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Research Article

Phylogenetic relationships among the freshwater genera of palaemonid shrimps (Crustacea: Decapoda) from Mexico: evidence of multiple invasions?

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ABSTRACT. Palaemonid shrimps form a large and diversified group distributed primarily in marine waters. Within the family Palaemonidae the subfamily Palaemoninae is composed of 26 genera and more than 370 species inhabiting marine and fresh waters in epigean and hypogean habitats. One of the relevant questions that have emerged in relation to the subfamily is how the invasion to freshwater has occurred in Mexico, where six freshwater genera belonging to the Palaemoninae (*Creaseria, Cryphiops, Macrobrachium, Palaemonetes, Neopalaemon* and *Troglomexicanus*), are present. The purpose of this study was to explore the relationships among these freshwater lineages through a phylogenetic analysis based on partial sequences of the 16S mitochondrial gene to elucidate if these genera are closely related and derived from a common ancestor or if each lineage has invaded the freshwater habitat independently. The analysis included species representing monotypic and diversified genera, from epigean and hypogean habitats and with complete and abbreviated larval development. The results suggest that the invasion of freshwater occurred on four different occasions and that the different lineages originated before the invasions of freshwater occurred.

Keywords: Palaemoninae, freshwater invasion, 16S mtDNA, phylogeny, Mexico.

Relaciones filogenéticas entre los géneros de camarones palaemónidos de agua dulce (Crustacea: Decapoda) de México: ¿evidencia de invasiones múltiples?

RESUMEN. Los camarones palaemónidos forman un grupo grande y diversificado distribuido principalmente en el ambiente marino. Dentro de la familia Palaemonidae la subfamilia Palaemoninae está formada por 26 géneros y más de 370 especies que habitan aguas marinas y dulces en hábitats epigeos e hipogeos. Una de las preguntas relevantes que ha emergido en relación a la subfamilia Palaemoninae es cómo ha ocurrido la invasión de especies en agua dulce, que en México, está representada por seis géneros dulceacuícolas (*Creaseria, Cryphiops, Macrobrachium, Palaemonetes, Neopalaemon* y *Troglomexicanus*). El propósito de este estudio es explorar las relaciones entre estos linajes dulceacuícolas mediante un análisis filogenético basado en secuencias parciales del gen 16S mitocondrial para determinar si estos géneros están cercanamente relacionados y derivan de un ancestro común o si cada linaje ha invadido el agua dulce independientemente. El análisis incluye especies que representan un género diversificado y monotípico, de hábitats epigeos e hipogeos, con desarrollo larval extendido y abreviado. Los resultados sugieren que la invasión del agua dulce ocurrió en por lo menos cuatro ocasiones diferentes y que los diferentes linajes se originaron antes de que la invasión del agua dulce ocurriera.

Palabras clave: Palaemoninae, invasión del agua dulce, 16S mtADN, filogenia, México.

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INTRODUCTION

The crustacean family Palaemonidae with more than 930 species is predominantly marine, but includes several important freshwater genera such as *Macrobrachium* Bate, 1868 (De Grave *et al*., 2009). The family is divided into the subfamilies Pontoniinae and Palaemoninae, the latter composed by 26 genera and more than 370 species, present in marine and freshwater environments, and inhabiting both epigean and hypogean water bodies (Jayachandran, 2001; De Grave *et al*., 2009).

A relevant topic in the evolution of this group is the invasion of freshwater (Ashelby *et al*., 2012), since typically freshwater epigean palaemonids, such as *Macrobrachium*, are dependent to a certain degree of marine or brackish waters to complete their larval development. However, a number of species in the subfamily are strictly freshwater inhabitants with populations completely isolated from brackish or marine waters, with reduced dispersal capabilities and often spatially constrained by geographic barriers. The strictly freshwater species have an abbreviated or partially abbreviated larval development with a reduced number of larval stages and fewer and relatively large eggs, allowing for the entire life cycle to take place in freshwater (Alvarez *et al*., 2002; Mejía *et al*., 2003).

In Mexico six genera of freshwater shrimps belonging to the subfamily Palaemoninae are distributed, creating a unique area of diversification along the Gulf of Mexico slope. These genera include endemic species with distribution ranges restricted to one or few sites (Fig. 1).

1. *Creaseria* Holthuis, 1950. Monotypic genus that includes *Creaseria morleyi* Creaser, 1936, with a wide-ranging distribution in the Yucatan Peninsula, inhabiting caves and sinkholes. *C. morleyi* is a strictly freshwater species with abbreviated development; it co-occurs with other cave crustaceans in the freshwater part of anchialine habitats. *Creaseria* is morphologically close to *Palaemon* (Iliffe, 1993).
2. *Cryphiops* Dana, 1852. Constitutes a freshwater genus that includes five hypogean species. The Mexican species are *C.* (*Bithynops*) *luscus* Holthuis, 1973 (Gruta del Arco, Rancho de San Rafael del Arco, La Trinitaria, Chiapas), *C.* (*B.*) *perspicax* Holthuis, 1977 (Cenote La Cueva, Chincultik ruins, Montebello lake district, La Trinitaria, Chiapas) and *C.* (*B.*) *villalobosi* Villalobos, Nates & Cantú, 1989, from rivers and streams in the Ocosingo valley, Chiapas (Villalobos *et al*., 1989). *Cryphiops* is morphologically related to *Macrobrachium* (Holthuis, 1952).
3. *Neopalaemon* Hobbs, 1973. A monotypic genus morphologically close to *Macrobrachium*, whose single described species *N. nahuatlus* Hobbs, 1973, is known only from the type locality in the Mexican state of Oaxaca (Cueva del Guano); it is a stygobitic population (Hobbs *et al*., 1977).
4. *Troglomexicanus* Villalobos, Alvarez & Iliffe, 1999. This genus comprises three freshwater hypogean species distributed in Mexican caves. It is closely related to *Troglocubanus* Villalobos, 1971, but the main difference resides in the lack of dorsal spines in the rostrum of the Mexican species. The species of *Troglomexicanus* are *T. perezfarfantae* Villalobos, 1971 (Sótano de la Tinaja, San Luis Potosí), *T. tamaulipasensis* Villalobos, Alvarez & Iliffe, 1999 (Cueva del Nacimiento del Río Frío, Tamaulipas) and *T. huastecae* Villalobos, Alvarez & Iliffe, 1999 (Manantial de San Rafael, San Luis Potosí) (Villalobos *et al*., 1999).
5. *Macrobrachium*. Represents the most species-rich genus in the subfamily with more than 240 described species (De Grave & Fransen, 2011), mainly distributed in tropical and subtropical waters. Most of the species have an extended larval development dependent on estuarine or brackish waters to be completed (Jayachandran, 2001). The Mexican strictly freshwater species from hypogean waters are *M. villalobosi* Hobbs, 1973 (Río San Antonio, Oaxaca) and *M. acherontium* Holthuis, 1977 (Grutas de Coconá, Tabasco); while *M. tuxtlaense* Villalobos & Alvarez, 1999 (streams of Laguna de Catemaco, Veracruz); *M. vicconi* Román, Ortega & Mejia, 2000 (Río Perlas, Chiapas); and *M. totonacum* Mejía, Alvarez & Hartnoll, 2003 (Río San Antonio, Oaxaca) are epigean species (Villalobos & Alvarez, 1999; Mejía *et al*., 2003).
6. *Palaemonetes* Heller, 1869. This genus groups around 30 species of brackish and freshwater shrimps distributed in tropical and subtropical waters around the world. *Palaemonetes* is morphologically close to *Calathaemon* (Bruce & Short, 1993). In Mexico five epigean freshwater species occur: *P. suttkusi* Smalley, 1964 (Cuatro Ciénegas, Coahuila); *P. mexicanus* Strenth, 1976 (Río Coy, San Luis Potosí; Rodríguez-Almaraz *et al*., 2010); *P. hobbsi* Strenth, 1994 (Río Mante, San Luis Potosí); *P. lindsayi* Villalobos & Hobbs, 1974 (La Media Luna, San Luis Potosí) and *P. kadiakensis* Rathbun, 1902, from Tamaulipas, Nuevo León and Veracruz (Strenth, 1994; Rodríguez-Almaraz & Muñiz-Martínez, 2008) (Fig. 1).

The purpose of this study was to explore the origin and evolution of the strictly freshwater shrimps in the subfamily Palaemoninae, which represent six genera occurring in Mexico, using a phylogenetic analysis based on partial sequences of the 16S mtDNA gene. The main question to be addressed is if the invasion of freshwater occurred once and then a secondary radiation, already in freshwater, produced the different genera that are distributed in Mexico or if several

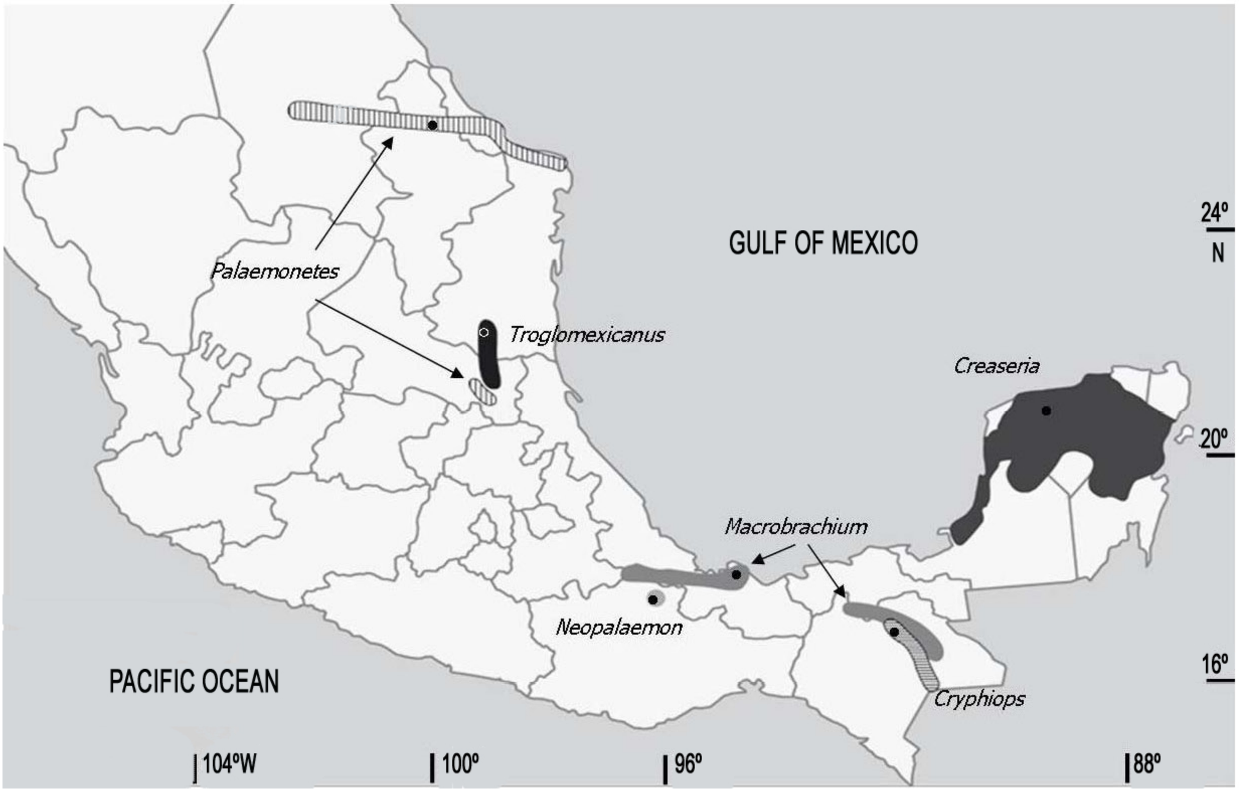

Figure 1. Distribution ranges of the strictly freshwater genera of the subfamily Palaemoninae in Mexico. circles correspond to the collection sites.

different invasions, from different lineages, have occurred producing a wide an interesting convergence.

MATERIALS AND METHODS

Samples and sequences

Twenty-two species belonging to ten genera from the subfamily Palaemoninae, including monotypic and specious genera, epigean and hypogean species, as well as species with extended and abbreviated development were selected. *Euryrhynchus wrzesniowskii* Miers, 1877, family Euryrhynchidae and *Gnathophylloides mineri* Schmitt, 1933, family Gnathophyllidae, were chosen as out-group's. The tissue samples used for sequencing for the following species were obtained from specimens deposited in the National Crustacean Collection (CNCR) of the Institute of Biology, National Autonomous University of Mexico: *Creaseria morleyi*, *Cryphiops luscus*, *C. villalobosi*, *Macrobrachium acanthurus* (Wiegmann, 1836), *M. tenellum* (Smith, 1871), *M. tuxtlaense*, *Neopalaemon nahuatlus*, *Palaemon northropi* (Rankin, 1898), *P. ritteri* Holmes, 1895, *Palaemonetes suttkusi* and *Troglomexicanus tamaulipasensis*. The sequences for the following species were obtained from the GenBank: *Macrobrachium rosenbergii* (De Man, 1879) (Australia); *M. rosenbergii* (Thailand); *Palaemon longirostris* H. Milne-Edwards, 1837; *P. pandaliformis* (Stimpson, 1871); *P. serenus* Heller, 1868; *P. intermedius* (Stimpson, 1860); *Palaemonetes atrinubes* (Dakin, 1915); *P. australis* (Bray, 1976); *Periclimenaeus wilsoni* (Hay, 1917); *Pontonia manningi* Fransen, 2000; *Pseudopalaemon chryseus* Kensley & Walker, 1982, *Euryrhynchus wrzesniowskii* and *Gnathophylloides mineri* (Table 1). Total DNA was extracted from the abdominal muscular tissue following the standard phenol-chloroform method (Hillis *et al*., 1996). A polymerase chain reaction (PCR) (Saiki *et al*., 1988), was performed to amplify one fragment of the ribosomal mitochondrial gene 16S rRNA. The primers used were 16Sar (5′-CGC CTG TTT ATC AAA AAC AT-3′) and 16Sbr (5′-CCG GTT TGA ACT CAG ATC ATG-3′) (Schubart *et al*., 2000). PCR amplification was carried out with an initial denaturation step at 92°C for 90 s, followed by 35 cycles at 92°C for 60 s, annealing temperature of 50°C for 60 s, and extension temperature of 72°C for

Table 1. Species included in the phylogenetic study, with their: distribution, type of larval development, habitat and CNCR/GenBank accession number.

Species	Distribution	Larval development	Habitat	Accession number
Creaseria				
C. morleyi	Yucatan Peninsula, Mexico	Abbreviated	Stygobitic	CNCR 22723 / JF491337
Cryphiops				
C. luscus	Chiapas, Mexico	Abbreviated	Stygobitic	CNCR 5759 / JF491343
C. villalobosi	Chiapas, Mexico	Abbreviated	Freshwater	CNCR 5760 / JF491348
Euryrhynchus				
E. wrzesniowskii	Guyana, Surinam and Brazil	Abbreviated	Freshwater	EU868654
Gnathophylloides				
G. mineri	Circumtropical	Extended	Marine	EU868659
Macrobrachium				
M. acanthurus	Georgia, U.S.A. to Brazil	Extended	Estuarine	CNCR 21758 / JF491345
M. tenellum	Baja California to Peru	Extended	Brackish	CNCR 22025 / JF491347
M. tuxtlaense	Veracruz, Mexico	Abbreviated	Freshwater	CNCR 13175 / JF491346
M. rosenbergii Australia	Indo-Pacific	Extended	Brackish	AY203920
M. rosenbergii Thailand	Indo-Pacific	Extended	Brackish	AY203911
Neopalaemon				
N. nahuatlus	Oaxaca, Mexico	Abbreviated	Stygobitic	CNCR 4396 / JF491338
Palaemon				
P. northropi	Atlantic	Extended	Coastal	CNCR 20747 / JF491339
P. longirostris	Europe	Extended	Estuarine	AJ640129
P. pandaliformis	Guatemala to Brazil	Extended	Estuarine	JF491340
P. ritteri	California, U.S.A. to Peru	Extended	Estuarine	CNCR 21015 / JF491341
P. serenus	Australia	Extended	Coastal	AF439518
P. intermedius	Australia	Extended	Marine	AF439516
Palaemonetes				
P. atrinubes	Australia	Extended	Brackish	AF439520
P. australis	Australia	Extended	Brackish	AF439517
P. suttkusi	Coahuila, Mexico	Abbreviated	Freshwater	CNCR 326 / JF491336
Periclimenaeus				
P. wilsoni	Gulf of Mexico	Extended	Marine	EU868702
Pontonia				
P. manningi	East and West Atlantic	Extended	Marine	EU868705
Pseudopalaemon				
P. chryseus	Brazil	Abbreviated	Freshwater	JF491342
Troglomexicanus				
T. tamaulipasensis	Tamaulipas, Mexico	Abbreviated	Stygobitic	CNCR 17030 / JF491344

90 s. This was followed by an additional extension for 180 s at 72°C. PCR products were purified using a Qiagen QIAquick PCR Purification Kit, and cycle-sequencing reactions were run with purified PCR products and the BigDye Terminator Kit on a Millipore Thermocycler. Reactions were cleaned using Sephadex columns and then sequenced using an ABI Prism 3100 automated DNA sequencer (Hillis *et al*., 1996).

Sequences were aligned using MAFFT software (Katoh *et al*., 2005), and visualized with BioEdit (Hall, 1999). The best evolutionary model for the nucleotide alignment was estimated using jModel Test assuming the Bayesian Information Criterion (BIC), in order to obtain the appropriate parameters to be considered in further analyses (Posada, 2008).

Phylogenetic analysis

The phylogenetic reconstruction involved the use of several approaches: maximum parsimony (MP), distance (neighbour joining NJ), maximum likelihood (ML) and Bayesian inference. The first three methods were run in PAUP version 4 (Swofford, 2002). For MP and ML we used a heuristic search adding sequences randomly and testing branch support with a 1000 resampling bootstrap. Bayesian analyses were run with MrBayes 3.2 (Ronquist *et al*., 2012). Each Bayesian search performed two independent runs starting with default prior values, random trees and three heated and one cold Markov chains that run for a million generations and sampled every 1000 generations to yield a posterior probability distribution of 1000 trees. After eliminating the first 250 trees as "burn-in", we constructed a 50% majority-rule consensus tree with nodal values representing the posterior probability of every recovered clade. The convergence of all parameters of the two independent runs was also assessed using the program Tracer 1.5 (Rambaut & Drummond, 2007). The different topologies were compared and a 50% consensus tree using PAUP was obtained.

RESULTS

Sequences

A total of 24 sequences were analyzed, including out-group, resulting in an alignment of 445 base pairs showing 227 variable sites. Nucleotide frequencies in the data matrix were A = 0.3246, G = 0.1841, C = 0.0812, and T = 0.4102. The evolutionary model that best fit the 16S sequences according to jModel Test with the BIC, was GTR+G+I (General Time Reversible plus gamma parameter $\gamma = 0.39$ plus invariable proportion sites I = 0.258) (Tavaré, 1986).

Phylogenetic analysis

The Bayesian consensus topology represented the phylogenetic relationships among members of the subfamily Palaemoninae. In this representation a basal clade grouping *Creaseria* and *Neopalaemon* is formed. Another two clearly separated clades result: the first one composed by *Palaemon* and *Palaemonetes*, and the second one divided in three groups: one includes the species of *Macrobrachium* with extended larval development, a second one comprises *Cryphiops*, *Macrobrachium* species with abbreviated larval development and *Pseudopalaemon*, and the third one corresponded to *Troglomexicanus* (Fig. 2).

DISCUSSION

The present study analyses the relationships among the strictly freshwater shrimps of the subfamily Palaemoninae distributed in Mexico considering also species of *Macrobrachium* with extended larval development, *Palaemonetes* from estuarine habitats, and the related genera *Palaemon* and *Pseudopalaemon*. The taxon sampling for this analysis was based on the close morphological and genetic relationships among these genera (Boulton & Knott, 1984; Murphy & Austin, 2003).

The obtained topology shows a basal group formed by *Creaseria* and *Neopalaemon*, both genera are monotypic and stygobitic, occurring throughout the Yucatan Peninsula and in northern Oaxaca, respectively (Hobbs *et al*., 1977; Alvarez & Iliffe, 2008). Similar to our result, Porter *et al.* (2005) obtained also a very early split of the ancestors of *Creaseria* from the *Macrobrachium*/*Cryphiops* and the *Palaemon*/*Palaemonetes* groups. Although the lineage from which *Creaseria* derives may be very old (Porter *et al*., 2005), *C. morleyi* probably evolved in the last 1-5 million years in which time the Yucatan Peninsula emerged and the first caves composing the current anchialine systems were formed (Beddows, 2003; Botello & Alvarez, 2010). Morphologically, *Creaseria* and *Neopalaemon* are very similar, differing in a few characters such as the hepatic and branchiostegal spines on the carapace, the setation of the fifth pereiopod and the shape of the telson and uropods (Hobbs *et al*., 1977).

The next division shows the separation of the *Macrobrachium*/*Cryphiops* and the *Palaemon*/*Palaemonetes* lines. In the former group *Troglomexicanus tamaulipasensis* clearly stands apart from the rest of the species. *Troglomexicanus* is closely related to *Troglocubanus*, which occurs in Cuba with four species and in Jamaica with a single species (Villalobos *et al*., 1999). Several authors agree in that both genera probably had the same marine ancestor (Villalobos, 1971; Hobbs *et al*., 1977; Villalobos *et al*., 1999). Villalobos (1971) proposed a Cretaceous origin for *Troglomexicanus* considering the probable time of formation of the Sierra del Abra in Tamaulipas, Mexico, where it occurs, while Chace & Hobbs (1969) proposed a Miocene origin for *Troglocubanus* with separate invasions of Cuba and Jamaica.

In the other section of the clade, *M. tuxtlaense* appears closely related to *Cryphiops villalobosi*, *C. luscus* and *Pseudopalaemon chryseus*, all of which are strictly freshwater species with abbreviated development. The close relationship between *Macrobrachium* and *Cryphiops* has already been described by Pileggi & Mantelatto (2010), whose results of a phylogenetic analysis show *C. brasiliensis* and *C. caementarius* completely nested within the diversity of species of *Macrobrachium*. However, it is interesting to note that *M. tuxtlaense* appears in our analysis more closely related to *P. chryseus* than to *Cryphiops* spp., even when important morphological differences, such as the presence of a mandibular palp in *Macrobrachium* and

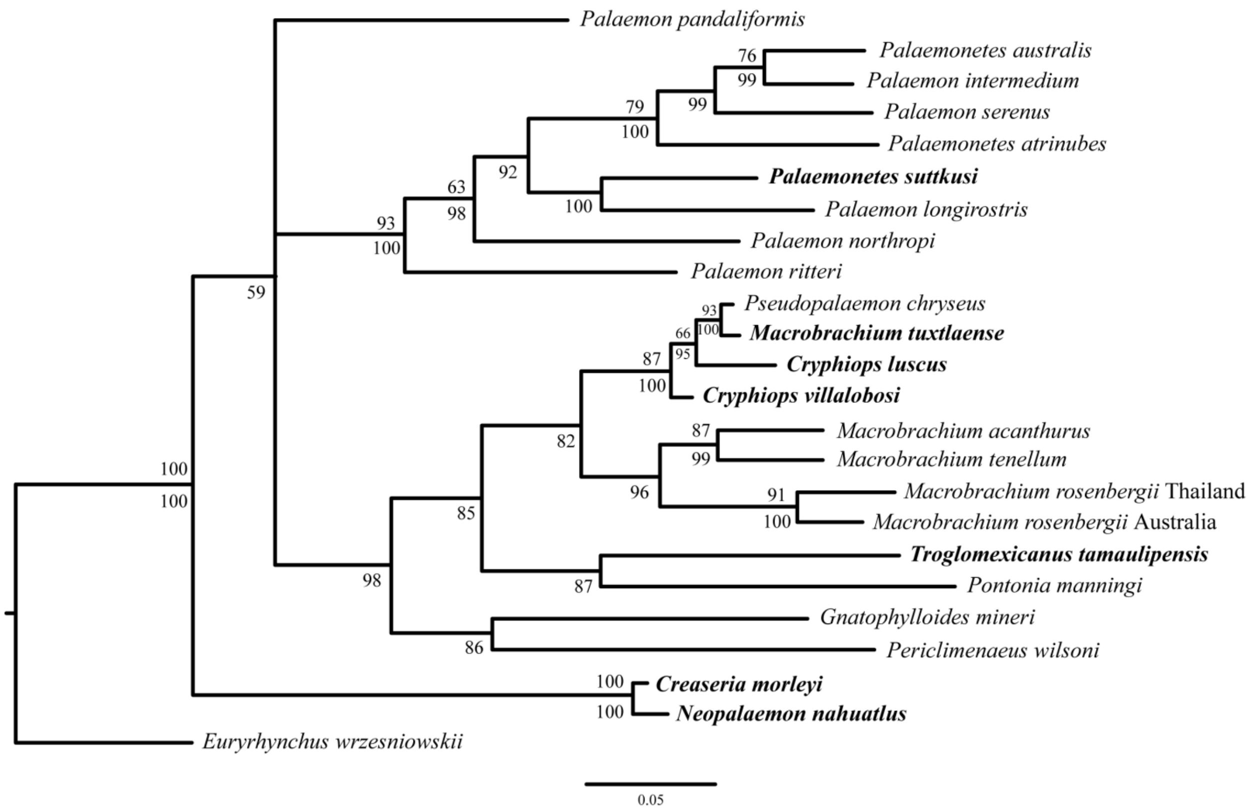

Figure 2. Consensus topology from the Bayesian analysis. Bootstrap values in the superior part of the branches. Posterior probabilities expressed as percentages in the inferior part; only values above 50% are included. The strictly freshwater species from Mexico appear in bold.

its absence in *Pseudopalaemon*, clearly separate them. *Macrobrachium acanthurus*, *M. tenellum* and *M. rosenbergii*, all with extended larval development for a different grouping.

The *Palaemon*/*Palaemonetes* clade confirms their morphological similarity showing the mixing of species of both genera (Walker & Poore, 2003). Porter *et al*. (2005) hypothesized that the split of the *Palaemon*/*Palaemonetes* lineage from the *Macrobrachium*/*Cryphiops* line occurred in early Cretaceous times. Both genera are cosmopolitan with brackish and fresh water species (Jayachandran, 2001). It is noteworthy that even within this clade, the two strictly freshwater species, *P. australis* and *P. suttkusi*, are situated in different branches, the former one grouped with the Australian species and the latter one with a European and the American species. *Palaemonetes suttkusi*, and the rest of the Mexican freshwater *Palaemonetes*, inhabits rivers that flow into the Gulf of Mexico. For this reason it is possible that the ancestor of these species belonged to the coastal Cretaceous fauna, and that its diversification was related to the uprising of the Sierra Madre Oriental that began about 70 mya (Cevallos-Ferriz & González-Torres, 2006).

The placement of the Mexican freshwater palaemonid shrimps in different branches of the obtained phylogeny and the proposed times of separation of the different lineages involved, suggest that the invasion of freshwater occurred at least four times corresponding to the ancestors of: (1) *Creaseria* and *Neopalaemon*; (2) *Troglomexicanus*; (3) *Macrobrachium* and *Cryphiops*; and (4) *Palaemonetes*. Murphy & Austin (2005) found that the presence of abbreviated development in a large set of *Macrobrachium* species did not have any relation to the phylogeny of the group, indicating a widespread convergence to solve the problems imposed by the freshwater habitat. In the present contribution this widespread convergence is extended to include species from another five genera, all of which display large eggs and abbreviated development. Thus the initial capability to invade the freshwater habitat must have been present in the ancestor of all of these different lineages, which Porter *et al*. (2005) hypothetically situate in early Cretaceous times.

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