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Phylogeny of *Calyptraeotheres* Campos, 1990 (Crustacea, Decapoda, Brachyura, Pinnotheridae) with the description of *C. pepeluisi* new species from the tropical Mexican Pacific

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Abstract

A reassessment of the adult and larval morphology as well as comparison with published molecular information confirms the monophyly of the genus *Calyptraeotheres* Campos, 1990, and its relationship with *Dissodactylus* Smith, 1870, *Clypeasterophilus* Campos & Griffith, 1990 and *Tumidotheres* Campos, 1990. *Calyptraeotheres pepeluisi* **new species**, is described from Michoacán, Mexico on the basis of a female specimen. The new species is distinguished from the other nominal species of the genus by having a subarcuate carapace with longer setae on its front and anterolateral margin, the eyes are dorsally visible, and a third maxilliped with a 2-segmented palp and a conical propodus.

Key words: Decapoda, Crustacea, Brachyura, Pinnotheridae, *Calyptraeotheres*, phylogeny, new species, Mexico

Introduction

The genus *Calyptraeotheres* Campos, 1990 comprises four species of pinnotherid crabs associated with limpets of the superfamily Calyptraeidea (*Crepidula* Lamarck, 1799, *Calyptraea* Lamarck, 1799 and *Crucibulum* Schumacher, 1817) (see Campos 1990, 1999; Hernández-Ávila & Campos 2006). Among the pinnotherids deposited in the National Crustacean Collection of the Universidad Nacional Autónoma de Mexico (CNCR), the first author discovered an ovigerous female that was collected off the coast of Michoacán, in the Pacific coast of Mexico. The morphology of this specimen concurs with *Calyptraeotheres*, and it was shown that the material belonged to a new species, related to *C. hernandezi* Hernández & Campos, 2006, and *C. granti* (Glassell, 1933). These three species share a third maxilliped with the palp of the endopod having only two segments (the dactylus is absent). An empirical and cladistic reassessment of the adult and larval morphology, respectively, and the comparison with the results provided from molecular data (Palacios-Theil *et al.* 2009) allow us to examine the monophyly of *Calyptraeotheres* and its presumptive phylogenetic relationships with alien genera.

Material and methods

The female holotype of *Calyptraeotheres pepeluisi* **new species** was dredged during the oceanographic expedition Atlas IV in July 1983 on board of the R/V El Puma of the Universidad Nacional Autónoma de México (UNAM). The holotype is deposited in the National Collection of Crustacean (CNCR) of the Instituto de Biología, UNAM. Abbreviations used include CL, carapace length; CW, carapace width; MXP3, third maxilliped; WL, walking legs; All measurements are in millimeters.

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Cladistic analysis. We conducted a new analysis with updated data on larval morphology compiled by Marques and Pohle (1995) (see corrections, deletions and additions in Table1). We rely on available literature and in actual zoeae hatched during field trips to San Felipe, Baja California, Mexico (*Fabia carvachoi* Campos, 1996, *Juxtafabia muliniarum* (Rathbun, 1918), *Austinotheres angelicus* (Lockington, 1877), *Calyptraeotheres granti* (Glassell, 1933) and Tortugas bay, Baja California Sur, Mexico (*F. subquadrata* Dana, 1851, *Bonita mexicana* Campos, 2009). For the present analysis, some species were united into 7 subgroups based on shared zoeal morphology (Table 1). The genus *Asthenognathus*, included in the Varunidae by Ng *et al.* (2008), was used as the outgroup. The computer program PAUP (Phylogenetic Analysis Using Parsimony, version 4.0b10; Swofford 2002) was used to process the data matrix. Bootstrap method with heuristic search analyses using parsimony as optimality criterion were performed with the following options in effect: 1000 bootstrap replicates; starting seed , 1; addition sequence, simple; one tree held at each step during stepwise addition; tree-bisection-reconnection (TBR) branch-swapping performed; MULPARS option activated; steepest descent option inactive; branches collapsed (creating polytomies) if maximum branch length is zero: topological constraints not enforced; trees unrooted; 'MulTrees' option in effect; accelerated transformation (ACCTRAN) was used as character-state optimization. All the characters were equally weighted, unordered and uninformative character 4 was deleted during the analysis. During the first part of the analysis, groups occurring at frequencies less than 50% (CONLEVEL default) were retained. During the second part of the analysis, *a posteriori* analysis was performed reweighting characters according their rescaled consistency index (RC). At the end, groups occurring in bootstrap frequencies less than 50% were collapsed.

TABLE 1. States of 7 morphological zoeal characters taken from Marques & Pohle (1995). We refer to this article for a full explanation of character states. *Buergeres holothuriae (Semper, 1880)* was omitted due to the inexactness of the original description and illustration. *Neoxenophtalmus garthi* was removed since it belongs in the family Ocypodidae (see Ng, et al, 2008). *Arcotheres rhombifer* is a senior synonym of *Pinnotheres latissimus* Bürger, 1895 (see, Ahyong & Ng 2007). Species and characters in bold were added or corrected from the original matrix (Marques & Pohle 1995) as indicated. [1]personal observations; [2]Bolaños *et al.* 2005; [3]Costlow & Bookhout 1966; [4]Gohar & Al-Kholy 1957; [5]Hong 1986; [6]Konishi 1981; [7]Saelzer & Hapette 1986;[8]Ocampo *et al.* 2010.

Species/group		Character states
Asthenognathus atlanticus Monod, 1933		00?0 000
Gemmotheres chamae (Roberts, 1975)		4121 043
Pseudopinnixa carinata Ortmann, 1894		211? 000
Fabia carvachoi Campos, 1996		2121 230
F. subquadrata Dana, 1851		2121 220
Juxtafabia muliniarum (Rathbun, 1918)		2121 220
Parapinnixa affinis Holmes, 1900		40?? 313
Pinnotheres taylori Rathbun, 1918		3121 055
Sakaina japonica Serène, 1964		2011 313
Tunicotheres moseri (Rathbun, 1918)		3131 053
Pinnotherid I	*Nepinnotheres pinnotheres* (Linnaeus, 1758)	4121 040
	***Ostracotheres tridacnae* (Rüppell, 1830)[4]**	**4**221 040
Pinnotherid II	***Austinotheres angelicus* (Lockington, 1877)[1]**	412**1** 041
	***Bonita mexicana* Campos, 2009[1]**	**4121 041**
Pinnotherid III	*Arcotheres modiolicola* (Bürger, 1895)	4121 042
	Arcotheres placunae (Hornell & Southwell, 1909)	4121 042
	Pinnotheres hickmani (Guiler, 1950)	???1 042
	P. pholadis De Haan, 1835	4121 042

continued next page

TABLE 1. (continued)

Species/group		Character states
	P. pisum (Linnaeus, 1767)	4121 042
	P. vicajii Chhapgar, 1957	41?1 042
	Viridotheres gracilis (Bürger, 1895)	4121 042
Pinnotherdi IV	***Arcotheres rhombifer* (Bürger, 1895)**	41?1 044
	A. aff. sinensis (Shen, 1932)	4121 044
	A. sinensis (Shen, 1932)	4121 044
	Nepinnotheres novaezelandiae (Filhol, 1885)	???1 044
	***Orthotheres barbatus* (Desbonne, 1867)**[2]	**4121 044**
	P. boninensis Stimpson, 1858	4121 044
	P. ridgewayi Southwell, 1911	4121 044
	Zaops ostreum (Say, 1817)	4121 044
Pinnotherid V	***Calyptraeotheres granti* (Glassell, 1933)**[1]	212**1** 010
	***C. politus* (Smith, 1870)**[1]	212**1** 010
	***C. garthi* (Fenucci, 1975)**[8]	212**1** 010
	Clypeasterophilus rugatus (Bouvier, 1917)	2121 010
	C. stebbingi (Rathbun, 1918)	2121 010
	Dissodactylus crinitichelis Moreira, 1901	2121 010
	D. lockingtoni Glassell, 1935	2121 010
	D. mellitae (Rathbun, 1900)	2121 010
	D. nitidus Smith, 1870	2121 010
	D. primitivus Bouvier, 1917	2121 010
	D. xantusi Glassell, 1936	2121 010
	***Pinnaxodes chilensis* (H. Milne Edwards, 1837)**[7]	212**1** 010
	***P. major* Ortmann, 1894**[5]	212**1** 010
	***P. mutuensis* Sakai, 1939**[6]	212**1** 010
	***Tumidotheres maculatus* (Say, 1818)**[3]	212**1** 010
Pinnixid I	*Austinixa cristata* (Rathbun, 1900)	21?? 230
	Pinnixa chaetopterana Stimpson, 1860	21?? 230
Pinnixid II	*P. cylindrica* (Say, 1818)	21?? 220
	P. longipes (Lockington, 1876)	2121 220
	P. aff. rathbunae Sakai, 1934	2121 220
	P. rathbunae Sakai, 1934	2121 220
	P. sayana Stimpson, 1860	21?? 220

Character 1. First zoea: antennal morphology: 0, with a protopodite and segmented endopodite; 1, with an unsegmented endopodite; 2, without endopodite and tapered protopodite with two rows of spinules distally; 3, has a much reduced protopodite with a short process; 4, with an extremely reduced bud-like protopodite, or it is considered absent.

Character 2. Zoeal stages: endopodite segmentation of the second maxilliped . 0, with three articles, 1; two articles; and 2, one article.

Character 3. Zoeal stages: endopodite setation of the maxilla (Fig. 3A–C). 0, 5 setae; 1, 4 setae; 2, 3 setae.

Character 4. Zoeal stages: number of abdominal somites. 0, 6 somites; 1, 5 somites.

Character 5. Zoeal stages: shape of the fifth abdominal somite (Fig. 5A–C). 0, no expansion; 1, slightly laterally expanded, 2, markedly laterally expanded.

Character 6. Zoeal stages: shape of the telson. Five types of telson were found among pinnotherid zoeae. 0, bifurcated and elongated. Its furcal shafts are very long, about 2/3 or more of the telson's length; 1, **bifurcated and elongated but the furcal shafts are less developed, representing about 1/2 of the total length of the telson**; 2, the whole telson is more compact and not as elongated as the previous; 3, similar than anterior but with a median projection on the furcal arch; 4, somewhat rounded, but the furcal shafts are greatly reduced to the size of the median projection; 5, **bifurcated and elongated but the furcal shafts are less developed, representing less than 1/2 of the total length of the telson**

Character 7. Zoeal stages: spines on the carapace, 0, with dorsal, rostral and lateral spines; 1, with the dorsal spine is extremely reduced; 2, with only rostral and lateral spines; 3, only a rostral spine is present; 4, without spines; 5, with only dorsal and rostral spines.

Systematic account

Family Pinnotheridae De Haan, 1833

Calyptraeotheres Campos, 1990

Type species. By original designation and monotypy *Calyptraeotheres granti* (Glassell, 1936).Gender masculine.

Diagnosis. Female: Carapace arcuate anteriorly, anterolateral margin cristate; regions poorly defined, with 2 longitudinal cervical depressions from orbits to middle of carapace; front slightly projecting; MXP3 obliquely placed in buccal cavity; ischium, merus completely fused; palp 2- or 3-segmented; carpus larger than propodus; dactylus, when present, minute, inserted distoventrally on propodus; exopod with thin, unsegmented flagellum. WL1-3 of similar shapes; WL4 relatively more slender than others; propodi of WL 1and 2 with tuft of short stiff setae on distoventral margin; dactyli of WL 1–3 similar in shape, those of WL 4 longest, sword-shaped. Abdomen covering thoracic sternum, with 6 abdominal somites and telson clearly separated.

Male: with carapace subpentagonal or suborbicular, regions poorly defined, dorsal region smooth, with short-spaced setae; anterolateral margin with fringe of simple setae. MXP3 similar to female. Abdomen with 6 somites, telson, well separated, widest at third somite, narrowing toward telson.

Distribution. Northeastern Pacific Ocean. *C. granti:* Mexico, throughout the Gulf of California and Magdalena Bay, west coast of Baja California Sur; *C. pepeluisi* **new species**: Michoacán, Mexico. **Southeastern Pacific Ocean.** *C. politus:* Ancón Bay, Perú to Castro, Chiloe I., Chile. **Caribbean Sea**. *C. hernandezi:* Cubagua I., Venezuela. **Southwestern Atlantic Ocean**. *C. garthi*: Rio Grande do Sul, Brazil; Mar del Plata, Necochea, Golfo de San Matias, Argentina (see Campos 1990; 1999; Hernández & Campos 2006).

Hosts. Gastropoda: Calyptraeidea: *Crepidula* Lamarck, 1799 *Calyptraea* Lamarck, 1799 and *Crucibulum* Schumacher, 1917 (Campos 1990; 1999; Hernández & Campos 2006).

Remarks. While the taxonomy of the genus *Calyptraeotheres* has been well documented, its systematics and phylogenetic relationship have been a matter of debate (see Campos 1990, 1999; Hernández-Ávila & Campos 2006; Marques & Pohle 1995). Marques & Pohle (1995), in their phylogenetic analysis of the Pinnotheridae based on larval morphology, placed *Pinnotheres politus* (junior synonym of *Caytraeotheres politus*) and *Tumidotheres maculatus* in their *Pinnotheres*-II group. They also concluded that both taxa were paraphyletic and transferred *P. politus* into *Tumidotheres* Campos, 1989. Later, Campos (1999) re-analyzed the adult morphological traits on which Marques and Pohle (1995) based their conclusion and discovered that *P. politus* did not possess any of the diagnostic adult features of *Tumidotheres* (see, Campos 1989). Nevertheless, the adult morphology of both male and female *P. politus* concurred very well with that of *Calyptraeotheres*, and this species was finally included in this genus (see Campos, 1999). Palacios-Theil *et al.* (2009) subsequently performed a molecular analysis of selected members of the family Pinnotheridae to ascertain their phylogenetic relationships. Their results suggested a close phylogenetic relationship between *Calyptraeotheres* and *Tumidotheres* which, collectively with the genera *Dissodactylus*, *Clypeasterophilus* and *Tunicotheres*, formed the so-called clade-IIC of the Pinnotherinae *sensu* Palacios-Theil *et al.* (2009, Fig.1; but see discussion on this subfamily in Campos 2009). Our new analysis, on the updated matrix of Marquez & Pohle (1995), permitted to recognize that members of the genera *Calyptraeotheres*, *Clypeasterophilus*, *Dissodactylus*, *Pinnaxodes* Heller, 1865 and *Tumidotheres* (see Table 1, Pinnotherid V) share the larval characters analyzed and in general possess a very similar morphology. The larval morphology and molecular results suggest a closely relationship between *Calyptraeotheres*, *Clypeasterophilus*, *Dissodactylus*, and *Tumidotheres* but, these results mutually do not confirm the relationship of these genera with *Tunicotheres* and *Pinnaxodes*. Our results on larval morphology support a more closely relationship between the monotypic *Tunicotheres* and *Pinnotheres taylori* and in a less degree with members of the subfamily Pinnotherinae *sensu* Campos (2009) (see Fig. 1–2). Remarkably, *Tunicotheres moseri* and *P. taylori* share a similar kind of host (tunicates) (Rathbun 1918; Campos 1996) and both have abbreviated larval development (see Hart 1935; Bolaños *et al.* 2004) which is highly derived. The systematics and classification of *Pinnotheres taylori* as well as of other crabs symbiotic of tunicates is currently under study by the first author, however, all the gathered morphological and ecological evidence suggest it, like *Tunicotheres*, neither belong in *Pinnotheres* nor in the subfamily Pinnotherinae *sensu* Campos (2009). The zoeae of this subfamily show a generalized and unique laterally convex telson with the furcal shafts greatly reduced to the size of the median projection and adults have a well developed protuberance on the basal antennal article (Campos 2009). Contrarily, the "tunicopinnos" have a telson subquadrate with two short lateral spines (see Hart 1935) and the antennal protuberance is absent (see Campos 1996). The discussion of the enigmatic molecular relationship between *Tunicotheres* and the *Dissodactylus* complex, is beyond the scope of the present paper, but probably this is the first documented molecular convergence within Pinnotheridea. Regarding *Pinnaxodes,* neither its adult morphology (Campos *et al.*, 1998; Takeda & Masahito 2000; Ng & Manning 2003) nor the molecular results suggest this genus is allied to *Calyptraeotheres* or other member of the clade IIC *sensu* PalaciosTheil et al (2009). We consider that the shared larval features between *Pinnaxodes* and other members of the Pinnotherid V group are probable homoplasies, like those observed in larvae of the *Pinnixa*-complex and *Fabia-Juxtafabia* (see Fig. 1; Palacios-Theil, *et al.* 2009: 457).

A preliminary analysis on selected adult morphological features of the carapace and third maxilliped of *Calyptraeotheres* suggests that is presumably more related to *Dissodactylus* and *Clypeasterophilus* than to *Tumidotheres*, although this would be in conflict with the molecular results of Palacios-Theil *et al.* (2009). The shared features between *Calyptraeotheres* and *Dissodactylus*-*Clypeasterophilus* include a glabrous subpentagonal-suborbicular carapace, and a third maxilliped with a fused ischium and merus and a carpus larger that the propodus in which, when present, a minute and rounded dactyl is inserted (Griffith 1987; Campos & Griffith 1990; Campos 1990; 1999; Ng & Manning 2003; Hernandez-Avila & Campos 2006). *Tumidotheres* has a tumid and suborbicular carapare and its surface is covered with short, dense, and deciduous tomentum and the carpus of the third maxilliped is shorter that the large propodus in which the long, narrow and saptulate dactylus is medially inserted (see Campos 1989). We consider that this preliminary conclusion requires an extensive morphological comparative study between all genera cited here, but emphasizing non-adaptive features.

In spite of the uncertainty on the phylogenetic affinity of the Pinnotherid V group, the only conclusion that can be fully sustained until now from an adult morphological viewpoint, is that each genus remains valid, an opinion which is supported by several unique apomorphies that uphold the monophyly of each taxon (Griffith 1987; Campos & Griffith 1990; Campos 1990; 1999; Campos *et al.* 1998; Takeda & Masahito 2000; Ng & Manning 2003; Hernandez-Avila & Campos 2006; Ocampo *et al.* 2010).

***Calyptraeotheres pepeluisi* new species**

(Figs. 3, 4)

Material. Holotype (CNCR26183), ovigerous female, 10 July 1983, collected by trawl, off Lázaro Cardenas port, Michoacán, Pacific coast of Mexico, oceanographic expedition Atlas IV on board of the R/V El Puma of the UNAM, June 1983, locality A-IV, C4-13, 18º 04'44" N 18º 05' 02" N, 102º 33' 18" W 102 º 33' 04".

Host. Unknown.

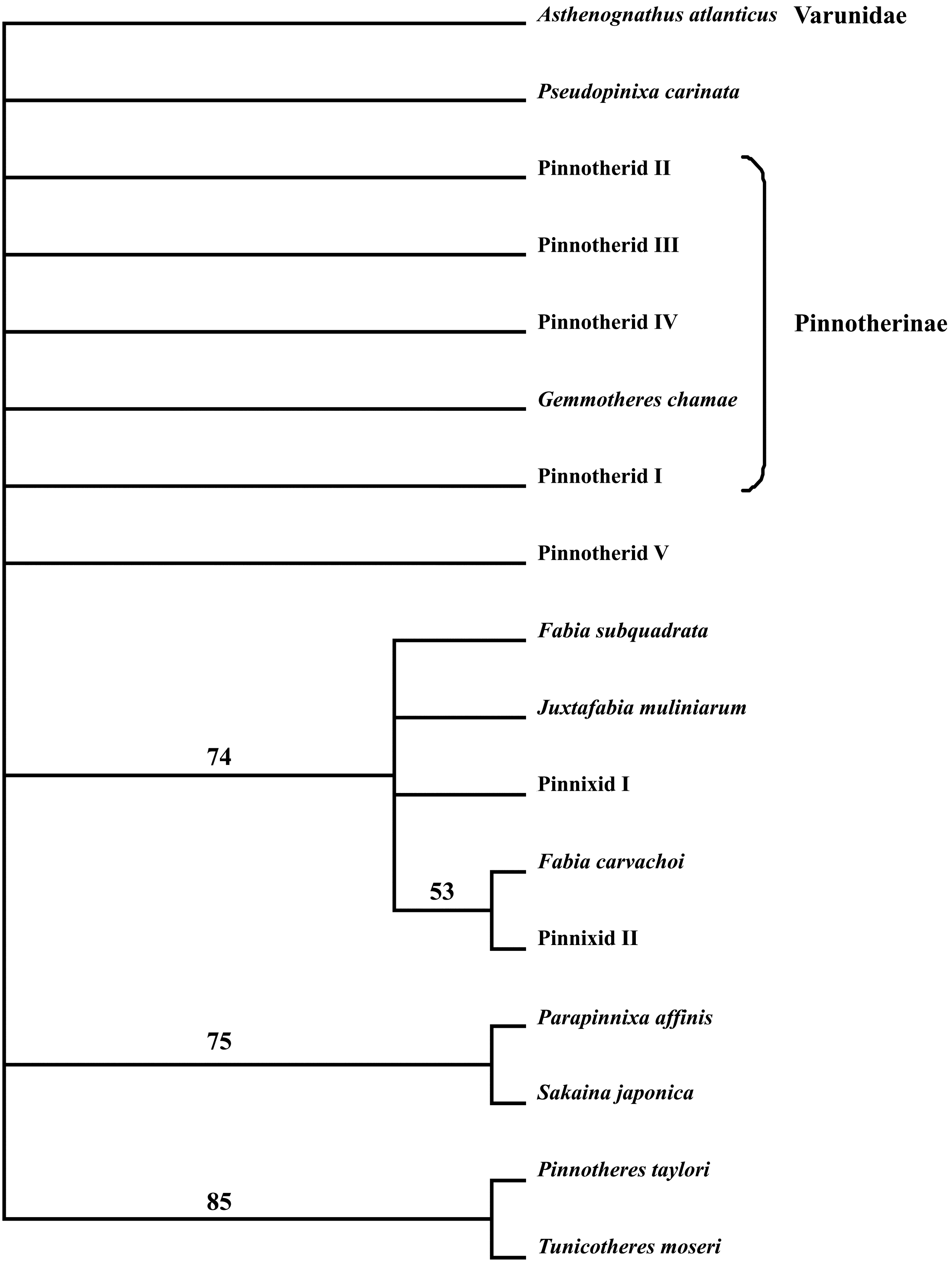

FIGURE 1. Strict consensus cladogram of 19 most parsimonious trees (length=27 CI = 0.667; RI = 0.625; RC = 0.417) obtained from heuristic parsimony analyses of unweighted and unordered characters. Subfamily name as proposed by Campos (2009) is indicated. Pinnotherid I–V and Pinnixid I–II are explained in Table 1. *Asthenognathus atlanticus* was used as the outgroup. Numbers above branches are the percentage of 1,000 bootstrap replicates that support the relevant nodes.

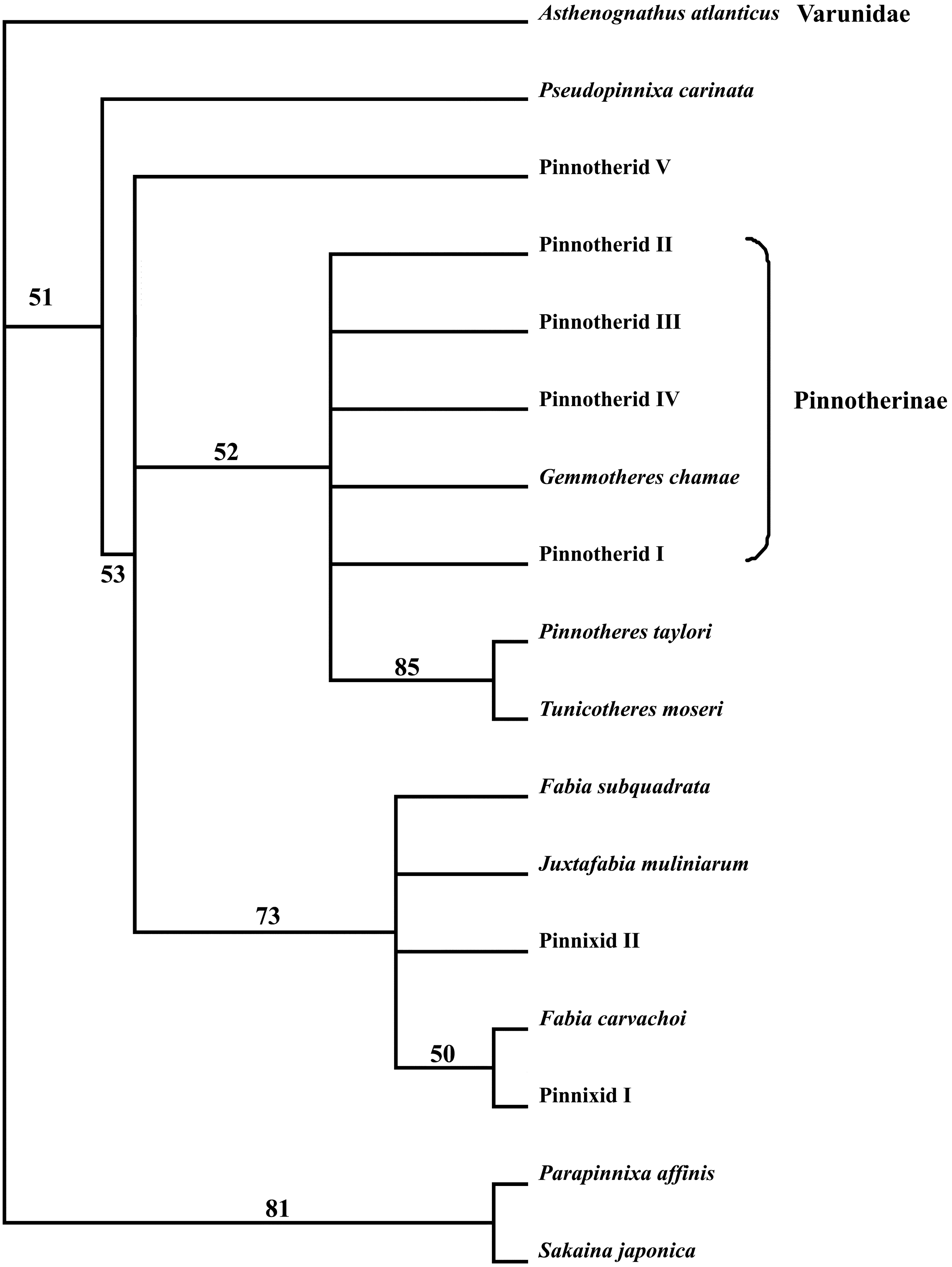

FIGURE 2. Strict consensus cladogram of 13.78 most parsimonious trees (length=13.45 CI = 0.865; RI = 0.896; RC = 0.7751) obtained from heuristic parsimony analyses of unordered characters. The data were *a posteriori* reweighted using the rescaled consistency index (RC). Subfamily name as proposed by Campos (2009) is indicated. Pinnotherid I–V and Pinnixid I–II are explained in Table 1. *Asthenognathus atlanticus* (Varunidae) was used as the outgroup. Numbers above branches are the percentage of 1,000 bootstrap replicates that support the relevant nodes.

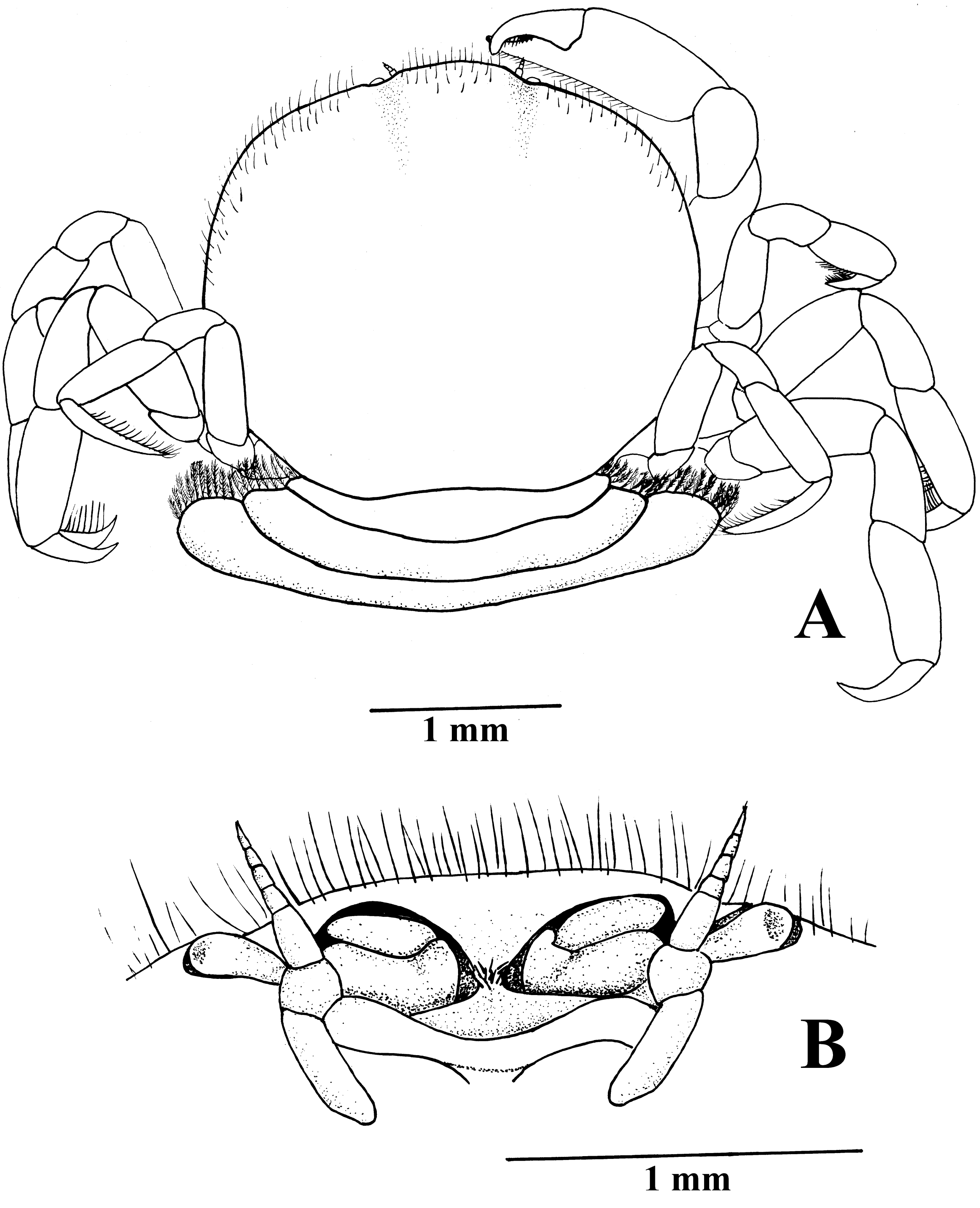

FIGURE 3. *Calyptraeotheres pepeluisi* **new species**, off Lázaro Cárdenas port, Michoacán, Mexico (CNCR26183). Adult female: A, dorsal view; B, partial frontal view.

Description of holotype female. Carapace suborbicular, with pilose sub-rectangular front, slightly projected, with medial shallow sulcus; anterolateral margin pilose, arcuate, cristate; regions poorly defined; posterior margin slightly curved; 2 cervical depressions from orbits to gastric region, converging posteriorly. Eyes visible in dorsal view. MXP3 placed obliquely, exopod with unsegmented flagellum; endopod with ischium and merus fused, widening distally, palp 2-segmented, articulating distally on inner margin; carpus

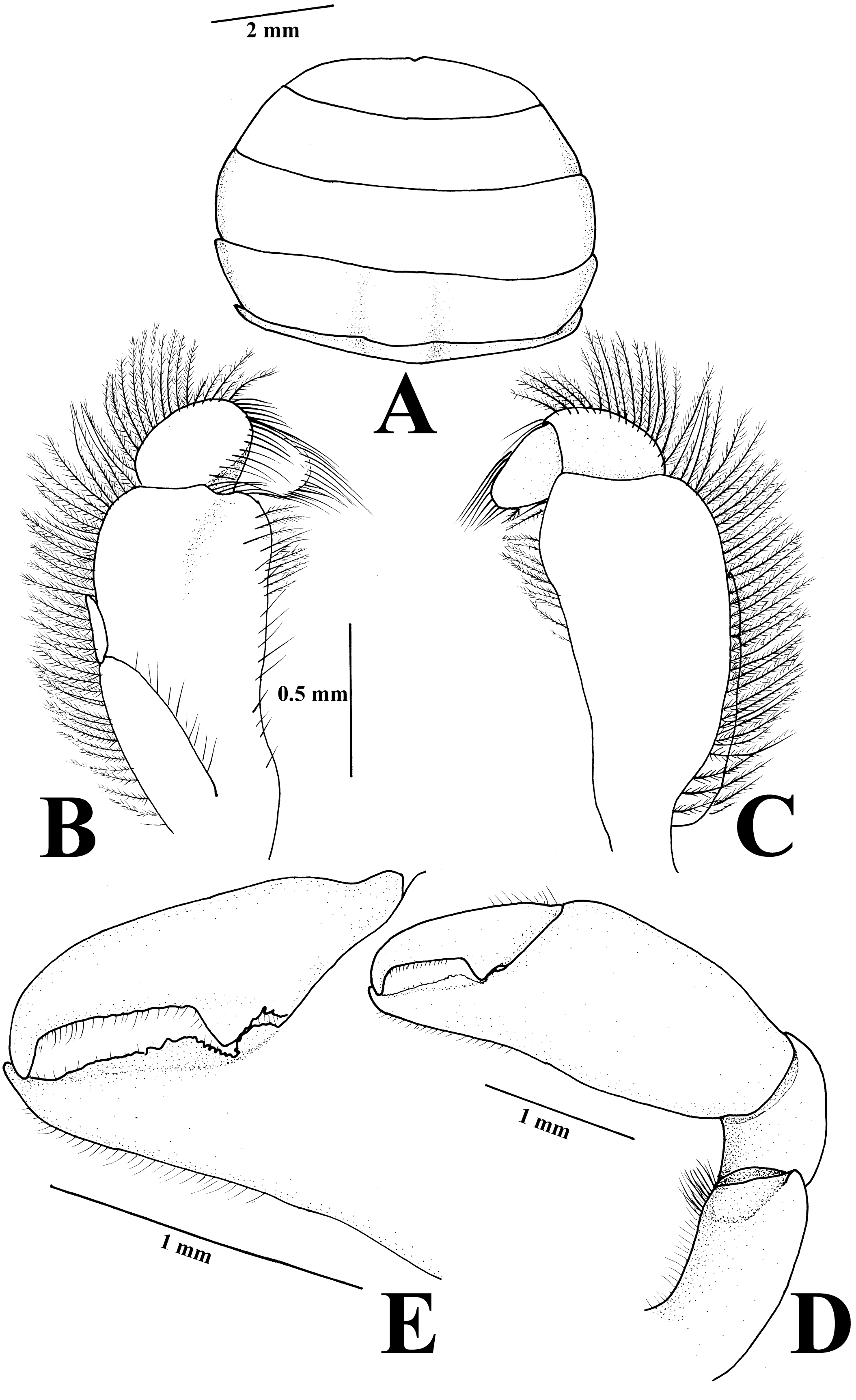

FIGURE 4. *Calyptraeotheres pepeluisi* **new species**, off Lázaro Cárdenas port, Michoacán, Mexico (CNCR26183). Adult female: A, abdomen, somites 3–6 and telson; B–C, MXP3, inner and outer views respectively; D, cheliped; E, tip of cheliped.

sub-trapezoidal, larger than sub-conical propodus; dactylus absent. Chelipeds stout, dorsodistal margin of carpus with small rounded projection; chela longer than combined merus-carpus length, palm widening distally, dorsal margin unarmed, ventral margin of propodus slightly curved with fringe of minute setae, dactylus curved, cutting margin with proximal tooth inserted in notch of propodus, fingers without gape when closed, tips crossed, both fingers with additional minute teeth; outer surface of chela slightly convex, inner surface convex dorso-proximally, slightly concave distally, with ventro-proximal depression. Relative length of WL in decreasing order 3 =2>1>4, margins unarmed, WL 1–3 of similar shape, WL 4 relatively slender. Dactyl falcate, relative length 4 > 3 > 2 > 1; dactyli shorter than propodi in WL 1–3, dactylus of WL 4 slightly larger than propodus. Abdomen with 6-somites, telson distinctly separated, covering sternum, reaching buccal cavity.

Etymology. This species is named in honor of our colleague and friend Pepe-Luis, the nickname of José Luis Villalobos-Hiriart (CNCR, Instituto de Biología, UNAM) for his numerous contributions to systematics and phylogeny of Decapoda and his invaluable support to our studies on pinnotherid crabs.

Type locality and distribution. Known only from the type locality, off the Lázaro Cárdenas port, Michoacán, Pacific coast of Mexico.

Taxonomic remarks. *Calyptraeotheres pepeluisi* **new species** is the third species of the genus recorded in the Pacific Ocean. It differs from the two austral (southern hemisphere) species, *C. garthi* (Atlantic: Argentina and Brazil) and *C. politus* (Pacific: Peru and Chile) by its 2-segmented MXP3 palp (Fig. 4B–C) instead of a 3-segmented palp (see Campos 1999, Fig. 4 A–B). Both *C. hernandezi* (Caribbean Sea: Venezuela) and *C. granti* (Mexican Pacific) share a 2-segmented MXP3 palp with *C. pepeluisi*, but this latter species is morphologically closer to the former species. *Calyptraeotheres hernandezi* and *C. pepeluisi* share a subarcuate carapace, with a fringe of setae on its anterolateral and frontal margins (Fig. 3A), a conical MXP3 propodus, and dorsally visible eyes. This resemblance provides evidence that *C. pepeluisi* is the Pacific counterpart of *C. hernandezi* and that both species probably evolved after the complete closure of the Isthmus of Panama 3.1–3.5 MYA (Keigwin, 1982; Coates & Obando, 1996). In spite of the fact that *C. pepeluisi*, *C. hernandezi* and *C. granti* have a 2-segmented MXP3 palp, it is remarkable that the shape of the propodus of this appendage in the former two species (conical) is quite different from that observed in the latter species (subtrapezoidal). Furthermore, in *C. granti* the eyes are not visible in dorsal view and it has a subpentagonal carapace with a glabrous margin instead of a subarcuate carapace, with the margin setose and eyes visible in dorsal view. *Calyptraeotheres pepeluisi* can be separated from *C. hernandezi* as follows: eyes proportionally smaller; posterior margin of carapace less concave; carapace without a shallow transverse T-shaped depression connecting both longitudinal sulci; and margins of ischium-merus and external margin of carpus with pinnate setae (simple setae in *C. hernandezi*). *Calyptraeotheres pepeluisi* can be separated from its Pacific congener, *C. granti*, as follows: carapace with the lateral margin arcuate instead of subparallel; eyes visible in dorsal view (not visible in dorsal view in *C. granti*), and MXP3 propodus conical, not obliquely truncated as in *C. granti*. The host for the new species is not known.

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