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Progressive troglomorphism of ambulatory and sensory appendages in three Mexican cave decapods

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Abstract

Sensory and ambulatory appendages were compared between epigeal and cave species of prawn and crayfish from Mexico. The cave prawn *Macrobrachium villalobosi* was compared with the epigeal *M. totonacum*. The cave crayfish *Procambarus cavernicola* and *P. oaxacae reddelli* were compared with the epigeal *P. olmecorum*. In both *Macrobrachium* and *Procambarus* the antennules and antennae of the cave species were longer in proportion to carapace length than in epigeal species. In the crayfish the cave species had a longer and narrower first pereopod, and also showed a greater development of setation on the antennules, antennae, and carapace. These are all considered examples of progressive troglomorphism. They will improve non-visual sensory capability in the aphotic and resource-poor cave environment.

Keywords: *Caves, decapods, morphological adaptations, progressive troglomorphism*

Introduction

Animals inhabiting caves have developed a variety of adaptations, or troglomorphisms, to better survive in this extreme environment. Some are regarded as progressive or constructive adaptations, such as enlargement of ambulatory, gnathal, and sensory appendages (Cooper 1969; Jones et al. 1992; Turk et al. 1996); increased setation to improve chemical receptor capacity (Allegrucci et al. 1992; Jones et al. 1992; Turk et al. 1996); development of specialized structures for lipid storage in the hepatopancreas (Vogt and Štrus 1992, 1999); increase of yolk in eggs to extend incubation time and decrease the larvae stages (Poulson and White 1969; Ueno 1987; Wilkens 1988, 1992; Culver et al.

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1995; Gillieson 1996); improved spatial orientation (Kellie et al. 2000; Li and Cooper 2001, 2002); and maximal feeding efficiency (Abele and Felgenhauer 1985).

Other adaptations involve the reduction or loss of structures, termed regressive evolution, regressive adaptation, or structural reduction (Lincoln et al. 1982; Banister 1984; Culver 1985; Kane and Richardson 1985). Examples include reduction or lack of pigmentation, reduction and loss of visual function, reduction of metabolic activity, and loss of the internal clock mechanism (Culver 1982; Hüppop 1985; Lamprecht and Weber 1985; Sket 1985; Camacho et al. 1992; Wilkens 1992).

This study presents an analysis of aspects of the morphology of three Mexican cave decapods from two families (Cambaridae and Palaemonidae) in comparison with epigeal congeners from the same areas. The two cave crayfish, *Procambarus cavernicola* Mejía-Ortiz et al., 2003 and *P. oaxacae reddelli* Hobbs, 1973a, are compared with the epigeal *P. olmecorum* Hobbs, 1987. The cavernicolous prawn *Macrobrachium villalobosi* Hobbs, 1973b is compared with the epigeal *M. totonacum* Mejía et al., 2003. The structures examined are those suspected as showing progressive troglomorphism, and possible causal factors are discussed. An earlier paper (Mejía-Ortiz and Hartnoll 2005) examined visual structures and pigmentation in the same crayfish species as examples of regressive troglomorphism.

Study area

The study area lies within the geological province of Cinturón Mexicano de Pliegues y Fallas, in the karst area of Sistema de la Sierra Madre del Sur, 18°15'–18°30'N, 96°30'–96°45'W (Figure 1). The following sites were sampled:

1. The Gabriel Cave in the Mojarra Hills, 18°27'25"N, 96°40'34"W, altitude 110 m. This is the habitat of *Procambarus cavernicola* and *Macrobrachium villalobosi* (Mejía-Ortiz et al. 2003).
2. The Mojarra Hill Stream, rising at 311 m, 18°25'6"N, 96°39'2"W. After flowing for approximately 500 m the waters vanish from the surface. The stream has a maximum width of 3 m, and several pools less than 1.5 m deep. During the dry season the stream disappears. This is the habitat of *Procambarus olmecorum*.
3. The San Antonio River Cave, entrance at 90 m, 18°28'8"N, 96°38'6"W. This cave is the habitat of *Procambarus oaxacae reddelli* and *M. villalobosi*.
4. The San Antonio River, emerging from the entrance to the San Antonio River Cave. The river forms a pool approximately 10 m wide at its origin (Mejía et al. 2003). This is the location of *Macrobrachium totonacum*.

Material and methods

The following material was collected at the above sites: *Procambarus oaxacae reddelli*, 29♀, 30♂; *P. cavernicola*, 68♀, 32♂; *P. olmecorum*, 64♀, 41♂; *Macrobrachium villalobosi*, 4♀, 2♂; and *M. totonacum*, 24♀, 8♂.

Specimens were sexed, and measured for total body length (TL), carapace length (CL), and length of antennules and antennae (right external branch). The first (crayfish) or second (prawns) pereopods were measured for length and width of palm (PL and PW), length of merus (M), carpus (C), propodus (P), and dactyl (D). All of the above were made with callipers to a precision of ± 0.01 mm.

Figure 1. Map of the study area in Oaxaca, Mexico. The four sampling sites are shown.

The above measurements were used to calculate a series of ratios: (1) total length/carapace length; (2) antennule length/carapace length; (3) antennal length/carapace length; (4) propodus length/carapace length; (5) palm length/palm width; (6) propodus length/dactyl length; (7) merus length/carpus length. These ratios were compared between sexes and species by *t*-test or ANOVA as appropriate.

The type and density of setae were examined on the antennules and antennae (*Macrobrachium* and *Procambarus*), and the carapace and dactyl of the third maxilliped (*Procambarus* only). An electron microscope was used for this (Hitachi Scan Electron 2460).

Results

Sexual dimorphism

In the three crayfish species there were no significant differences between sexes in any of the ratios. In *Macrobrachium totonacum* significant differences between sexes were found only for the ratios antennule/carapace length, antennae/carapace length and dactyl/palm length (Table I). Due to the small sample size for *M. villalobosi* it was not possible to examine sexual dimorphism.

Table I. *Macrobrachium totonacum*—comparison of proportions between females and males (mean values for the ratios are given for each sex, and the results of comparison by *t*-test).

Ratio	Females	Males	<i>P</i> value
Total length/carapace length	2.34	2.35	0.8213
Antennule/carapace length	1.10	1.50	0.0025 ^a
Antenna/carapace length	2.20	3.0	0.0025 ^a
Propodus/carapace length	0.43	0.41	0.068
Propodus/dactyl length	2.34	2.16	0.2747
Palm length/palm width	3.43	3.41	0.9094
Dactyl/palm length	0.72	0.88	0.0204 ^a
Merus/carpus length	0.88	0.81	0.1325

^aSignificantly different.

Comparison between species of Procambarus

Since the preceding analysis showed no significant differences between sexes, data from both sexes were combined for inter-specific comparison. For each ratio the mean values and results of the ANOVA are given in Table II. All were significantly different, except the ratio of total length/carapace length.

The ANOVA results were further examined by LSD tests. These showed that all three species differed significantly in the ratio of antennae/carapace length. However, in the other six ratios, *P. olmecorum* differed significantly from both *P. cavernicola* and *P. oaxacae reddelli*, but there were no significant differences between the latter two species.

Weight/length relationships were also compared. The regressions of wet weight on total length were as follows:

$$\begin{array}{ll} P. olmecorum & \log_{10} WW = -3.962 + 2.58 \log_{10} TL \\ P. oaxacae reddelli & \log_{10} WW = -5.132 + 3.28 \log_{10} TL \\ P. cavernicola & \log_{10} WW = -3.416 + 2.24 \log_{10} TL \end{array}$$

These regressions were used to calculate the weights for specimens of each species with a total length of 40 mm (a median value for the size ranges studied): the values were 1.49, 1.32, and 1.46 g, respectively.

Table II. Comparison of proportions between *Procambarus olmecorum*, *P. cavernicola*, and *P. oaxacae reddelli* (mean values are given for the ratios, and results of comparison by ANOVA).

Ratio	<i>P. olmecorum</i>	<i>P. cavernicola</i>	<i>P. oaxacae reddelli</i>	<i>P</i> value
Total length/carapace length	2.23 ± 0.369	2.19 ± 0.345	2.14 ± 0.113	0.251
Antennule/carapace length	0.37 ± 0.091	0.50 ± 0.118	0.50 ± 0.098	<0.0001 ^a
Antenna/carapace length	1.27 ± 0.363	1.66 ± 0.441	1.85 ± 0.354	<0.0001 ^a
Propodus/carapace length	0.48 ± 0.121	0.68 ± 0.155	0.69 ± 0.161	<0.0001 ^a
Propodus/dactyl length	1.82 ± 0.247	1.92 ± 0.190	1.88 ± 0.165	0.0052 ^a
Palm length/palm width	1.56 ± 0.372	2.29 ± 0.382	2.43 ± 0.398	<0.0001 ^a
Dactyl/palm length	1.07 ± 0.207	1.00 ± 0.247	0.99 ± 0.106	0.027 ^a
Merus/carpus length	1.83 ± 0.349	2.20 ± 0.436	2.10 ± 0.304	<0.0001 ^a

^aSignificantly different.

Comparison between species of *Macrobrachium*

Although there were some differences between sexes in *M. totonacum* (Table I), the small samples of *M. villalobosi* necessitated combination of data from both sexes for comparison between the two species (Table III). There were no statistical differences in the ratios of total length/carapace length, antennule length/carapace length, or palm length/palm width. *Macrobrachium totonacum* was significantly higher for the ratios propodus/dactyl length, and propodus/carapace length. *Macrobrachium villalobosi* was significantly higher for the ratios merus/carpus length, antennae/carapace length, and dactyl/palm length.

Studies of setation

Setation on the carapace and the dactyl of the third maxilliped are shown in Figure 2 for the three species of *Procambarus*. On the carapace there are numerous pinnate setae in all species (Figure 2A, B, D, E, G, H), but they are denser in the two stygobite species. The mean densities were four setae per mm for the epigeal *P. olmecorum*, compared with six setae per mm² for *P. oaxacae reddelli* and eight setae per mm² for *P. cavernicola*. The dactyl of the third maxilliped in *P. cavernicola* was longer and with abundant setation (Figure 2I), but in *P. oaxacae reddelli* (Figure 2F) and *P. olmecorum* (Figure 2C) it was shorter and with fewer setae.

On both the antennules and antennae the epigeal *P. olmecorum* (Figure 3A, B) had notably fewer setae than the stygobite species *P. cavernicola* (Figure 3C, D) and *P. oaxacae reddelli* (Figure 3E, F). Setae are particularly abundant on the antennae of *P. oaxacae reddelli*. However, differences were less apparent in the *Macrobrachium* species. The antennae were very similar in setation in the two species (Figure 3G, I). At the tip of the antennule *M. villalobosi* has more setae along the shaft (Figure 3J), whilst on *M. totonacum* they are concentrated on the apex (Figure 3H).

Discussion

Sexual dimorphism has been widely documented for epigeal crayfish and prawns (Weagle and Ozburn 1970; Lobao et al. 1986; Valenti et al. 1987, 1994; Hernández-Guzmán et al. 1999), notably in the proportions of the chelae. In the epigeal environment the main selective force that induces sexual differentiation in chelae is reproductive behaviour, since in general males show aggressive and dominant behaviour to conspecifics (Bovbjerg 1970;

Table III. Comparison of proportions between *Macrobrachium totonacum* and *M. villalobosi* (mean values are given for the ratios, and results of comparison by *t*-test).

Ratio	<i>M. totonacum</i>	<i>M. villalobosi</i>	<i>P</i> value
Total length/carapace length	2.34 ± 0.097	2.28 ± 0.109	0.1677
Antennule/carapace length	2.12 ± 0.456	2.55 ± 0.243	0.0527
Antenna/carapace length	2.40 ± 0.684	3.79 ± 0.218	<0.0001 ^a
Propodus/carapace length	0.41 ± 0.065	0.33 ± 0.032	0.00902 ^a
Propodus/dactyl length	2.21 ± 0.269	1.81 ± 0.253	0.0455 ^a
Palm length/palm width	3.42 ± 0.308	3.62 ± 0.226	0.1963
Dactyl/palm length	0.79 ± 0.140	1.05 ± 0.086	0.00380 ^a
Merus/carpus length	0.85 ± 0.095	0.75 ± 0.038	0.0411 ^a

^aSignificantly different.

Figure 2. Electron micrographs of carapace surface, magnification of surface, and dactyl of third maxilliped, respectively, of *Procambarus olmecorum* (A–C), *P. oaxacae reddelli* (D–F), and *P. cavernicola* (G–I).

Rabeni 1985; Söderbäck 1991). However, our results show no sexual differentiation for cave crayfish in the shape and size of chela (data were inadequate to test for sexual differences in the cave prawn studied). This is because the elongation of the chelae, that characterizes cave crayfish (Hobbs et al. 1977; Cooper and Cooper 1997), occurs similarly in both sexes. In the cave environment the main selective force driving the elongation of the ambulatory and sensory appendages is the limited availability of food, which is characteristic from these environments (Barr 1967; Poulson and White 1969; Sbordoni 1980; Culver 1982), a situation with equal influence on both females and males.

Hobbs et al. (1977) considered that cave crustaceans showed a more delicate construction than their epigeal relatives, because the cave species show ambulatory and sensorial appendages more slender than epigeal crustaceans. However, this study indicated that the cave species showed a similar construction of the body in comparison with their epigeal congeners, at least in terms of the total length/carapace length ratio. Nor did the weight/length relationships for the *Procambarus* species show consistently lower values for the cave species, though *P. oaxacae reddelli* is slightly lighter.

The main morphological differences observed between epigeal and cave species involved length of antennules and antennae, and length and proportions of the first (crayfish) or second (prawns) pereopods, structures of sensory importance in the cave environment. In

Figure 3. (A–F) Electron micrographs of segments from antennae (left column) and antennules external branch (right column), respectively, of *Procambarus olmecorum* (A, B), *P. cavernicola* (C, D), and *P. oaxacae reddelli* (E, F); (G–J) electron micrographs of segments of antennae (left column) and tip of antennules (right column), respectively, of *M. totonacum* (G, H) and *M. villalobosi* (I, J).

both *Macrobrachium* and *Procambarus* the antennules and antennae of the cave species studied here are longer in proportion to carapace width than in the epigeal species. In the *Macrobrachium* spp. there are differences in the proportions of the second pereopod, but the pattern is not clear. However, in *Procambarus* the cave species have a longer and narrower first pereopod. In *Procambarus* the cave species also show a greater development of setation on the antennules, antennae, and carapace.

Such modifications, which will improve sensory capability, have been considered as progressive troglomorphism (Cooper 1969; Jones et al. 1992; Turk et al. 1996). Culver (1987) stated that the more highly cave adapted species should have relatively longer antennae, as seen here. In a comparison of cave and surface-dwelling species of the crayfish *Orconectes*, Ziemba et al. (2003) found longer antennules in the cave species. Possibly *P. oaxacae reddelli* shows a more progressive troglomorphism than *P. cavernicola*: their sensory setae are more abundant, the ratio between antennal length and carapace length is greater, and the chelae are narrower (though the last two differences were not found significant). There are clear examples of progressive troglomorphism in the cave crayfish studied, complementing the regressive troglomorphism earlier described in the same species (Mejía-Ortiz and Hartnoll 2005).

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