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Research Article

Geometric morphometric analysis of the variations in cephalothorax shape of the freshwater prawn *Macrobrachium tenellum*, Smith (Decapoda Palaemonidae) from two different coastal basins in Oaxaca, Mexico

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ABSTRACT. Morphological variations of *Macrobrachium tenellum* prawns from two populations from locations in the Copalita and Colotepec riverine basins in the seashore of Oaxaca, Mexico, were studied with geometric morphometry techniques. The purpose was to find and explain significant differences in shape and size between the cephalothorax and the rostrum. Differences between sexes and populations were intended to prove intra and inter-populations. Results suggest low intrapopulation differences but significant interpopulation variation between specimens from different places, while a regression analysis suggests a higher correlation between shape and size only in males. The higher differences in places between and within sexes could be explained due to differences in environmental pressure. A positive allometry bias in males could indicate a sexual selection mechanism affecting mating.

Keywords: *Macrobrachium tenellum*; cephalothorax; rostrum; morphometrics; allometry; dimorphism

INTRODUCTION

Most freshwater crustaceans migrate as part of their life cycle, which can lead to a wide spatial distribution, making studying their populations complex. On species with wide spatial distribution, it is normal to find variations in environmental and ecological factors (adaptability, defense, competition), and this might produce morphological differences (Walker 1994, Carter et al. 1996, Bolker et al. 2003, Bolnick et al. 2003, Werner & Peacor 2003). A way to reinforce such studies is by assessing differences or similarities in shape between specimens of different populations (Torres et al. 2014a,b).

Morphometric studies are useful for delineating the shapes of various populations and species over geographical ranges, providing evidence of regional differences in crustaceans. Studies that analyze morphological differences might reveal selective factors affecting the phenotypic response to certain environmental issues, helping to understand how morphology influences the promotion of a particular phenotype (Anastasiadou et al. 2009, Kaliontzopoulou et al. 2010). The geometric morphometric (GM) technique is a tool for visualizing and quantifying these morphological differences (Adams et al. 2013). It has proven useful in natant decapods to compare geographically separated populations (Anastasiadou et al. 2009). This technique analyzes the shape and size variability using coordinates of homologous "reference points" or landmarks (Bookstein 1991, Zelditch et al. 2004). It is particularly useful with diverse genera, with a high degree of adaptability in colonizing new habitats due to the significant capacity of long-distance migration

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(Anastasiadou & Leonardos 2008), as occurs with *Macrobrachium* prawns. This genus has been previously analyzed with geometric morphometry techniques. Such is the case of *M. niponesse* (Cheng et al. 2015), where at least two morphologically different groups were detected, one divided into two subgroups. Authors attribute these differences to the fact that animals in each group come from two different migratory routes that potentially have a geographic barrier separating them with little chance of gene flow between them, and this eventually produced two populations with distinct morphological attributes.

It has been stated that the main variations among *Macrobrachium* populations occurred in the rostrum, cephalothorax, and telson (*M. borellii*, Torres et al. 2014a). Zimmermann et al. (2012) and Torres et al. (2014a) studied variations in the cephalothorax shape of *M. borellii* and *M. australe* linking those variations with biological factors. For example, habitats that differ greatly in soil type (stones, gravel, mud), submerged vegetation, or their hydrodynamics could produce subtle long-term differences in the shape of these structures depending on how these features are combined. Other authors (Alibert et al. 2001, Krapivka et al. 2007) stated that interspecific phenotypic comparisons of shape and size with GM techniques allow to detect morphological variations in the cephalothorax. Such variations, called allometry, are one of the main developmental phenomena related to diversification among different genera or species (Klingenberg 1996). Diversification places this structure highly functional in freshwater prawns (Mazancourt et al. 2017). Morphometric variation information between populations can provide a basis for its structure and might explain environmentally induced variations (Cheng et al. 2015). Caridean *Macrobrachium* prawns have peripheral distributional patterns, colonizing freshwater and estuarine habitats (Garcia-Guerrero et al. 2013). It could cause, over time, shape and size variations in separate populations from habitats with different physical, trophic, or hydrodynamic features (De Grave et al. 2008).

Macrobrachium tenellum (Smith, 1871), a freshwater prawn of rivers and coastal lagoons from the America Pacific coast, is distributed from Sinaloa in northern Mexico to the north of Peru (García- Guerrero et al. 2013). *M. tenellum* natural habitat fragmentation and its ability to spread and adapt to different scenarios place the species as a useful model for analyzing this phenomenon. The present research aims to compare two *M. tenellum* populations from different hydrological basins to find shape variations that can be adaptations to habitats and explain such differences at the population level.

MATERIALS AND METHODS

Sampling

One hundred twenty *M. tenellum* adult prawns were collected from ten spots all inside two different hydrological basins: Copalita River (96°48'43"W, 15°48'37"N) and Colotepec River (97°01'38"W, 15°49'46"N) both delivering freshwater water to the coast of Oaxaca, Mexico. The distance between them is 104.5 km. Sampling was done by walking inside the riverbanks with a hand net (rectangular 40×30 cm spoon with 0.5 cm type net), moved among the submerged vegetation to remove the specimens. Before sampling them, all non-*Macrobrachium* fauna were manually removed. Once collected, they were killed by placing them in freezing water and then fixed in 20% formalin in agreement with García-Guerrero & Hendrickx (2005). A single visit to the sampling site was carried out during June, which is the month when the hydrodynamics of the region allows efficient sampling of this species. Once in the laboratory, only 76 intact adults identified as *M. tenellum* were considered for the analysis. Those were rinsed, preserved in alcohol (70%), labeled, and stored individually. Sex was determined as in Espinosa-Chaurnaud et al. (2011). Photographs were taken using a blue plastic foam for support and contrast with an Axiocam 506 color camera attached to a Carl Zeiss Axio Zoom V16 (Carl Zeiss, Oberkochen, Germany) microscope.

Morphometric and statistical analysis

Landmarks digitalization. The MakeFan8 (Sheets 2014) software was used to register shape variations in the cephalothorax. The cephalothorax template design was defined by a comb and a circle of 10 and 38 landmarks, respectively (for the latter, only the points of the lower margin were marked); the comb was fixed with a point on the upper base of the rostrum and the upper posterior angle of the cephalothorax and the circle with two points; the apex of the branchiostegal spine and the eye orbital angle. For the rostrum, two combs of 14 and 15 landmarks were used on the upper and lower margin, respectively. The software tpsUtil v.1.76 and tpsDig v2.31 (Rohlf 2015) were used for the digitalization of the landmarks and to obtain the "tps" file.

The statistical analyzes were executed with *MorphoJ* v.1.0 6d software (Klingenberg 2011) through a Procrustes superposition aligned by main axes that projects the data to the tangent space by an orthogonal projection to correct size and orientation (Fig. 1). The performed analysis were:

a) Principal component analysis (PCA) to determine the patterns of the two main variations in the thin plate spline and the position of each specimen in the morpho space between and within populations.

b) Canonical variation analysis (CVA) and discriminant function analysis (DFA) to measure the shape features that best distinguish different groups labeled a priori; sex and place for the first and only one attribute for two groups in the last one. The *P*-value for the permutation test was performed with 10,000 and 1000 rounds, respectively. Differences were expressed in Procrustes distances (PD).

c) A regression analysis was applied to predict the values of one dependent variable (shape) from the independent variable's (size) values to test if size is form-dependent under the null hypothesis of independence. The permutation test against the null hypothesis with 10000 randomization rounds.

d) For the allometry analysis a multivariate regression was executed among sexes to test the possible evolutionary changes in shape that can be associated with size or to which degree the change in shape is associated with size.

RESULTS

Intrapopulational analysis

Discriminant function analysis (DFA). Differences in deformation of the thin plates among populations were almost in the same vector directions between sexes for each place (Fig. 2). Variations among male and female of both places is observed as a larger cephalothorax and a smaller rostrum length in males. However, only Copalita specimens were statistically different since deformation vectors and Procrustes distances are greater among them (Table 1).

Differences within sexes

PCA and DFA tests show that differences in cephalothorax shape are larger in females than in males (Figs. 3-4). For the PCA, the variation in each component is different, mainly in the first one and in the pattern of the morpho-space occupation. In males, almost all the defined areas are superimposed. For females, the superimposed areas occupy approximately half of different space (males: PC1 66.52%, PC2 16.08%, PC3 5.42% (Fig. 3); females: PC1 49.15%, PC2 22.75%, PC3 11.96% (Fig. 4)). Likewise, the differences among means within sexes show that in females are larger with statistically significant differences in Procrustes distances (Table 2).

Differences between sexes and localities

The DFA test shows more variation in shape between both populations in general than among the sexes. Suppose the shape of both sexes is compared. In that case, the difference is observed with the thin plate spline as a small variation in cephalothorax that consists in an increase in the length of this structure in males and a minor reduction in rostrum length, with no statistical significance for the Procrustes distances (Fig. 5a, Table 3). In the case of the difference in shape between populations from different places, variations are more notorious; in Copalita specimens, the cephalothorax seems to be smaller and the rostrum larger, mainly in its apical half, with statistical differences (Fig. 5b, Table 3).

For the CVA, cephalothorax shape results were useful to distinguish the groups considering both sex and place, except for the Colotepec population (Table 4). The main differences expressed along the axis of CV1 account for the total variance of 62.35%, and the CV2 has a contribution ratio of 32.85% with no statistical significance for the groups along this axis (Figs. 6a-b).

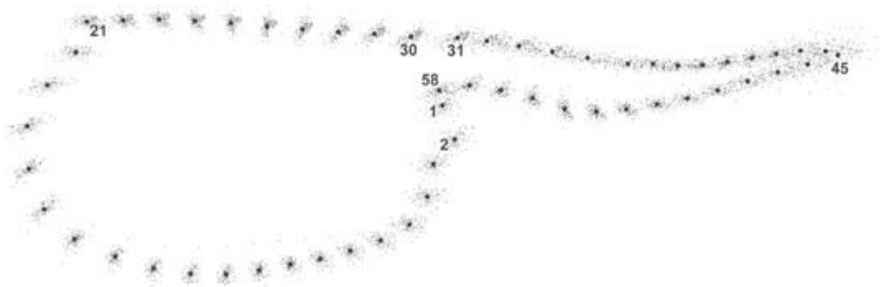

Figure 1. Landmarks and overlap Procrustes superimposition for cephalothorax and rostrum in *Macrobrachium tenellum* specimens.

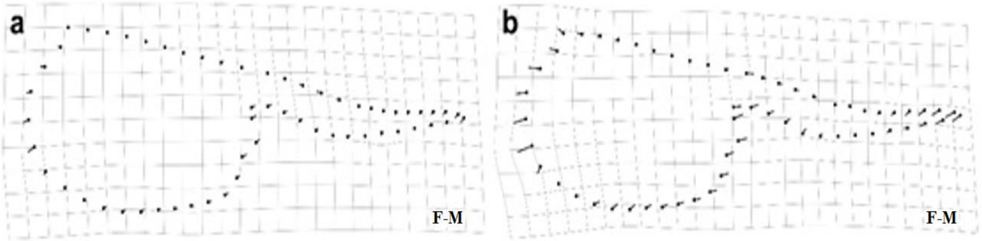

Figure 2. Difference of rostrum and cephalothorax shape between both sexes in *Macrobrachium tenellum* specimens in a) Colotepec, b) Copalita. F: females, M: males. Scale factor 2.5.

Table 1. Discriminant function for intrapopulation differences between sexes. F: females, M: males, PD: Procrustes distances.

Locality	Difference between means			*P*-values for permutation tests	
	PD	T-square	*P*-value	PD	T-square
Colotepec F-M	0.0093	245.7283	0.9994	0.4220	0.0310
Copalita F-M	0.0186	575.6787	0.9685	0.0390	<0.0001

For the allometry, there is a stronger association between shape and size in males (19.68%, $P < 0.001$) than in females (0.76%, $P = 0.8064$), in where the largest males have smaller rostrums, and the smaller, longer ones (Fig. 7).

DISCUSSION

Body shape is recognized as a prime attribute in functional biology and ecology (Hart & Bychek 2011). Differences in body shape and size are expected when several populations of the same species inhabit different habitats, from running waters of mountain streams to low rivers and lakes or coastal bodies of varying salinity having different components and soil. Such differences among individuals of the same species should be adaptations to different habitat pressure (Rosenfield 2002, Smith & Brown 2002). Morphological traits such as carapace and abdomen length and width can be strongly affected by water hydrodynamics, and its temperature and different vegetation cover or soil might stimulate morphological and size differences in rostrum and carapace (Zimmermann et al. 2012). It has been suggested, for example, that less or a lack of ornamentation would be an adaptation to life among rocks, sand stratum, or rivers and streams (Giri & Collins 2004), and specimens from running waters are more slender than specimens inhabiting lakes (Giri & Loy 2008). Schmitt (1942) states that these differences are evolutionary responses to population fragmentation facilitated by possible species plasticity. Geometric morphometry assesses those differences (Giri & Collins 2014, Torres et al. 2014a) by analyzing the relationships between two or more separated populations (Konan et al. 2010). This analysis helps understand the causes and effects of distribution patterns in different populations on temporal or geographical scales (Cardini et al. 2007, Vonlanthen et al. 2009).

In agreement with Mc Dowall (2007), the ability of dispersion and colonization of new habitats of amphidromic species, such as *Macrobrachium* prawns, requires adaptations to settle in habitats often different in terms of hydrodynamic and physicochemical parameters. In *Macrobrachium* prawns, such adaptations probably allow them to migrate and are strategies for colonizing new habitats. In agreement with Anastasiadou & Leonardos (2008), some species prefer eurythermal or euryhaline habitats, while others prefer well-oxygenated waters with submerged aquatic vegetation. Some populations are in lentic habitats with slow-flowing waters, muddy substrates, poor or abundant aquatic vegetation, or different trophic states. All these combinations might cause subtle differences in shape or size with time, aiming to take the best possible advantage of a particular habitat. When analyzing such differences, geometric morphometry helps to elucidate whether populations occupying different freshwater habitats could exhibit morphological differences, which could be adaptations to different habitat pressure and, thus, explained as habitat effect (Miner et al. 2005). There are few previous

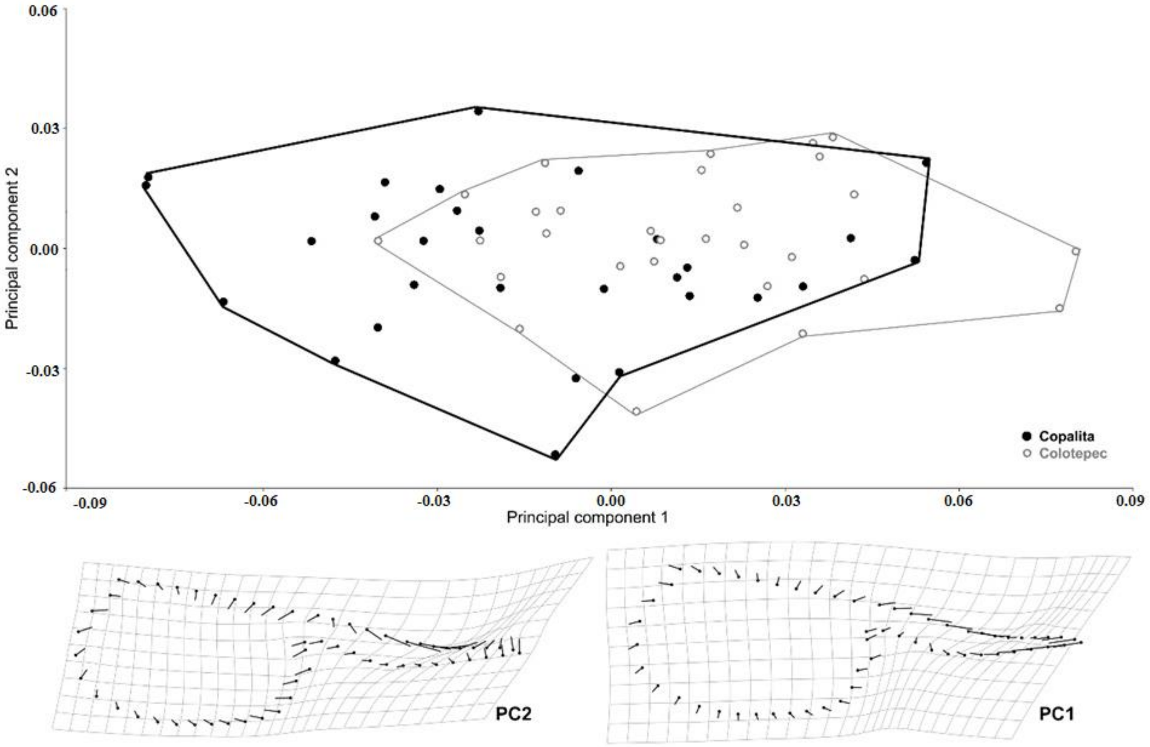

Figure 3. Accumulative contribution of variance of the cephalothorax in *Macrobrachium tenellum* males from Copalita and Colotepec rivers.

research on this issue for *Macrobrachium* prawns, but they confirm what occurs in the present research. Different environmental pressures could cause variations in shape. Konan et al. (2010) observed in *M. vollenhovenii* that specimens from close populations are more alike than those distant. In freshwater crabs, Torres et al. (2014a) state that there is a similar shape between three different close populations. Morphometric differences among populations of crustaceans about habitat differences have also been analyzed by Dimmock et al. (2004), Rufino et al. (2004), Anastasiadou & Leonardos (2008), Konan et al. (2010) and Srijaya et al. (2010). However, more research is needed to explore how body parts change shape or size because of isolation from other populations, even if the habitats are equivalent. Previous research has stated that body length is associated with environmental factors such as a biomechanical response to locomotion needs, which depends on water flow and feeding behavior (Zimmermann et al. 2012, Mazancourt et al. 2017). Moraes et al. (2018) evaluated the variation of the cephalothorax and rostrum at different developmental stages, focusing on the correlation patterns between shape and size and phenotypic covariation between both structures.

Geometric morphometric techniques with Decapoda are applied mostly on marine shrimps (Tzeng et al. 2001, 2004, Anastasiadou & Leonardos 2008, Anastasiadou et al. 2009, Konan et al. 2010). As in present research, such research describes that habitat differences might cause subtle variations in body shape among populations. In *M. tenellum*, as occur with other crustaceans, differences in biota, water hydrodynamic, or bottom cause significant differences. In the present research, prawns from the Copalita river basin had significant differences in the rostrum and cephalothorax shape in comparison with those from Colotepec (Fig. 2, Table 1), even considering the differences within specimens from the same place. In the analysis of the same-sex specimens, variations in the shape of both cephalothorax and rostrum between males and females were observed, being greater in females (Figs. 3-4, Table 2). In the first case, some possible causes could be variations in growth rate among specimens, causing heterogeneous populations. Commonly, crustaceans grow despairingly even in the same population and habitat (Hartnoll 1978), clearly explained by analyzing the allometric relationships between shape and size (centroid) of the rostrum in prawn species (Torres et al. 2014b). In the second case,

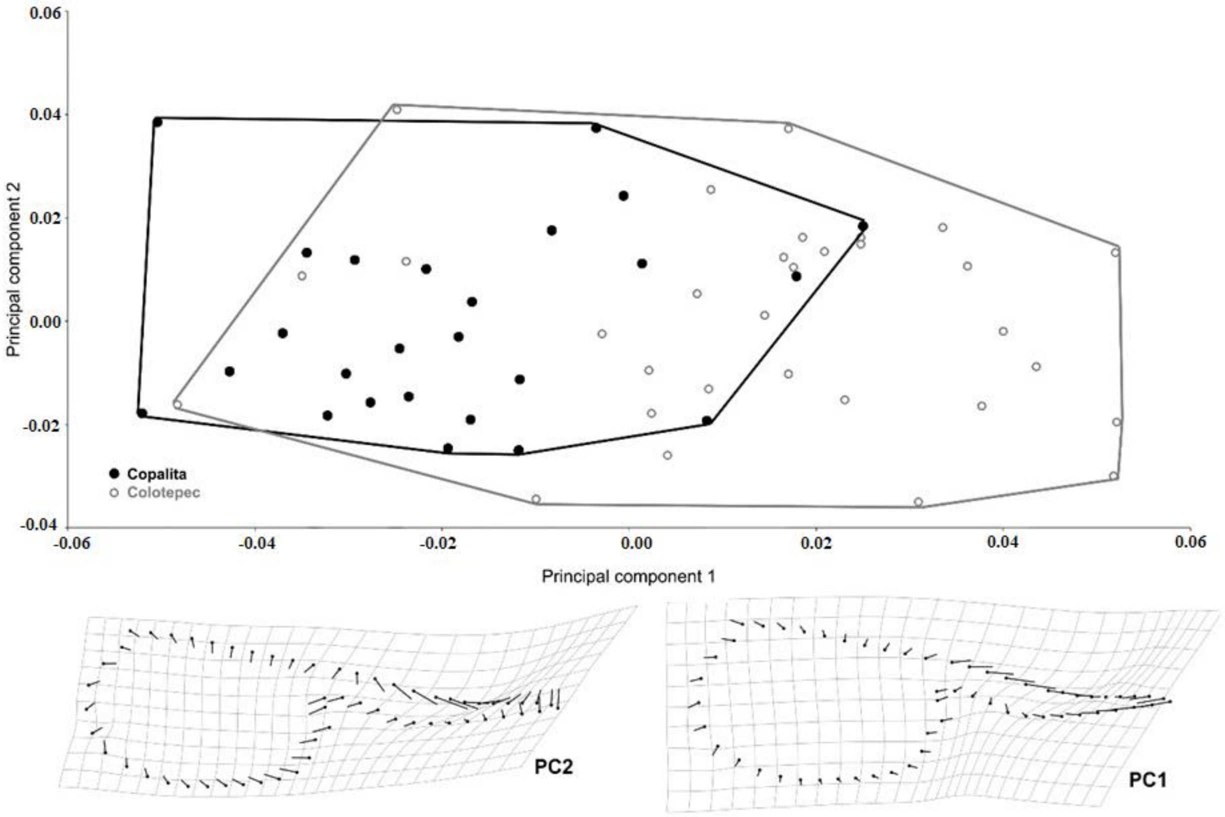

Figure 4. Accumulative contribution of variance of the cephalothorax in *Macrobrachium tenellum* females from Copalita and Colotepec rivers.

Table 2. Discriminant function for interpopulation differences within sexes. PD: Procrustes distances.

Locality	Difference between means Female-male			*P*-values for permutation tests	
	PD	T-square	*P*-value	PD	T-square
Males	0.0292	667.41	0.9655	0.0030	<0.0001
Females	0.0372	618.32	0.9657	<0.0001	<0.0001

few studies in morphometrics allow us to understand how a particular body part is modified because of isolation or sexual selection. Some previous research checking variations in the shape of the rostrum and its relationship with the rest of the cephalothorax has shown that this is habitat-dependent (Sardà & Demestre 1989, Kapiris & Thessalou-Legaki 2001, May-Kú et al. 2006, Kapiris & Kavvadas 2009, Ocasio-Torres et al. 2014). Sexual dimorphism, competition, or environmental pressure can also cause such differences (Konan et al. 2010). In this sense, Kapiris & Thessalou-Legaki (2001) mention for Aristidae shrimps that males with shorter rostrums can mate easier. However, in the present research, differences between sexes for both populations were not statistically different (Fig. 5a), but there were between places, as shown (Fig. 5b; Table 3). The absence of sexual dimorphism was also found by Moraes et al. (2018) in *Xiphopenaeus kroyeri* specimens.

Nonetheless, other research has stated that sexual dimorphism is expressed as shape variations in the back of the cephalothorax, possibly because of the differences in distance between the perishing and the pleon, which seems to be an adaptation to different requirements for egg carrying, as previously observed by Giri & Collins (2004), Rufino et al. (2004), Giri & Loy (2008) and Barría et al. (2011), a common trend, especially in different genus. Torres et al. (2014a) found that *M. borellii* and *Palaemonetes antennarius* females have such differences, even considering that other research did not find such differences. For

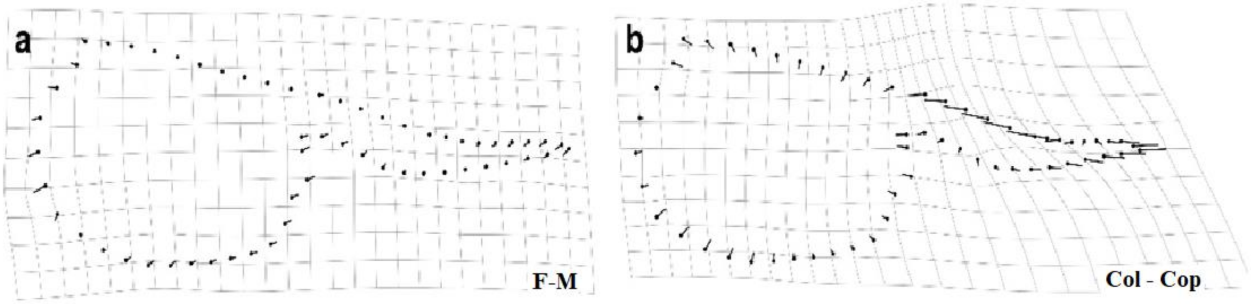

Figure 5. Difference in forms between sexes and localities of *Macrobrachium tenellum* prawns. a) females-males, and b) Colotepec-Copalita. Scale factor 2.5.

Table 3. Discriminant function for interpopulation differences between sexes and localities. PD: Procrustes distances.

Locality	Difference between means Female-male			*P*-values for permutation tests	
	PD	T-square	*P*-value	PD	T-square
Sex	0.0127	401915.43	0.1399	0.0620	0.0100
Locality	0.0326	14132.21	0.6518	<0.0001	<0.0001

Table 4. Discriminant function between sexes in both localities (col: Colotepec, cop: Copalita). F: females, M: males, PD: Procrustes distances.

Sex and locality	Difference between means				*P*-values for permutation tests		
	PD	MD	T-square	*P*-value	PD	T-square	MD
Fcol-Fcop	0.0372	20.49	618.18	0.9657	<0.0001	<0.0001	<0.0001
Fcol-Mcol	0.0093	17.36	245.66	0.9994	0.4390	0.0300	<0.0001
Fcol-Mcop	0.0294	24.17	1062.20	0.9143	0.0003	<0.0001	<0.0001
Fcop-Mcol	0.0407	31.69	909.58	0.9154	<0.0001	<0.0001	<0.0001
Fcop-Mcop	0.0186	20.82	575.53	0.9685	0.0350	<0.0001	<0.0001
Mcol-Mcop	0.0292	25.78	667.20	0.9656	0.0013	<0.0001	<0.0001

example, in *M. vollenhovenii*, even in distant places, specimens have no significant differences in carapace shape (Konan et al. 2010). In agreement with this author, this might occur due to the connection between basins, which promote genetic flow between populations (Kupfer & Meitzen 2012). However, this seems not to be the case in the present research since each environment produces in each population, different morphotypes, as previously observed by Simanjuntak & Eprolurahman (2019) for several *Macrobrachium* species. It is in these cases and as in the present investigation that geometric morphometry techniques can evaluate the similarities in shape that these populations have between basins. (Alibert et al. 2001, Sadeghi et al. 2009, Torres et al. 2014a).

The only previous research dealing with the rostrum with geometric morphometric techniques was designed with one landmark to analyze the effect of this body part on the overall variance of the shape of the cephalothorax, known as the "Pinocchio effect" (Zimmermann et al. 2012). In the present research, a configuration with 31 and 27 landmarks was used to analyze the shape of the cephalothorax and rostrum, recognizing in detail the intensity and direction of change of both structures. In this sense, the regression test results between size and shape indicate a positive allometry effect in males under the criteria of the Gould-Mosimann school (Klingenberg 2016). This phenomenon of size-related change with morphological traits is important because differential growing and development is one of the main causes of evolutionary diversification (Huxley 1932). Allometry could relate to biological requirements in locomotion, thermo-regulation, defense, or sexual behavior (Hone et al. 2012, Lavine et al. 2016). However, as in present research, divergent growth patterns between sexes may be due to a gradual sex dimorphism (Sanger et al. 2013). The positive allometry in size and sexual

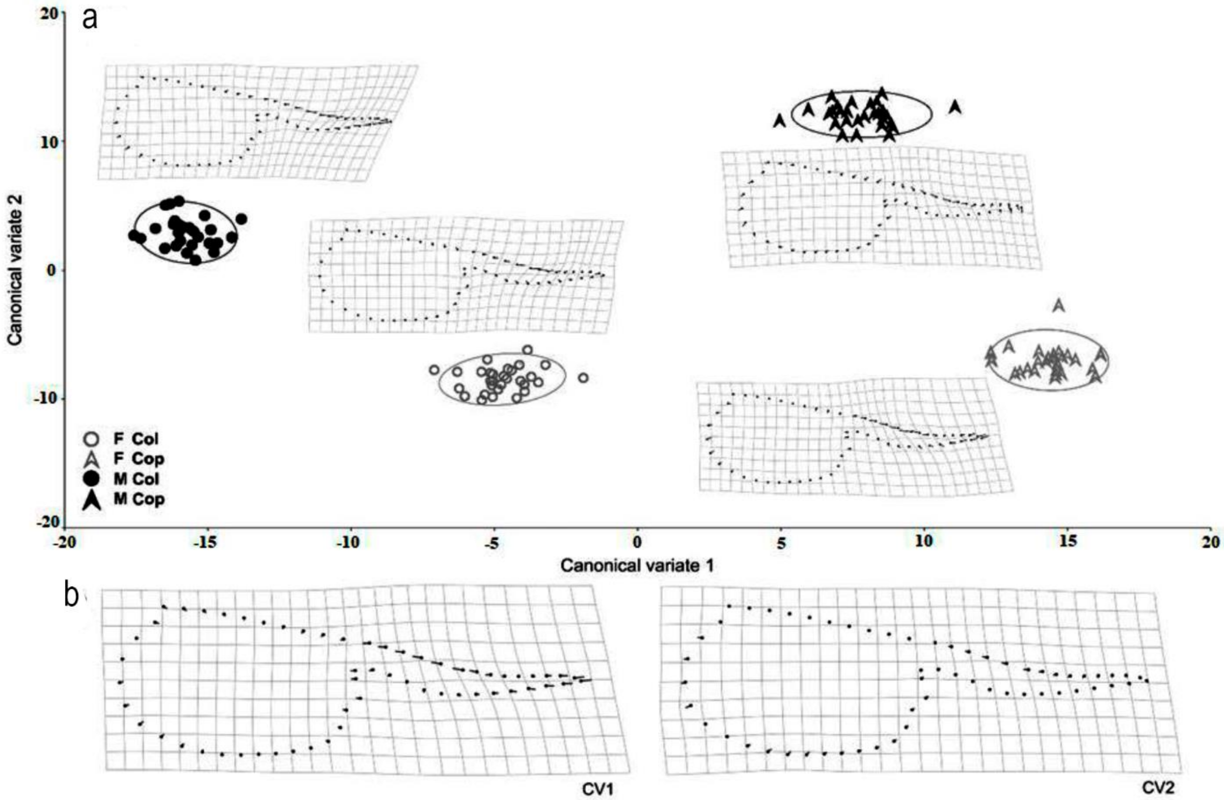

Figure 6. Canonical variation analysis (CVA) results. a) CV1 and CV2 plots with groups formed by the sex and locality of *Macrobrachium tenellum* prawns (confidence ellipses with a probability of 90%), and b) shape variance in the tps of the CV1 and CV2.

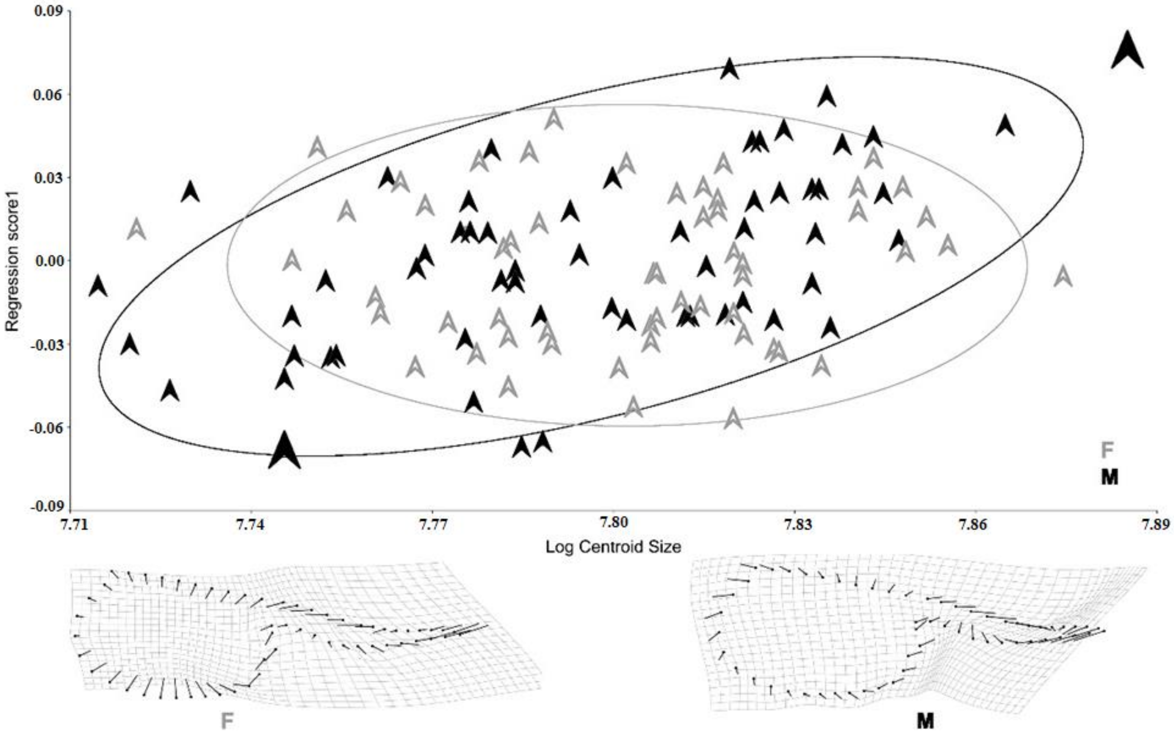

Figure 7. Regression scores on centroid size log plot for each sex in *Macrobrachium tenellum* prawns from Copalita and Colotepec rivers. The large dots represent the extremes of expression with their corresponding tps.

dimorphism, both male-biased, might suggest sexual selection mechanisms promoting the evolution of the rostrum. However, most research on other species of Decapoda did not observe sexual dimorphism in the rostrum (Moraes et al. 2018).

Previous research also suggests that the positive allometry and sexual dimorphism in certain structures are caused by sexual selection (Bonduriansky 2007, Emlen 2008, Tomkins et al. 2010, Ramírez-Ponce et al. 2017). Other features, such as the complexity of cephalic ornaments, can promote an increase in size within clades (Gates 2016, Raia et al. 2016), but this does not seem to be the case in the present research. The fact that rostral shape can be related to competition or sexual issues has important evolutionary implications (Collins 2001). If males with short rostrums, like Aristidae, can mate easily (Kapiris & Thessalou-Legaki 2001), then in *M. tenellum*, this phenotype matches the larger males. A larger size would give them an additional advantage during competition and mating. *M. tenellum* morphometric differences between populations are likely a consequence of different colonization scenarios or routes through which species migrated and are finally separated, totally or partially. Further isolation can cause, through time, such morphological differences.

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REFERENCES

Adams, D.C., Rohlf, F.J. & Slice, D. 2013. A field comes of age: geometric morphometrics in the 21st century. Hystrix, the Italian Journal of Mammalogy, 24: 7-14. doi: 10.4404/hystrix-24.1-6283

Alibert, P., Moureau, B., Dommergues, J.-L. & David, B. 2001. Differentiation at a microgeographical scale within two species of ground beetle, *Carabus auronitens* and *C. nemoralis* (Coleoptera, Carabidae): a geometrical morphometric approach. Zoologica Scripta, 30: 299-311.

Anastasiadou, C. & Leonardos, I.D. 2008. Morphological variation among populations of *Atyaephyra desmarestii* (Millet, 1831) (Decapoda: Natantia: Atyidae) from freshwater habitats of north-western Greece. Journal of Crustacean Biology, 28: 240-247. doi: 10.1163/20021975-99990370

Anastasiadou, C., Liasko, R. & Leonardos, I.D. 2009. Biometric analysis of lacustrine & riverine populations of *Palaemonetes antennarius* (H-Milne Edwards, 1837) (Crustacea, Decapoda, Palaemonidae) from north-western Greece. Limnologica, 39: 244-254. doi: 10.1016/j.limno.2008. 07.006

Barría, E.M., Sepúlveda, R.D. &. Jara, C.G. 2011. Journal of Crustacean Biology, 31: 231-239. doi: 10.1651/10-3324.1

Bolker, B., Holyoak, M., Krivan, V., Rowe, L. & Schmitz, O. 2003. Connecting theoretical & empirical studies of trait-mediated interactions. Ecology, 84: 1101-1114.

Bolnick, D.I., Svanbäck, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D. & Forister, M.L. 2003. The ecology of individuals: incidence & implications of individual specialization. American Naturalist, 161: 1-28.

Bonduriansky, R. 2007. Sexual selection and allometry: a critical reappraisal of the evidence and ideas. Evolution: International Journal of Organic Evolution, 61: 838-849. doi: 10.1111/j.1558-646.2007.00081.x

Bookstein, F.L. 1991. Morphometric tools for landmark data. Geometry and biology. Cambridge University Press, Cambridge.

Cardini, A., Jansson, A.U. & Elton, S. 2007. A geometric morphometric approach to the study of eco-geographical and clinal variation in vervet monkeys. Journal of Biogeography, 34: 1663-1678. doi: 10.1111/j.1365-2699.2007.01731.x

Carter, J.L., Fend, S.V. & Kennelly, S.S. 1996. The relationships among three habitat scales and stream benthic invertebrate community structure. Freshwater Biology, 35: 109-124.

Cheng, P., Tzong-Der, T., Chun-Han, S., Ta-Jen, C. & Ying-Chou, L. 2015. Morphometric variation of the oriental river prawn (*Macrobrachium nipponense*) in Taiwan. Limnologica, 52: 51-58.

Collins, P. 2001. Relative growth of the freshwater prawn *Macrobrachium borelli* (Nobili, 1896) (Decapoda: Palaemonidae). Nauplius, 9: 53-60.

De Grave, S., Cai, Y. & Anker, A. 2008. Global diversity of shrimps (Crustacea: Decapoda: Caridea) in freshwater. Hydrobiologia, 595: 287-293.

Dimmock, A., Williamson, I. & Mather, P.B. 2004. The influence of environment on the morphology of *Macrobrachium australiense* (Decapoda: Palaemonidae). Aquaculture International, 12: 435-456.

Emlen, D.J. 2008. The evolution of animal weapons. Annual Review of Ecology, Evolution, and Systematics, 39: 387-413. doi: 10.1146/annurev.ecolsys.39.110707.173502

Espinosa-Chaurand, L.D., Vargas-Ceballos, M.A., Guzmán-Arroyo, M., Nolasco-Soria, H., Carrillo-Farnés, O., Chong-Carrillo, O. & Vega-Villasante, F. 2011. Biología y cultivo de *Macrobrachium tenellum*: estado del arte. Hidrobiológica, 21: 99-117.

García-Guerrero, M. & Hendrickx, M.E. 2005. Fecundity and reproductive period of *Paradella dianae* and *Uromunna* sp. (Peracarida, Isopoda) associated with prop roots of *Rhizophora mangle* in a tropical coastal lagoon, SE Gulf of California, México. Crustaceana, 78: 769-780.

García-Guerrero, M.U., Becerril-Morales, F., Vega-Villasante, F. & Espinosa-Chaurand, L.D. 2013. Los langostinos del género *Macrobrachium* con importancia económica y pesquera en América Latina: conocimiento actual, rol ecológico y conservación. Latin American Journal of Aquatic Research, 41: 651-675. doi: 103856/vol41-issue4-fulltext-3

Gates, T.A. 2016. Bony cranial ornamentation linked to rapid evolution of gigantic theropod dinosaurs. Nature Communications, 7: 1-10.

Giri, F. & Collins, P.A. 2004. A geometric morphometric analysis of two sympatric species of the family Aeglidae (Crustacea, Decapoda, Anomura) from the La Plata basin. Italian Journal of Zoology, 71: 85-88. doi: 10.1080/11250000409356555

Giri, F. & Collins, P. 2014. Clinal variation in carapace shape in the South American freshwater crab *Aegla uruguayana* (Anomura: Aeglidae). Biological Journal of the Linnean Society, 113: 914-930. doi: 10.1111/bij.12382

Giri, F. & Loy, A. 2008. Size and shape variation of two freshwater crabs in Argentinean Patagonia: the influence of sexual dimorphism, habitat, and species interactions. Journal of Crustacean Biology, 28: 37-45. doi: 10.1651/07-2824R.1

Hart, R.C. & Bychek, E.A. 2011. Body size in freshwater planktonic crustaceans: an overview of extrinsic determinants and modifying influences of biotic interactions. Hydrobiologia, 668: 61-108. doi: 10.1007/s10750-010-0400-y

Hartnoll, R.G. 1978. The determination of relative growth in crustacea. Crustaceana, 34: 281-293.

Hone, D.W.E., Naish, D. & Cuthill, I.C. 2012. Does mutual sexual selection explain the evolution of head crests in pterosaurs and dinosaurs? Lethaia, 45: 139-156. doi: 10.1111/j.1502-3931.2011.00300.x

Huxley, J.S. 1932. Problems of relative growth. Methuen & Co. Ltd., London.

Kaliontzopoulou, A., Carretero, M.A. & Llorente, G.A. 2010. Sexual dimorphism in traits related to locomotion: ontogenetic patterns of variation in *Podarcis* wall lizards. Biological Journal of the Linnean Society, 99: 530-543. doi: 10.1111/j.1095-8312.2009.01385.x

Kapiris, K. & Kavvadas, S. 2009. Morphometric study of the red shrimp *Aristeus antennatus* in the Eastern Mediterranean. Aquatic Ecology, 43: 1061-1071. doi: 10.1007/s10452-008-9224-5

Kapiris, K. & Thessalou-Legaki, M. 2001. Sex-related variability of rostrum morphometry of *Aristeus antennatus* (Decapoda: Aristeidae) from the Ionian Sea (Eastern Mediterranean, Greece). In: Paula, J.P.M., Flores, A.A.V. & Fransen, C.H.J.M. (Eds.). Advances in Decapod Crustacean Research. Developments in Hydrobiology, 154: 123-130. Springer, Dordrecht. doi: 10.1007/978-94-017-0645-2_12

Klingenberg, C.P. 1996. Multivariate allometry. In: Marcus, L.F., Corti, M., Loy, A., Naylor, G.J.P. & Slice, D.E. (Eds.). Advances in Morphometrics, 284: 23-49. doi: 10.1007/978-1-4757-9083-2_3

Klingenberg, C.P. 2011. MorphoJ: an integrated software package for geometric morphometrics. Molecular Ecology Resources, 11: 353-357. doi: 10.1111/j.1755-0998.2010.02924.x

Klingenberg, C.P. 2016. Size, shape, and form: concepts of allometry in geometric morphometrics. Development Genes and Evolution, 226: 113-137. doi: 10.1007/s00427-016-0539-2

Konan, K.M., Adépo-Gourène, A.B., Ouattaraa, A., Nyingy, W.D. & Gourène, G. 2010. Morphometric variation among male populations of freshwater shrimp *Macrobrachium vollenhovenii* Herklots, 1851 from Côte d'Ivoire rivers. Fisheries Research, 103: 1-8. doi: 10.1016/j.fishres.2010.01.005

Krapivka, S., Toro, J.E., Alcapán, A.C., Astorga, M., Presa, P., Pérez, M. & Guiñez, R. 2007. Shell-shape variation along the latitudinal range of the Chilean blue mussel *Mytilus chilensis* (Hupe, 1854). Aquaculture Research, 38: 1770-1777. doi: 10.1111/j.1365-2109.2007.01839.x

Kupfer, J.A. & Meitzen, K.M. 2012. Modeling flood inundation & hydrological connectivity across the Congaree River floodplain, Congaree National Park. Proceedings of the 2012 South Carolina Water Resources Conference, South Carolina.

Lavine, L., Gotoh, H., Brent, C.S., Dworkin, I. & Emlen, D.J. 2016. Exaggerated trait growth in insects. Annual

Review of Entomology, 60: 1-20. doi: 10.1146/annurev-ento-010814-021045

May-Kú, M.A., Ordóñez-López, U. & Defeo, O. 2006. Morphometric differentiation in small juveniles of the pink spotted shrimp (*Farfantepenaeus brasiliensis*) and the southern pink shrimp (*F. notialis*) in the Yucatan Peninsula, Mexico. Fishery Bulletin, 104: 306-310.

Mazancourt, V., Marquet, G. & Keith, P. 2017. The "Pinocchio-shrimp effect": first evidence of variation in rostrum length with the environment in *Caridina* H. Milne-Edwards, 1837 (Decapoda: Caridea: Atyidae). Journal of Crustacean Biology, 37: 249-257. doi: 10.1093/jcbiol/rux025

McDowall, R.M. 2007. On amphidromy, a distinct form of diadromy in aquatic organisms. Fish and Fisheries, 8: 1-13.

Miner, B.G., Sultan, S.E., Morgan, S.G., Padilla, D.K. & Relyea, R.A. 2005. Ecological consequences of phenotypic plasticity. Trends in Ecology and Evolution, 20: 685-692. doi: 10.1016/j.tree.2005.08.002

Moraes, S.A.S.N., Alencar, C.E.R.D., Fransozo, A., Costa, R.C., Castilho, A.L. & Freire, F.A.M. 2018. Sexual and ontogenetic morphometric variation in *Xiphopenaeus kroyeri* (Crustacea, Decapoda, Penaeidae): a new approach with linear and angular morphometric data. Invertebrate Reproduction & Development, 62: 143-153. doi: 10.1080/07924259.2018.1461691

Ocasio-Torres, M.E., Crowl, T.A. & Sabat, A.M. 2014. Long rostrum in an amphidromous shrimp induced by chemical signals from a predatory fish. Freshwater Science, 33: 451-458. doi: 10.1086/675500

Raia, P., Passaro, F., Carotenuto, F., Maiorino, L., Piras, P., Teresi, L., et al. 2016. Cope's rule and the universal scaling law of ornament complexity. American Naturalist, 186: 165-175. doi: 10.1086/682011

Ramírez-Ponce, A., Garfias-Lozano, G. & Contreras-Ramos, A. 2017. The nature of allometry in an exaggerated trait: the postocular flange in *Platyneuromus* Weele (Insecta: Megaloptera). Plos One, 12: e0172388. doi: 10.1371/journal.pone.0172388

Rohlf, F.J. 2015. The tps series of software. Hystrix, the Italian Journal of Mammalogy, 26: 1-4.

Rosenfield, J.A. 2002. Pattern and process in the geographical ranges of freshwater fishes. Global Ecology and Biogeography, 11: 323-332. doi: 10.1046/j.1466-822X.2002.00287.x

Rufino, M., Abelló, P. & Yule, A.B. 2004. Male and female carapace shape differences in *Liocarcinus depurator* (Decapoda: Brachyura): an application of geometric morphometrics analysis to crustaceans. Italian Journal of Zoology, 71: 79-83. doi: 10.1080/11250000409356554

Sadeghi, S., Adriaens, D. & Dumont, H.J. 2009. Geometric morphometric analysis of wing shape variation in ten European populations of *Calopteryx splendens* (Harris, 1782) (Zygoptera: Odonata). Odonatologica, 38: 341-357.

Sanger, T.J., Sherratt, E., McGlothlin, J.W., Brodie III, E.D., Losos, J.B. & Abzhanov, A. 2013. Convergent evolution of sexual dimorphism in skull shape using distinct developmental strategies. Evolution, 67: 2180-2193. doi: 10.1111/evo.12100

Sardà, F. & Demestre, M. 1989. Shortening of the rostrum and rostral variability in *Aristeus antennatus* (Risso, 1816) (Decapoda: Aristeidae). Journal of Crustacean Biology, 9: 570-577. doi: 10.1163/1937 24089X00584

Schmitt, W.L. 1942. The species of Aegla, endemic South American fresh-water crustaceans. Proceedings of the United States National Museum, 91: 431-520.

Sheets, H.D. 2014. MakeFan. Integrated morphometric package. [http://www.philadb.com/an-behav/imp/]. Reviewed: November 2, 2019.

Simanjuntak, R.G. & Eprolurahman, R. 2019. Geometric morphometrics analysis of chelae and carapace of the freshwater prawn *Macrobrachium* Bate, 1868. Biogenesis: Jurnal Ilmiah Biologi, 7: 58-66. doi: 10.24252/bio.v7i1.7803

Smith, K.F. & Brown, J.H. 2002. Patterns of the diversity, depth range, and body size among pelagic fishes along a gradient of depth. Global Ecology Biogeography, 11: 313-322. doi: 10.1046/j.1466-822X.2002.00286.x

Srijaya, T.C., Pradeep, P.J., Mithun, S., Hassan, A., Shaharom, F. & Chatterji, A. 2010. A new record on the morphometric variations in the populations of horseshoe crab (*Carcinoscorpius rotundicauda* Latreille) obtained from two different ecological habitats of Peninsular Malaysia. Our Nature, 8: 204-211. doi: 10.3126/on.v8i1.4329

Tomkins, J.L., LeBas, N.R., Witton, M.P., Martill, D.M. & Humphries, S. 2010. Positive allometry and the prehistory of sexual selection. American Naturalist, 176: 141-148. doi: 10.1086/653001

Torres, M.V., Collins, P.A. & Giri, F. 2014a. Morphological variation of freshwater crabs *Zilchiopsis collastinensis* and *Trichodactylus borellianus* (Decapoda, Trichodactylidae) among localities from the middle Paraná River basin during different hydrological periods. ZooKeys, 457: 171-186. doi: 10.3897/zookeys.457.6726

Torres, M.V., Giri, F. & Collins, P.A. 2014b. Geometric morphometric analysis of the freshwater prawn *Macrobrachium borellii* (Decapoda: Palaemonidae) at a microgeographical scale in a floodplain system. Ecological Research, 29: 959-968. doi: 10.1007/s11284-014-1184-8

Tzeng, T.D. 2004. Stock identification of sword prawn *Parapenaeopsis hardwickii* in the East China Sea and Taiwan Strait inferred by morphometric variation. Fisheries Science, 70: 758-764. doi: 10.1111/j.1444-2906.2004.00868.x

Tzeng, T.D., Chiu, C.S. & Yeh, S.Y. 2001. Morphometric variation in red-spot prawn (*Metapenaeopsis barbata*) in different geographic waters of Taiwan. Fisheries Research, 53: 211-217. doi: 10.1016/S0165-7836(00)00286-1

Vonlanthen, P., Roy, D., Hudson, A.G., Largiadèr, C.R., Bittner, D. & Seehausen, O. 2009. Divergence along a steep ecological gradient in lake whitefish (*Coregonus* sp.). Journal of Evolutionary Biology, 22: 498-514. doi: 10.1111/j.1420-9101.2008.01670.x

Walker, I. 1994. The benthic litter-dwelling macrofauna of the Amazonian forest stream Taruma-rim: patterns of colonization and their implications for community stability. Hydrobiologia, 291: 75-92. doi: 10.1007/BF00044437

Werner, E.E. & Peacor, S.D. 2003. A review of trait-mediated indirect interactions in ecological communities. Ecology, 84: 1083-1100. doi: 10.1890/0012-9658(2003)084[1083:AROTII]2.0.CO;2

Zelditch, M.L., Swiderski, D.L., Sheets, H.D. & Fink, W.L. 2004. Geometric morphometrics for biologists: a primer. Elsevier-Academic Press, San Diego.

Zimmermann, G., Bosc, P., Valade, P., Cornette, R., Améziane, N. & Debat, V. 2012. Geometric morphometrics of carapace of *Macrobrachium australe* (Crustacea: Palaemonidae) from Reunion Island. Acta Zoologica, 93: 492-500. doi: 10.1111/j.1463-6395.2011.00524.x

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