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A new species and two new genera of pinnotherid crabs from the northeastern Pacific Ocean, with a reappraisal of the subfamily Pinnotherinae de Haan, 1833 (Crustacea: Brachyura: Pinnotheridae)

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Abstract

Two monotypic genera, *Enigmatheres* **new genus**, and *Bonita* **new genus**, are described to receive *Fabia canfieldi* Rathbun, 1918, and *Bonita mexicana* **new species** respectively. *Enigmatheres* can be distinguished from other Pinnotheridae by the third maxilliped having a gently curved outer margin, with a carpus that is larger than the conical propodus and a dactylus that is inserted on the middle third of the ventral margin of the propodus, walking legs 2 that are asymmetrical in length and the dactyli of walking legs 1, 3 and 4 that are short, slender, conical, slightly curved up to hooked and hard tip. *Bonita* can be distinguished from other Pinnotheridae by the presence of two sulci on the carapace, protruding anterolateral margins of the carapace, walking leg 3 asymmetrical in length and larger than other walking legs, and walking leg 4 with a clavate propodus. These two new genera and 25 additional ones (nine with hesitation), including *Pinnotheres* Bosc, 1802 (type genus of Pinnotherinae de Haan, 1833), share a carapace that is soft and thin, walking legs 1-4 that are slender and feeble, antennae with a protuberance on the basal segment and the known zoea larvae being very similar, particularly with an abdomen that widens from somite 1 to 5 and a telson that is laterally convex and posteriorly trilobed. These adult and larval shared features support the monophyly of these genera and clearly diagnose the subfamily Pinnotherinae de Haan, 1833 *sensu stricto*.

Key words: Crustacea, Pinnotheridae, Pinnotherinae, *Enigmatheres* **new genus**, *Bonita mexicana* **new genus**, **new species**, Baja California, Mexico

Resumen

Dos géneros monotípicos, *Enigmatheres* **nuevo género**, y *Bonita* **nuevo género**, son descritos para recibir a *Fabia canfieldi* Rathbun, 1918 y *Bonita mexicana* **nueva especie** respectivamente. *Enigmatheres* se puede separar de otros Pinnotheridae por presentar el margen externo del isquio-mero del tercer maxilípedo suavemente curveado, con el carpo de este último más grande que el propodio cónico y el dáctilo que se inserta sobre el tercio medio del margen ventral del propodio, las patas caminadoras 2 son asimétricas en longitud y los dáctilos de las patas caminadoras 1, 3 y 4, son cortos, delgados, cónicos y se curvan ligeramente hasta la punta dura en forma de gancho. *Bonita* se puede separar de otros Pinnotheridae por la presencia de dos surcos sobre el caparazón, los márgenes anterolaterales del caparazón proyectado, las patas caminadora 3 asimétrica en longitud y más grandes que las otras patas caminadoras y los propodios de las patas caminadoras 4 con forma de clava. Estos dos nuevos géneros y otros 25 más (nueve con reserva), incluyendo a *Pinnotheres* Bosc 1802 (género tipo de la familia Pinnotheridae de Haan, 1833), comparten un caparazón suave y delgado, las patas caminadoras 1-4 delgadas y débiles, la antena con una protuberancia en su artejo basal y la morfología de las larvas zoeas muy semejante, particularmente el abdomen que se ensancha del somito 1 al 5 y el telson que es lateralmente convexo y posteriormente trilobulado. Las semejanzas morfológicas de los adultos y las larvas zoeas apoyan la monofila de estos géneros y diagnostican claramente a la subfamilia Pinnotherinae de Haan, 1833 *sensu stricto*.

Palabras clave: Crustacea, Pinnotheridae, Pinnotherinae, *Enigmatheres* **nuevo género**, *Bonita mexicana* **nuevo género, nueva especie**, Baja California, México

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Introduction

Current studies on the American species of the family Pinnotheridae prompted a re-evaluation of the taxonomy of the enigmatic Californian species *Fabia canfieldi* Rathbun, 1918, and the members historically included in the subfamily Pinnotherinae. As part of a revision of the genus *Fabia* Dana, 1851, Campos (1996b) concluded that *F. canfieldi* was incorrectly assigned to this genus due the lack of an obtuse angle on the internal margin of the third maxilliped and the propodus of this appendage being shorter than the carpus. The generic status of *F. canfieldi* has remained unresolved, however, awaiting a study of the holotype and the collection of additional material. Collections of pinnotherid crabs made at Tortugas Bay on the west coast of Baja California Peninsula, México, provided several female specimens new to this area (see Campos, 2007) which were tentatively identified as *F. canfieldi*. Further study of this material and a comparison with the *F. canfieldi* holotype (USNM 8445) revealed that both belong to different taxa and that the Mexican pinnotherid crabs represent a new genus and new species. In addition, the subfamily Pinnotherinae de Haan, 1833 is re-diagnosed to include its type genus, *Pinnotheres* Bosc, 1802, and 26 (nine tentatively) additional genera which appear to constitute a monophyletic group.

Material

In addition to the new genera and new species described, 85 species were studied for a comparative purpose. Types and voucher material examined are deposited in the American Museum of Natural History, New York, USA (AMNH); Colección Nacional de Crustáceos, Instituto de Biología, Universidad Nacional Autónoma de México, Distrito Federal, México (CNCR); Colección Nacional de Equinodermos, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Distrito Federal, México (CNE); Colección de Macroinvertebrados, Instituto de Ciencias del Mar y Limnología (Estación Mazatlán), Universidad Nacional Autónoma de México, Sinaloa, México (EMU); Crustacean Collection, Department of Biology, University of Louisiana, Lafayette, U.S.A (ULLZ); Museo Argentino de Ciencias Naturales, Instituto Nacional de Investigaciones de las Ciencias Naturales, Buenos Aires, Argentina (MACN); Museo Marino de Margarita, Isla Margarita, Venezuela (MMM); Muséum national d'Histoire naturelle, Paris, France (MNHN); National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. (USNM); Natural History Museum of Los Angeles County, California, USA (formerly at the Allan Hancock Foundation) (AHF), and Naturalis, Nationaal Naturhistorisch Museum (formerly Rijksmuseum van Natuurlijke Historie), Leiden, The Netherlands (RMNH).

The additional species studied include: *Arcotheres guinotae* Campos, 2001, MNHN B9498; *A. palaensis* (Bürger 1895), USNM 256948; *Austinixa* sp., CNCR 11601, 11602; *A. cristata* (Rathbun, 1900), USNM; *A. felipensis* (Glassell, 1935), UABC; *Austinotheres angelicus* (Lockington, 1877), USNM 71334, 67723, UABC, EMU; *Austinotheres sp.*, ULLZ 5547; *Calyptraeotheres granti* (Glassell, 1933), UABC, CNCR 1425; *C. garthi* (Fennucci, 1975), MACN 26315, 26316, 29265, 26700; *C. politus* (Smith, 1869), USNM 40448; *C. hernandezi* Hernández-Ávila and Campos, 2006, UABC, MMM.cr.03651 to 57; *Calyptraeotheres* sp., CNCR 3821; *Clypeasterophilus rugatus* (Bouvier, 1917) CNE-UNAM 7046; *C. ususfructus* (Griffith, 1987), EMU-2635, 2636, USNM, CNCR 5247; *Dissodactylus lockingtoni* Glassell, 1935, UABC; *D. nitidus* Smith, 1870, UABC; *D. xanthusi* Glassell, 1936, USNM 7154; *D. glasselli* Rioja, 1944, EMU; *D. crinitichelis* Moreira, 1901, CNE-UNAM 7047, USNM 23430, 23429; *D. mellitae* (Rathbun, 1900), USNM 57303; *Epulotheres* sp., UABC; *Fabia byssomiae* (Say, 1818), USNM 25648; *F. concharum* (Rathbun, 1893), UABC, USNM 234206, 234207; *F. emiliai* (Melo, 1971), MACN 16689, 16546; *F. felderi* Gore, 1986, USNM 228615; *F. malaguena* (Garth, 1948), AMNH 10012; *F. subquadrata* Dana, 1851, UABC, USNM, AHF 1467-42; *Fabia* sp., ULLZ 8563, 8564, 8565; *F. tellinae* Cobb, 1973, FSPC-I 7623, 7624, 7625, 7626; *Gemmotheres chamae* (Roberts, 1975), USNM 139098; *Glassella costaricana* (Wicksten, 1982), UABC, AHF 806; *Glassella* sp., CNCR 12225; *Globihexapus paxillus* Schweitzer and Feldmann, 2001, UABC (fossil) ; *Holothuriophilus pacificus*

(Poeppig, 1836), ULLZ 5569; *Holothuriophilus* sp., UABC; *Indopinnixa sipunculana* Manning and Morton, 1987, USNM 221697, 222500; *Juxtafabia muliniarum* (Rathbun, 1918), UABC, USNM 23443, 18217, 229724; *Limotheres nasutus* Holthuis, 1975, USNM 151039; *Nepinnotheres pinnotheres* (Linnaeus, 1758), USNM 264743; *Opisthopus transversus* Rathbun, 1893, USNM 50997, UABC; *Orthotheres unguifalcula* Glassell, 1936, USNM; *O. barbatus* (Desbonne, 1867), ULLZ 5559; *O. strombi* (Rathbun, 1905), ULLZ; *Ostracotheres tridacnae* (Rüppell, 1830) MNHN B.10578, RMNH-D 1542; *O. spondyli* Nobili 1905, RMNH-D 22681; *Parapinnixa affinis* Holmes, 1900, UABC; *P. bolagnosi* Hernandez-Avila and Campos, 2007, MMM. cr. 0352; *P. nitida* (Lockington, 1877), EMU 3753; *Pinnaxodes floridensis* H. W. Wells and Wells, 1961, ULLZ, USNM 186366; *P. chilensis* (Milne Edwards, 1837), USNM 22112, 49238; *P. gigas* Green, 1992, UABC; *Pinnixa barnharti* Rathbun, 1918, UABC, USNM 31510, LACM 35-189.1; *P. darwini* Garth,1960, AHF 3812; *P. franciscana* Rathbun, 1918, USNM 110633, 110671; *P. littoralis* Holmes, 1894, UABC; *P. longipes* (Lockington, 1876), USNM 110636; *P. occidentalis* Rathbun, 1893, EMU; *P. pembertoni* Glassell, 1935, UABC; *P. richardsoni* Glassell, 1936, UABC; *P. scamit* Martin and Zmarzly, 1994, USNM 267500, UABC; *P. schmitti* Rathbun, 1918, USNM; *Pinnixa* sp., EMU 0842; *P. tomentosa* Lockington, 1877, UABC; *P. trasversalis* (H. Milne Edwards and Lucas, 1844), UABC; *P. tubicola* Holmes, 1894, USNM 20860, UABC; *P. tumida* Stimpson, 1858, UABC; *P. valerii* Rathbun, 1931, UABC, EMU 3769; *P. valdiviensis* Rathbun, 1907, UABC (photographs); *Pinnotheres hemphilli* Rathbun, 1918, USNM 6420; *P. orcutti* Rathbun, 1918, USNM 49215, EMU 3747; *P. pisum* (Linnaeus, 1758), UABC; *P. pichilinquei* Rathbun,1923, USNM 57004; *P. shoemakeri* Rathbun, 1918, ULLZ 902; *Pinnotherelia laevigata* H. Milne Edwards and Lucas, 1843, UABC, USNM 125585; *Raytheres clavapedatus* Glassell, 1935, UABC; *Scleroplax granulata* Rathbun, 1893, UABC, ULLZ, USNM 17497; *Tetrias scabripes* Rathbun, 1898, EMU 3744, 4026; *Tumidotheres maculatus* (Say, 1818), USNM, MACN 26697, 26311, CNCR 2540; *T. margarita* (Smith, 1969), UABC, USNM 229723, EMU; *Tunicotheres moseri* (Rathbun, 1918), USNM 74954; *Zaops geddesi* (Miers, 1880), USNM 23767, 51000; *Z. ostreum* Rathbun, 1900, UABC, USNM, CNCR 2252, 2571.

The following abbreviations are used: MXP3= third maxilliped; the walking legs 1-4 are referred as to WL1-4.

Systematics

Pinnotheridae de Haan, 1833

Enigmatheres new genus

(Fig. 1A–E)

Type species *Fabia canfieldi* Rathbun, 1918, by present designation and monotypy.

Diagnosis. MXP3 with ischium and merus indistinguishably fused, inner and outer margin gently curved, lacking obtuse angle; carpus larger than conical propodus; small, narrow dactylus inserted on middle third of medioventral margin of propodus. Relative length of WL 2 > 3 > 1 > 4; WL2 asymmetrical, right one third longer than left; dactyli short, slender and conical, slightly curved up to hooked, hard tip, except right dactylus of WL2 that is longer than other dactili and straight to the tip.

Etymology. From the Latin *enigma* (= mystery) to recognize that knowledge on the distribution and host species are still incomplete after more than nine decades since the discovery of the type species. Gender feminine.

***Enigmatheres canfieldi* (Rathbun, 1918), new combination**
(Fig. 1A–E)

Raphonotus subquadratus Rathbun, 1904: 106 (part: specimen from Monterey, California, *fide* Rathbun, 1918). (Not *Raphonotus subquadratus* Dana, 1851).
Fabia canfieldi Rathbun, 1918: 12, 101, 102, 106–107, pl. 24, fig. 5–7, text-fig. 57; Schmitt, 1921: 254–255, pl.39, fig. 5–6: Balss, 1957: 1420; Schmitt *et al*., 1973: 7, 22: Dai, 1980: 136; Campos, 1996b: 1174–1175; Ng *et al*., 2008: 249 (listed).

Distribution and host. Known from only Monterey, California, the type locality; in folds of the keyhole limpet *Megathura crenulata* (Sowerby, 1825).

Material examined. Holotype of *Fabia canfieldi* Rathbun, 1918: 1 damaged female (USNM 8445).

Redescription of holotype. Carapace damaged (crushed as to be for the most part beyond description). Front devoid of setae, with short, longitudinal median depression.

Third maxilliped obliquely placed in buccal cavity; ischium, merus indistinguishably fused; palp 3-segmented; carpus larger than conical propodus; dactylus small, narrow, inserted on middle third of medioventral margin of propodus. Exopod with 2-segmented flagellum (Fig. 1A–B).

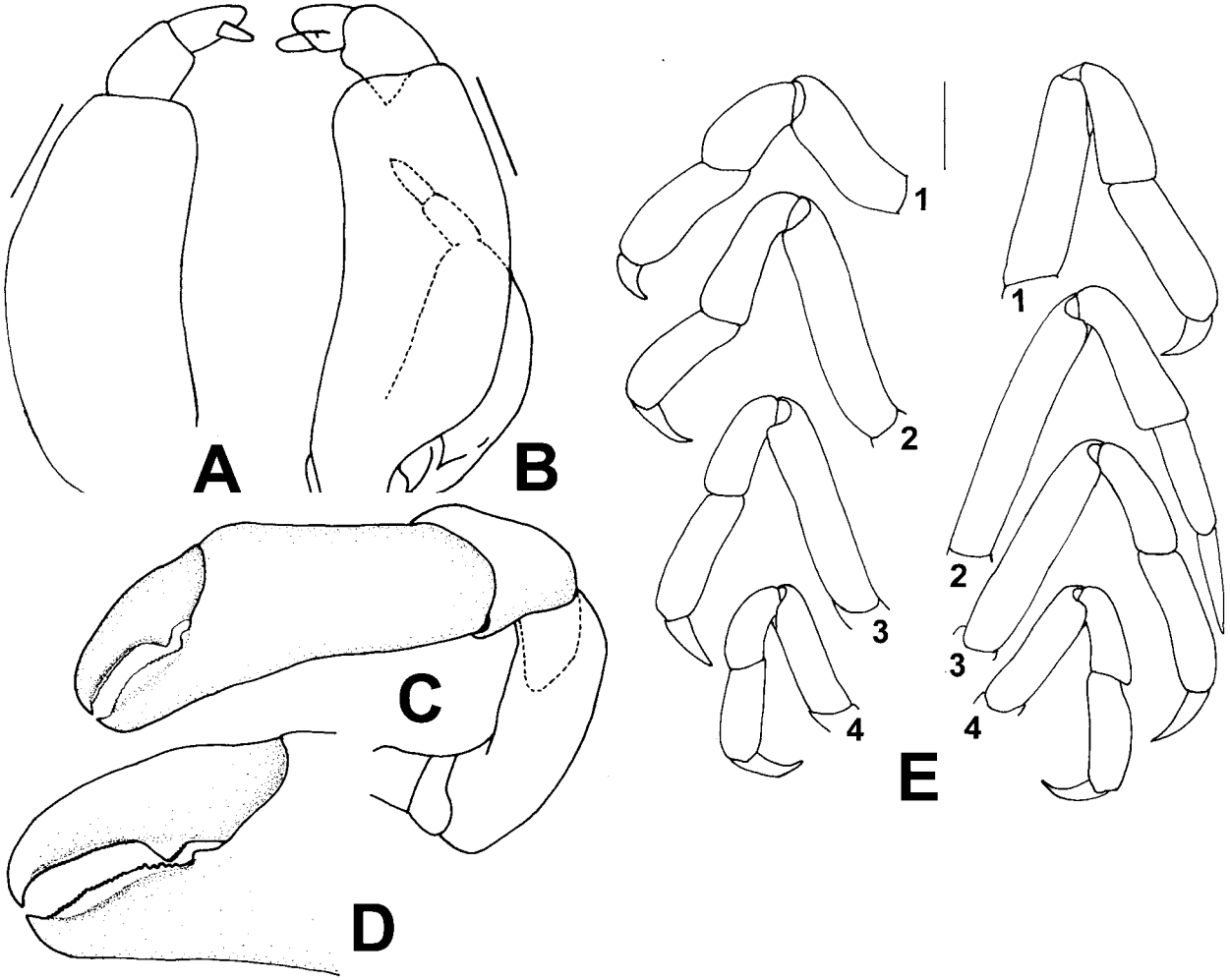

FIGURE 1. *Enigmatheres canfieldi* (Rathbun, 1918) **new combination**, Monterey, California (USNM 8445). Adult female: A–B, left outer and right inner view of MXP3; C, left cheliped; D, pollex and dactylus of left cheliped; E, left and right walking legs, respectively. Scales: A = 0.57 mm; B = 0.47 mm; C–D not at scale; E = 1 mm.

Chelipeds elongated (Fig. 1C), palm slightly increasing in width distally, fingers shorter than palm, slightly deflexed, ventral margin of propodus slightly concave; fingers not gaping when closed, setose along

inner surface; with prehensile tooth at proximal third of cutting edge of dactylus, smaller one at base of pollex; cutting edge of both fingers with small teeth (Fig. 1C).

Walking legs subcylindrical, naked, relative length 2 > 3 > 1 > 4; second leg asymmetrical, right 1/3 longer than left; WL1 stouter than others; propodi slightly curved, slightly stouter at distal end than at proximal, except right WL2 which tapers to distal end; longest right WL2 dactylus differs from others dactili in being nearly straight to tip; other dactyli shorter, slender, conical, more curved toward hooked, hard tip (Fig. 1E).

Abdomen of six somites and telson well separated.

Remarks. The presence of a thin, translucent and soft carapace, enlarged carpus of MXP3 and asymmetrical WL2 are characters that suggest *Enigmatheres* is related to the genus *Austinotheres* Campos, 2002. *Enigmatheres* differs from *Austinotheres* in the gently curved outer margin of the MXP3 ischium-merus, and by the insertion of the dactylus on the middle third of the ventral margin of the conical propodus. *Austinotheres* has an obtuse angle on the MXP3 outer margin and the dactylus of this appendage is inserted further distally on the propodus. *Austinotheres* can be also distinguished from *Enigmatheres* by its slender and long walking legs, with blade-shaped and slightly curved dactyli. Both *Enigmatheres* and *Austinotheres* can be distinguished from other pinnotherids by the asymmetrical WL2 and the shape and relative length of the MXP3 palp articles, particularly the carpus being larger than the propodus, as well as the small and narrow dactylus being inserted medially or distally on the medioventral margin of the propodus. Others genera currently in the Pinnotheridae have symmetrical walking legs and/or the dactylus of MXP3 is inserted on the middle or proximal ventral margin of a propodus which is always larger than the carpus.

***Bonita,* new genus**
(Figs. 2–5B, 8B)

Type species. *Bonita mexicana* **new species**, by present designation and monotypy.

Diagnosis. Carapace thin, easily wrinkled, tumid, anterolateral margins protruding beyond frontal margin, two longitudinal sulci extending form orbits to middle of carapace; WL3 asymmetrical, left longer than right, dactylus blade-shape; WL4 more robust than others, with clavate propodus, short, conical dactylus. Abdomen large, concave, margin involutes.

Etymology. From the Latin *bellus* (= beauty) alluding to the beauty facie of the crab. Gender feminine.

***Bonita mexicana* new species**
(Figs. 2–5B, 8B)

Distribution and host. Known only from the type locality, Point Sofia, Tortugas Bay, Baja California Sur, México (27º 41.943’ N;114º 52.542’W). Found in the mantle cavity of *Pseudochama exogyra* (Conrad, 1837) (Mollusca, Pelecypoda, Family Chamidae) cemented to rocky reef.

Type material. Female holotype, (CNCR-25300), 6 females paratypes (CNCR-25301, USNM), 26–27 Dec 1989.

Other material examined. 1 female (UABC), Dec. 1990; 3 females (UABC), 2 Jan 1992; 7 females (UABC), 2–3 Dec. 1994, Point Sofia, Tortugas Bay, Baja California Sur, México.

Description. Carapace subhexagonal, tumid, regions well defined, smooth, shiny, anterolateral margins protruding beyond frontal margin; 2 longitudinal, deep sulci extending form orbits to middle of carapace; posterior margin somewhat sinuous (Fig. 2B). Orbits small, eyes oval, visible in dorsal view. Prominent protuberance at posterior end of basal segment of antenna (Fig. 2A). MXP3 obliquely placed on buccal cavity, ischium, merus indistinguishably fused, inner, outer margin gently curved, lacking obtuse angle (Fig. 3 D–E);

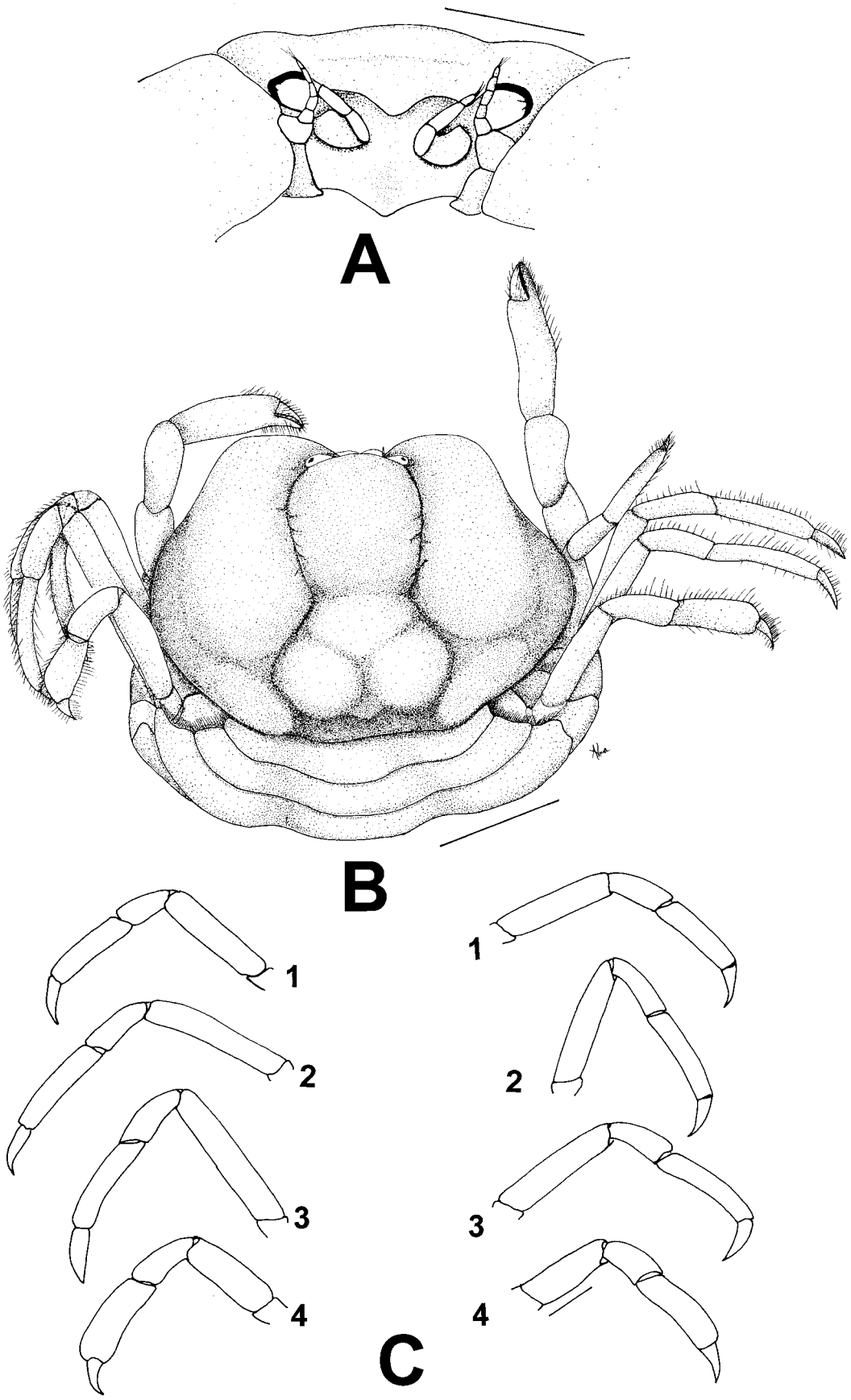

FIGURE 2. *Bonita mexicana* **new genus**, **new species**, Point Sofia, Tortugas Bay, Baja California Sur, México (CNCR 25300). Adult female: A, partial frontal view; B, dorsal view; C, left and right WL 1–4, respectively. Scales: A = 0.23 mm; B = 2.76 mm; C = 1.00 mm.

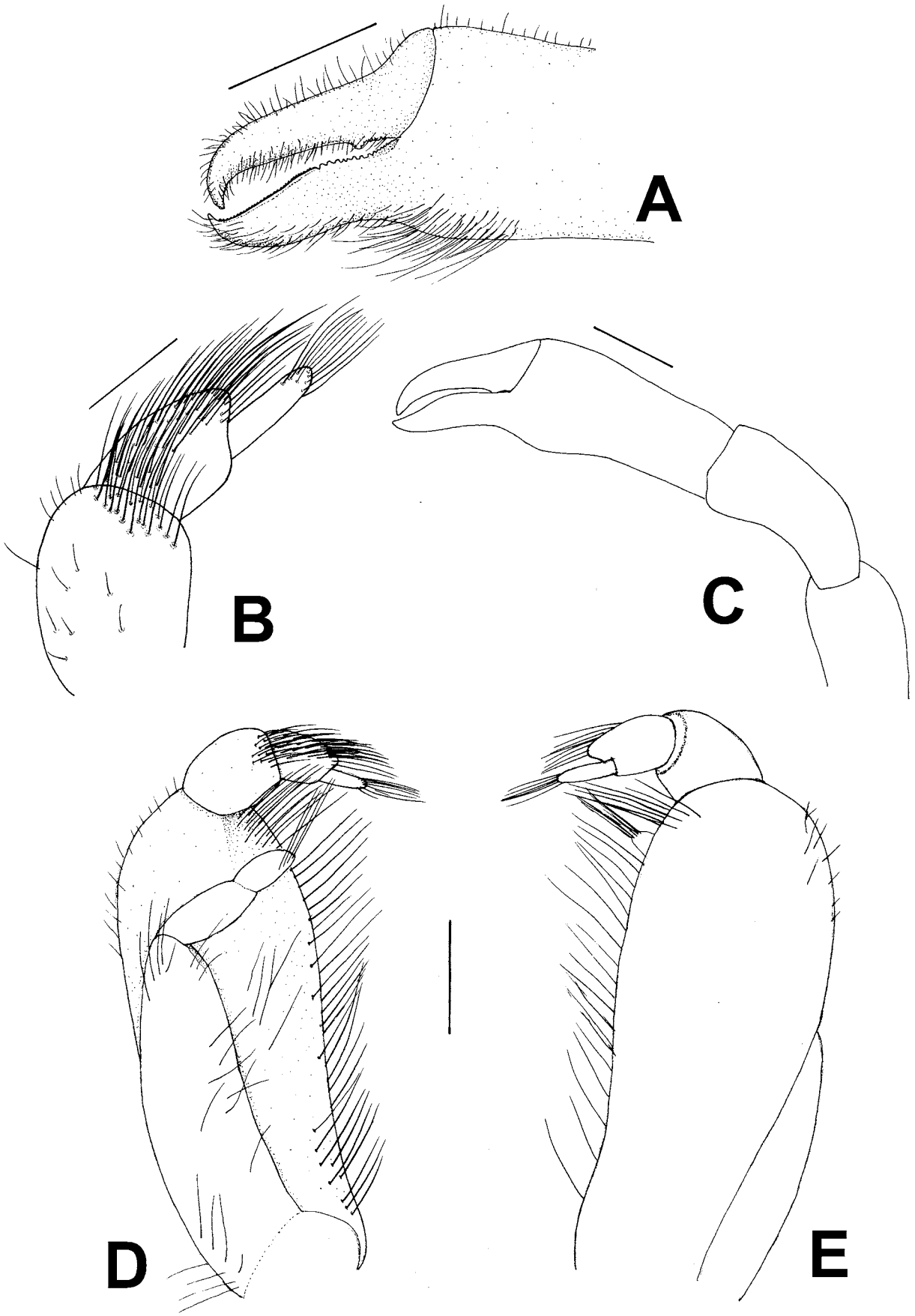

FIGURE 3. *Bonita mexicana* **new genus**, **new species**, Point Sofia, Tortugas Bay, Baja California Sur, México (CNCR 25300). Adult female: A, left dactylus and pollex of chela; B, MXP3 palp; C, left cheliped; D–E left MXP3, inner and outer view, respectively, Scales: A, C = 1.00 mm; B = 0.23 mm; D–E = 0.57 mm.

palp 3-segmented; carpus larger than propodus, latter extending distally, dactylus digitiform distally inserted on distoventral angle of propodus (Fig. 3 B). Exopod of MXP3 with 2-segmented flagellum (Fig. 3D).

Chelipeds elongated (Fig. 3C), chelae subcylindrical; manus increasing in width distally; pollex slightly deflexed, ventral margin proximally concave, distally convex; dactylus wide at base, distally with sharp-hooked, hard tip; cutting edge of dactylus with small proximal tooth, both fingers with additional minute teeth (Fig. 3 A).

Walking legs slender, relative length 3 > 2 > 1 > 4; WL3 asymmetrical, left 1.2 times longer than right (Fig. 2C). Propodi with margins subparallel except those of WL4 distally expanded. Dactyli curved at tip, relative length 3 > 2 > 4 > 1, those of longer WL3 blade-shaped.

Abdomen greatly enlarged, with 6 somites and telson well separated (Fig. 4 A), strongly concave, laterally covering ischia, margin with tomentum, involuted, (Fig. 4B–C), distally covering the buccal cavity.

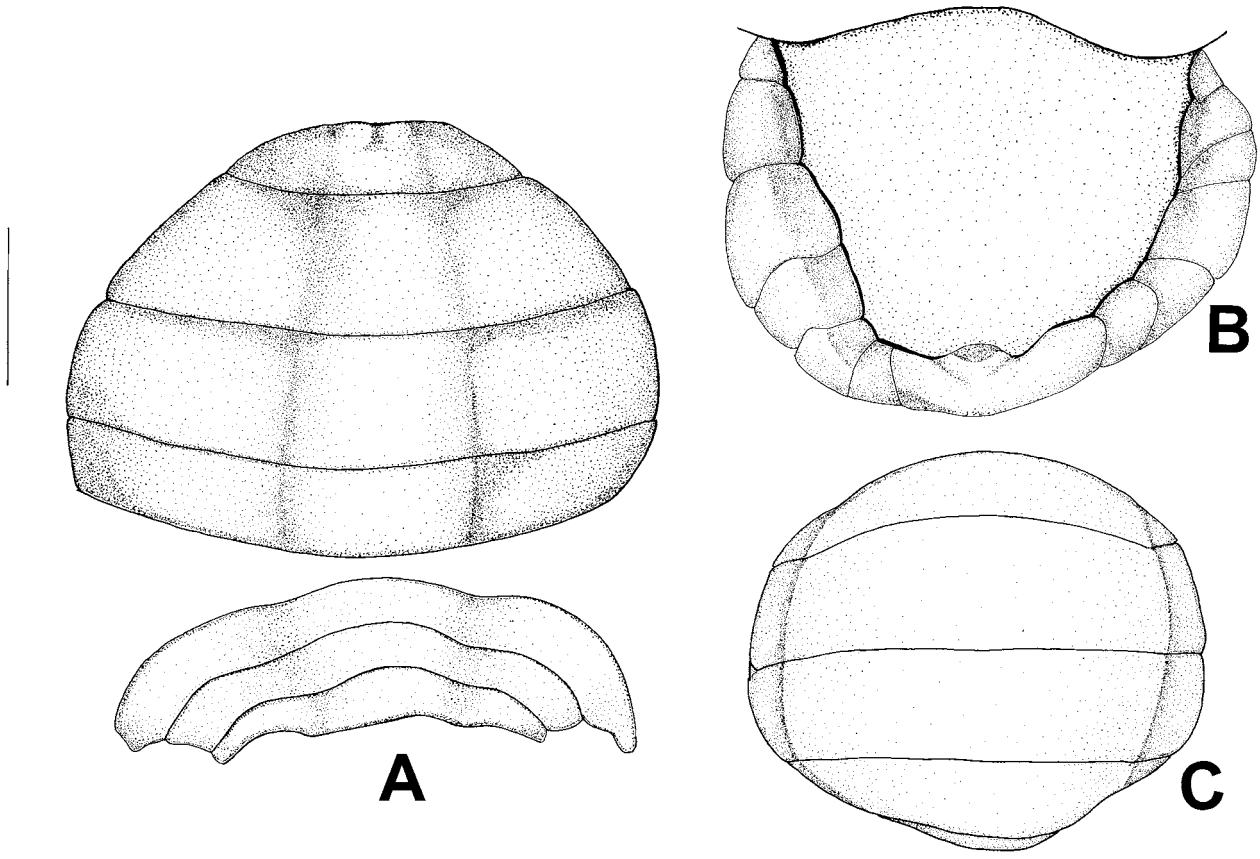

FIGURE 4. *Bonita mexicana* **new genus**, **new species**, Point Sofia, Tortugas Bay, Baja California Sur, México (CNCR 25300). Adult female, abdomen and telson: A, C, outer surface; B, inner surface. Scales: A = 2.76 mm; B = 2.64 mm; C = 3.47 mm.

Male. Unknown.

Etymology. The name *mexicana* refers to the country where the type material was collected.

Remarks. The soft carapace, the protuberance on the basal article of the antennae, the transversely placed MXP3 on the buccal cavity, the slender and feeble walking legs and the well-separated six-segmented abdomen and telson are features shared between *Bonita* and the genera *Arcotheres* Manning, 1993 (see Campos & Manning, 2001), *Austinotheres* Campos, 2002, *Epulotheres* Manning, 1993, *Gemmotheres* Campos, 1996, *Nannotheres* Manning & Felder, 1996, *Orthotheres* Sakai, 1969, *Ostracotheres* H. Milne-Edwards, 1853, *Pinnotheres* Bosc, 1802, *Raytheres* Campos, 2002, and *Zaops* Rathbun, 1900. However, the presence of a thin, translucent, easily wrinkled carapace and the enlarged MXP3 carpus suggest that *Bonita* is

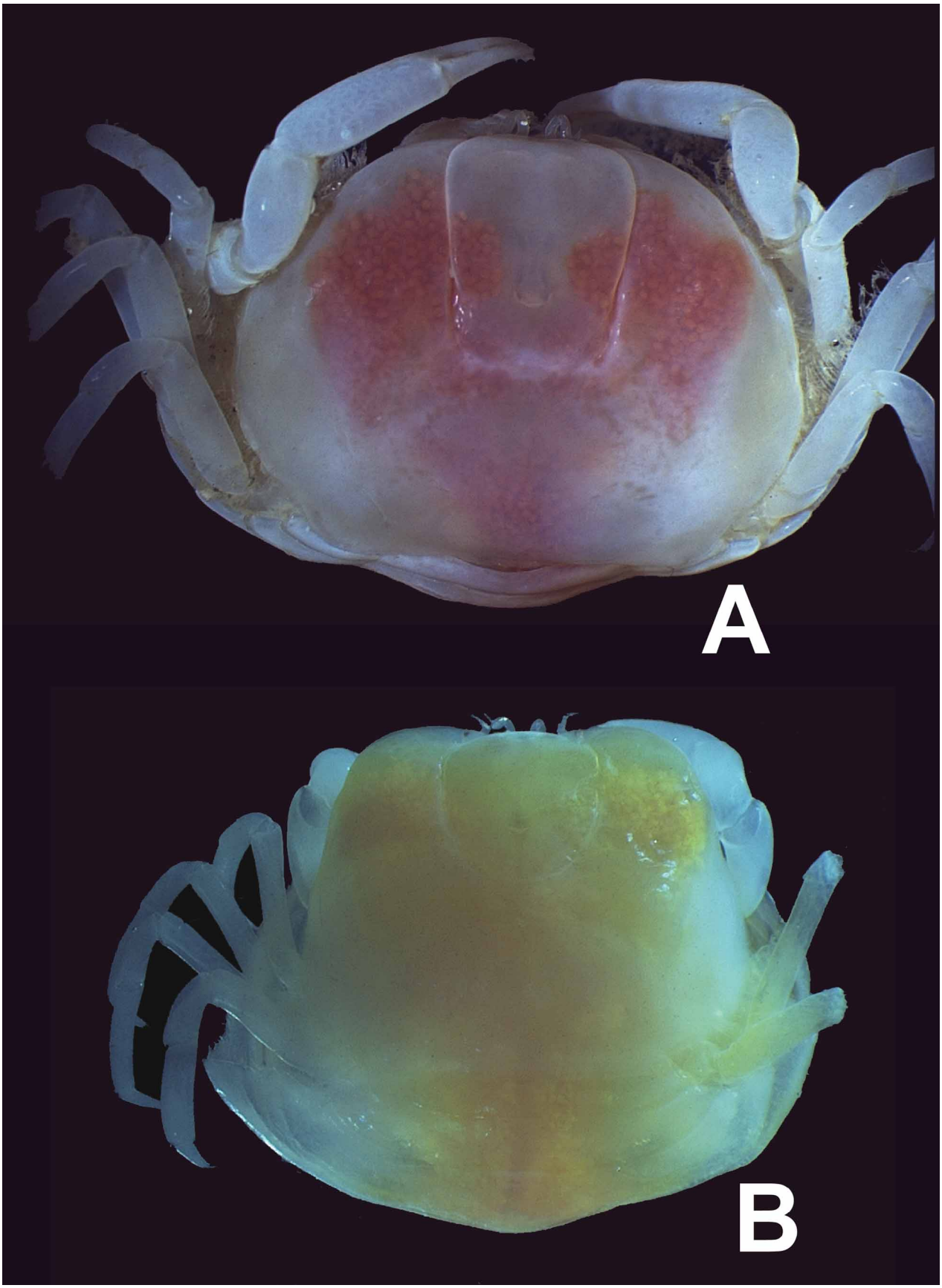

FIGURE 5. Adult female, dorsal view: A, *Fabia subquadrata* (Dana, 1851), San Vicente, Ensenada, Baja California, México (UABC); B, *Bonita mexicana*, **new genus**, **new species**, Point Sofia, Tortugas Bay, Baja California Sur, México (UABC). Carapace width in mm, A = 13.4; B = 7.2.

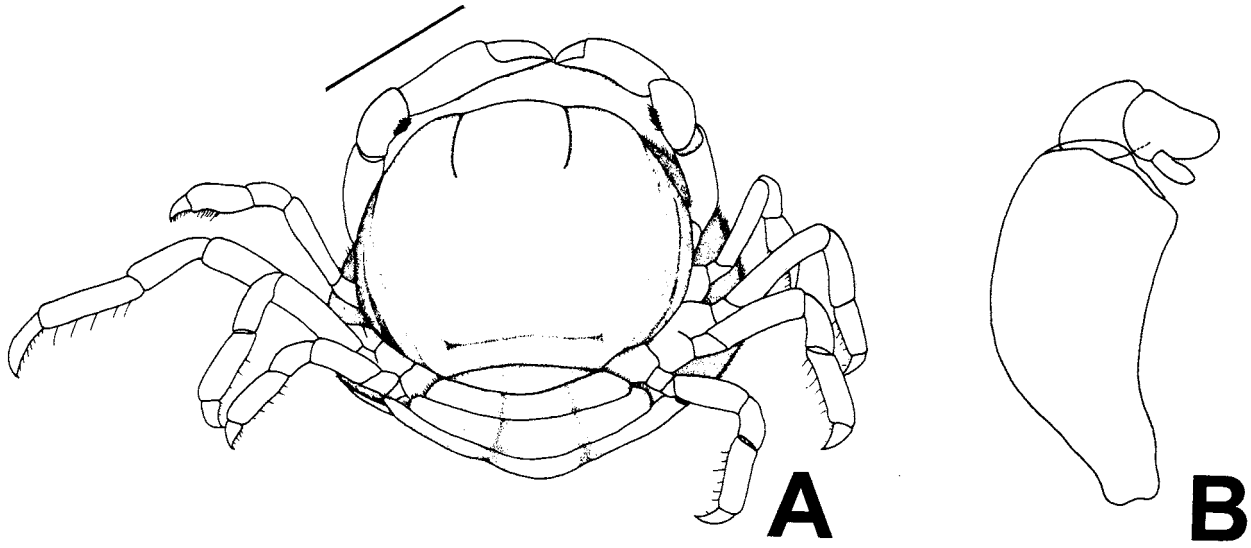

FIGURE 6. *Fabia carvachoi* Campos, 1996, El Pescador Camp, San Felipe, Baja California, México (from, Campos, 1996b: figs. 2A–B). Adult female, A, dorsal view; B, outer view of MXP3. Scale: 6.8 mm.

allied to the eastern Pacific genera *Austinotheres* and *Enigmatheres*. In contrast, the remarkably asymmetrical and enlarged WL3 is a character shared with the American genus *Epulotheres* Manning, 1993 and the Indo-West Pacific genus *Arcotheres* Manning, 1993 (see Manning, 1993b; Manning & Felder, 1996 and Campos & Manning, 2001). The remaining genera of the subfamily Pinnotherinae have symmetrical walking legs or asymmetrical WL2. *Bonita* can be easily distinguished from all the above genera by the presence of two sulci on the carapace, the anterolateral margins of carapace protrude beyond the frontal margin and by the clavate WL4 propodus. The two deep sulci on the carapace in *Bonita* are also present in members of the genus *Fabia* Dana, 1851 (Fig. 5). This feature may suggest that these two genera are allied. However, the genus *Fabia* differ from *Bonita* in the anterolateral margins of the carapace, that do not protrude beyond the frontal margin, the WL2 that are the longest, the propodi of the WL4 with their margins subparallel and the MXP3 with a propodus larger that the carpus and the dactylus inserting in an angular notch in the ventral middle third of the propodus (see Campos, 1996b; Fig. 2–3 vs. 6 A–B). These differences support the sulci of the carapace should be regarded as convergences. Noticeably is that the larval zoeal morphology of *Bonita*, particularly the shapes of the abdomen and telson, are similar to that of species of *Arcotheres*, *Austinotheres*, *Gemmotheres*, *Nepinnotheres*, *Orthotheres*, *Ostracotheres*, and *Pinnotheres* (Fig. 8). In contrast, the abdomen and telson in larval zoeal of *Bonita* markedly differ from those observed in the genera *Fabia*/*Juxtafabia* and *Pinnixa* (Fig. 7). These latter genera shared some larval features of the abdominal somites (see Marquez and Phole, 1995) which have recently been regarded as convergence of two independent monophyletic groups (see, Palacios-Thiel, *et al.*, 2008). I consider *Bonita* and their allied genera represent another monophyletic group within the Pinnotheridae, as strongly suggest the shared adult and larval morphology herein discussed as well as the molecular evidence recently provided by Palacios-Thiel, *et al.*, (2008).

Reappraisal of the subfamily Pinnotherinae De Haan, 1833.

Type genus. *Pinnotheres* Bosc, 1801.

Diagnosis. Carapace soft, thin; MXP3 obliquely placed in buccal cavity: MXP3 ischium and merus indistinguishably fused, palp smaller than ischium-merus; antennae with protuberance on basal segment; walking legs symmetrical or asymmetrical, slender, feeble; abdomen of six somites and telson well separated.

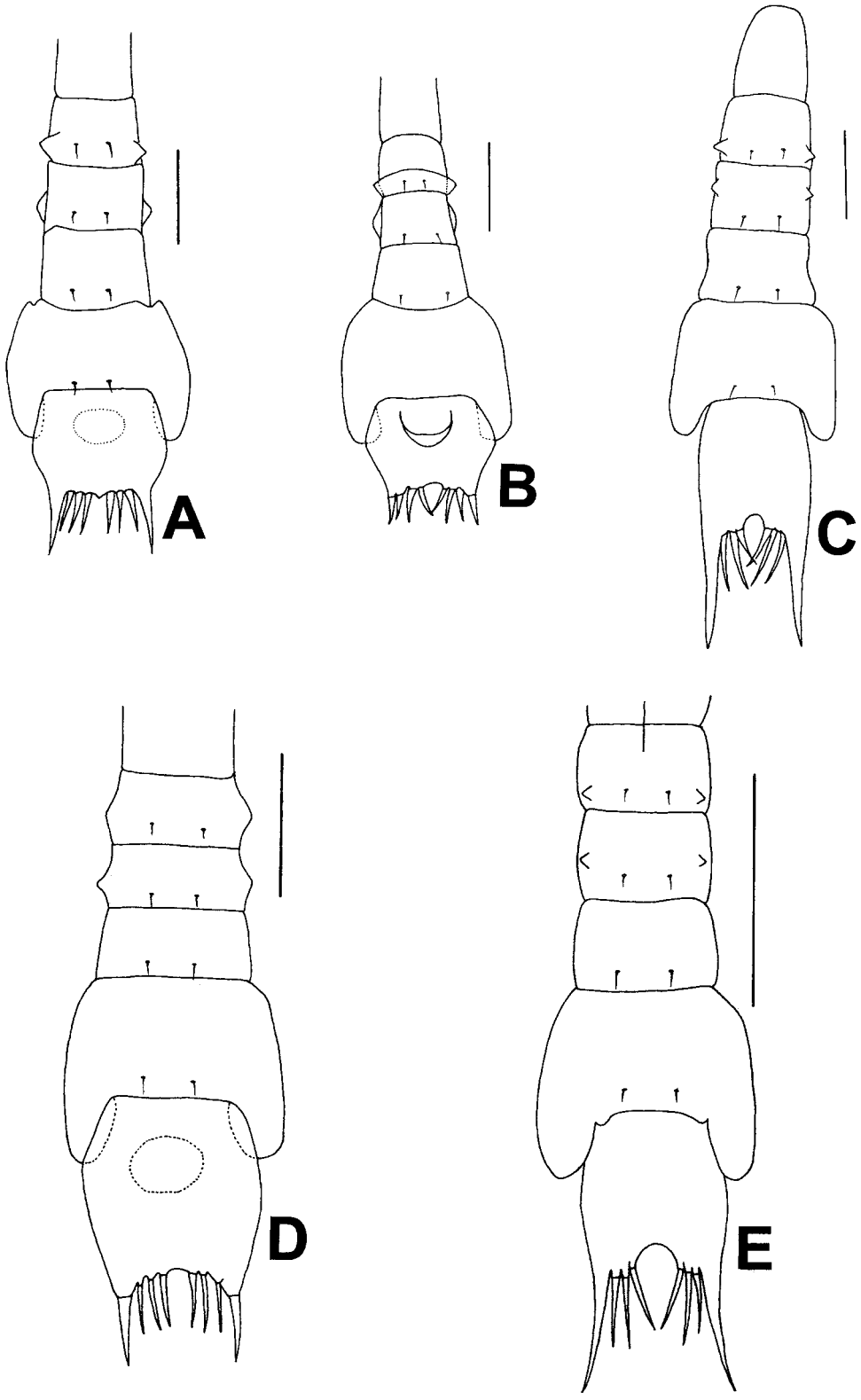

FIGURE 7. Dorsal view of abdomen and telson zoeal 1. A, *Fabia carvachoi* Campos, 1996, El Pescador Camp, San Felipe, Baja California, México (from Campos, 1993: fig. 2C); B, *Juxtafabia muliniarum* (Rathbun, 1918), El Pescador Camp, San Felipe, Baja California, México (from Campos, 1993: fig 2A); C, *Pinnixa longipes* (Lockington, 1876), Tomales Bay, California (from Bousquette, 1980: fig. 4A); D, *Fabia subquadrata* Dana, 1851, Todos Santos Bay, Ensenada, Baja California (from Campos, 1993: fig 2B); E, *Pinnixa aff. rathbuni* Sakai, 1934, Oshoro Bay, Hokkaido, Japan (from Konishi, 1983:282, fig 14C). Scale value, A–D= 0.1 mm, E=0.05 mm.

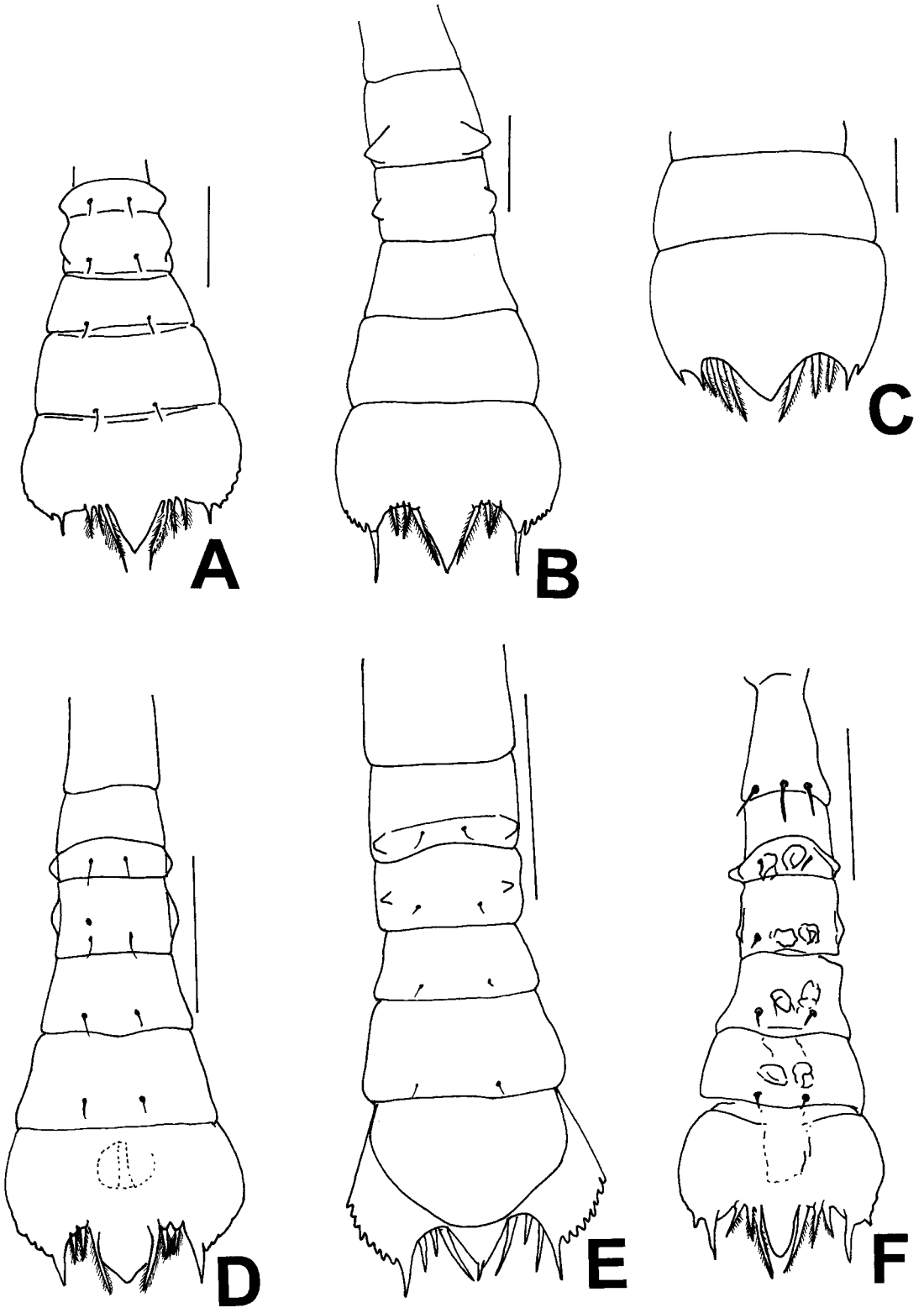

FIGURE 8. Dorsal view of abdomen and telson of zoea-1 stage: A, *Pinnotheres sinensis* Shen, 1932, Oshoro Bay, Hokkaido, Japan (from Konishi, 1983: fig 3A); B, *Bonita mexicana* **new genus**, **new species**, Point Sofia, Tortugas Bay, Baja California Sur, México (UABC); C, *Ostracotheres tridacnae* (Rüppell, 1830) (from Gohar & Al-Kholy, 1957: fig 39); D, *Austinotheres angelicus* (Lockington), El Pescador Camp, San Felipe, Baja California, México; E, *Gemmotheres chamae* (Roberts, 1975), North Carolina, USA (from Roberts, 1975: fig 1C); F, *Pinnotheres pisum* (Linnaeus), Plymouth, England (from Atkins, 1955: fig. 5D). Scale = 0.01 mm.

TABLE 1. Reassessment of the genera included in the subfamily Pinnotherinae De Haan, 1833. List compiled from Sakai (1969), Schmitt *et al.* (1973), Campos (1989a, b, 1990, 1993, 1996a, b, 1999, 2001, 2002), Campos & Griffith (1990), Manning (1993a, 1993b, 1996, 1998), Manning & Felder (1996), Manning & Galil (2000), Campos & Manning (2001), Kazmi & Manning (2003), Ng & Manning (2003), Ahyong & Ng (2005, 2007a, b, 2008) and Ng *et al.* (2008). ?X = Tentative assignment.

Genus	Pinnotherinae De Haan, 1833	To be determined (work in progress)
Abyssotheres Manning & Galil, 2000	?X	
Afropinnotheres Manning, 1993	?X	
Alain Manning, 1998	?X	
Alainotheres Manning, 1993	?X	
Arcotheres Manning, 1993	X	
Austinotheres Campos, 2002	X	
Bonita Campos, new genus	X	
Buergeres Ng & Manning, 2003		X
Calyptraeotheres Campos, 1990		X
Clypeasterophilus Campos & Griffith, 1990		X
Dissodactylus Smith, 1870		X
Durckheimia De Mann, 1889	X	
Enigmatheres Campos, new genus	X	
Epulotheres Manning, 1993	X	
Ernestotheres Manning, 1993	?X	
Fabia Dana, 1851		X
Gemmotheres Campos, 1996	X	
Holotheres Ng & Manning, 2003		X
Holothuriophilus Nauck, 1880		X
Hospitotheres Manning, 1993	?X	
Juxtafabia Campos, 1993		X
Limotheres Holthuis, 1975	X	
Nannotheres Manning & Felder, 1996	X	
Nepinnotheres Manning, 1993	X	
Opisthopus Rathbun, 1894		X
Orthotheres Sakai, 1969	X	
Ostracotheres H. Milne Edwards, 1853	X	
Parapinnixa Holmes, 1894		X
Pinnaxodes Heller, 1865		X
Pinnotheres Bosc, 1802	X	
Raytheres Campos, 2002	X	
Sakaina Serène, 1964		X
Scleroplax Rathbun, 1893		X
Sindheres Kazmi & Manning, 2003	X	
Serenotheres Ahyong & Ng, 2003		X
Tridacnatheres Ahyong & Ng, 2005	X	
Tumidotheres Campos, 1989		X
Tunicotheres Campos, 1996		X

to be continued.

TABLE 1. (continued)

Genus	Pinnotherinae De Haan, 1833	To be determined (work in progress)
Viridotheres Manning, 1996	?X	
Visayeres Ahyong and Ng, 2007	?X	
Waldotheres Manning, 1993	?X	
Xanthasia White, 1846	X	
Zaops Rathbun, 1900	X	

Remarks. A comparison among genera traditionally included within the subfamily Pinnotherinae (see Table 1) recognizes several similarities between *Pinnotheres* (type genus of Pinnotherinae) and the following 17 genera: *Arcotheres* Manning, 1993, *Austinotheres* Campos, 2002, *Bonita* **new genus**, *Durckheimia* De Man, 1889, *Enigmatheres* **new genus**, *Epulotheres* Manning, 1993, *Gemmotheres* Campos, 1996, *Limotheres* Holthuis, 1975, *Nannotheres* Manning & Felder, 1996, *Nepinnotheres* Manning, 1993, *Orthotheres* Sakai, 1969, *Ostracotheres* H. Milne Edwards, 1853, *Raytheres* Campos, 2002, *Sindheres* Kazmi & Manning, 2003, *Tridacnatheres* Ahyong & Ng, 2005, *Xanthasia* White, 1846, and *Zaops* Rathbun, 1900. The consistent and distinct characters noted in the above diagnosis, particularly the soft, thin carapace and the protuberance in the basal antennal article (unique in this group, Fig. 2A), allow for the differentiation of a presumably monophyletic group that comprises the subfamily Pinnotherinae de Haan, 1833 *sensu stricto*. Concomitantly with the characters shared by adults, the known zoeae of these genera show a generalized and distinct abdomen shape that increases from the first to the fifth somite and a laterally convex telson with two short lateral furcal shafts and a median trilobed projection (Fig. 7). These shared larval features should also be used to characterize members of the subfamily Pinnotherinae. Nine genera have been tentatively included or retained within this subfamily (Table 1): *Abyssotheres* Manning & Galil, 2000, *Afropinnotheres* Manning, 1993, *Alain* Manning, 1998, *Alainotheres* Manning, 1993, *Ernestotheres* Manning, 1993, *Hospitotheres* Manning, 1993, *Viridotheres* Manning, 1996, *Visayeres* Ahyong & Ng, *2007*, and *Waldotheres* Manning, 1993. The inclusion of these genera within the Pinnotherinae should be nevertheless reassessed in light of the present findings. Conversely, seventeen genera previously included in the Pinnotherinae (see Table 1) should be excluded since they do not agree either with the adult or larval characters: *Buergeres* Ng & Manning, 2003, *Dissodactylus* Smith, 1870, *Clypeasterophilus* Campos & Griffith, 1990, *Fabia* Dana, 1853, *Holotheres* Ng & Manning, 2003, *Juxtafabia* Campos, 1993, *Parapinnixa* Holmes, 1894, *Sakaina* Serène, 1964, *Scleroplax* Rathbun, 1893, *Calyptraeotheres* Campos, 1990, *Opisthopus* Rathbun, 1894, *Pinnaxodes* Heller, 1865, *Serenotheres* Ahyong & Ng, 2003, *Tumidotheres* Campos, 1989, *Tunicotheres* Campos, 1996, and *Holothuriophilus* Nauck, 1880. The subfamily assignment for these genera will be discussed in a forthcoming publication.

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Literature cited

Ahyong, S.T. & Ng, P.K.L. (2005) Review of *Durckheimia* and *Xanthasia*, with descriptions of two new genera (Decapoda: Brachyura: Pinnotheridae). *Journal of Crustacean Biology*, 25 (1), 116–129.

Ahyong, S.T. & Ng, P.K.L. (2007a) *Visayeres acron*, a new genus and species of pinnotherid crab (Crustacea: Decapoda: Brachyura) from the Philippines. *Raffles Bulletin of Zoology*, supplement 16, 187–189.

Ahyong, S.T. & Ng, P.K.L. (2007b) The pinnotherid type material of Semper (1880), Nauck (1880) and Bürger (1895) (Crustacea: Decapoda: Brachyura). *Raffles Bulletin of Zoology*, supplement 16, 191–226.

Ahyong, S.T. & Ng, P.K.L. (2008) *Alain raymondi*, a new species of deepwater pinnotherid crab (Crustacea: Decapoda: Brachyura) from the Philippines, commensal with holothurians. *Zootaxa* 1919: 61–68.

Atkins, D. (1955) The post-embryonic development of British Pinnotheres (Crustacea). *Proceedings of the Zoological Society of London*, 124, 687–715.

Balss, H. (1957) Decapoda, VIII: Systematik, *In*: H.G. Bronn. *Klassen und Ordungen des Tierreichs*, Band 5, Abteilung I, 7 (12), 1505–1672.

Bosc, L. A-G. (1802) *Histoire naturelle des Crustacés, contenant leur description et leurs moeurs, avec figures dessinées d'après nature*, Paris, Deterville, 1, 1–258.

Bousquette, G. D. (1980) The larval development of *Pinnixa longipes* (Lockington, 1877) (Brachyura, Pinnotheridae) reared in the laboratory. *Biological Bulletin*, 159, 592–605.

Campos, E. (1989a) Comments on taxonomy of the genus *Orthotheres* Sakai, 1969 (Crustacea, Brachyura, Pinnotheridae). *Bulletin of Marine Science*, 4(3), 1123–1128.

Campos, E. (1989b) *Tumidotheres*, a new genus for *Pinnotheres margarita* Smith, 1860 and *Pinnotheres maculatus* Say, 1818 (Crustacea, Brachyura, Pinnotheridae). *Journal of Crustacean Biology*, 9(4), 672–679.

Campos, E. (1990) *Calyptraeotheres*, a new genus of Pinnotheridae for the limpet-crab *Fabia granti* Glassell, 1933 (Crustacea, Brachyura). *Proceedings of the Biological Society of Washington*, 103(2), 364–371.

Campos, E. (1993) Systematics and taxonomic remarks on *Pinnotheres muliniarum* Rathbun, 1918 (Crustacea: Brachyura: Pinnotheridae). *Proceedings of the Biological Society of Washington*, 106(1), 92–101.

Campos, E. (1996a) Partial revision of Pinnotherid crab genera with a two-segmented palp on the third maxilliped (Decapoda: Brachyura). *Journal of Crustacean Biology*, 16(3), 556–563.

Campos, E. (1996b) Partial revision of the genus *Fabia* Dana, 1851 (Crustacea: Brachyura: Pinnotheridae). *Journal of Natural History*, 30, 1157–1178.

Campos, E. (2001) A new crab species of the genus *Arcotheres* Manning, 1993, from Thailand (Crustacea: Brachyura: Pinnotheridae). *Zoosystema*, 23(3), 493–497.

Campos, E. (2002) Two new genera of pinnotherid crabs from the tropical eastern Pacific (Brachyura: Pinnotheridae). *Journal of Crustacean Biology*, 16(3), 556–563.

Campos, E. (2007) Pinnotheridae. *In*, Carlton, J.T. *The Light and Smith Manual, Intertidal Invertebrates from Central California to Oregon*. 4th edition, University of California Press, pp. 643–647.

Campos, E. & Griffith, H. (1990) *Clypeasterophilus*, a new genus to receive the small-palped species of the *Dissodactylus* complex (Brachyura: Pinnotheridae). *Journal of Crustacean Biology*, 10(3), 550–553.

Campos, E. (1999) Inclusion of the Austral *Pinnotheres politus* (Smith, 1870) and *Pinnotheres garthi* Fenucci, 1975 within the genus *Calyptraeotheres* Campos, 1990. *Proceedings of the Biological Society of Washington*, 112, 536–540

Campos, E. & Manning, R.B. (2001) Authorship and diagnosis of the genus *Arcotheres* Manning, 1993 (Crustacea: Brachyura: Pinnotheridae). *Raffles Bulletin of Zoology*, 49(1), 167–170.

Dai, Ai-Yun (1980) *Fabia obtusidentata* Dai, sp. nov. *In*: Dai, Ai-Yun, Zhong-qi, Feng, Yu-zhi, Song & Guo-xiao Chen. New species and new records of family Pinnotheridae from Hainan Island. *Acta Zootaxonomica Sinica*, 5, 129-142

[in Chinese, with English summary].
Dana, J.D. (1851) On the classification of the crustacean Grapsoidea. *American Journal of Science and Arts*, series 2(12), 283–291.
Gohar, H.A.F. & Al-Kholy, A.A. (1957) The larvae of some brachyuran Crustacea (from the Red Sea). *Publications of the Marine Biological Station*, Al Ghardaga, Egypt, 9, 143–176.
Kazmi, Q.B. & Manning, R.B. (2003) A new genus and species of pinnotherid crabs from Karachi, northern Arabian Sea (Crustacea, Decapoda, Brachyura). *Journal of Natural History*, 37, 1085–1089.
Konishi, K. (1983) Larvae of pinnotherid crabs (Crustacea: Brachyura) found in the plankton of Oshoro Bay. *Hokkaido University series Vl, Zoology*, 23(3), 266–295.
Lockington, W.N. (1877) Description of a new genus and species of Crustacea. *Proceeding of the California Academy of Science*, 7, 55–56.
Manning, R.B. (1993a) West African pinnotherid crabs, subfamily Pinnotherinae (Crustacea, Decapoda, Brachyura). *Bulletin du Muséum National d'Histoire Naturelle, Paris*, 4e série A, 14 (1–4), 125–177.
Manning, R.B. (1993b) *Epulotheres angelae*, new genus, new species, a pinnotherid crab from the Caribbean Sea (Decapoda: Pinnotheridae). *Journal of Crustacean Biology*, 13(4), 801–804.
Manning, R.B. (1996) *Viridotheres marionae*, a new genus and species of pinnotherid crab from West Africa (Crustacea: Decapoda: Brachyura). *Zoologische Mededelingen*, Leiden 70(19), 271–273
Manning, R.B. (1998) A new genus and species of pinnotherid crab (Crustacea, Decapoda, Brachyura) from Indonesia. *Zoosystema*, 20(2), 357–362
Manning, R.B. & Felder, D. L. (1996) *Nannotheres moorei*, a new genus and species of minute pinnotherid crabs from Belize, Caribbean Sea (Crustacea: Decapoda: Pinnotheridae). *Proceedings of the Biological Society of Washington*, 109(2), 311–317.
Manning, R.B. & Galil, B. (2000) A new genus of pinnotherid crab from the Indian Ocean (Crustacea Decapoda, Brachyura. *Proceedings of the Biological Society of Washington*, 113(1), 66–69.
Marques, F. & Pohle, G. (1995) Phylogenetic analysis of the Pinnotheridae (Crustacea, Brachyura) based on larval morphology, with emphasis on the *Dissodactylus* species complex. *Zoologica Scripta*, 24(4), 347–364.
Ng, P.K.L. & Manning, R.B. (2003) On two new genera of pea crabs parasitic in holothurians (Crustacea: Decapoda: Brachyura: Pinnotheridae) from the Indo-West Pacific, with notes on allied genera. *Proceedings of the Biological Society of Washington*, Vol. 116 (4), 901–919.
Ng, P.K.L., Guinot, D. & Davie, P.J.F. (2008) Systema Brachyurorum: Part 1. An annotated checklist of extant brachyuran crabs of the world. *The Raffles Bulletin of Zoology*, supplement 17, 1–286.
Palacios-Thiel, E., Cuesta, J.A., Campos, E., & Felder, D.L. (2009). Molecular genetic Re-examination of subfamilies and polyphyly in the family Pinnotheridae (Crustacea: Decapoda). *In*, Martin, J.W., Crandall, K.A. and Felder, D.L. *Decapod Crustacean Phylogenetics*. Crustacean Issues, CRC Press. 423-441.
Roberts, M.H. (1975) Larval development of *Pinnotheres chamae* reared in the laboratory. *Chesapeake Science*, 16(4), 242–252.
Rathbun, M.J. (1904) Decapod crustaceans of the northwest coast of North America. *Harriman Alaska Expedition* 10, 1–190.
Rathbun, M.J. (1918) The grapsoid crabs of America. *Bulletin of the United States National Museum*, 97, 1–461.
Sakai, T. (1969) Two new genera and twenty-two new species of crabs from Japan. *Proceedings of the Biological Society of Washington*, 82, 243–280.
Schmitt, W.L. (1921) *The marine decapod Crustacea of California*. University of California Publications in Zoology, 23, 1–470.
Schmitt, W.L., McCain, J.C. & Davidson, E.S. (1973) *Fam. Pinnotheridae, Brachyura I: Decapoda I. In*, H.-E. Gruner & L.B. Holthuis, eds. Crustaceorum Catalogus. W. Junk, Den Haag 3, 1–160.