

Research Article

***Austinotheres angelicus* (Lockington, 1877): the correct name for the symbiotic crab *Juxtafabia muliniarum sensu* Cabrera-Peña *et al.* (2001) (Crustacea, Brachyura, Pinnotheridae)**

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ABSTRACT. The taxonomic identity of the symbiotic crabs *Juxtafabia muliniarum sensu* Cabrera-Peña *et al.* (2001) was revised. The morphology of these specimens, collected in the estuary of Punta Morales, Pacific coast of Costa Rica, in the oyster *Saccostrea palmula* did not agree with *J. muliniarum* but concurs well with topotypes and voucher material of *Austinotheres angelicus* from the Gulf of California, Mexico. *Austinotheres angelicus* belongs to the subfamily Pinnotherinae *sensu* Campos, 2009, and the morphology of *A. angelicus* supports its close relationship with *Bonita mexicana* and *Enigmatheres canfieldi*. The presence of a soft and thin carapace colored with deep chocolate brown with dark purple tones, a conspicuous protuberance in the basal antennal article, a third maxilliped with an ischio-merus fused with its inner margin angled, a carpus larger than the propodus, and a digitiform and small dactylus subdistally inserting on the ventral margin of the propodus are diagnostic features for *A. angelicus*. These characteristics separate this species from other pinnotherid crabs from the entire Pacific Ocean.

Keywords: *Juxtafabia muliniarum*, taxonomy, Pinnotheridae, Brachyura, Crustacea.

***Austinotheres angelicus* (Lockington, 1877): nombre correcto para el cangrejo simbiótico *Juxtafabia muliniarum sensu* Cabrera-Peña *et al.* (2001) (Crustacea, Brachyura, Pinnotheridae)**

RESUMEN. Se revisó la identidad taxonómica del cangrejo simbiote *Juxtafabia muliniarum sensu* Cabrera-Peña *et al.* (2001). La morfología de los especímenes recolectados en el estuario de Punta Morales, costa Pacífica de Costa Rica, en el ostión *Saccostrea palmula* no concordaron con *J. muliniarum* pero concurren bien con topotipos y material verificado de *Austinotheres angelicus* del Golfo de California, México. *Austinotheres angelicus* pertenece a la subfamilia Pinnotherinae *sensu* Campos, 2009 y su morfología apoya su cercana relación con *Bonita mexicana* y *Enigmatheres canfieldi*. La presencia de un caparazón blando y delgado, de color chocolate intenso con tonos púrpura oscuros, una conspicua protuberancia en el artejo basal de la antena, un tercer maxilipedio con el isquio-merus fusionado con su margen interno angulado, un carpus más grande que el propodus y el pequeño dactilo digitiforme que se inserta sobre el margen ventral del propodus son características diagnósticas para *A. angelicus*. Estas características separan a esta especie de otros pinotéridos del océano Pacífico.

Palabras clave: *Juxtafabia muliniarum*, taxonomía, Pinnotheridae, Brachyura, Crustacea.

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INTRODUCTION

Ongoing studies on the pinnotherid crabs of Costa Rica continue to yield new information on the species recorded for this country. The present study deals with *Juxtafabia muliniarum sensu* Cabrera-Peña *et al.* (2001), a symbiont of the oyster *Saccostrea palmula*

Carpenter, 1857. *Juxtafabia* Campos, 1993 is a monotypic genus, closely related to *Fabia* Dana, 1851 (Campos, 1993, 1996). Females of both genera share an asymmetrical pair of pereopods 3 (walking legs 2), longer than the others, and males possess two or more abdominal somites fused (Campos, 1993, 1996). In addition, both males and females in both genera lack a

tubercle on the basal article of the antennae (Campos, 2009). Recently, Dr. Maurizio Protti-Quesada (Escuela de Ciencias Biológicas, Universidad Nacional, Heredia, Costa Rica) allowed us to examine some of the specimens formerly studied by Cabrera-Peña *et al.* (2001) in order to revise their taxonomic identification. Specimens studied by these authors were compared with all the known genera and species of the American Pinnotheridae, including the type species of the genus *Juxtafabia* (Campos, 1993), *J. muliniarum* (Rathbun, 1918). The morphology of males and females of the symbiotic crab of the oyster *S. palmula* did not match with that of *Juxtafabia*. In the present study, the taxonomic identity of *J. muliniarum sensu* Cabrera-Peña *et al.* (2001) is emended, providing a diagnostic description for this species and a morphological comparison with all pinnotherid crabs of America.

MATERIALS AND METHODS

Both, specimens studied by Cabrera-Peña *et al.* (2001) and new material collected in the intertidal zone of the estuary of Punta Morales, Puntarenas, Pacific coast of Costa Rica, in the oyster *Sacosstrea palmula* (see details in the next section) were analyzed. In addition, 26 species of different pinnotherid genera were studied for a comparative purpose. Material obtained from the following institutions were analyzed: Laboratorio de Sistemática de Invertebrados, Universidad Autónoma de Baja California, México (UABC); Colección Nacional de Crustáceos, Instituto de Biología, Universidad Nacional Autónoma de México, Distrito Federal, Mexico (CNCR); Colección Nacional de Equinodermos, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Distrito Federal, Mexico (CNE); Colección de Macroinvertebrados, Instituto de Ciencias del Mar y Limnología (Estación Mazatlán), Universidad Nacional Autónoma de México, Sinaloa, Mexico (EMU); Crustacean Collection, Department of Biology, University of Louisiana, Lafayette, USA (ULLZ); Muséum national d'Histoire naturelle, Paris, France (MNHN); National Museum of Natural History, Smithsonian Institution, Washington D.C., USA (USNM); Natural History Museum of Los Angeles County, California, USA (formerly at the Allan Hancock Foundation) (AHF), and Naturalis, Nationaal Natuurhistorisch Museum (formerly Rijksmuseum van Natuurlijke Historie), Leiden, The Netherlands (RMNH). The species studied include: *Austinotheres angelicus* (Lockington, 1877), USNM 71334, 67723, UABC, EMU; *Austinotheres* sp., ULLZ 5547; *Calyptraeothers granti* (Glassell, 1933), UABC, CNCR 1425; *Epulothers* sp., UABC; *Fabia subquadrata* Dana, 1851, UABC, USNM, AHF 1467-42; *Fabia* sp., ULLZ 8563, 8564, 8565; *Gemmothers chamae* (Roberts,

1975), USNM 139098; *Glassella costaricana* (Wicksten, 1982), UABC; *Holothuriophilus pacificus* (Peppig, 1836), ULLZ 5569; *Holothuriophilus trapeziformis* Nauck, 1880, UABC; *Juxtafabia muliniarum* (Rathbun, 1918), UABC, USNM 23443, 18217, 229724; *Limotheres nasutus* Holthuis, 1975, USNM 151039; *Opisthopus transversus* Rathbun, 1893, USNM 50997, UABC; *Orthotheres ungifalcula* Glassell, 1936, USNM; *Ostracotheres tridacnae* (Ruppell, 1830) MNHN B.10578, RMNH-D 1542; *Parapinnixa nitida* (Lockington, 1877), EMU 3753; *Pinnaxodes floridensis* H.W. Wells & Wells, 1961, ULLZ, USNM 186366; *P. chilensis* (Milne-Edwards, 1837), USNM 22112, 49238; *P. gigas* Green, 1992, UABC; *Pinnixa* spp, UABC; *Pinnotheres pisum* (Linnaeus, 1758), UABC; *Pinnotherelia laevigata* H. Milne Edwards & 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; *Tumidothers 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.

Other abbreviations used include: MZUCR: Museo de Zoología, Universidad de Costa Rica; SDNH: San Diego Natural History, California, USA; CL: carapace length; CW: carapace wide; MXP3: third maxilliped; P1: pereopod 1 (cheliped), P2-P5: pereopods 2-5 (walking legs 1-4).

Systematics

Order Decapoda Latreille (1802)
 Suborder Pleocyemata Burkenroad (1963)
 Infraorder Brachyura Linnaeus (1758)
 Section Eubrachyura de Saint Laurent (1980)
 Family Pinnotheridae de Haan (1833)
 Genus *Austinotheres* Campos (2002)
Austinotheres angelicus (Lockington, (1877)
 (Figs. 1a-1f, 2a)

Synonymy: For previous synonymy, see Schmitt *et al.* (1973): 10, 38.

Pinnotheres angelicus: Lemaitre & Alvarez-Leon (1992): 36-76; Hendrickx (1995): 142.

Austinotheres angelicus: Campos (2002): 328-335; 2009: 30, 40; Ng *et al.* (2008): 248; Palacios-Theil *et al.* (2009): 459, 464, 466; Campos & Hernández-Ávila (2010): 42. *Juxtafabia muliniarum* [not *J. muliniarum* (Rathbun, 1918)]: Cabrera-Peña *et al.* (2001): 889-894.

Type species

Pinnotheres angelicus Lockington 1877, by the original designation and monotypy.

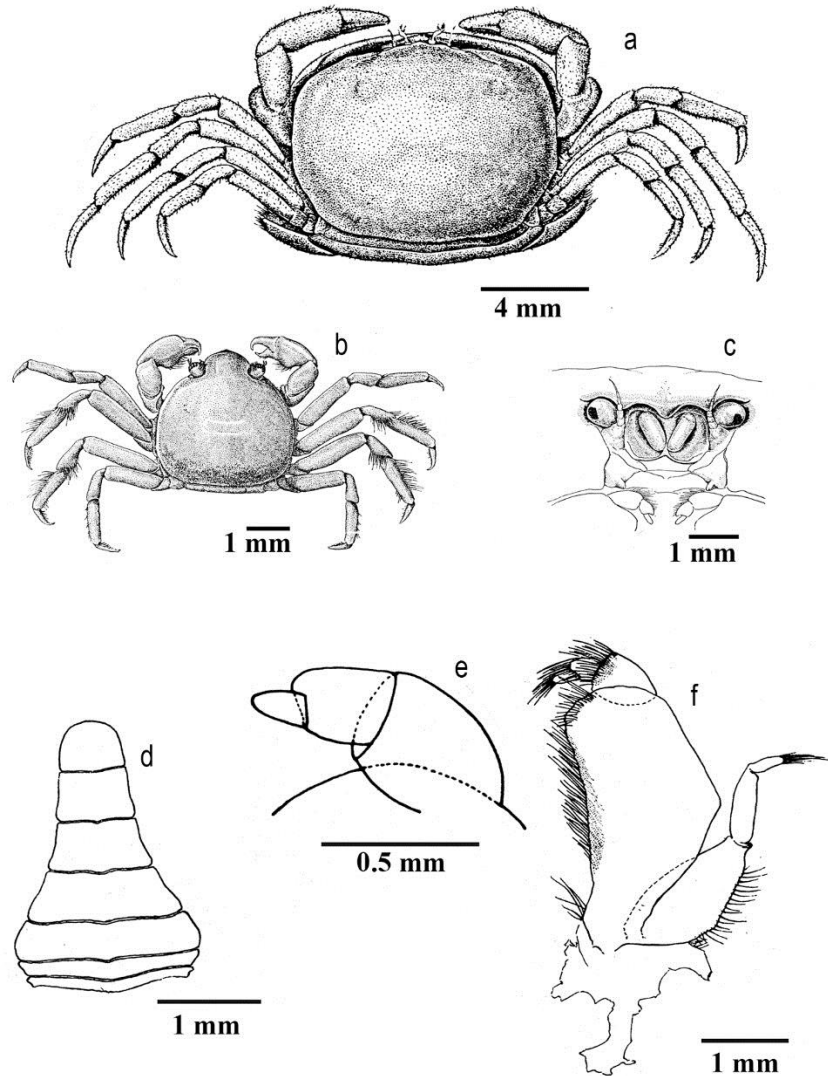


Figure 1. *Austinotheres angelicus*. a,c,e,f) adult female, b, d) adult male, from Bahía de los Angeles, Baja California, Mexico, SDNH 759: a) dorsal view, b) dorsal view, c) frontal region of carapace, d) abdomen, e) palp of MXP3, f) MXP3, (a-f, from Glassell, 1935).

Geographic distribution and host

San Felipe, Baja California, upper Gulf of California, Mexico to Colombia (Lemaitre & Alvarez-León, 1992; Campos, 2002). In *Myrakeena angelica* (Rochebrune, 1895) and *Saccostrea palmula* Carpenter, 1857.

Material examined

1 ♂, 4 ♀, San Felipe, Baja California, Mexico, USNM 71334, 67723; 30 ♀, 30 ♂, Campo El Pescador, 4 km north of San Felipe, Baja California, Mexico, 18 September 1986, in the oyster *Myrakeena angelica* (Rochebrune, 1895), UABC, USNM 205688; 5 ♀, San José Island, Baja California Sur, Mexico, Albatross, 16 May 1889, USNM 17467; 3 ♀, Bahía de los Angeles,

BC, Mexico, May 1982, in *Myrakeena angelica*, USNM210921; 2 ♀, Punta Morales Beach, Puntarenas, Costa Rica, 7 June 1992, USNM 256984; 2 ♂, 8 ♀ (4 ovigerous) Punta Morales, Playa Blanca (Golfo de Nicoya) in *Saccostrea palmula*, M. Protti & A. Baeza, coll, MZUCR 2617-01; 34 ♂, 107 ♀, 15 juveniles, same locality, habitat and host, 18-19 April 2009, MZUCR-2782-01; same locality, habitat and host, 7 November 2009, MZUCR 2782-01; 4 ♂, 12 ♀ (1 juvenile), same locality, habitat and host, 30 October 2010, MZUCR 2832-01; 4 ♂, 9 ♀ (2 ovigerous), same locality, habitat and host, 30 October 2010, MZUCR-2831-01; 11 ♂, 61 ♀ (6 juveniles, 28 ovigerous), same locality, habitat and host, 30 October 2010, MZUCR-2833-01, Rita Vargas coll.

Description

Female (after Campos, 2002). Carapace suborbicular, regions ill-defined, smooth, shiny, thin, easily wrinkled; anterior margin strongly arcuate and not protruding anteriorly; posterior margin wide, slightly sinuous, sides rounded. Front advanced, laterally rounded. Orbits and eyes oval, hidden from dorsal view. Antenna with a prominent tubercle at posterior end of basal joint of antenna. MXP3 obliquely placed on buccal cavity, ischium and merus indistinguishably fused, palp of three articles, joined end to end; carpus larger than propodus and dactylus combined, propodus extending distally, small dactylus distally inserted on ventral margin of propodus. Exopod of MXP3 with a 2-segmented flagellum. Pereopod 1 (chelipeds) elongate, manus slightly compressed and increasing in width distally; pollex slightly deflexed, swollen in basal half, with small teeth on cutting edge; dactylus slightly curved, with small proximal tooth on cutting edge; curved tips cross each other and leave a small gap when fingers are closed. P2-P5 slender, relative length $P3 > P4 > P2 > P5$; P3 asymmetrical, right from 1.10 to 1.22 longer than left. Dactyli of P2-P5 slightly curved at tip, relative length $3 > 4 > 2 > 5$, those of P3 subequal to or longer than respective propodi. Abdomen extremely large, with six somites, and telson free articulated; margin with tomentum, laterally covering ischia and distally buccal cavity and eyes.

Male

(After Campos, 2002). Much smaller than female. Carapace flat, suborbicular; front projecting, triangular, tip bent ventrally to a blunt point, not visible in dorsal view; surface hard, lightly pubescent, punctuate; cardiac region faintly defined. Eyestalk large and stout, diminishing from base to tip; pubescent on upper frontal surface; cornea large. A small tubercle at posterior end of basal joint of antenna. MXP3 similar to that of female. Pereopod 1 (chelipeds) stout, similar, slightly pubescent, palm smooth, swollen on basal half, tapering distally; exterior of manus crossed longitudinally by granulated ridge. Pollex short, stout, hooked at tip; a large ridge-like tooth occupying entire central portion; a deep notch at gape. Dactyli long and curved at tip; armed with two well-developed teeth at proximal end, the distal one the larger; fingers fitting together when closed, curved tips crossing each other; a row of setae on ventral margin of hand. P2-P5 slender, relative length $P3 = P4 > P2 > P5$. Dactyli long and straight, with tips hooked, acuminate. Propodus of P3-P5 crested with setae. Lower distal edges of carpus of P3-P4 with setae. Abdomen of six somites, and telson free articulated, widest at third segment, which represents almost $\frac{3}{4}$ of entire length; gradually narrowing from third somite to telson, which is obtusely rounded. Abdomen and sternum pubescent.

Color in life

Carapace and chelipeds of male a deep chocolate brown; finger of chelipeds and ambulatory legs much lighter. Carapace and chelipeds of female a deep chocolate brown; ambulatory legs from light cream color to white (modified from Glassell, 1935).

Hosts

Austinotheres angelicus is a holosymbiont of oysters (Ostreidae) including *Myrakeena angelica* (Rochebrune, 1895) and *Saccostrea palmula* (Carpenter, 1857). The only other two American pinnotherid crabs, which are symbionts of oysters of the genus *Crassostrea* in the Atlantic Ocean include *Zoaps ostreum* and *Z. geddesi* (see Rathbun, 1918; Schmitt *et al.*, 1973; Campos & Manning, 2000). In addition, several hundreds of *Modiolus capax* (Conrad, 1837) from the Gulf of California were collected in the intertidal zone of San Felipe, and Los Angeles Bay, Baja California, and La Paz Bay, Baja California Sur, Mexico. Like Glassell (1935) we were unable to verify Rathbun's (1918) record of *A. angelicus* in *M. capax*. Only *Fabia concharum* (Rathbun, 1893) and *Opisthopus transversus* Rathbun, 1893 have been confirmed as symbionts of *M. capax* but from the west coast of Baja California Sur, Mexico (Campos *et al.*, 1992; Campos, 1996).

DISCUSSION

The morphological analyses of the specimens collected in Punta Morales, Pacific coast of Costa Rica, in *Saccostrea palmula* and their comparison with topotypes of *Austinotheres angelicus* collected in Los Angeles Bay and another in San Felipe, Baja California, in *Mayrakeena angelica*, has led to the conclusion that the Costa Rican specimens belong to *A. angelicus* (Fig. 1). The genus *Austinotheres* Campos, 2002 along with other 17 genera worldwide has been included in the subfamily Pinnotherinae *sensu stricto* by Campos (2009). The consistent and distinct characters of this group include a soft and thin carapace, and a conspicuous protuberance at the basal antennal article, which is conspicuous in *A. angelicus* (Fig. 2a). Although *Juxtafabia muliniarum* has a carapace soft and thin, it is lacking such a protuberance at the basal antennal article (Fig. 2b). In addition, adult females of *J. muliniarum* have the dactyl of P5 longer than the other pereopods (Fig. 3a); males of this genus, and those of *Fabia* share long swimming setae on external face of carpus and propodus of P3 and P4, and two or more abdominal somites fused (Figs. 3b, 3d; Campos, 1993, 1996; Campos & Manning, 1998). Females of *A. angelicus* have the dactylus of P3 longer than the others pereopods, and males have all abdominal somites and

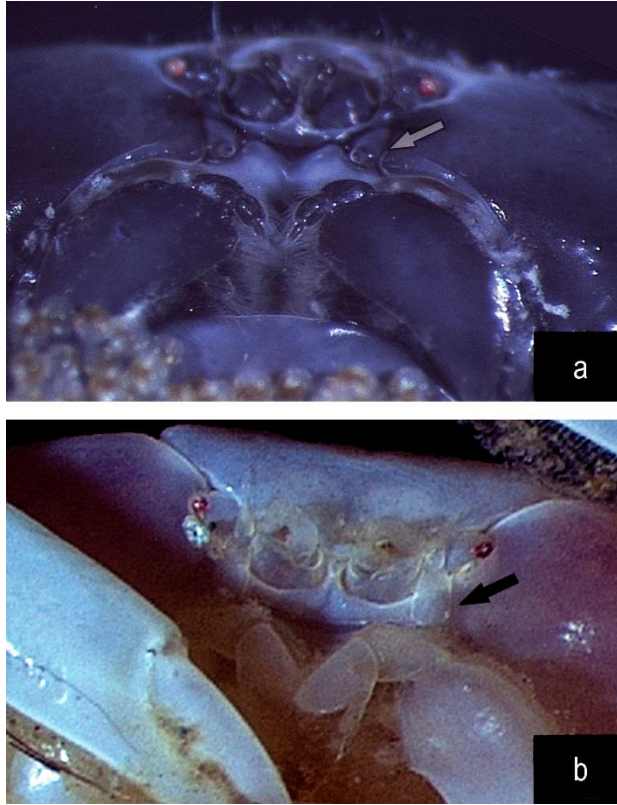


Figure 2. Frontal view. a) *Austinotheres angelicus* from San Felipe, Baja California, Mexico, UABC uncatalogued, arrow indicates the conical tubercle of basal antennal segment; b) *Fabia subquadrata*, Todos Santos Bay, Ensenada, Baja California, Mexico, UABC uncatalogued, arrow indicate the basal antennal segment without a conical tubercle. a) CL = 9.9 mm, b) CL = 13.4 mm.

telson well separated (Fig. 1d). The oyster crab, *A. angelicus*, as well as *Enigmatheres canfieldi* (Rathbun, 1918) (type species of *Enigmatheres* Campos, 2009) and *Bonita mexicana* Campos, 2009 (type species of *Bonita* Campos, 2009) comprise a subgroup within the Pinnotherinae *sensu* Campos (2009) that share a third maxilliped with a palp of three segments, being the carpus longer than the propodus (Figs. 1e, 1f). These shared and exclusive features of these species allow their taxonomic separation from other members of this subfamily. The presence of an even and smooth carapace, and the P3 longer than the others (Fig. 1a) permit to separate *A. angelicus* from *B. mexicana*, which has the carapace tumid with two longitudinal sulci arising from the orbits and extending to the middle the of carapace, and the P4 longer than the others. On the other hand, *E. canfieldi* and *A. angelicus* can be distinguished from other pinnotherines by the asymmetrical P3 and because the propodus of the third maxilliped is shorter than the carpus (Figs. 1e, 1f).

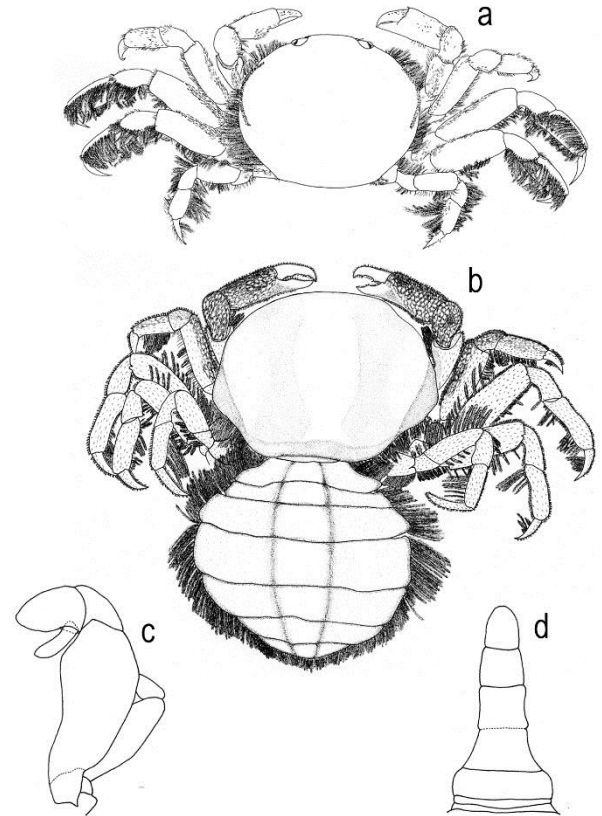


Figure 3. *Juxtafabia muliniarum*: a,c) adult male, b,d) adult female, from Laguna Percebú, San Felipe, Baja California, México, UABC uncatalogued: a) dorsal view; b) dorsal view; c) third maxilliped; d) abdomen. a) CL = 7 mm, b) CL = 3.14 mm.

Others species in the Pinnotherinae *sensu* Campos, 2009, except *B. mexicana*, have symmetrical walking legs, and the propodus of the third maxilliped is always larger than the carpus (Figs. 2b, 3c). *A. angelicus* differs from *E. canfieldi* in the obtuse angle of the outer margin of the ischium-merus of the third maxilliped (Fig. 1f) and by the insertion of the dactylus of this appendage on the distal third of the ventral margin of the propodus (Figs. 1e, 1f). *E. canfieldi* has a gently curved outer margin of the MXP3, and the insertion of the dactylus is on the middle third of the ventral margin of the propodus. The oyster crab, *A. angelicus*, can be also distinguished from *E. canfieldi* by its slender and long walking legs with long, blade-shaped and slightly curved dactyli. The walking legs of *E. canfieldi* are relatively stouter, and the dactyli are shorter, conical and slightly curved up to hooked and hard tip.

In summary, the following diagnostic characteristics as well as its symbiotic relationship with oysters (Ostreidae) permit to distinguish *A. angelicus* from other pinnotherid crabs from the entire Pacific Ocean: 1) the presence of a soft and thin carapace

colored deep chocolate brown with dark purple tones, 2) a conspicuous protuberance in the basal antennal article (Fig. 2a), 3) a third maxilliped with a ischium-merus fused with its inner margin angled, 4) a carpus longer than the propodus, and 5) a digitiform dactylus insert subdistally (Figs. 1e, 1f).

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REFERENCES

- Cabrera-Peña, J., M. Protti-Quesada, M. Urriola-Hernández, O. Sáenz-Vargas & R. Alfaro-Hidalgo. 2001. Body size and fecundity of *Juxtafabia muliniarum* (Brachyura: Pinnotheridae) associated with *Saccostrea palmula* (Bivalvia: Ostreidae), Costa Rica. *Rev. Biol. Trop.*, 49: 889-894.
- Campos, E. 1993. Systematics and taxonomic remarks on *Pinnotheres muliniarum* Rathbun, 1918 (Crustacea: Brachyura: Pinnotheridae). *Proc. Biol. Soc. Wash.*, 106: 92-101.
- Campos, E. 1996. Partial revision of pinnotherid crab genera with a two-segmented palp on the third maxilliped (Decapoda: Brachyura). *J. Crustacean Biol.*, 16: 556-563.
- Campos, E. 2002. Two new genera of pinnotherid crabs from the tropical eastern Pacific (Decapoda: Brachyura: Pinnotheridae). *J. Crustacean Biol.*, 22: 328-336.
- Campos, E. 2009. 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). *Zootaxa*, 2022: 29-44.
- Campos, E. & I. Hernández-Ávila. 2010. Phylogeny of *Calyptraeothers* Campos, 1990 (Crustacea, Decapoda, Brachyura, Pinnotheridae) with the description of *C. pepeluisi* new species from the tropical Mexican Pacific. *Zootaxa*, 2691: 41-52.
- Campos, E. & R.B. Manning. 1998. *Pinnotheres malaguena* Garth, 1948, a new member of the genus *Fabia* Dana, 1851 (Crustacea: Brachyura: Pinnotheridae). *Proc. Biol. Soc. Wash.*, 111: 912-915.
- Campos, E. & R.B. Manning 2000. The identities of *Pinnotheres nudus* Holmes, 1895 and *P. nudus sensu* Weymouth, 1910 (Crustacea: Decapoda: Pinnotheridae). *Proc. Biol. Soc. Wash.*, 113: 799-805.
- Campos, E., A.R. de Campos & J. Ramirez. 1992. Remarks on distribution and hosts for symbiotic crustaceans of the Mexican Pacific (Decapoda and Isopoda). *Proc. Biol. Soc. Wash.*, 105: 753-759.
- Glassell, S.A. 1935. New or little known crabs from the Pacific coast of northern Mexico. *Trans. San Diego Soc. Nat. Hist.*, 8: 91-106.
- Hendrickx, M.E. 1995. Checklist of brachyuran crabs (Crustacea: Decapoda) from the eastern tropical Pacific. *Bull. Inst. Roy. Sci. Nat. Belgique, Biol.*, 65: 125-150.
- Lemaitre, R. & R. Álvarez-León. 1992. Crustáceos decápodos del Pacífico Colombiano: lista de especies y consideraciones zoogeográficas. *An. Inst. Invest. Mar. Punta de Betín*, 21: 33-76.
- Ng, P.K.L., D. Guinot & P.J.F. Davie. 2008. Systema Brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world. *Raffles Bull. Zool., Suppl.* 17: 1-286.
- Palacios-Theil, E., J.A. Cuesta, E. Campos & D.L. Felder. 2009. Molecular genetic re-examination of subfamilies and polyphyly in the family Pinnotheridae (Crustacea: Decapoda). In: J.W. Martin, K.A. Crandall & D.L. Felder (eds.). *Decapod crustacean phylogenetics*. CRC Press, Boca Raton, pp. 457-474.
- Rathbun, M.J. 1918. The grapsoid crabs of America. *Bull. U.S. Nat. Mus.*, 97: 1-461.
- Schmitt, W.L., J.C. McCain & E.S. Davidson. 1973. Fam. Pinnotheridae, Brachyura I: Decapoda I. In: H.-E. Gruner & L.B. Holthuis (eds.). *Crustaceorum catalogus*. W. Junk, Den Haag, 3: 1-160.

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