

Allometric Growth in *Creaseria morleyi* (Creaser, 1936) (Decapoda: Palaemonidae), from the Yucatan Peninsula, Mexico

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ABSTRACT.—The palaemonid shrimp *Creaseria morleyi* is widely distributed along the northern portion of the Yucatan Peninsula inhabiting submerged cave systems. A high degree of morphological variation is evident in the shape of the carapace and the relative lengths of the first two pereiopods in the larger organisms. In order to find an explanation for these changes in taxonomically important characters, a morphometric analysis was undertaken. Several body parts as well as individual articles of the first and second pereiopods were measured for a total of 24 variables. The equation $Y = aX^b$, was used to calculate the divergence from isometry in relation to carapace length. Males ranged in total length from 31.6 to 49.3 mm and females from 31.8 to 65.6 mm. For males, all regressions considering body variables showed negative allometry, except for gonopod length. For females, the only variable showing positive allometry was carapace width, suggesting that as females increase in size the carapace becomes wider than longer. Regarding the first pereiopod, almost all variables showed negative allometry; males and females did not differ markedly in this respect. For the second pereiopod, males showed negative allometry; however, for females, chela related dimensions exhibited positive allometric growth, consistent with the diverging morphology of the larger females. Regressions for males and females were significantly different describing a sexual dimorphism. Graphic representations of the tendencies show that significant changes in the morphology, or in the level of allometry, occur in females at sizes between 46 and 60 mm of total length.

KEYWORDS.—*Creaseria morleyi*, Palaemonidae, allometric growth, cave fauna

INTRODUCTION

The karstic nature of the Yucatan Peninsula promotes the formation of submerged cave systems and sinkholes locally known as cenotes (Reddell 1981). These environments are inhabited by an endemic biota composed of teleostean fishes and crustaceans; with the latter group being dominant both in terms of number of taxonomic groups and individuals present (Wilkins 1982). Among crustaceans, decapods are the more abundant and diverse with seven genera and ten species (Iliffe 1993).

The palaemonid shrimp *Creaseria morleyi* (Creaser, 1936), represents a monotypic genus closely related to *Palaemon*, characterized by the presence of antennal and branchiostegal spines, the absence of a branchiostegal groove, a two-jointed mandibular palp, reduced eyes, and unpig-

mented eyes and body (Holthuis 1952). In contrast with most other cave adapted species, whose distribution range is reduced to one or a few localities (Holthuis 1986; Vilalobos et al. 1999), *C. morleyi* is widely distributed along the northern portion of the Yucatan Peninsula; until 1983 it was known from 46 sites (Reddell 1981; Pérez-Aranda 1983a).

This endemic shrimp was originally described as *Palaemon morleyi* (Creaser, 1936) based on a type series composed of eight organisms, among which the holotype had a total length (TL) of 33.5 mm. The genus *Creaseria* was proposed by Holthuis (1952), who examined females that measured up to 42 mm TL. In these two studies, as well as in several later ones, a certain degree of morphological variation was reported among adult females measuring between 35 and 60 mm TL, in the relative length of the appendix masculina of males, and in the shape and number of teeth on the ros-

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trum in both sexes (Hobbs and Hobbs 1976; Hobbs et al. 1977; Hobbs 1979; Pérez-Aranda 1983a). During recent sampling trips conducted throughout the Yucatan Peninsula, males of up to 44 mm TL and females of up to 66 mm TL were captured. A high degree of morphological variation was evident in the larger organisms, mainly in the shape of the carapace and the relative lengths of the articles of the first two pereopods (Fig. 1). Further, important differences emerged with respect to the figures that appear in Hobbs and Hobbs (1976, fig. 8) and Hobbs et al. (1977, fig. 19) which had been commonly used to identify the species. This situation becomes relevant if we consider that the morphology of the first two pereopods, together with the shape and number of teeth on the rostrum are the two most important taxonomic characters to differentiate among species in the family Palaemonidae (Holthuis 1952; Mejía et al. 2003; Walker and Poore 2003).

In order to find an explanation for the noticeable changes in proportions of the several regions and appendages in *C. morleyi*, a morphometric analysis was undertaken. Previous studies with palaemonid shrimps have extensively used allometric or relative growth to define the change in shape and proportion that takes place gradually over a series of molts (Hartnoll 1982; Román-Contreras and Campos-Lince 1993; Cartaxana 2003; Mossolin and Bueno 2003; Mariappan and Balasundaram 2004).

Sometimes an abrupt change in shape and proportion occurs at a single molt, frequently called puberty molt, separating the last juvenile stage from the first sexually mature one (Hartnoll 1985).

The aim of this study was to explore if an abrupt increment in size and proportion of the different body parts, based on allometric growth, could be used to explain the presence of two different morphologies in the freshwater shrimp *C. morleyi* from the Yucatan Peninsula. We found that important differences in the allometric growth of the second pereopod are evident, particularly in females where significant changes in the morphology occur at sizes between 46 and 60 mm TL.

MATERIALS AND METHODS

Fifty-nine *Creaseria morleyi* (20 males and 39 females), deposited in the Colección Nacional de Crustáceos (CNCR), Instituto de Biología, Universidad Nacional Autónoma de México, were studied from 17 different localities in the Yucatan Peninsula: 1, Pozo Chaak (20°21'36"N, 89°45'36"W; 1 male, CNCR 1640; Aug 27, 1992); 2, Cenote de Sihunchen (20°41'40"N, 89°40'44"W; 6 males, 2 females, CNCR 22733, 22734, 22738; May 3, 2004); 3, Cenote de San Isidro (20°7'64"N, 89°37'18"W; 3 females, CNCR 318, 320; Jun 15, 1938); 4, Cenote Cuxtal (20°47'19"N, 89°35'26"W; 1 male, 6 females, CNCR 22720; Jul 21, 2003); 5, Cenote Noh-

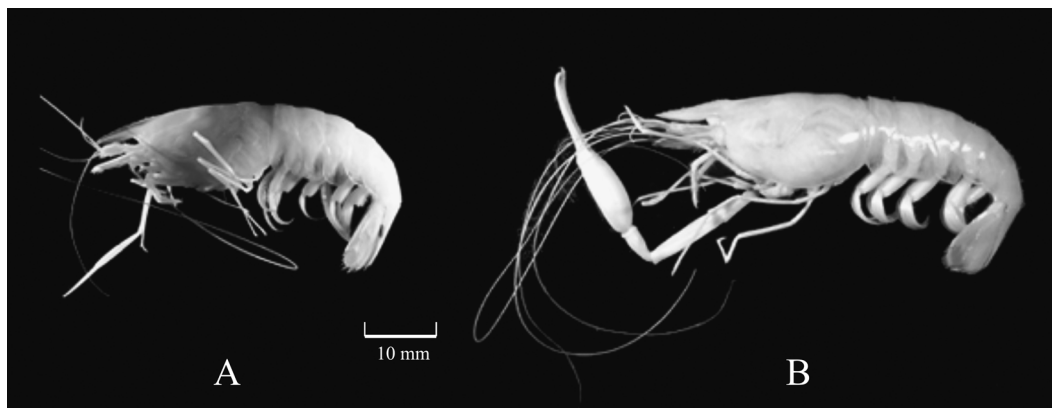


FIG. 1. *Creaseria morleyi* females: A, female with small second pereopod; B, female with large second pereopod. Scale bar represent 10 mm.

chen (20°29'51"N, 89°35'20"W; 2 females, CNCR 22722, 24621; May 1, 2004); 6, Grutas de Tzab-Nah (20°43'49"N, 89°28'28"W; 3 males, 4 females, CNCR 12579, 22717, 22725, 22726, 22736; Jul 29, 2003); 7, Cenote Tza-Itza (20°43'49"N, 89°27'57"W; 1 male, 2 females, CNCR 22724, 22729; Dec 4, 2003); 8, Cenote Kabahchen (20°23'14"N, 89°23'43"W; 2 females, CNCR 22718, 24620; Jul 29, 2003); 9, Cenote de Hoctun (20°51'23"N, 89°11'44"W; 1 male, 3 females, CNCR 22716, 22721, 22723, 22732; May 5, 2004); 10, Cenote de Santo Domingo (19°46'07"N, 88°40'04"W; 3 males, 6 females, CNCR 22735; Aug 7, 2004); 11, Cenote de Las Ruinas (19°37'46"N, 88°33'07"W; 2 males, 2 females, CNCR 22728, 24611, 24612; Aug 7, 2004); 12, Grutas de Balancanche (20°39'31"N, 88°32'05"W; 1 female, CNCR 319; Jun 15, 1938); 13, Cueva Chac Mol (20°38'47"N, 88°24'53"W; 1 female, CNCR 330; Jun 15, 1938); 14, Cueva de Punta Laguna (20°38'47"N, 87°38'23"W; 1 female, CNCR 24616; Dec 9, 2003); 15, Noh Aktun (20°23'36"N, 87°37'01"W; 2 males, CNCR 24617; Dec 7, 2003); 16, Cueva de San Dimas (20°22'13"N, 87°35'17"W; 3 females, CNCR 22727, 24618, 24619; Dec 7, 2003); 17, Cenote Hoil (20°21'24"N, 87°19'70"W; 1 male, CNCR 22725; Feb 12, 2004) (Fig. 2).

Total length (TL), cephalothoracic length

(CFL), rostrum length (RL), caparace length (CL), caparace width (CW), abdomen length (AL), abdomen width (AW), telson length (TL), total length of the appendage as well as length of the five individual articles of the first and second pereiopods, and gonopod length (GL) in the case of males, were measured with a caliper or with a stereomicroscope fitted with an ocular micrometer (0.01 mm) (Fig 3).

Due to the sexual dimorphism exhibited by adults of *C. morleyi*, males and females were analyzed separately. Since the rostrum can be very variable in shape and length, carapace length (CL, Fig. 3) was used as the main independent variable in the regression analysis (Mariappan and Balasundaram 2004).

The equation $Y = aX^b$, was used to obtain the relationships between CL and the remaining variables. In its linear form, $\log y = \log a + b X$, where a slope = 1 denotes isometric growth, slope > 1 is positive allometric growth, and slope < 1 is negative allometric growth (Hartnoll 1982). The data were log transformed before computing the regression equations (Sokal and Rohlf 1995). Divergences from isometry on the slope values were tested with a Student's *t*-test ($\alpha = 0.05$). Analysis of covariance was used to test for significant differences in slopes between sexes (Zar 1999).

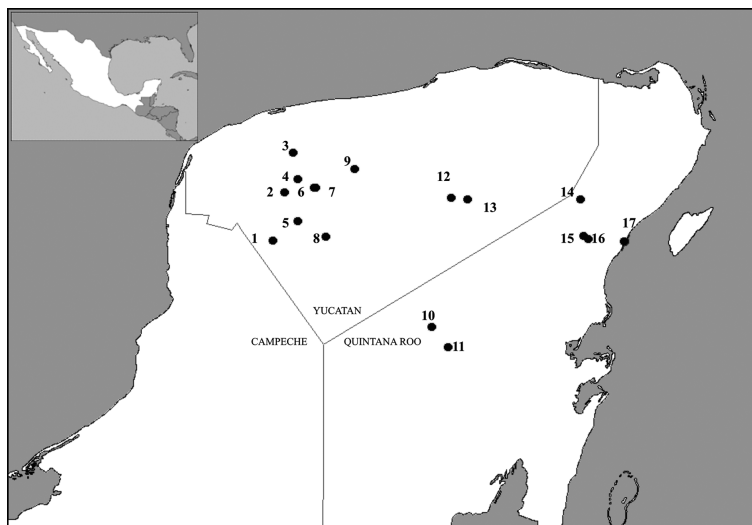


FIG. 2. Map of the Yucatan Peninsula, Mexico, indicating the sites where *Creaseria morleyi* were collected.

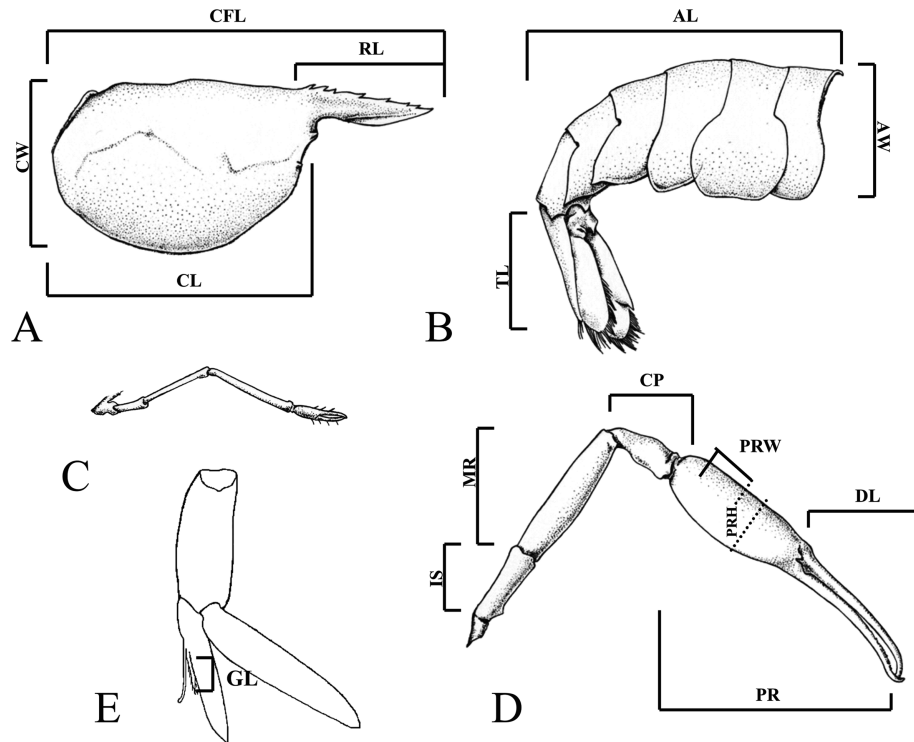


FIG. 3. *Creaseria morleyi*, schematic drawings of the body parts measured. A, cephalothorax: CFL, cephalothoracic length; CL, carapace length; CW, carapace width; RL, rostrum length. B, abdomen and telson: AL, abdomen length; AW, abdomen width; TL, telson length. C and D, first and second pereopods: IS, ischium length; MR, merus length; CP, carpus length; PR, propodus length; PRW, propodus width; PRH, propodus height; DL, dactylus length. E, second pleopod: GL, gonopod length.

With the purpose of describing the relative growth of the first two pairs of pereopods and determining the size at which significant changes in their proportions occur, females of *C. morleyi* were classified as having small or large pereopods, as seen in Figure 1. To graphically analyze the tendencies, total length was plotted against the length of the different pereopodal articles; least squares estimates were used to illustrate the relationships. All data were treated with the NCSS statistical package (Hintze 2004).

RESULTS

Twenty males and 39 females were included in the analysis; males ranged in total length from 31.6 to 49.3 mm ($\bar{x} = 39.9 \pm 1.2$ mm), and females from 31.8 to 65.6 mm ($\bar{x} = 44.3 \pm 1.6$ mm). All regressions ob-

tained appear in Table 1, with CL being used as the independent variable in all cases. The regressions are divided into three sections: those involving cephalothorax, abdomen and telson, and gonopod length for males; those of the first pereopod; and those of the second pereopod. For males, all regressions considering body variables showed negative allometry, except for GL where positive allometry was obtained (Table 1). For females, similar results were obtained; however, the only variable showing positive allometry was CW, suggesting that as females increase in size the carapace becomes wider than longer (t -test, $p < 0.05$) (Fig. 4).

Regarding the first pereopod, in males all variables show negative allometry except for the length of the carpus which exhibits positive allometry and propodus height with an isometric growth. Females

TABLE 1. Results from regression analyses of morphometric data of *Creaseria moriei* with log-transformed data. Carapace length, CL was used as the independent variable. TL, total length; CFL, cephalothoracic length; RL, rostrum length; CW, carapace width; AL, abdomen length; AW, abdomen width; TL, telson length; GL, gonopod length; TP, total pereopod length; IS, ischium length; MR, merus length; CR, carpus length; PR, propodus length; PRW, propodus width; PRH, propodus height; DL, dactylus; 0, isometry; -, negative allometry; +, positive allometry; *, statistically significant at $p < 0.05$; ns, statistically not significant at $p > 0.05$; ***, statistically significant at $p < 0.05$; $F_{1,56} = 4.013$.

Variable	Regression equation		r ²		t		Allometry		Comparison of slopes
	Males	Females	Male	Female	Male	Female	Male	Female	
Growth in relation to carapace length (CL)									
TL	0.760 + 0.796 log CL	0.768 + 0.788 log CL	0.895	0.909	12.371*	18.997*	-	-	392.90***
CFL	0.377 + 0.817 log CL	0.307 + 0.873 log CL	0.891	0.824	12.098*	13.001*	-	-	149.08***
RL	0.124 + 0.699 log CL	0.148 + 0.673 log CL	0.623	0.840	5.458*	13.171*	-	-	115.28***
CW	-0.127 + 0.902 log CL	-0.313 + 1.072 log CL	0.896	0.932	12.441*	22.171*	-	+	350.94***
AL	0.368 + 0.797 log CL	0.387 + 0.777 log CL	0.767	0.828	7.701*	13.169*	-	-	139.97***
AW	-0.192 + 0.912 log CL	-0.180 + 0.907 log CL	0.739	0.923	7.143*	20.752*	-	-	237.80***
TL	0.041 + 0.790 log CL	0.043 + 0.714 log CL	0.644	0.868	5.546*	15.369*	-	-	131.98***
GL	-1.596 + 1.492 log CL		0.671	0.671	6.064*		+		
First pereopod									
TP	0.187 + 0.864 log CL	0.223 + 0.830 log CL	0.879	0.938	11.117*	22.394*	-	-	377.67***
IS	-0.419 + 0.686 log CL	-0.548 + 0.806 log CL	0.521	0.759	4.296*	10.335*	-	-	66.92***
MR	-0.426 + 0.952 log CL	-0.341 + 0.874 log CL	0.859	0.923	10.471*	20.184*	-	-	321.88***
CR	-0.670 + 1.165 log CL	-0.507 + 1.014 log CL	0.831	0.902	9.416*	17.460*	+	+	253.09***
PR	-0.135 + 0.582 log CL	-0.091 + 0.545 log CL	0.813	0.850	8.841*	13.670*	-	-	167.15***
PRW	-1.080 + 0.683 log CL	-0.937 + 0.533 log CL	0.282	0.395	2.656*	4.640*	-	-	19.44***
PRH	-1.664 + 1.371 log CL	-0.911 + 0.579 log CL	0.117	0.578	1.545 ^{ns}	6.729*	0	-	10.41***
DL	-0.401 + 0.660 log CL	-0.379 + 0.615 log CL	0.367	0.684	3.232*	8.451*	-	-	43.87***
Second pereopod									
PD	0.484 + 0.789 log CL	0.356 + 0.954 log CL	0.588	0.744	3.777*	8.697*	-	-	39.62***
IS	-0.287 + 0.724 log CL	-0.426 + 0.872 log CL	0.734	0.781	5.255*	9.642*	-	-	52.34***
MR	-0.033 + 0.749 log CL	-0.168 + 0.918 log CL	0.512	0.748	3.237*	8.796*	-	-	37.60***
CR	-0.262 + 0.711 log CL	-0.319 + 0.777 log CL	0.532	0.883	3.369*	14.062*	-	-	73.19***
PR	0.038 + 0.865 log CL	-0.101 + 1.057 log CL	0.546	0.630	3.466*	6.782*	-	+	24.86***
PRW	-0.723 + 0.675 log CL	-1.188 + 1.211 log CL	0.260	0.688	1.876 ^{ns}	4.830	0	+	9.67***
PRH	-0.671 + 0.665 log CL	-1.216 + 1.277 log CL	0.375	0.521	2.451*	5.423*	-	+	11.88***
DL	-0.331 + 1.002 log CL	-0.335 + 1.066 log CL	0.528	0.606	3.346*	6.447*	+	+	24.69***

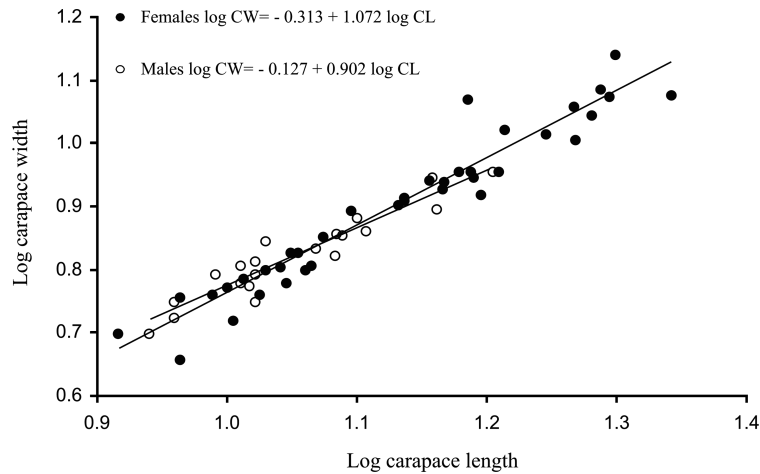


FIG. 4. Relationships between the carapace length and carapace width for males and females of *Creaseria morleyi* (log-transformed data).

show a similar pattern with all measurements exhibiting negative allometry except for carpus length, which is positive. In general terms, the first pereiopod does not differ markedly between males and females, but there is an evident difference in the growth of the propodus and dactylus in females.

With respect to the second pereiopod, dactylus length in males shows positive allometry and propodus height an isometric growth; the rest of the variables show negative allometry. For females, chela related dimensions such as propodus length, width and height, and dactylus length show a positive allometric growth, consistent with the diverging morphology of the larger females (Fig. 1). A closer inspection reveals that females with large chelae can be clearly separated from those with small chelae showing a noticeably different level of allometry (Fig. 5). The change in the relative proportions of the chela occurs at sizes ranging from 46.9 to 59.2 mm TL.

All regressions for males and females were significantly different (Fisher test, analysis of covariance; Table 1) describing a marked sexual dimorphism.

DISCUSSION

Although *Creaseria morleyi* is widely distributed across all the karstic areas of the Yucatan Peninsula and can be present in

remote and inaccessible sites, some of the populations mentioned in previous studies have not been found recently, and others have probably disappeared. An example of this situation is the several localities cited around the city of Merida (Pérez-Aranda 1983a). In addition to the shrinking habitat problem, cave environments in the Yucatan generally support small populations of aquatic animals due to their oligotrophic nature (Pérez-Aranda 1983b). Due to these two effects, *C. morleyi* is becoming rare and for the same reason, the number of organisms used for this analysis represents a uniquely large data set.

The sexual dimorphism seen in *C. morleyi* becomes more evident when the larger individuals are compared. Several species of *Palaemon*, which is closely related to *C. morleyi* (Holthuis 1952), show a similar pattern of sexual dimorphism; *Palaemon northropi* and *P. ritteri* females exhibit stronger and larger chelae on the second pereiopod than males (Guerao et al. 1994; Cartaxana 2003; Kim 2005). In contrast, in the genus *Macrobrachium* adult males are larger than females and their second pereiopods, traditionally used as diagnostic characters, are more developed (Anger and Moreira 1998; Mossolin and Bueno 2003; Mariappan and Balasundaram 2004).

The type of growth shown by *C. morleyi* in relation to total length indicates negative

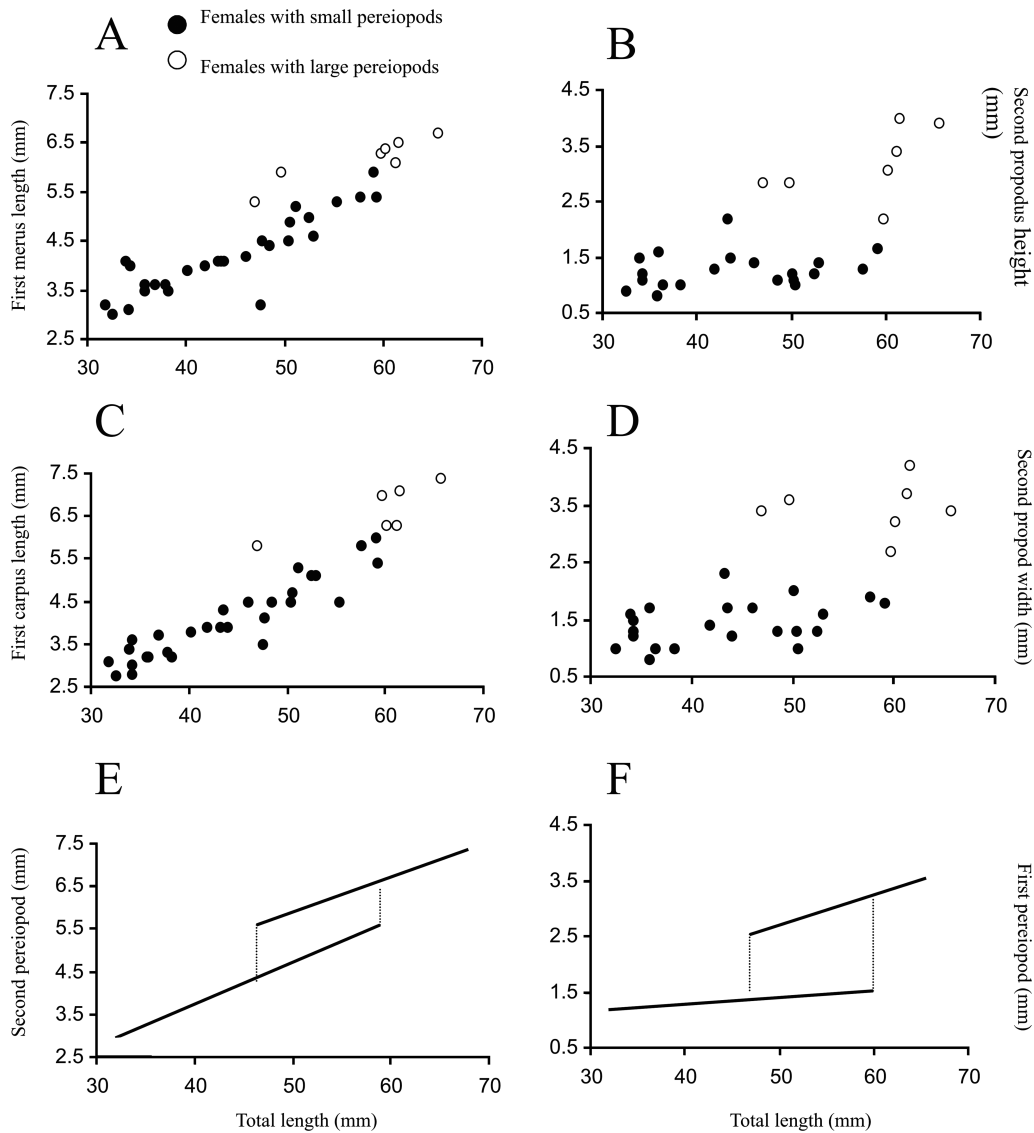


FIG. 5. Relationships between total length and several article lengths of the first and second pereiopods of females of *Creaseria morleyi*. A, total length vs. merus of first pereiopod length; B, total length vs. propodus of second pereiopod width; C, total length vs. carpus length of first pereiopod; D, total length vs. second propodus height; E, theoretical behavior of the growth of the first pereiopod; F, theoretical behavior of the growth of the second pereiopod. E and F calculated with the least squares method.

allometry, or that the carapace increases in length at a faster rate than total length. This pattern is also exhibited by other palaemonids such as *Palaemon northropi*, *P. pandaliformis*, *Macrobrachium acanthurus* and *M. olfersii* (Anger and Moreira 1998); in *P. longirostris*, however, males show a positive allometric growth (Cartaxana 2003).

In particular, the carapace of female *C. morleyi* tends to increase more in width than in length, a feature that is evident when the largest females are examined (Fig. 1). Another important feature of the largest females is the second pereiopod which changes dramatically, through what could be called a puberty molt (Hartnoll

1985) (Fig. 5). This increment in the size of the chela is similar to what happens in other decapod species with marked heterochely (Negreiros-Fransozo and Fransozo 2003; Mariappan and Balasundaram 2004).

Puberty molts as described by Hartnoll (1982; 1985) involve a change in the level of allometry, an interval during which the puberty molt can take place, and a mature morphology associated with reproduction. In the case of *C. morleyi*, the first two elements are clearly present when the lengths of various articles of the second pereopod are plotted against total length (Figs. 5a-d). However, since no reports of ovigerous *C. morleyi* exist, it remains somewhat speculative to call this a puberty molt. Puberty molts have been studied only occasionally in palaemonids; however, this has been observed in the cephalothorax of *Macrobrachium borellii* (Collins and Petriella 1999).

With the description of the significant change in morphology of the second pereopod of *C. morleyi* through allometric growth, we can conclude that all specimens belong to the same species. Graphic representations of the tendencies (Figs. 5e-f), show that significant changes in the morphology take place in females during a period of growth that occur between 46 mm and 60 TL.

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LITERATURE CITED

- Anger, K., and G. S. Moreira. 1998. Morphometric and reproductive traits of tropical caridean shrimps. *J. Crust. Biol.* 18(4):823-838.
- Cartaxana, A. 2003. Growth of the prawn *Palaemon longirostris* (Decapoda, Palaemonidae) in Mira river and estuary, SW Portugal. *J. Crust. Biol.* 23(2): 251-257.
- Collins, P., and A. Petriella. 1999. Growth pattern of isolated prawns of *Macrobrachium borellii* (Crustacea, Decapoda, Palaemonidae). *Invertebr. Reprod. Dev.* 36(1):87-91.
- Creaser, E. P. 1936. Crustaceans from Yucatan. In *Cenotes of Yucatan: A Zoological and Hydrographic Survey*, eds. A. S. Pearse, E. P. Creaser and F. G. Hall, 117-132. Washington: Carnegie Institution.
- Guerao, G., J. Pérez-Baquera and C. Ribera. 1994. Growth and reproductive biology of *Palaemon xiphias* Risso, 1816 (Decapoda: Caridea: Palaemonidae). *J. Crust. Biol.* 14(2):280-288.
- Hartnoll, R. G. 1982. Growth. In *The Biology of Crustacea: embryology, morphology and genetics*, ed. D. E. Bliss, 2:111-196. New York: Academic Press.
- Hartnoll, R. G. 1985. Growth, sexual maturity and reproductive output. In *Crustacean Issues: factors in adult growth*, ed. A. M. Wenner, 3:101-128. Rotterdam: A. A. Balkema.
- Hintze, J. 2004. NCSS and PASS: Number cruncher statistical systems. <http://www.ncss.com>. Kaysville, Utah.
- Hobbs III, H. H. 1979. Additional notes on cave shrimps (Crustacea, Atyidae and Palaemonidae) from the Yucatán Peninsula, México. *Proc. Biol. Soc. Wash.* 92(3):618-633.
- Hobbs III, H. H., and H. H. Hobbs, Jr. 1976. On the troglobitic shrimps of the Yucatán Peninsula, Mexico (Decapoda, Atyidae and Palaemonidae). *Smithson. Contrib. Zool.* 240:1-23.
- Hobbs, Jr. H. H., H. H. Hobbs III, and M. A. Daniel. 1977. A review of the troglobitic decapod crustaceans of the Americas. *Smithson. Contrib. Zool.* 244: 1-183.
- Holthuis, L. B. 1952. A general revision of the Palaemonidae (Crustacea, Decapoda, Natantia) of the Americas. II. The subfamily Palaemonidae. *Allan Hanc. Found. Publ., Occas. Pap.* 12:1-396.
- Holthuis, L. B. 1986. Decapoda. In *Stygofauna Mundi: A faunistic, distributional, and ecological synthesis of the world fauna inhabiting subterranean waters*, ed. L. Botosaneanu, 589-615. Amsterdam: Brill and Backhuys.
- Iliffe, T. M. 1993. Fauna troglobia acuática de la Península de Yucatán. In *Biodiversidad Marina y Costera de México*, eds. S. I. Salazar-Vallejo and E. González, 673-686. México: Comisión Nacional para el Conocimiento y Uso de la Biodiversidad and Centro de Investigaciones de Quintana Roo.
- Kim, S. 2005. Population structure, growth, mortality, and size at sexual maturity of *Palaemon gravieri*

- (Decapoda: Caridea: Palaemonidae). *J. Crust. Biol.* 25(2):226-232.
- Mariappan, P., and C. Balasundaram. 2004. Studies on the morphometry of *Macrobrachium nobilii* (Decapoda, Palaemonidae). *Braz. arch. biol. technol.* 47(3): 441-449.
- Mejía, L. M., F. Alvarez, and R. G. Hartnoll. 2003. A new species of freshwater prawn, *Macrobrachium totonacum* (Decapoda, Palaemonidae), with abbreviated development from Mexico. *Crustaceana* 76(1):77-86.
- Mossolin, E. C., and S. L. S. Bueno. 2003. Relative growth of the second pereopod in *Macrobrachium offersii* (Wiegmann, 1836) (Decapoda, Palaemonidae). *Crustaceana* 76(3):363-376.
- Pérez-Aranda, L. 1983a. Palaemonidae: *Creaseria morleyi*. *Fauna de los Cenotes de Yucatán*. 1:1-11. Mérida: Universidad de Yucatán.
- Pérez-Aranda, L. 1983b. Atyidae: *Typhlatya pearsei*. *Fauna de los Cenotes de Yucatán*. 3:1-11. Mérida: Universidad de Yucatán.
- Negreiros-Fransozo, M. L., and V. Fransozo. 2003. A morphometric study of the mud crab, *Panopeus austrobesus* Williams, 1983 (Decapoda, Brachyura) from a subtropical mangrove in South America. *Crustaceana* 76(3):281-294.
- Reddell, J. R. 1981. *A review of the cavernicole fauna of Mexico, Guatemala, and Belize*. Texas: Texas Memorial Museum.
- Román-Contreras, R., and L. S. Campos-Lince. 1993. Aspectos reproductivos y aproximación a un modelo de crecimiento para una población de *Macrobrachium acanthurus* (Wiegmann, 1836) en el río Palizada, Campeche, México. *An. Inst. Cienc. Mar Limnol. Univ. Nac. Auton. Mex.* 20(1):78-96.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry*. New York: W. H. Freeman and Company.
- Villalobos, J. L., F. Alvarez and T. M. Iliffe. 1999. New species of troglobitic shrimps from Mexico, with the description of *Troglomexicanus*, new genus (Decapoda: palaemonidae). *J. Crust. Biol.* 19(1):111-122.
- Walker, T. M., and G. C. B. Poore. 2003. Rediagnosis of *Palaemon* and differentiation of southern Australian species (Crustacea: Decapoda: Palaemonidae). *Mem. Mus. Vict.* 60(2):243-256.
- Wilkins, H. 1982. Regressive evolution and phylogenetic age: the history of colonization of freshwaters of Yucatan by fish and crustacea. *Ass. Mex. Cave Stud. Bull.* 8:237-243.
- Zar, J. H. 1999. *Biostatistical Analysis*. 4rd ed. New Jersey: Prentice Hall.