobe**, bearing two plumose setae; outer lobe with 9 setal-teeth. Maxilla2 and maxilliped palp normal for the family.

Pereon. Gnathopod 1, coxa longer than broad, with well-defined central shelf on posterior margin; basis broadening at the middle, with downward curved setae; merus shorter than carpus, postero-distal acute corner; carpus with robust setae on ventral lobe; propodus broad, expanded distally, **posterior margin concave; palm concave without protuberance in middle part, defined by angle armed with two equal length** straight **stout setae**; dactylus reaching to end of palm **and not medially swollen**. Gnathopod 2 coxa longer than broad, with well-defined central shelf on posterior margin; basis bearing curved setae on dorsal margin, without postero-distal lobe; ischium quadrate; merus with postero-distal acute angle; carpus with small projection between

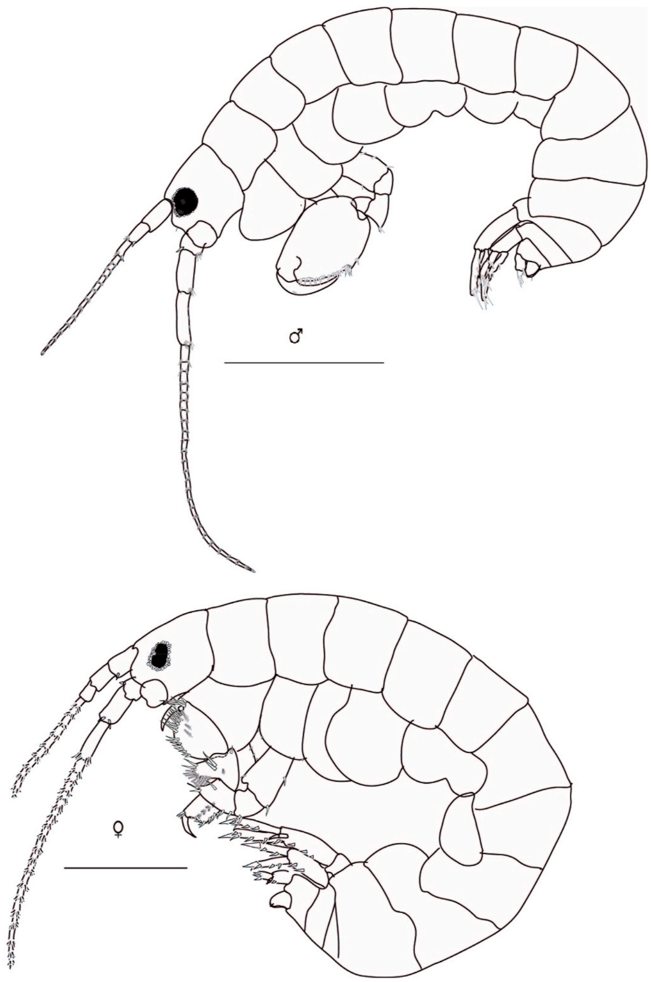

Fig. 5. *Parhyale bushehri* **sp. nov**., holotype, male, 5.4 mm (INIOC1–42S), Bushehr port and allotype, female 7.5 mm, (INIOC 1-43S), Bushehr port. Scale 1 mm.

merus and propodus, absent in larger male; propodus oval, without delimitation in anterior and posterior margins, **posterior margin without protuberance**; palm acute with several stout setae, with two large robust setae on posterodistal corner at the beginning; dactylus subequal to palm. Pereopods 3–4 alike, without large robust striated setae on propodus. Pereopod 5 much shorter than pereopods 6–7, propodus with 2 medial setae on anterior margin, with setae on posterior margin. Pereopods 6–7 propodus with 3 groups of setae on anterior margin, **and 5 groups on the posterior margin**.

Pleon. Epimera 2–3 with semi-quadrate posteroventral corner and two setae on posterior angle. Uropod 1 **with a distolateral seta;** rami subequal, inner ramus with two setae, **outer ramus with two marginal seta.** Uropod 2 rami subequal, inner ramus with two setae, outer ramus **with two marginal seta.** Uropod 3 biramous, extending beyond the telson; **peduncle with a stout seta distally;** outer ramus shorter than peduncle with 5 distal robust setae; inner ramus minute, scale-like. Telson deeply cleft, as long as peduncle of third uropod, subtriangular, apically round, with two apical fine setae on each lobe.

Female (sexually dimorphic characters). Gnathopod 1 carpus lobate, **subquadrate propodus**; palm transverse, defining angle with two stout setae. Gnathopod 2 slightly larger than gnathopod 1, **subquadrate propodus and transvers palm**.

Remarks. The new species of *Parhyale* in the western Indian Ocean; *P. bushehri* sp. nov. is diagnosed by combined extracted GM characters and morphological characters.

The marked differentiated characters by geometric morphometric analysis are as follows: the straight margin in posterio-distal part of propodus and the smooth palm marked with two equal straight stout setae in first male gnathopod, less propodus delimitation in the second male gnathopod, transvers palm and subquadrate propodus in the first and second female gnathopods. Fig. 8 is illustrated the variations in the male and female gnathopods in the western Indian Ocean species of the genus *Parhyale*.

The revealed diagnostic characters of *P. bushehri* by complementary morphological analysis are as follows: palp of first maxilla not reach to the base of outer plate (extend to outer plate in *P. piloi*), present of seta groups on the posterior margin of seventh pereopods (lacking in *P. darvishi* but present in *P. basrensis* and *P. piloi*), bearing distolateral robust seta on the peduncle of first uropod (lacking in *P. basrensis*), outer ramus of first uropod with robust setae (lacking on *P. piloi* and *P. darvishi*) second uropod with two robust seta (lacking in *P. darvishi*), bearing one distal stout seta on the peduncle of third uropod (2 stout setae on *P. basrensis* and *P. piloi*). The main differentiated characters in *P. darvishi* groups are tabulated in Table 3.

4. Conclusion

There are three views to justify shape variations in the gnathopods of crustaceans. Based on adaptational view, the environmental factors such as temperature, salinity and chlorophyll-a concentrations can affect the morphological traits (Dugan et al. 1994). No correlation was found between shape variations of adjacent populations (Fig. 3.4) which have same ecological elements based on the extracted map by Barth & Khan (2008) and Sheppard et al. (2010). Therefore, this hypothesis is rejected.

In the second view, variations are affected by sex (Claverie & Smith 2007; Wilhelm and Venarsky, 2009) or allometry (Rosenberg 2002). In the previous study on family Hyalidae, the allometric variations in the shape of carpal lob of second male gnathopod were reported by Serejo (2004) and Momtazi and Maghsoudlou (2016). But, no ontological variations were reported in the propodus article of G1 and G2. Therefore, the shape variations in Bushehr population could not be assigned to allometric changes. Also, the dimorphism of gnathopods shape variations described in *P. darvishi* by Momtazi & Maghsoudlou (2016) were confirmed in the current research. But, the revealed shape variations discriminated Bushehr population of *P. darvishi* from other populations was found in both sexes in the separate analysis. Thus, the effect of sex in shape variation was rejected here. It must be considered that in spite of previous studies in this family (Bousfield & Hendrycks 2002; Myers et al. 2017; Iaciofano & Lo Brutto 2017; Lo Brutto and Iaciofano, 2018) which were emphasized on the taxonomic value of male gnathopod shapes, the present results draw attention to the differences in female samples.

The last hypothesis for the reason of gnathopod shape variations in crustacean is geographical barriers that are considered as a factor which leads to genetic differences and reproductive isolation (Contreras & Jaramillo 2003; Rufino et al. 2006). The geological history of the shorelines of the PG is complicated and subjected in various studies (Lambeck, 1996; Pourkerman et al. 2018; Beni et al. 2021). There is no available evidence for the geographical barriers in PG, but based on the primary studies in the region, the Bushehr port is considered for bearing potential submarine springs (Farzin et al. 2018), special topology

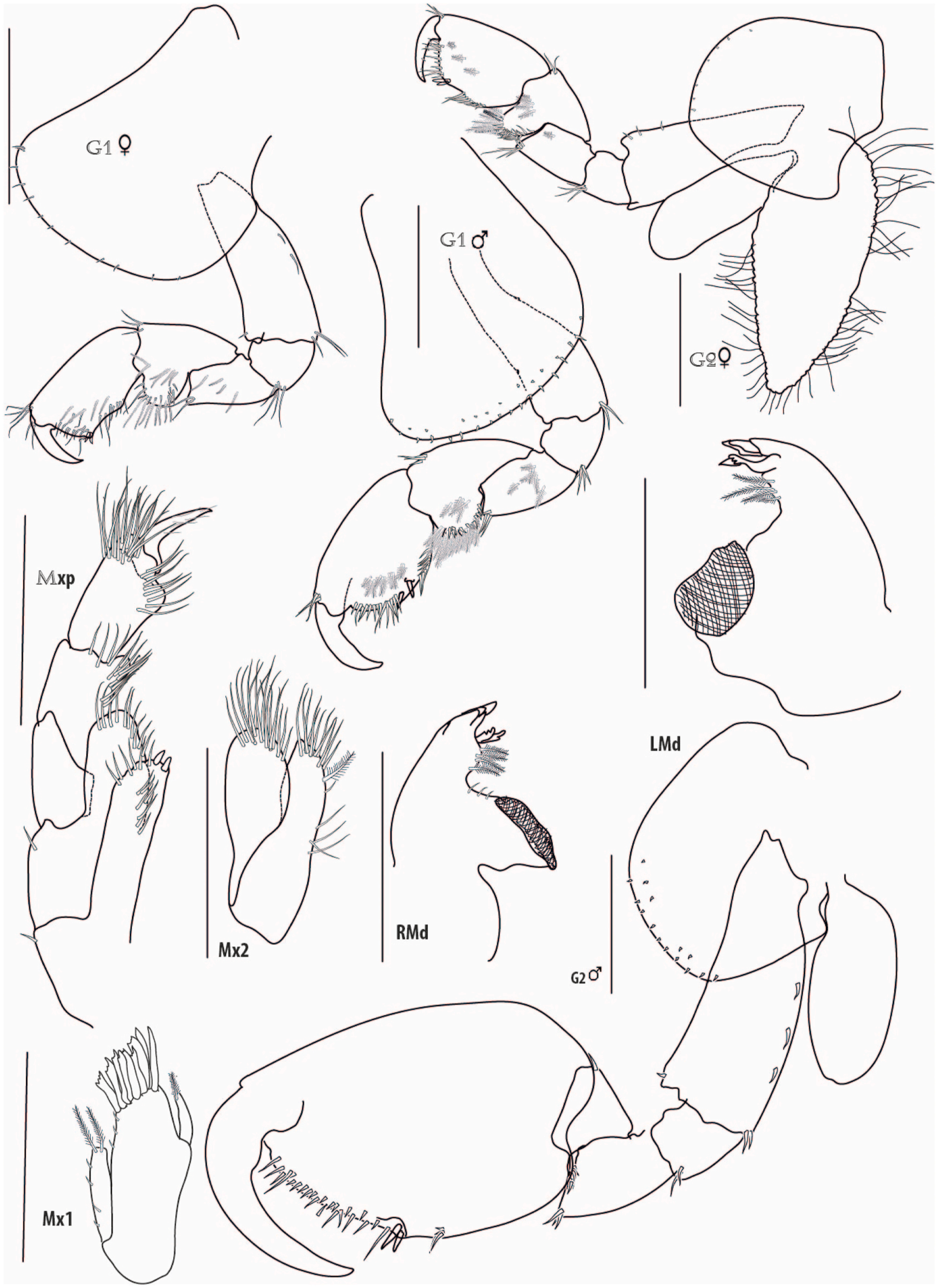

Fig. 6. *Parhyale bushehri* **sp. nov.**, holotype, male, 5.4 mm (INIOC1–42S), Bushehr port and allotype, female 7.5 mm, (INIOC 1-43S), Bushehr port. Scale 1 mm. Scale 0.5 mm.

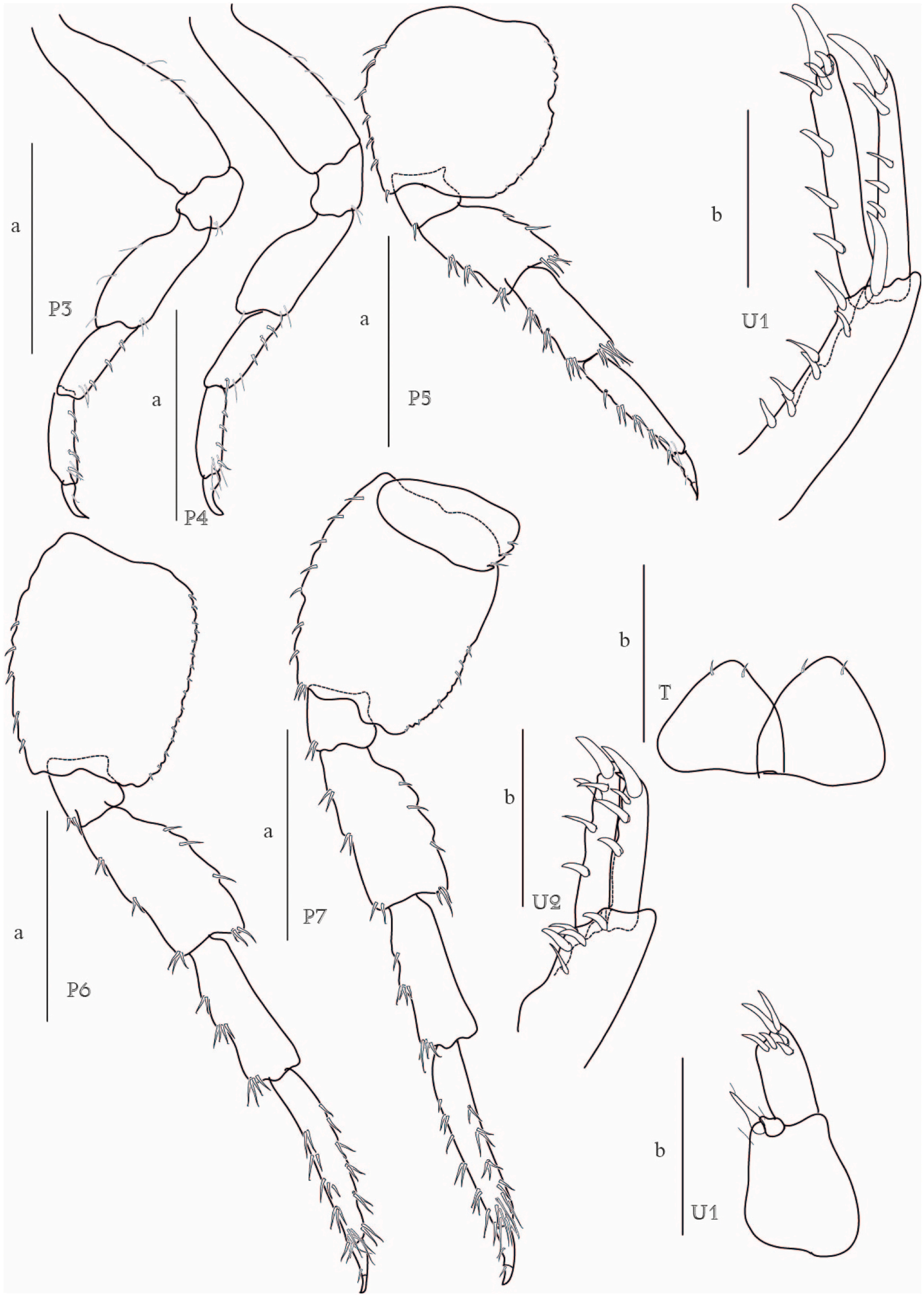

Fig. 7. *Parhyale bushehri* **sp. nov**., holotype, male, 5.4 mm, (INIOC1–42S), Bushehr port. Scale a = 1 mm and b = 0.5 mm.

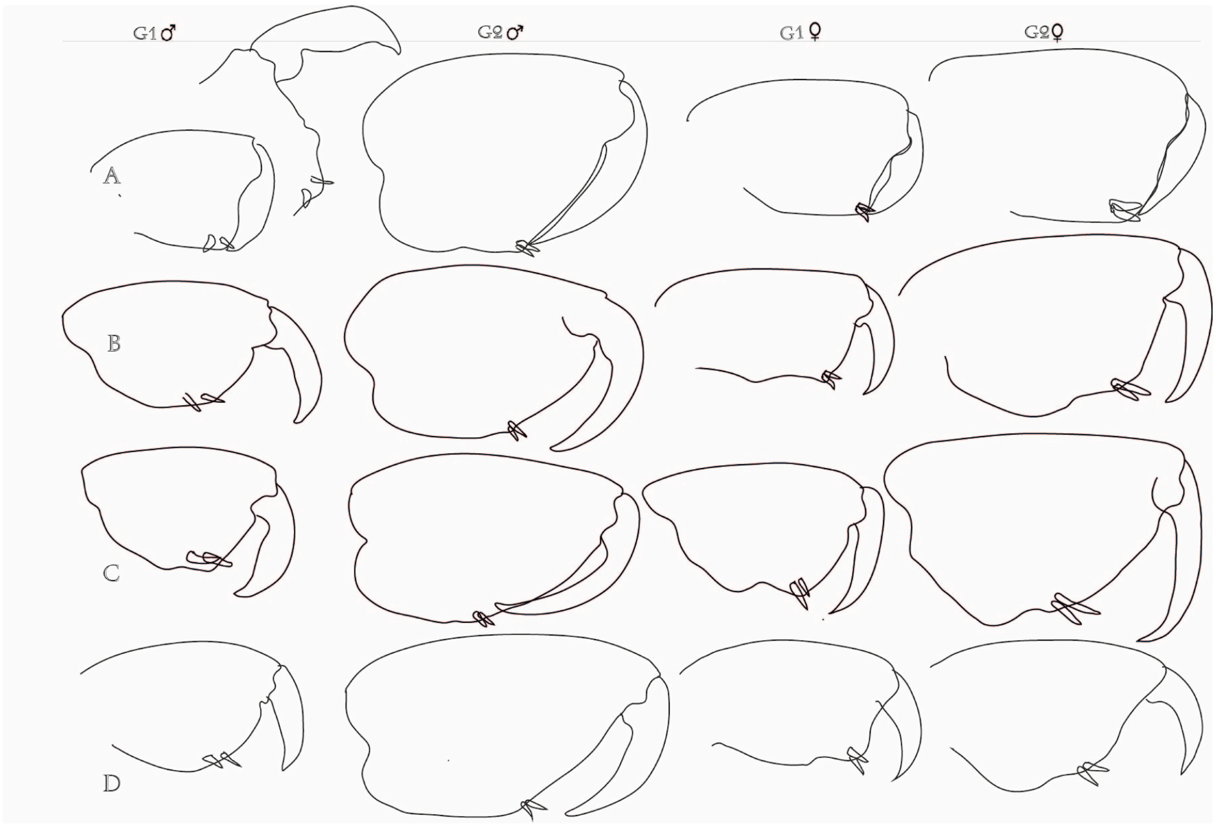

Fig. 8. The shape variations in first and second gnathopods of species of *Parhyale darvishi* group. A: *P. basrensis* (redraw from Salman 1986), B: *P. bushehri*, C: *P. darvishi* (draw from fresh material of type locality) and D: *P. piloi* (redraw from Myers et al. 2017).

Table 3
Morphological diagnostic characters in species of *Parhyale darvishi* group.

species	Reference	Palp of Mx1	Propodus of G1♀	Propodus of G1♂	Propodus of G2 ♀	posterior margin of propodus of G2 ♂	P7 posterior margin of propodus	U1, outer rammus	U1, peduncle distolateral R.S	U2, outer rammus
P. basrensis	Salman (1986)	Not reach to O.P	Palm acute	Grasping spines curved	Palm acute	With depression	With 5 setae group	With three R.S	absent	With two R.S
P. darvishi	Momtazi & Maghsoudlou (2016)	Not reach to O.P	Palm acute	Grasping spines curved	Palm acute	With depression	naked	naked	present	naked
P. bushehri sp.nov.	Present study	Not reach to O.P	Palm transvers	Grasping spines straight	Palm transvers	Without depression	With 5 setae group	With three R.S	Present	With two R.S
P. piloi	Myers et al. (2017)	Longer than O.P	Palm transvers	Grasping spines straight	Palm transvers	Without depression	With three distributed setae	naked	present	With two R.S

(Pourkerman et al. 2018) and hydrothermal regime (Alosairi et al. 2011). These findings suggest the probability of microhabitats' existence in Bushehr port which could mean an accelerated speciation.

Consequently, however, the morphological surveys are efficient in amphipod taxonomy to find new species, using geometric morphometric method and statistical approach could also be employed to clarify the descriptions and uncover additional cryptic variations.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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