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3 DE MAZANCOURT *ET AL.*, MORPHOLOGICAL VARIATION WITH THE ENVIRONMENT

4 IN *CARIDINA*

5

6 **The “Pinocchio-shrimp effect”: first evidence of variation in rostrum**

7 **length with the environment in *Caridina* H. Milne-Edwards, 1837**

8 **(Decapoda: Caridea: Atyidae)**

9

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18

#### ABSTRACT

19 External morphology has always been the first criterion used to separate species of shrimps,  
20 especially in the freshwater genus *Caridina* H. Milne-Edwards, 1837, but more doubts have been  
21 expressed regarding the relevance of some of the morphological characters. We collected 27  
22 specimens of *Caridina* from seven different localities during field work conducted on the island of  
23 Pohnpei (Federated States of Micronesia). After genetic verification that they all belonged to the  
24 same species, 19 morphological variables were measured and correlated with the elevation of the  
25 collecting stations using correlation analyses. We provide evidence that the length of the rostrum

26 showed strong negative correlation with the elevation. This could be explained either by the  
27 physical stress exerted on the rostrum by the stronger water currents in the stations at a higher  
28 elevation, as a defence against predators in the lower stations, or a combination of both possibilities.  
29 The taxonomy of these shrimps is thus challenging and should not rely only on rostrum length, but  
30 on other characters such as the number of teeth on the dorsal margin of the carapace, which is not  
31 correlated with rostrum length and therefore, with the environment.

32

33 **Key words:** correlation analysis, effect of elevation, freshwater shrimps, Micronesia, morphology,  
34 taxonomy

35

36

## INTRODUCTION

37 The freshwater shrimp genus *Caridina* H. Milne-Edwards, 1837 is one of the most diverse of  
38 Caridea (De Grave *et al.*, 2015) with 298 described species thus far (World Register of Marine  
39 Species (WoRMS), December 2016; <http://www.marinespecies.org/>), and an important ecological  
40 component of tropical freshwater ecosystems (Pringle *et al.*, 1993; Covich *et al.*, 1999). This high  
41 diversity is a challenge for taxonomists, as the boundaries among species are not always clear from  
42 a morphological point of view as well as from a molecular perspective. The main morphological  
43 character used to identify the species of *Caridina* is generally the length, shape, and armature of the  
44 rostrum. This character, however, has been proven to be plastic in shrimps, tending to vary among  
45 individuals within a single species (De Grave, 1999), sometimes in adaptation to environmental  
46 constraints (Jugovic *et al.*, 2010). There is therefore a need to be very cautious and proceed with an  
47 integrative approach when dealing with the taxonomy of caridean shrimps (Page *et al.*, 2005; Page  
48 & Hughes, 2011).

49 A survey of the freshwater fauna conducted on the island of Pohnpei (Federated States of  
50 Micronesia) by a team from the Muséum national d'Histoire naturelle (MNHN), Paris collected a  
51 large number of atyid shrimps from different rivers and habitats (Keith *et al.*, 2012). Some of these

52 specimens showing a long rostrum were attributed to *Caridina brachydactyla* De Man, 1908,  
53 whereas others, showing a short rostrum, were identified as *Caridina mertoni* Roux, 1911,  
54 following the previous identifications made from Guam, another Micronesian island, by Leberer &  
55 Cai (2003). A molecular analysis (see below) of these specimens indicated that they belong to the  
56 same species, referred to here to as *Caridina sp.* We therefore treated them as such to test the  
57 hypothesis that morphological variation is related to environmental factors. We performed a  
58 correlation analysis of 19 morphological variables on 27 specimens with the elevation of the station  
59 where the specimens were collected.

60

## 61 MATERIALS AND METHODS

### 62 *Sampling*

63 A total of 14 stations were sampled using electrofishing (see Ng *et al.*, 2017) in the four main  
64 streams of Pohnpei, Federated States of Micronesia, and 27 shrimp specimens were captured in  
65 seven of these stations at different altitudes. Out of these seven stations, three were located below  
66 the first major waterfall in each of the rivers (Table 1; Fig. 1).

67

68 <Table 1>

69 <Fig. 1>

70

### 71 *Molecular analysis*

72 We used the same protocol given by Mazancourt *et al.* (2017) to obtain sequences of 16S rRNA and  
73 COI gene for all the 27 specimens studied to perform a phylogenetic analysis.

74

### 75 *Morphological analysis*

76 Each specimen was dissected and the appendages prepared for microscopic observation.

77 Microphotographs were taken using an Olympus UTV1X-2 camera mounted on an Olympus BX51

78 stereomicroscope. The images obtained were treated using the AnalySIS Work v5.0 software  
79 (Olympus Soft Imaging System) to measure 19 morphological variables (Table 2). Correlation  
80 analyses were performed using Statistica v.10 software (StatSoft), providing 2D scatterplots,  
81 regression, and r coefficients.

82

83 &lt;Table 2&gt;

84

85 **RESULTS**86 *Sampling*

87 The species of fishes, particularly the shrimp predators, were reported for each station. For stations  
88 1, 5, 8, and 10, which were located above the first waterfall of each river, the only predator able to  
89 climb up was the eel *Anguilla marmorata* Quoy & Gaimard, 1826.; The flagtails *Kuhlia marginata*  
90 (Cuvier, 1829) and *K. rupestris* (Lacépède, 1802) were present in station 3; for the station 7, *K.*  
91 *rupestris* and *A. marmorata* in station 7, and *A. marmorata*, *K. marginata*, and *Eleotris fusca*  
92 (Forster, 1801) in station 9.

93

94 *Molecular analysis*

95 After a molecular analysis based on two mitochondrial genes (16S and COI) (Fig. 2), we found that  
96 all of our specimens were all very close genetically (> 1% p-distances).

97

98 &lt;Fig. 2&gt;

99

100 *Morphological analysis*

101 Of the 19 variables tested, five showed a significant correlation ( $r > 0.5$ ) with elevation (Fig. 3).  
102 These variable were, from the highest to the lowest absolute r value, rostrum length to carapace  
103 length ratio (variable 15; Fig. 3b,  $r = -0.9277$ ), number of teeth on ventral margin of rostrum

104 (variable 18; Fig. 3d,  $r = -0.6480$ ), unarmed part of rostrum length to armed part length ratio  
 105 (variable 16; Fig. 3e,  $r = -0.6868$ ), pereopod 2 carpus length-to-width ratio (variable 8; Fig. 3j,  $r =$   
 106  $-0.6318$ ), and pereopod 3 propodus length-to-width ratio (variable 10; Fig. 3o,  $r = -0.5302$ ).

107

108 *<Figs. 3a-e, 3f-i, 3j-m, 3n-p, 3q-s>*

109

110 In order to refine the analysis, we hypothesized that the variables related to the rostrum would be  
 111 linked to its length instead of elevation. To test this hypothesis, another correlation analysis was  
 112 performed on the three concerned variables (16, 17, and 18) with rostrum length to carapace length  
 113 ratio (Fig. 4).

114

115 *<Fig. 4>*

116

117 We found that there was a strong correlation between rostrum length and variables 18 and  
 118 16 (Fig. 4b,  $r = 0.67166$ , and 4c,  $r = 0.81086$ , respectively). Out of the 19 variables tested, three are  
 119 directly linked to elevation (variable 15, rostrum length to carapace length ratio; variable 8,  
 120 pereopod 2 carpus length-to-width ratio; and variable 10, pereopod 3 propodus length-to-width  
 121 ratio), with only the former showing a strong correlation ( $r > \pm 0.9$ ; Fig. 5).

122

123 *<Fig. 5>*

124

125 These correlations show that the specimens living at higher altitudes had a shorter rostrum  
 126 (and therefore, a shorter unarmed dorsal margin and fewer ventral teeth), a shorter pereopod 2  
 127 carpus, and a shorter pereopod 3 propodus than specimens living at lower altitudes.

128

129

## DISCUSSION

130 This is the first time that variation in a morphological character, the length of the rostrum in this  
131 case, is demonstrated to be linked to an environmental factor in *Caridina*. The elevation that was  
132 tested in this study is most likely not linked directly to the morphological changes observed. Indeed,  
133 several parameters can be shown to be related to elevation. The speed of the current increases with  
134 elevation, which would result in stronger mechanical forces being applied on the rostrum, limiting  
135 its growth. Furthermore, a longer rostrum tends to be more fragile and breaks easily, and might  
136 offer more current resistance, hindering movements in fast-flowing areas. The flow is certainly  
137 slower in the estuary at sea level, and little stress is applied on the rostrum, hence its long shape,  
138 whereas higher in the course, the slope of the stream is more important and the current faster. This  
139 phenomenon has been shown in another freshwater shrimp *Macrobrachium australe* (Guérin,  
140 1838), with a longer rostrum in lentic habitats in contrast to a shorter rostrum in lotic habitats  
141 (Zimmermann *et al.*, 2012). This would also be valid for the other two morphological variables  
142 linked with elevation (i.e., pereopod 2 carpus length and pereopod 3 propodus length), the higher  
143 in the stream, the shorter and broader the legs, presumably an adaptation to better resist stronger  
144 currents.

145 Morphological adaptations to hydrodynamic parameters have been highlighted in  
146 crustaceans before, such as the evolution towards an elongated shape in shrimp-like crustaceans  
147 (Spaargaren, 1999). We can argue, however, that there can be areas at higher altitudes of the stream  
148 with little or no current, as the slope is not steady along all of its length. Another parameter linked  
149 to the altitude is temperature. The higher the elevation of the stream, the cooler the water, because  
150 of lower air temperatures as well as thicker vegetation cover providing more shade. Temperature  
151 could influence the morphology as growth would be slower at lower temperatures due to a lower  
152 metabolism of the animal (Lee & Fielder, 1981), resulting in a shorter rostrum. This variation with  
153 temperature has been shown in freshwater shrimp species of *Macrobrachium* (Dimmock *et al.*,  
154 2004). Unfortunately, the water temperature at each station was not measured in our study so no  
155 correlation could be tested. The temperature difference between the estuary and the upper course in

156 such tropical island can be up to more than 5°C (PK, unpublished data), which could significantly  
157 impact the metabolism and the growth of organisms living there. The amount of food available  
158 could also limit the growth of the shrimp. This species is a detritivore feeding in particular on  
159 decaying plants, which would tend to accumulate in downstream areas of slow current to the  
160 detriment of upstream fast-flowing zones. These last two parameters have indeed been  
161 demonstrated to significantly affect the size of atyid shrimps (Pérez-Reyes *et al.*, 2015).

162         The sediment size of the substrate also varies with slope and current speed. The substrate is  
163 composed of large blocks in steep-slope, fast-flowing areas, but replaced with sand or gravel in  
164 areas with a gentler slope (Keith *et al.*, 2010). This would imply that the shrimp could use the  
165 spaces between the rocks to hide from predators and a long rostrum would be undesirable for  
166 crawling in these narrow spaces. A long rostrum does not therefore hinder the shrimp living lower  
167 in the stream where the sediment provides fewer hideouts. On the contrary, as indicated by Jugovic  
168 *et al.*(2010) and Occasio-Torres *et al.* (2015), a long rostrum could be a protection against  
169 predators, making the shrimp more difficult to swallow. Predator pressure would be greater in the  
170 lower course than in the upper course, because many shrimp-eating fishes like species of Eleotridae  
171 or Kuhliidae are present in the lower course of rivers (Covich *et al.*, 2009; Keith *et al.*, 2010) and  
172 are unable to climb waterfalls. This limitation in the distribution and mobility of predators affects  
173 the distribution of others organisms. Atyids are more abundant in the areas situated above waterfalls  
174 where predators are less numerous (Covich *et al.*, 2009). We found the individuals with the longest  
175 rostra in the three stations (3, 7, and 9) where the most predators were present, which were all  
176 below the first waterfall and at the lowest altitudes. This kind of defensive feature is supposedly  
177 present in some species of the freshwater gastropods *Clithon* Montfort, 1810, in which specimens  
178 encountered in brackish water exhibit spikes on their shell, whereas specimens of the same species  
179 living higher in the river have smooth shells (Haynes, 2005). These spikes could be a protection  
180 against predators (Eichhorst, 2016). Eels, which are also known to be shrimp predators, however,  
181 are able to crawl upward these waterfalls (Keith *et al.*, 2010), which would still make some kind of

182 defensive adaptation useful for prey living there. This kind of morphological adaptation against  
183 predation could be chemically induced by kairomones from predators, as shown in *Xiphocaris*  
184 *elongata* (Guérin-Méneville, 1857) (Ocasio-Torres *et al.*, 2014) and species of *Troglocaris*  
185 Dormitzer, 1853 (Jugovic *et al.*, 2010). If the presence of a long rostrum was only linked to the  
186 presence or absence of predators, one would expect only two classes of length, short and long, but  
187 we nevertheless showed that there is a continuum following a gradient, which is not related to the  
188 abundance of predators in the sampled stations.

189 To ease future citations of the phenomenon we describe here, we decided to name the  
190 elongation of the rostrum at lower altitudes in freshwater shrimps the “Pinocchio-shrimp effect”.  
191 This name is in relation to the commercial name of *Caridina gracilirostris* in the aquarium trade,  
192 known for having a long and slender rostrum. This is not to be confused with the “Pinocchio effect”  
193 *sensu* Chapman (1990), Zelditch *et al.* (2004), and Zimmerman *et al.* (2012), which refers to  
194 Procrustes-based morphometric analyses in which a variation that is localized to a single landmark  
195 can be smeared out across many in the superimposition consensus.

196 This observed variation of the morphology of this species with environmental parameters  
197 shows that some of the characters widely used in the taxonomy of *Caridina* might not be as reliable  
198 as it was thought. We found here that rostrum length, but also the length of the unarmed portion of  
199 the dorsal part of the rostrum and the number of ventral teeth are highly plastic in this species, and  
200 presumably in others. We nevertheless found that the number of dorsal teeth seems surprisingly  
201 unrelated to the length of the rostrum (Fig. 4a), and therefore with the elevation, making it a more  
202 reliable taxonomic character. We strongly suggest to always perform some type of molecular work  
203 to studying and describing a new species of *Caridina* in order to unravel this kind of variation  
204 within a species, focus on the morphology, and uncover any type of variation. This would provide  
205 enough characters to confidently identify the species in the field. It is likely that the different  
206 described species in the genus exhibit the same kind of polymorphism that has been shown here.  
207 Species with a short rostrum like *C. mertoni* and *C. sundanella* Holthuis, 1978 need to be studied in

208 order to ensure that other species with a long rostrum do not actually belong to species having such  
 209 polymorphism. The taxon investigated in this study is probably neither *C. brachydactyla* nor *C.*  
 210 *mertoni* so an in-depth taxonomic study should follow.

211

212

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222

223

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300  
301

## Figure captions

302

303

304 **Figure 1.** NJ tree of concatenated COI and 16S of the specimens studied. The numbers at nodes  
305 indicate bootstrap numbers. The letter M indicates specimens identified as *Caridina mertoni*  
306 because of their short rostrum and the letter B indicates specimens identified as *Caridina*  
307 *brachydactyla* because of their long rostrum.

308

309 **Figure 2.** Pohnpei Island, Federated States of Micronesia, showing sampling stations (see Keith *et*  
310 *al.*, 2012). Crosses indicate the position of the first major waterfall for each sampled river.

311

312 **Figure 3.** Correlation scatterplots of the 19 morphological variables with the elevation (in m); **a-e**,  
313 rostrum/cephalothorax; **f-i**, pereopod 1; **j-m**, pereopod 2; **n-p**, pereopod 3; **q-s**, pereopod 5.  
314 Above scatterplots, r coefficient, and equation of the regression line present for variables with  
315 significant correlations. Dashed lines indicate the 0.95 confidence interval.

316

317 **Figure 4.** Correlation scatterplots of the three rostrum-related variables with the length of the  
318 rostrum. Equation of the regression line present when correlations are significant. Dashed lines  
319 indicate the 0.95 confidence interval.

320

321 **Figure 5.** Correlation scatterplot of the rostrum length over carapace length with elevation. Some of  
322 the specimens are illustrated to show the variation.

323