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## Life-history traits of the Amazonian freshwater shrimps *Euryrynchus amazoniensis* and *E. burchelli* (Decapoda: Caridea: Euryrynchidae)

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### ABSTRACT

The family Euryrynchidae comprises freshwater shrimps with a disjunct distribution, occurring mainly in the Amazon basin. Basic biological information for this group, which is comparatively recent in evolutionary terms, is still lacking. The present study provides the first morphometric and biological data for *Euryrynchus amazoniensis* and *E. burchelli*, analysing relative growth, sexual dimorphism and patterns of heterochely and handedness in both sexes. Specimens were collected from floodplain areas of two rivers in Manaus, northern Brazil. Individuals were measured for carapace length and for the articles of the chelipeds. In both species, males were larger than females and exhibited proportionally more developed chelipeds. No significant handedness pattern was observed, indicating that the larger cheliped may occur on either side of the body. In *E. amazoniensis*, relative growth analyses revealed strong sexual dimorphism, with males allocating more energy to cheliped development. Furthermore, the morphological analyses and evidence indicate the presence of different male morphotypes in this species, a pattern commonly reported for other freshwater carideans, but previously unrecorded for Euryrynchidae. Overall, the results indicate that *E. amazoniensis* and *E. burchelli* share morphological patterns typical of other freshwater shrimps but also exhibit evolutionary particularities reflecting unique reproductive and ecological strategies, thereby expanding current knowledge of the biology of Euryrynchidae.

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## Introduction

The caridean shrimps of the family Euryrynchidae constitute a small group of freshwater shrimps composed of four distinct genera, *Eurindicus* De Grave, Arjun & Raghavan, *Euryrynchina* Powell, *Euryrynchoides* Powell, and *Euryrynchus* Miers, which currently comprise 11 valid species (Pachelle and Tavares 2018). From a taxonomic perspective, this family belongs to the superfamily Palaemonoidea and, for a long time, was considered a subfamily within Palaemonidae (Bruce 1993; Chace and Bruce 1993; Holthuis 1993). Later, however, it was elevated to family rank based on a combination of morphological characters (Martin and Davis 2001). Among the most distinctive features are the proximal antennular flagellum divided along its length into two branches, with flattened segments on the inner ramus; the uropodal protopodite bearing a well-developed posterolateral extension; and the exopodal diaeresis bearing large cuspidate setae along its margin (Martin and Davis 2001; De Grave *et al.* 2007).

The geographical distribution of this family is considered disjunct (De Grave *et al.* 2018). The genus *Euryrynchus* (seven species) is endemic to northern South America, occurring exclusively within the Amazon rainforest. In contrast, *Euryrynchina* (two species) and *Euryrynchoides* (monotypic) are restricted to West Africa, whereas *Eurindicus* (monotypic) occurs in southern India. This fragmented distribution has led to the hypothesis that the origin of these organisms is associated with the Gondwana supercontinent (De Grave *et al.* 2018; Pachelle and Tavares 2018).

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Most known species of *Euryrhynchus* occur in areas of the Brazilian Amazon rainforest, with the exception of *Euryrhynchus pemoni* Pereira, which has been recorded only in Venezuela, Guyana and French Guiana (Pachelle and Tavares 2018). Among the species occurring in Brazil, *Euryrhynchus amazoniensis* Tiefenbacher, *E. burchelli* Calman, and *E. wrzesniowski* Miers, stand out as the most abundant, being found across several northern Brazilian states, including Amapá, Amazonas, Pará and Roraima (Pachelle and Tavares 2018). Several studies have addressed this group over time, particularly focusing on these more common species. Most of these investigations consist of occurrence records from different regions of the Amazon rainforest, often accompanied by short natural history notes regarding reproductive and ecological aspects of these shrimps (Gordon 1935; Holthuis 1959; Kensley and Walker 1982; Pereira 1985; García-Dávila and Magalhães 2003; Valencia and Campos 2010; Pimentel and Magalhães 2014; Pachelle and Tavares 2018; Santos *et al.* 2018b). In contrast, only a few studies have directly examined the biological aspects of euryrhynchids through a spatiotemporal scale or population-based approaches (Walker and Ferreira 1985; Magalhães 1988; Walker 2001; Oliveira *et al.* 2017).

In general, these organisms exhibit an extremely abbreviated larval development (Magalhães 1988), even when compared with other shrimp species that follow a similar pattern. In euryrhynchids, this development is considered extreme, as it comprises only a single larval stage in which the larvae hatch from the eggs already benthic in habit and morphologically similar to juveniles (Magalhães 1988). This contrasts with species that exhibit the standard abbreviated development, in which larvae typically pass through three distinct stages before reaching the juvenile phase (Magalhães and Walker 1988; Magalhães 2016). Associated with this developmental pattern, ovigerous females of Euryrhynchidae carry few embryos, on average between 10 and 25, which are relatively large in size and volume compared to those of other freshwater carideans (Walker 2001; Oliveira *et al.* 2017).

Additionally, some studies have examined the distribution of *E. amazoniensis* and *E. burchelli* in a short, shallow tributary approximately 40 km in length, which contributes to the drainage of a network of small streams flowing into the Negro River (Walker and Ferreira 1985; Walker 2001). These studies demonstrated the sympatric occurrence of the two species. Despite this overlap, *E. amazoniensis* was found to be more abundant in the upper reaches of the river, whereas *E. burchelli* occurred more frequently in the lower section. The same studies also reported that both species exhibit seasonal reproduction, with ovigerous females recorded mainly during the rainy months (January to July), when the water level of the Negro River begins to rise (Walker and Ferreira 1985).

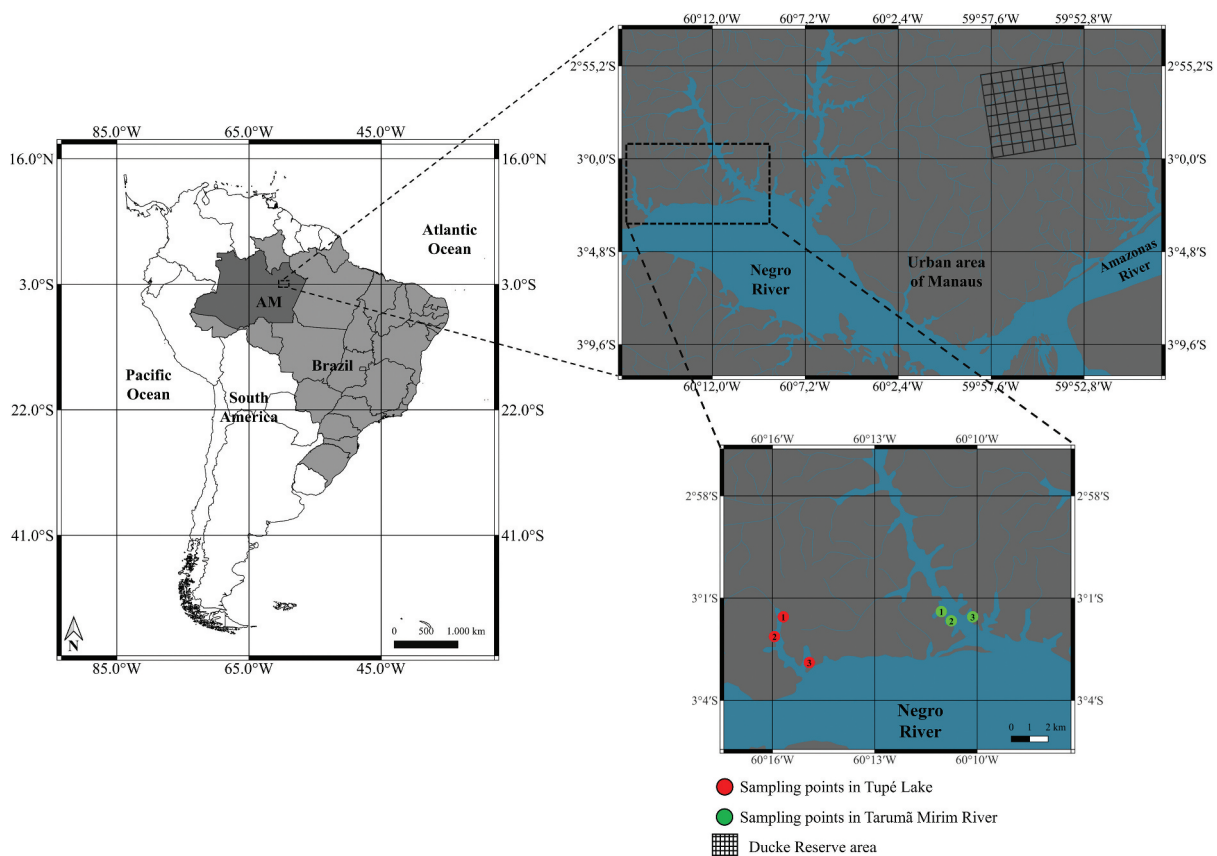
The information presented above represents the main biological data currently known for euryrhynchid shrimps. However, there remains a considerable lack of knowledge regarding this group. For instance, there are no records describing basic biological traits such as population structure, patterns of sexual dimorphism, growth and morphometric characteristics. Baseline data are essential, as understanding basic biological aspects of a species provides a foundation for more complex studies aimed at assessing population health and behaviour in their natural habitats (Willis *et al.* 2007). This need becomes even more critical in regions exposed to intense anthropogenic impacts and large-scale environmental changes driven by climate variation, such as the Amazon rainforest (Fearnside 2005; Lapola *et al.* 2023).

In this context, the present study analysed populations of two euryrhynchid shrimp species, *E. amazoniensis* and *E. burchelli*, from the northern region of Brazil. The main objectives were to describe the morphometric patterns, relative growth and sexual dimorphism in both species and, based on these data, to infer their possible mating system, a fundamental biological trait still unknown for Euryrhynchidae.

## Material and methods

### Sampling and identification of shrimps

The organisms analysed in this study were collected in January 2024 from floodplain areas of Lake Tupé (Site 1: 3.02647°S, 60.26539°W; Site 2: 3.03008°S, 60.26864°W; Site 3: 3.03725°S, 60.24906°W) and the Tatumã-Mirim River (Site 1: 3.01625°S, 60.18444°W; Site 2: 3.01806°S, 60.18383°W; Site 3: 3.02003°S, 60.16842°W). All sampling sites are located within the municipality of Manaus, state of Amazonas, northern Brazil (Figure 1).



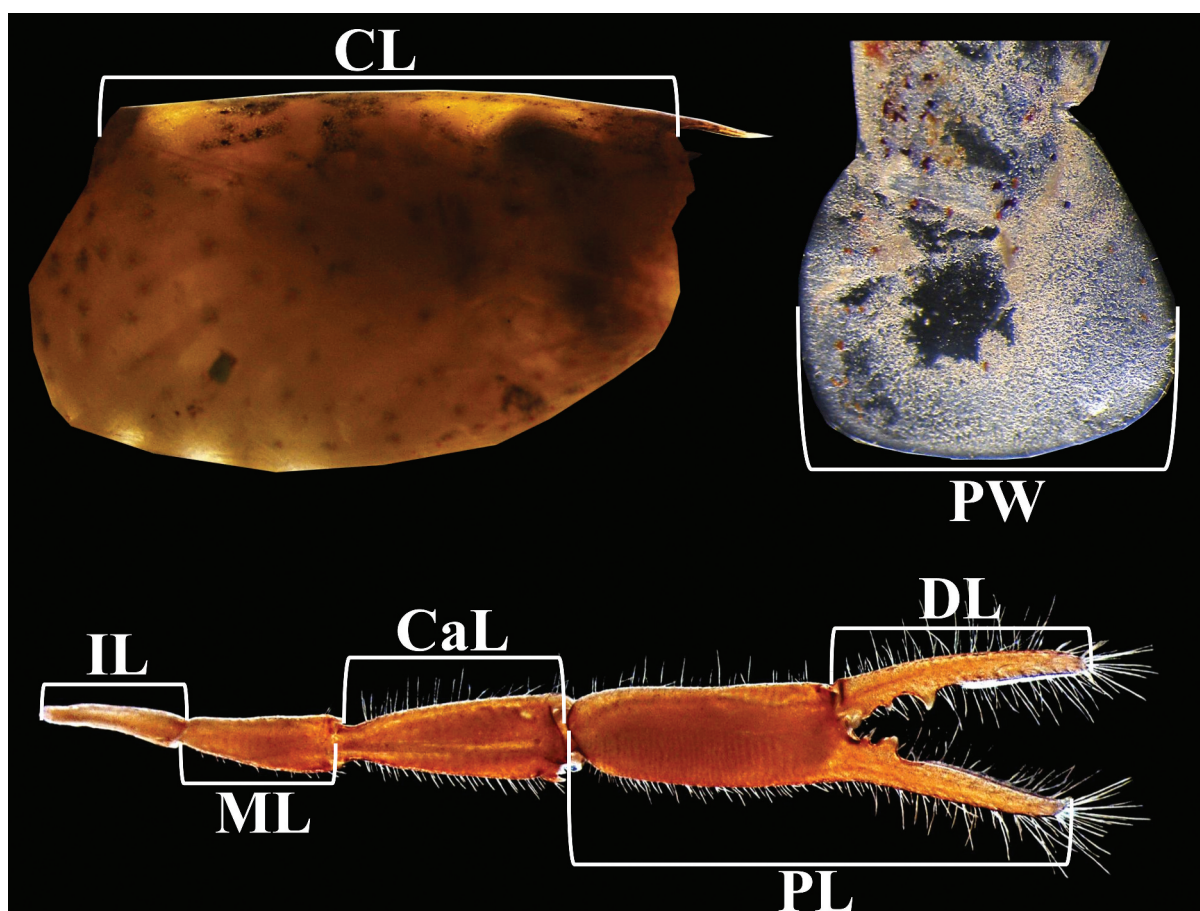
**Figure 1.** Location of the sampling sites in Lake Tupé (red points) and Taramã-Mirim River (green points). AM = State of Amazonas.

The sampling effort consisted of four collectors performing active searches for 1 h at each sampling site in both localities. Collections were carried out using circular hand nets with a 3 mm mesh diameter, swept through submerged vegetation, leaf litter and macrophytes. Each net was inserted and dragged through the vegetation to capture organisms associated with the substrate, which were subsequently sorted and placed in transport containers filled with water from the sampling site. After collecting, the specimens were transported to the laboratory, separated by morphospecies, euthanised by chilling ( $-20^{\circ}\text{C}$ ) and preserved in 95% ethanol.

Species identification was based on diagnostic characters specific to Euryrhynchidae, such as the presence of spines on the articles of the larger cheliped, as well as the morphology of the carapace and the endopod of the second pair of pleopods (Kensley and Walker 1982; Pachelles and Tavares 2018). Sex determination was performed by analysing the morphology of the second pair of pleopods, considering the sexually modified shape of the endopod of this appendage. Males of *E. amazoniensis* and *E. burchelli* exhibit a modified endopod compared to that of females (see Figures 17 and 29 in Pachelles and Tavares 2018).

### Morphometrics

Shrimps were measured for carapace length (CL), the second pleonal pleura width (PW) and the length of the articles composing the second pair of chelipeds (Figure 2). The articles of both chelipeds of the second pair were measured – ischium (IL), merus (ML), carpus (CaL), propodus (PL) and dactylus (DL) (Figure 2) – since *E. amazoniensis* and *E. burchelli* exhibit strongly heterochelous chelipeds, i.e. chelipeds of distinct sizes and shapes. Only individuals with intact structures (without damage or missing articles or appendages) were included in the analyses. Thus, for the morphometric analyses of the chelipeds, only specimens with both second pereopods completely preserved were considered. All structures were dissected to facilitate measurements, which were taken under a Leica® MZ stereomicroscope equipped with an image capture system. The structures were photographed and subsequently measured using the Leica Application Suite software.



**Figure 2.** Morphological structures analysed in the present study. The markings on each structure indicate the measurement points. CL corresponds to carapace length, and PW to the width of the second pleonal pleura. IL, ML, CaL, PL and DL correspond to the lengths of the ischium, merus, carpus, propodus and dactylus, respectively. All structures shown belong to a specimen of *Euryrhynchus amazoniensis*.

All individuals of the same species collected from different sampling sites were pooled for analysis. This approach aimed to increase the representativeness of each species without compromising the reliability of the results, since the sampling points were geographically close and the morphometric characters evaluated are highly conserved.

### Statistical analysis

The morphometric data set for each structure, grouped by species, was first tested for normality using the Shapiro-Wilk test. Based on the results, differences between males and females were analysed using either the *t*-test or the Mann-Whitney (*U*) test ( $\alpha = 0.05$ ).

As *E. amazoniensis* and *E. burchelli* exhibit heterochely, cheliped handedness was also assessed to determine whether a consistent pattern was present regarding the position of the larger cheliped relative to body side. For this purpose, the side on which the larger cheliped occurred was recorded, and the results were expressed as percentages of occurrence. Additionally, a chi-square ( $\chi^2$ ) test was performed to evaluate whether the pattern of handedness differed significantly between the body sides.

Subsequently, the difference in size between the larger and smaller chelipeds was evaluated to determine whether it was statistically significant. In this analysis, the total length of each cheliped was measured, and the values were compared using either the paired *t*-test or the paired Wilcoxon test ( $\alpha = 0.05$ ), depending on data normality. Additionally, morphological variation between males and females was investigated using principal component analysis (PCA) in order to assess the possible occurrence of male morphotypes. The morphometric variables analysed, including CL, IL, ML, CaL, PL and DL (considering only the articles of the

larger cheliped), were previously log-transformed ( $\log_{10}$ ) to reduce distributional asymmetry and minimise allometric effects. The PCA was performed based on the correlation matrix to standardise the variables and prevent scale differences from disproportionately influencing the ordination. All statistical analyses were conducted using PAST v. 5.3 (Hammer *et al.* 2011).

Analyses of relative growth were carried out to characterise the type of development (allometric or isometric) for the morphometric relationships evaluated. These analyses were conducted separately for males and females, without distinguishing between juveniles and adults. Therefore, preliminary analyses commonly used in relative growth studies (e.g. k-means clustering, discriminant analysis or analysis of covariance) were not required, as these are typically applied to identify and compare different ontogenetic groups (juveniles and adults) (Sampedro *et al.* 1999; Nogueira *et al.* 2022a; Jaconis *et al.* 2023; Rezende-Gois *et al.* 2023).

The relative growth analysis was performed to examine the growth pattern of body structures in relation to the independent variable (CL). Scatter plots were constructed from the measurements of each body structure, and the morphometric data were fitted to the allometric equation  $y = ax^b$  (Hartnoll 1974, 1978; Hawkins and Hartnoll 1982), linearised as  $\log y = \log a + b \times \log x$ . In this equation,  $y$  represents the length of a specific body structure (dependent variable),  $x$  corresponds to CL (independent variable),  $a$  is the intercept and  $b$  is the allometric coefficient (slope). The allometric constant  $b$  was calculated for each morphometric relationship, and the resulting values indicated the type of growth: isometric ( $b = 1$ ), positively allometric ( $b > 1$ ) or negatively allometric ( $b < 1$ ; Zar 2010). The null hypothesis ( $H_0: b = 1$ ) was tested using Student's  $t$ -test ( $\alpha = 0.05$ ).

## Results

A total of 249 individuals of *E. amazoniensis* were collected, including 144 females and 105 males. In contrast, *E. burchelli* was less abundant, with only 29 individuals collected, of which 20 were females and 9 males. Due to the low abundance of *E. burchelli*, its specimens were not subjected to all analyses originally proposed in the present study. Therefore, this species was evaluated only for sexual dimorphism, and its patterns of handedness and heterochely were described using pooled-sex data, with no sex-based analytical separation. This approach maximised the use of the available material and provided baseline information on this still poorly studied species.

### *Euryrhynchus amazoniensis*

The morphometric data of all measured structures in *E. amazoniensis* showed a non-normal distribution (Shapiro-Wilk test,  $p < .05$ ). In general, males exhibited significantly larger values for all body variables than females, except for PW, whose mean values did not differ significantly between sexes (Mann-Whitney test,  $U = 6.489$ ;  $p = .06$ ). However, males still showed slightly higher mean PW values ( $1.93 \pm 0.35$  mm) compared to females ( $1.85 \pm 0.37$  mm) (Table 1).

Males and females of *E. amazoniensis* showed no significant handedness in their chelipeds, indicating that the larger and smaller chelipeds may occur on either side of the body, without a defined pattern (Chi-square test: overall  $-\chi^2 = 2.18$ ;  $p = .14$ ; males  $-\chi^2 = 1.37$ ;  $p = .24$ ; females  $-\chi^2 = 0.87$ ;  $p = .35$ ). Considering males and females together, 57.14% of the analysed individuals had the larger cheliped on the left side of the body, whereas in 42.86% of the cases it was located on the right side. When analysed separately, males had the larger cheliped on the left side in 58.33% and on the right side in 41.67% of the cases, while females exhibited the larger cheliped on the left in 56.14% and on the right in 43.86% of the cases (Figure 3).

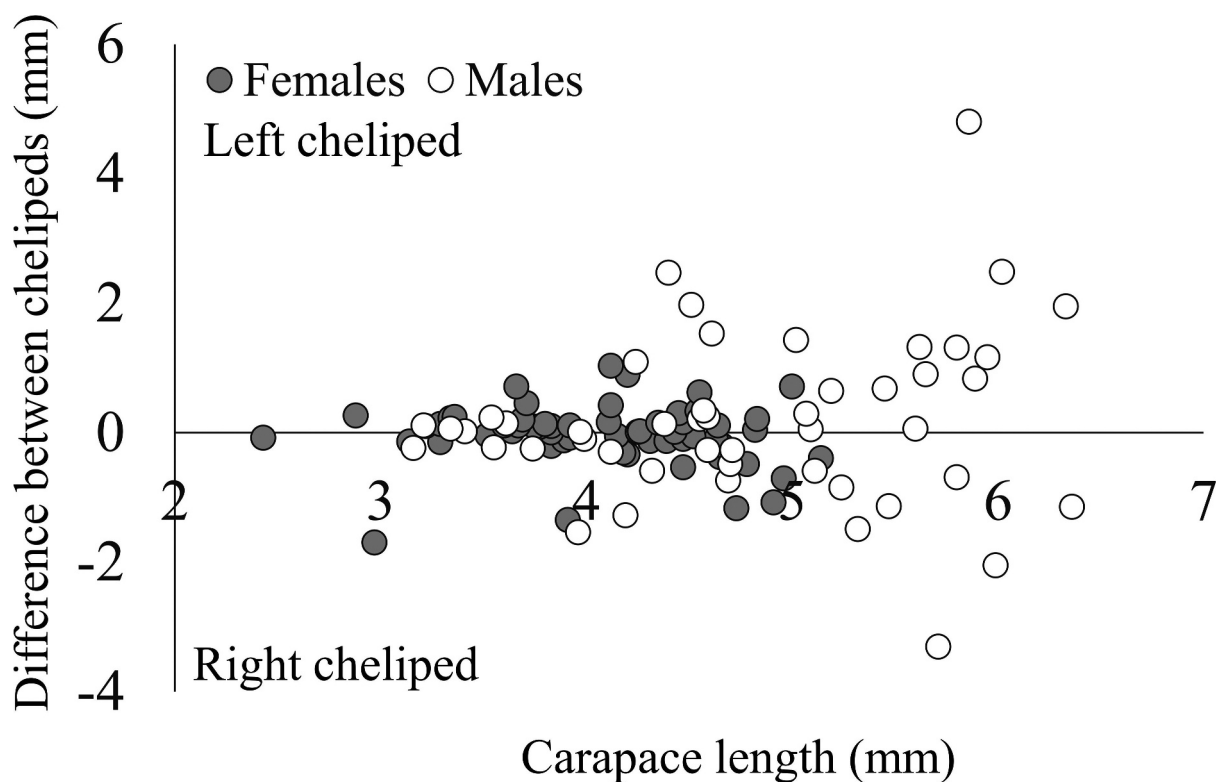
Since no consistent pattern of cheliped handedness was observed, the size difference between these structures was evaluated by comparing the larger and smaller cheliped of each individual. Both sexes showed a significant heterochelous difference between chelipeds (Wilcoxon test; males  $-p < .001$ ; females  $-p < .001$ ). In males, the mean lengths of the larger and smaller chelipeds were  $10.22 \pm 2.83$  mm and  $9.30 \pm 2.37$  mm, respectively. In females, the means were smaller, with  $7.74 \pm 1.27$  mm for the larger cheliped and  $7.43 \pm 1.17$  mm for the smaller one. Additionally, the degree of heterochely increased considerably with body size (Figure 3).

**Table 1.** Morphometric data of males and females of *Euryrhynchus amazoniensis*. 'Smaller' and 'larger' refer to the articles of the smaller and larger cheliped, respectively.

Structure	Sex	Mean $\pm$ SD	Min–Max	U	<i>p</i>
CL	Males	4.57 $\pm$ 0.87	3.04–6.36	4961.5	< .001*
	Females	4.04 $\pm$ 0.65	2.43–5.98		
PW	Males	1.93 $\pm$ 0.35	1.27–2.66	6489	.06
	Females	1.85 $\pm$ 0.37	1.09–3.77		
IL (smaller)	Males	1.31 $\pm$ 0.33	0.73–2.19	784.5	< .001*
	Females	1.07 $\pm$ 0.17	0.64–1.42		
ML (smaller)	Males	1.78 $\pm$ 0.40	1.16–2.98	783.5	< .001*
	Females	1.49 $\pm$ 0.22	1.07–1.9		
CaL (smaller)	Males	1.89 $\pm$ 0.51	1.13–3.82	675.5	< .001*
	Females	1.48 $\pm$ 0.25	0.85–2.11		
PL (smaller)	Males	4.32 $\pm$ 1.2	2.04–7.41	717	< .001*
	Females	3.38 $\pm$ 0.6	2.06–4.78		
DL (smaller)	Males	2.31 $\pm$ 0.67	1.05–3.99	729.5	< .001*
	Females	1.79 $\pm$ 0.31	1.04–2.45		
IL (larger)	Males	1.4 $\pm$ 0.37	0.79–2.51	782	< .001*
	Females	1.13 $\pm$ 0.21	0.53–1.57		
ML (larger)	Males	1.86 $\pm$ 0.42	1.14–3.2	723.5	< .001*
	Females	1.52 $\pm$ 0.21	1–1.88		
CaL (larger)	Males	2.01 $\pm$ 0.54	1.04–3.53	660.5	< .001*
	Females	1.55 $\pm$ 0.28	0.93–2.63		
PL (larger)	Males	4.95 $\pm$ 1.56	2.23–9.64	619	< .001*
	Females	3.54 $\pm$ 0.68	2.16–5.03		
DL (larger)	Males	2.56 $\pm$ 0.82	1.09–4.99	645	< .001*
	Females	1.84 $\pm$ 0.39	1.07–2.71		

CaL = carpus length; CL = carapace length; DL = dactylus length; IL = ischium length; Max = maximum value; Min = minimum value; ML = merus length; PL = propodus length; PW = second pleonal pleura width; SD = standard deviation.

The PCA based on morphometric data revealed that some males and females occupy the same morphospace. However, certain males exhibited distinct morphometric characteristics, being distributed in different

**Figure 3.** Handedness and heterochely in males and females of *Euryrhynchus amazoniensis*.

regions of the morphospace (Figure 4). The first principal component (PC1) explained 90.24% of the data variation (eigenvalue = 5.41), whereas the second principal component (PC2) explained 3.68% of the data variation (eigenvalue = 0.22), together accounting for 93.92% of the total observed variation (Figure 4). Male dispersion appears to be influenced by the variables of the larger cheliped, specifically the ischium (loading values: PC1 = 0.3922 and PC2 = 0.7218), merus (PC1 = 0.4125 and PC2 = -0.035), carpus (PC1 = 0.4086 and PC2 = -0.402), propodus (PC1 = 0.4212 and PC2 = -0.269) and dactylus (PC1 = 0.415 and PC2 = -0.331), with carapace length showing a moderate influence (loading values: PC1 = 0.3994 and PC2 = 0.3661) (Figure 4).

The pattern of body development, or relative growth, for most morphometric relationships showed clear distinctions between males and females of *E. amazoniensis*, except for CL vs CaL of the smaller cheliped, in which both sexes exhibited isometric growth (Table 2). In the relationship between CL vs PW, males showed negative allometric growth, whereas females exhibited isometry (Table 2; Figure 5). Regarding the smaller cheliped, males displayed isometric growth for CL vs IL, CL vs ML and CL vs CaL, and positive allometry for CL vs PL and CL vs DL (Table 2; Figure 5). In contrast, females showed negative allometry for CL vs IL and CL vs ML, and isometric growth for CL vs CaL, CL vs PL and CL vs DL (Table 2; Figure 5).

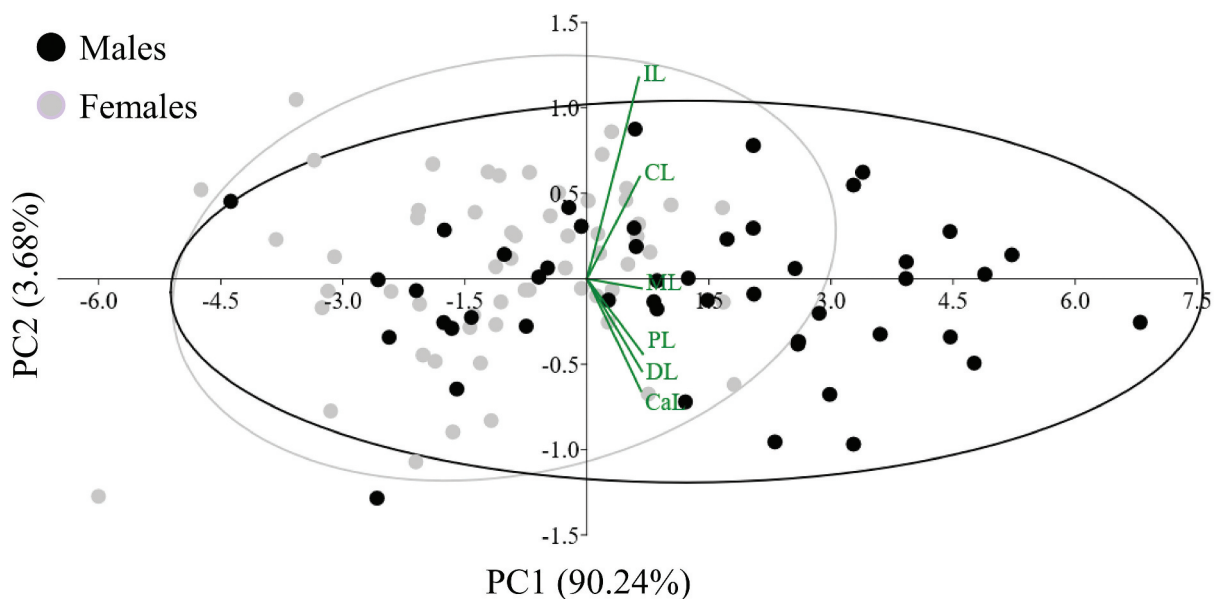
Finally, when analysing the morphometric relationships of the larger cheliped, males exhibited positive allometry for almost all relationships (CL vs IL, CL vs CaL, CL vs PL and CL vs DL), except for CL vs ML, which showed isometric growth (Table 2; Figure 6). In females, isometric growth was observed in CL vs IL, CL vs PL and CL vs DL, while negative allometry was detected in CL vs ML and CL vs CaL (Table 2; Figure 6).

### *Euryrhynchus burchelli*

The morphometric data for most of the structures measured in *E. burchelli* showed a normal distribution (Shapiro-Wilk test,  $p > .05$ ), except for carapace length, which exhibited a non-normal distribution (Shapiro-Wilk test,  $W = 0.80$ ;  $p < .01$ ).

On average, males exhibited higher body measurements than females for all variables analysed (Table 3). However, no significant differences were detected for some of them, specifically for CL (Mann-Whitney test,  $U = 56$ ;  $p = .11$ ), PW (t-test,  $t = 1.01$ ;  $p = .32$ ) and ML (t-test,  $t = 1.33$ ;  $p = .20$ ).

Specimens of *E. burchelli* showed no significant handedness in their chelipeds, indicating that the larger and smaller chelipeds may occur on either side of the body without a defined pattern (Chi-square test,  $\chi^2 = 0.07$ ;  $p = .80$ ). Considering all individuals, 53.33% had the larger cheliped on the left side of the body, while 46.67% had it on the right side (Figure 7).



**Figure 4.** Principal component analysis (PCA) of morphometric data for males and females of *Euryrhynchus amazoniensis*. CaL = carpus length; CL = carapace length; DL = dactylus length; IL = ischium length; ML = merus length; PL = propodus length.

**Table 2.** Linear regression and allometric pattern data of *Euryrhynchus amazoniensis*. 'Smaller' and 'larger' refer to the articles of the smaller and larger cheliped, respectively.

Morphometric relationship	Group	N	a	b	r <sup>2</sup>	T (b = 1)	p	Allometry
CL vs PW	Males	144	-0.2854	0.8662	0.85	3.77	< .001	-
	Females	105	-0.3541	1.0202	0.72	0.38	< .001	=
CL vs IL (smaller)	Males	48	-0.6684	1.1459	0.74	1.47	< .001	=
	Females	58	-0.4755	0.8278	0.56	1.78	< .001	-
CL vs ML (smaller)	Males	48	-0.434	1	0.76	0.0004	< .001	=
	Females	58	-0.3283	0.8229	0.69	2.41	< .001	-
CL vs CaL (smaller)	Males	48	-0.4562	1.0673	0.63	0.57	< .001	=
	Females	58	-0.3915	0.9165	0.6	0.84	< .001	=
CL vs PL (smaller)	Males	48	-0.2174	1.2428	0.71	2.11	< .001	+
	Females	58	-0.1025	1.0325	0.71	0.37	< .001	=
CL vs DL (smaller)	Males	48	-0.5419	1.3172	0.71	2.6	< .001	+
	Females	58	-0.3936	1.0557	0.75	0.68	< .001	=
CL vs IL (larger)	Males	48	-0.6632	1.1803	0.75	1.81	< .001	+
	Females	58	-0.5142	0.9266	0.51	0.61	< .001	=
CL vs ML (larger)	Males	48	-0.4399	1.039	0.81	0.52	< .001	=
	Females	58	-0.2737	0.7479	0.61	3.21	< .001	-
CL vs CaL (larger)	Males	48	-0.5163	1.1942	0.74	1.9	< .001	+
	Females	58	-0.3157	0.8229	0.48	1.75	< .001	-
CL vs PL (larger)	Males	48	-0.3334	1.4949	0.8	4.63	< .001	+
	Females	58	-0.0983	1.0569	0.66	0.57	< .001	=
CL vs DL (larger)	Males	48	-0.6156	1.4877	0.78	4.27	< .001	+
	Females	58	-0.3924	1.0688	0.55	0.54	< .001	=

- = negative allometry; + = positive allometry; = = isometry; a = intercept; b = slope; CL = carapace length; CaL = carpus length; DL = dactylus length; IL = ischium length; ML = merus length; PL = propodus length; PW = second pleonal pleura width.

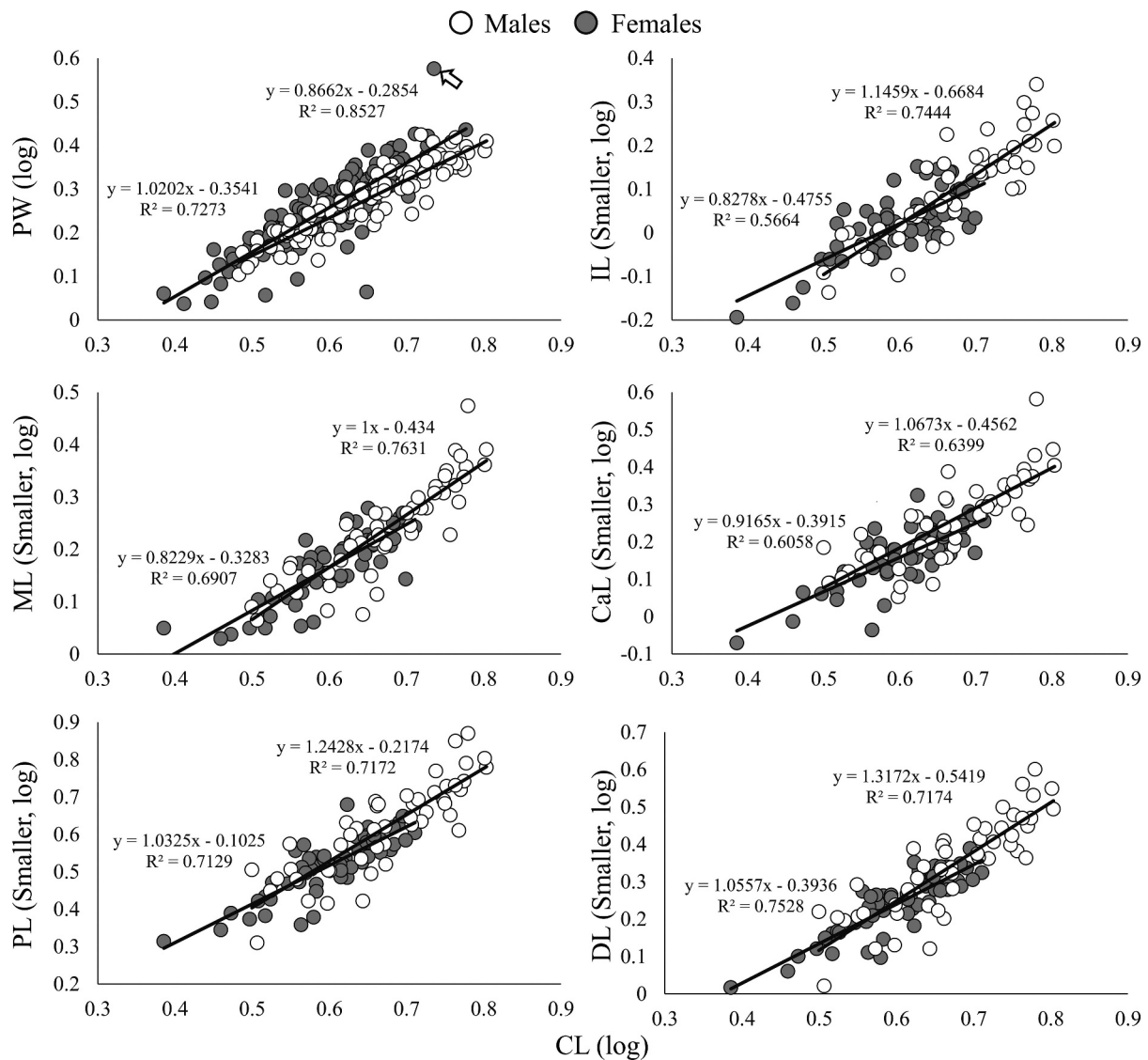
Due to the absence of handedness, the size difference between chelipeds was evaluated by comparing the larger and smaller cheliped of each individual. Males and females, analysed together, showed a significant difference in cheliped size (paired *t*-test,  $t = 7.47$ ;  $p < .001$ ). On average, the larger and smaller chelipeds measured  $6.31 \pm 0.96$  mm and  $5.80 \pm 1.06$  mm, respectively.

## Discussion

The present study provides the first morphometric data on body size and relative growth patterns in euryrhynchid shrimps, with particular emphasis on the chelipeds. The results revealed consistent developmental patterns for these structures and suggest the possible existence of different male morphotypes in *E. amazoniensis*. Furthermore, the morphometric patterns observed show strong similarities to those described for other groups of freshwater shrimps, particularly those of the family Palaemonidae (Mossolin and Bueno 2003; Santos *et al.* 2022; Nogueira *et al.* 2022b; Nogueira and Almeida 2023).

In both species analysed, males were significantly larger than females, exhibiting distinct mean values in most of the morphometric comparisons performed. Although not all differences were statistically significant, a particularly notable result was observed for PW, which also showed higher mean values in males of both species. In caridean shrimps in general, females exhibit more developed pleonal pleurae than males, especially the second pleuron, a feature commonly associated with the formation of an expanded brooding chamber and, consequently, with greater reproductive success due to an increased capacity for embryo incubation (Pantaleão *et al.* 2012; Pescinelli *et al.* 2018; Ghizelli-Fraga *et al.* 2021). The difference observed in the present study, in which males exhibited, on average, higher PW values than females, may be related to the size-dependent nature of this structure. Thus, as males reach larger body sizes than females, and considering that PW increases as a function of body size (Nogueira *et al.* 2026), it is plausible that larger individuals exhibit wider pleonal pleurae. However, when considering the results of the relative growth analyses *i.e.*, when the effect of body size is controlled, females are observed to have a proportionally larger second pleonal pleuron than males, and to exhibit greater energetic investment in the development of this structure.

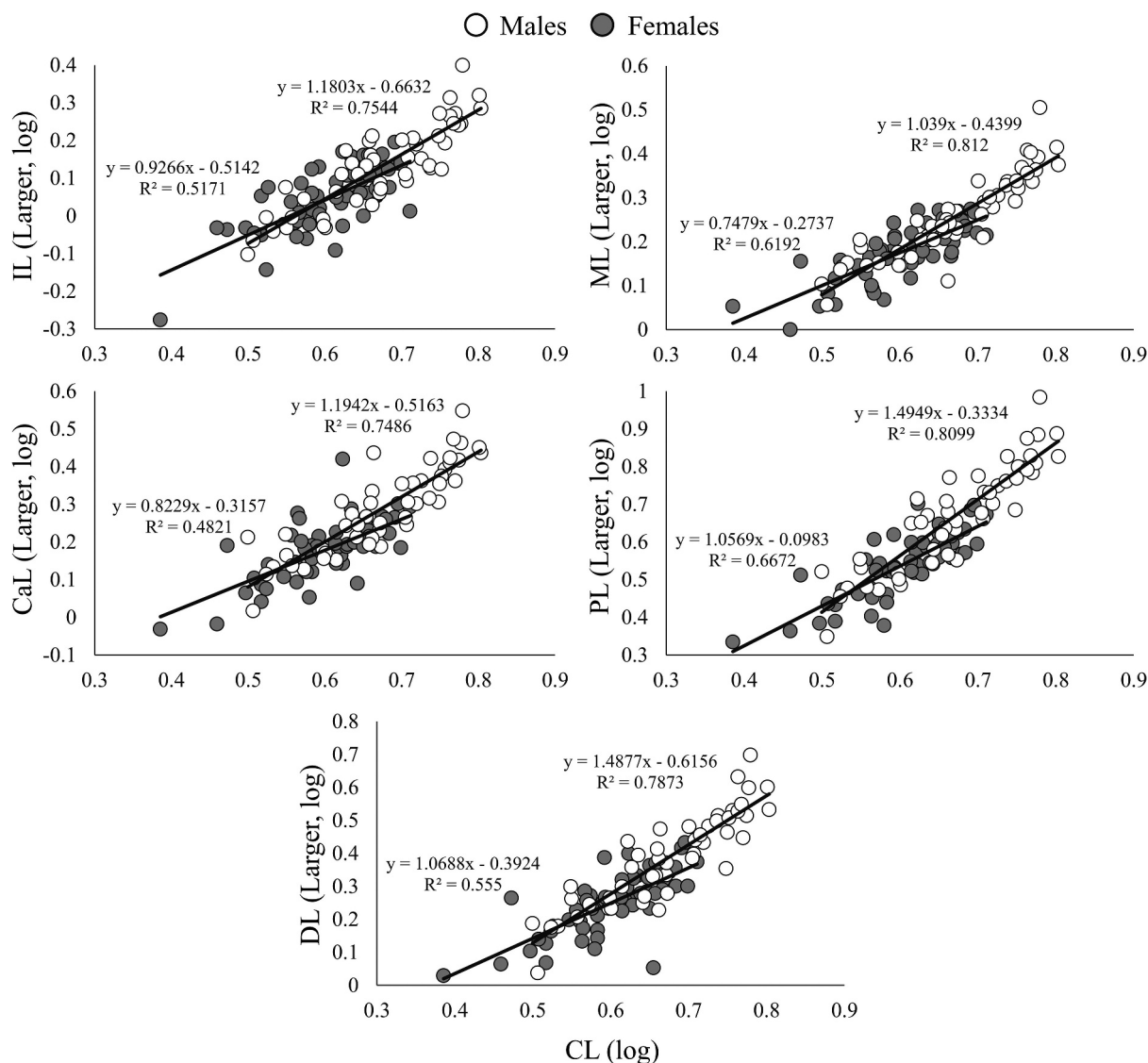
As mentioned earlier, one of the unique characteristics of Euryrhynchidae is their extremely abbreviated larval development, during which embryos complete most larval stages while still inside the egg (Magalhães 1988). These embryos are remarkably large due to the high yolk content required to sustain embryonic development. Despite the large size of the embryos, females apparently do not allocate a high energetic demand to the expansion of the incubation chamber, as indicated by the isometric pattern observed in this



**Figure 5.** Relative growth of males and females of *Euryrhynchus amazoniensis*. The arrow in the PW graph indicates an ovigerous female, which exhibits a modification of the second pleonal pleura known as the breeding dress. CaL = carpus length; CL = carapace length; DL = dactylus length; IL = ischium length; ML = merus length; PL = propodus length; PW = second pleonal pleura width.

study. In addition, an examination of data available in the literature reveals that most species with abbreviated larval development exhibit isometric patterns in PW development, similarly to *E. amazoniensis* (Nogueira *et al.* 2019a, 2019b, 2022a; Gasparotto *et al.* 2024). In contrast, this pattern differs from that observed in caridean shrimp species with extended larval development, which carry small embryos during the ovigerous stage and generally show positive allometric growth of PW (Paschoal *et al.* 2013; Pescinelli *et al.* 2018a, 2018b; Ghizelli-Fraga *et al.* 2021; Talamonte *et al.* 2022). Thus, PW development appears to be under weaker selective pressure in groups with abbreviated larval development, such as Euryrhynchidae, in which the number of embryos produced is naturally reduced due to their large size. A relative increase in the female incubation chamber would likely not result in substantial reproductive gains, since the number of embryos that can be incubated is constrained by their large volume. This condition may represent an adaptive energy-saving strategy in these species, with reduced investment in pleural expansion and greater allocation of energy to other biological processes, such as yolk production, thereby increasing embryonic survival.

The pattern of handedness and heterochely in decapod crustaceans has been extensively studied in brachyuran and anomuran crabs. In these groups, a defined pattern of handedness is generally observed,



**Figure 6.** Relative growth of males and females of *Euryrhynchus amazoniensis*. CaL = carpus length; CL = carapace length; DL = dactylus length; IL = ischium length; ML = merus length; PL = propodus length.

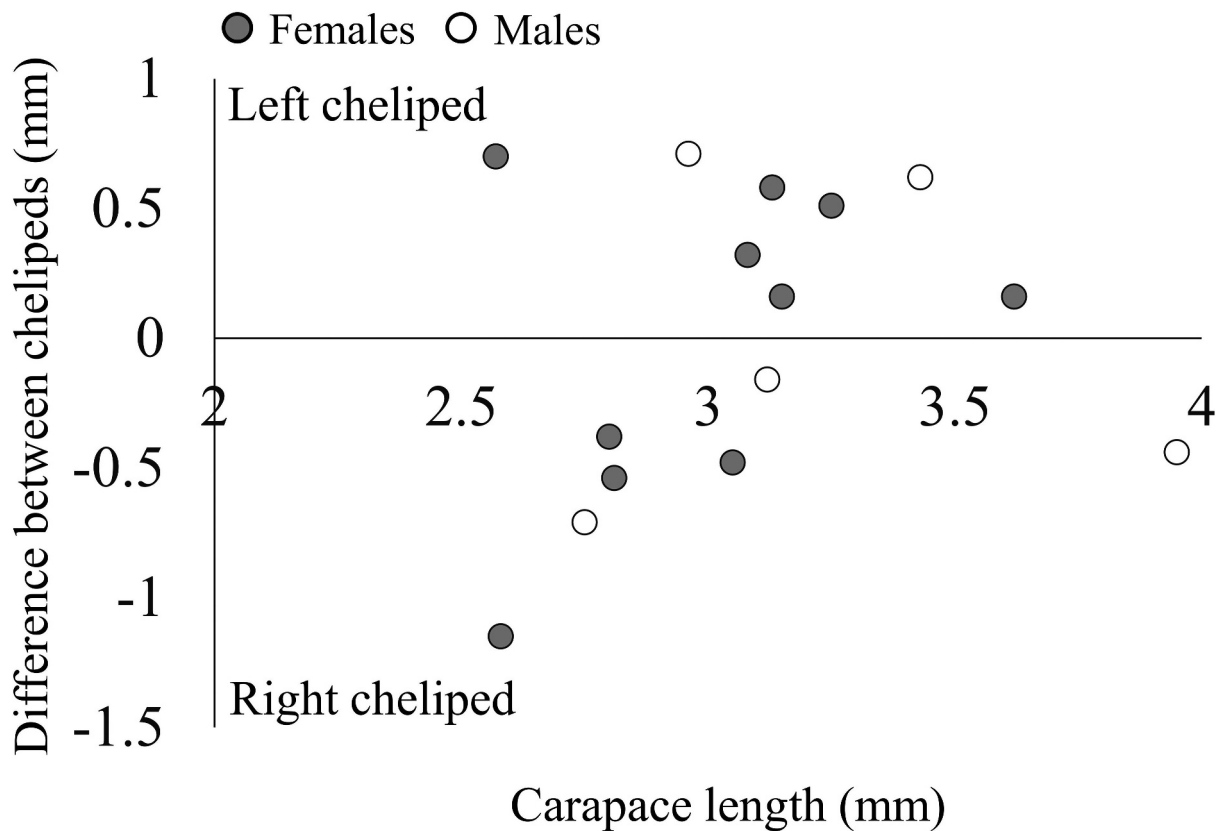
with the larger cheliped predominantly located on a specific side of the body (Santos *et al.* 2018a; Pescinelli *et al.* 2020; da Silva *et al.* 2021). This pattern suggests the influence of genetic factors in the development of this structure, reflecting a stable directional asymmetry (Palmer 2016). In shrimps, however, this feature has received less attention and has only recently begun to be investigated in greater depth. Studies involving palaemonid and alpheid shrimps (Mossolin and Bueno 2003; Palmer 2016; Nogueira *et al.* 2022a; Nogueira and Almeida 2023) have indicated that, unlike brachyurans and anomurans, there is no fixed pattern of handedness among carideans, as the larger cheliped may develop on either side of the body. According to the results of the present study, euryrhynchids appear to follow the same pattern observed in these other shrimp groups, suggesting that the absence of a defined handedness may represent a general trend among heterochelous caridean shrimps. The occurrence of reverse asymmetry – that is, the ability to switch the dominant side of the larger cheliped – may represent an adaptive strategy that reduces the energetic costs associated with regenerating this structure after loss. In such cases, energetic investment is redirected towards the smaller cheliped, which undergoes morphological modifications to assume the role of the larger cheliped, thereby minimising the costs of regeneration.

During the analyses of *E. amazoniensis*, a small group of males was observed to possess a distinct propodus morphology when compared with most other males. In addition, the PCA revealed that male individuals were distributed across different regions of the morphospace, indicating an intrasexual morphological variation.

**Table 3.** Morphometric data of males and females of *Euryrhynchus burchelli*. ‘Smaller’ and ‘larger’ refer to the articles of the smaller and larger cheliped, respectively. The asterisk indicates statistically significant results.

Structure	Sex	Mean ± SD	Min–Max	U/t	p
CL	Males	3.42 ± 1.07	2.01–5.82	56 (U)	.11
	Females	2.87 ± 0.38	2.01–3.62		
PW	Males	1.58 ± 0.43	0.98–2.52	1.01 (t)	.32
	Females	1.44 ± 0.28	0.98–1.97		
IL (smaller)	Males	0.94 ± 0.12	0.8–1.09	2.36 (t)	.03*
	Females	0.75 ± 0.17	0.8–0.96		
ML (smaller)	Males	1.45 ± 0.24	1.14–1.71	1.33 (t)	.2
	Females	1.27 ± 0.24	1.14–1.63		
CaL (smaller)	Males	1.28 ± 0.22	1–1.48	2.32 (t)	.03*
	Females	1.01 ± 0.21	1–1.37		
PL (smaller)	Males	2.92 ± 0.38	2.42–3.47	2.68 (t)	.01*
	Females	2.38 ± 0.36	2.42–2.88		
DL (smaller)	Males	1.47 ± 0.21	1.22–1.75	2.8 (t)	.01*
	Females	1.18 ± 0.18	1.22–1.38		
IL (larger)	Males	0.96 ± 0.16	0.81–1.17	2.83 (t)	.01*
	Females	0.74 ± 0.14	0.81–0.95		
ML (larger)	Males	1.54 ± 0.14	1.4–1.72	2.47 (t)	.02*
	Females	1.32 ± 0.17	1.4–1.56		
CaL (larger)	Males	1.32 ± 0.22	1.15–1.61	2.23 (t)	.04*
	Females	1.08 ± 0.18	1.15–1.36		
PL (larger)	Males	3.3 ± 0.32	2.85–3.68	3.01 (t)	.01*
	Females	2.76 ± 0.32	2.85–3.3		
DL (larger)	Males	1.59 ± 0.23	1.33–1.92	3.25 (t)	< .01*
	Females	1.3 ± 0.13	1.33–1.5		

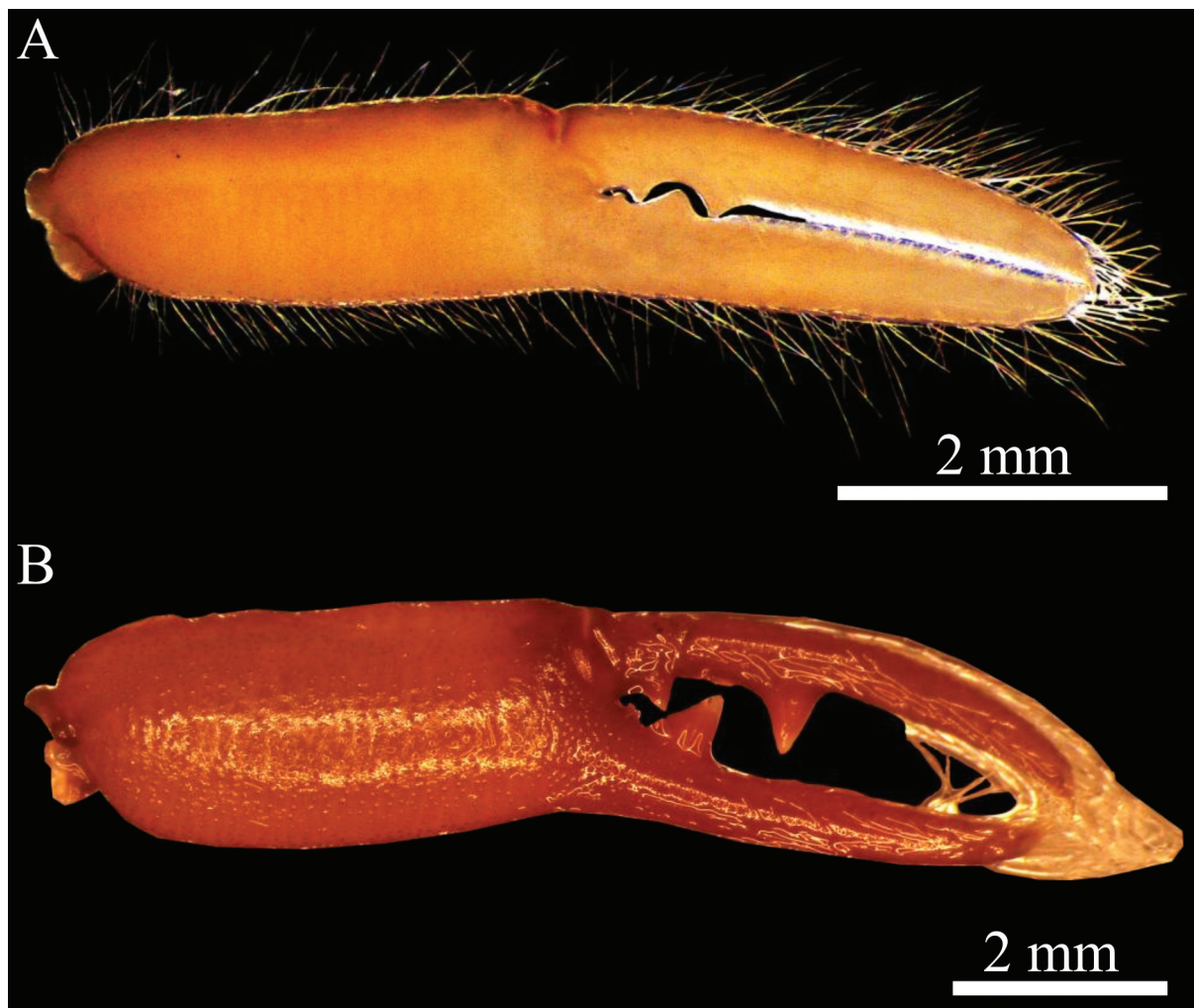
CL = carapace length; DL = dactylus length; CaL = carpus length; IL = ischium length; Max = maximum value; Min = minimum value; ML = merus length; PL = propodus length; PW = second pleonal pleura width; SD = standard deviation.



**Figure 7.** Handedness and heterochely in males and females of *Euryrhynchus burchelli*.

These males, characterised by proportionally larger chelipeds, exhibited a slightly more robust propodus palm and highly pronounced teeth on both the fixed and movable fingers, forming a conspicuous gap between them (Figure 8). These morphological differences represent strong evidence for the occurrence of male morphotypes in *E. amazoniensis*, a phenomenon already documented for several freshwater shrimps, particularly among species of the genus *Macrobrachium* Spence Bate, (Kuris *et al.* 1987; Wortham and Maurik 2012; Karplus and Barki 2019; Nogueira *et al.* 2020; Santos *et al.* 2022). In *Macrobrachium* species with well-defined morphotypes, overlap in body size between different male morphotypes is common, with the main distinguishing traits being the size and morphology of the chelipeds. In such cases, variation is mainly expressed in the ornamentation pattern and the morphology of the propodus and dactylus (Kuris *et al.* 1987; Nogueira *et al.* 2022b; Santos *et al.* 2022). In the present study, the limited number of individuals exhibiting distinct morphological features prevented a formal description of potential morphotypes, as is typically performed through more detailed morphometric and morphological analyses. Nevertheless, the results provide strong evidence that *E. amazoniensis* exhibits this type of intrasexual dimorphism, suggesting that the occurrence of dominant male morphotypes may also extend to the family Euryrhynchidae.

The relative growth of body structures in *E. amazoniensis* followed an expected pattern, very similar to that observed in palaemonid shrimps exhibiting sexual dimorphism, in which males tend to be larger than females (Collins 2001; Mossolin and Bueno 2003; Nogueira *et al.* 2019). In all morphometric relationships involving both the smaller and larger chelipeds, males exhibited higher allometric coefficients than females,



**Figure 8.** Morphological variation in the propodus of males of *Euryrhynchus amazoniensis*. (A) Standard propodus morphology observed in most males. The illustrated specimen had a carapace length of 5.95 mm. (B) Propodus morphology observed in some males from the largest size classes. The illustrated specimen had a carapace length of 6.02 mm.

indicating greater investment in the development of these structures. This differential growth pattern reinforces the functional importance of chelipeds in males. Although these appendages serve similar purposes in both sexes, such as food capture and object manipulation, in males, they also play an additional role in agonistic behaviours and competition for mates (Mariappan *et al.* 2000; Palaoro and Peixoto 2022), a limited resource that directly influences reproductive success. Thus, the greater investment in cheliped growth may reflect this selective pressure, as possessing more developed chelipeds can enhance male mating success and, consequently, overall reproductive fitness.

The results obtained in this study indicate that males of both species are larger than the females and possess proportionally more developed chelipeds. In *E. amazoniensis*, males also appear to allocate greater energetic investment towards the development of these structures, in addition to the probable occurrence of distinct male morphotypes. Thus, as proposed by Bauer (2023), the presence of sexual dimorphism in both body size and weaponry (chelipeds) suggests that the *Euryrhynchus* species analysed here may adopt a 'neighbourhood of dominance' mating system. In this system, males tend to be larger, possess robust chelipeds and display aggressive behaviours during competition for mates (Correa and Thiel 2003; Karplus and Barki 2019; Bauer 2023). Although the morphological and morphometric evidence presented here strongly supports this hypothesis, confirmation of this pattern requires complementary analyses, including population-based and behavioural studies focused on describing copulatory and agonistic interactions.

During the present study, an ovigerous female of *E. amazoniensis* was collected, carrying a small number of large embryos within its incubatory chamber, consistent with previous reports in the literature (Walker 2001; Oliveira *et al.* 2017). It is known that females of caridean shrimps, prior to reaching the ovigerous or incubation stage, undergo a special moult that induces modifications in pleonal structures to accommodate the embryos more efficiently, a process known as breeding dress (Bauer 2023). The extent of these morphological modifications varies among different taxonomic groups (Yonge 1955; Bauer 2023). In the case of the family Euryrhynchidae, however, such information was previously unavailable. Based on the analysis of this ovigerous female, it was observed that the width of the second pleuron increases by approximately 40% compared to that of a non-ovigerous female of similar body size. Furthermore, the incubatory chamber, formed by the first three pleonal pleurae, nearly encloses the embryos due to the vertical and lateral expansion of these structures, forming an almost completely closed chamber that protects the offspring (Figure S1). Considering that the production of these embryos represents a highly energy-demanding biological process, given the large size and volume of the eggs and their high yolk content, it is plausible to interpret these structural modifications as an additional form of parental care, aimed at protecting the embryos and enhancing reproductive success in *E. amazoniensis*.

Although the data from the present study was not obtained from a population-based perspective, since no sequential collections were conducted, *i.e.* there was no temporal scale, it is possible to establish comparisons with previous studies carried out in the same sampling area approximately 20 to 40 years ago (Walker and Ferreira 1985; Walker 2001). In those earlier studies, a distributional pattern was observed between *E. amazoniensis* and *E. burchelli* in the Tarumã-Mirim River, in which the former was more abundant in the upper reaches of the river, while the latter predominated in the lower portions, with greater overlap between the two species occurring in the intermediate areas. This pattern remained consistent throughout different years of sampling. However, after several decades, the site was revisited by the authors of the present study, and new collections revealed an opposite scenario: in the lower sections of the Tarumã-Mirim River, *E. amazoniensis* was markedly more abundant, far surpassing *E. burchelli* in number. This inversion in the distribution pattern may be associated with multiple factors, including the progressive urbanisation of the riverbanks over recent decades and the consequent increase in organic matter load in the lower reaches, which may have favoured *E. amazoniensis* in these areas. Additionally, it is worth noting that the present collections were conducted during one of the most severe drought and heat events ever recorded in the Amazon (Espinoza *et al.* 2024). Therefore, the observed shift in the relative abundance of these species may also reflect an ecological response to extreme climatic conditions, potentially inducing a downstream migration of individuals from the upper portions of the river. These findings highlight how severe climatic events and ongoing deforestation in the Amazon biome can significantly alter the distribution patterns and population structure of aquatic organisms.

In summary, the results of the present study substantially expand the current knowledge on the biology and morphometric patterns of shrimps belonging to the family Euryrhynchidae, providing the first qualitative and quantitative evidence of relative growth and sexual dimorphism in these shrimps. The analyses revealed that *E. amazoniensis* and *E. burchelli* share morphological patterns typical of freshwater carideans, but also exhibit particular traits that directly reflect adaptations related to their evolutionary history and life strategies, such as their extremely abbreviated larval development and the differential investment in reproductive structures. Furthermore, the indication of possible male morphotypes in *E. amazoniensis* suggests that intrasexual dimorphism, so far undocumented for Euryrhynchidae, may be more widespread within the family. These findings not only contribute to the understanding of the reproductive and evolutionary strategies of these shrimps but also provide a foundation for future ecological and taxonomic studies on the group, particularly in light of the rapid environmental transformations that are negatively affecting the Amazon biome.

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## Disclosure statement

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