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## Description of a new genus and species of Pseudothelphusidae Ortmann, 1893 (Decapoda: Brachyura) from Panama, and new records and remarks on the zoogeography of *Trichodactylus quinquedentatus* Rathbun, 1893 (Trichodactylidae) in Central America

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### ABSTRACT

A collection of freshwater crabs from Central America resulted in the description of a new genus and two new species of pseudothelphusid crabs from Panama, and the record of the trichodactylid *Trichodactylus quinquedentatus* Rathbun, 1893 from Honduras and Panama. A new monotypic genus, *Emberacarcinus* n. gen., is erected to accommodate *Potamocarcinus darienensis* Magalhães, Campos & Türkay, 2013. The two new species can be distinguished from their respective congeners by the structures of the male first gonopods: *Ptychophallus bilobatus* n. sp. has a bilobed mesial process whereas *Potamocarcinus tapirrhynchus* n. sp. exhibits a mesial process as a stout, rounded projection obliquely directed apical-cephalically and partially fused to the mesial lobe of the apical crest. The taxonomic affinities of both species with their closest congeners are treated, and the zoogeographic implication of the new records of *T. quinquedentatus* in Central America is discussed.

**Key Words:** biodiversity, biogeography, Central and South American freshwater fauna, Neotropical region, taxonomy

### INTRODUCTION

Panama harbors a remarkably rich freshwater crab fauna despite its relatively small territory (75,517 km<sup>2</sup>). Our knowledge of this fauna began in the late nineteenth century with the description of *Pseudothelphusa colombianus* Rathbun, 1893 (now in *Ptychophallus* Smalley, 1964) from the Chiriquí province, but increased mainly during the second half of the twentieth century with the descriptions of several new taxa by Pretzmann (1965, 1968a, 1968b, 1971, 1978), Rodríguez (1994), Campos & Lemaitre (1999, 2002), and Magalhães *et al.* (2013). Ábrego & Cornejo (2015) provided a checklist of freshwater decapods from Panama based on the records available in the literature, and listed 20 species of freshwater crabs. Although their list included *incertae sedis* taxa and some species with unconfirmed records, this number is close to the 17 species currently recognized in the country (Magalhães *et al.*, 2015). Such diversity of the Panamanian freshwater crab fauna is similar to that of Costa Rica (15 species) and Guatemala (17 species), the other Central American countries recently surveyed for this group (Magalhães *et al.*, 2015; Wehrmann *et al.*, 2016).

The Zoological Reference Collection (ZRC) of the Lee Kong Chian Natural History Museum (previously Raffles Museum), National University of Singapore has accumulated a small but important collection of freshwater brachyuran crabs. Some of this material has already been used in other studies (e.g. Ng & Guinot, 2001; Shih *et al.*, 2015; Ng & Castro, 2016). ZRC passed the collection of Neotropical crabs to the first author for study as part of his revision of the Neotropical fauna. The taxonomic and zoogeographic results derived mainly from the study of this material are reported here.

### MATERIALS AND METHODS

Specimens are deposited at the Colección Zoológica Dr. Eustorgio Méndez, Instituto Conmemorativo de Estudios de la Salud (CoZEM), Panama City, Panama; Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil; Museu de Zoologia, Universidade de São Paulo (MZUSP), São Paulo, Brazil; National Museum of Natural History, Smithsonian Institution (USNM), Washington D.C.; and ZRC. Measurements of carapace are in

millimeters, carapace width was measured across the carapace at its widest point, and carapace length was measured along the midline, from the frontal to the posterior carapace margin. Both measurements follow the number and sex of the specimens examined and are given between parenthesis as (carapace breadth × carapace length). The following abbreviations are used in the text: carapace width (cw), carapace length (cl), male first (G1) and second (G2) gonopods, third maxilliped (mxp3), cheliped (P1), pereopods 2 to 5 (P2–P5), and sternal sulci between adjacent thoracic sternites (s4/s5). Localities without geographic coordinates were georeferenced using Google Earth® software and GeoNames (<http://www.geonames.org/>), and the coordinates given in brackets. The distribution maps were generated using the QGIS software, v. 2.14.16 (<http://www.qgis.org/ptBR/site/>). Line drawings were made by CM with the aid of a Wild M8 (Wild, Heerbrugg, Switzerland) stereomicroscope equipped with a drawing tube, then scanned and edited in Adobe Photoshop® CS 2 software. The plates were mounted in CorelDraw® X3 software. Terminology used in the description of the G1 was adapted from Smalley (1964a), Villalobos & Álvarez (2010), and Magalhães *et al.* (2015).

## SYSTEMATICS

**Family Pseudothelphusidae** Ortmann, 1893

**Tribe Hypolobocerini** Pretzmann, 1971

**Genus *Ptychophallus*** Smalley, 1964

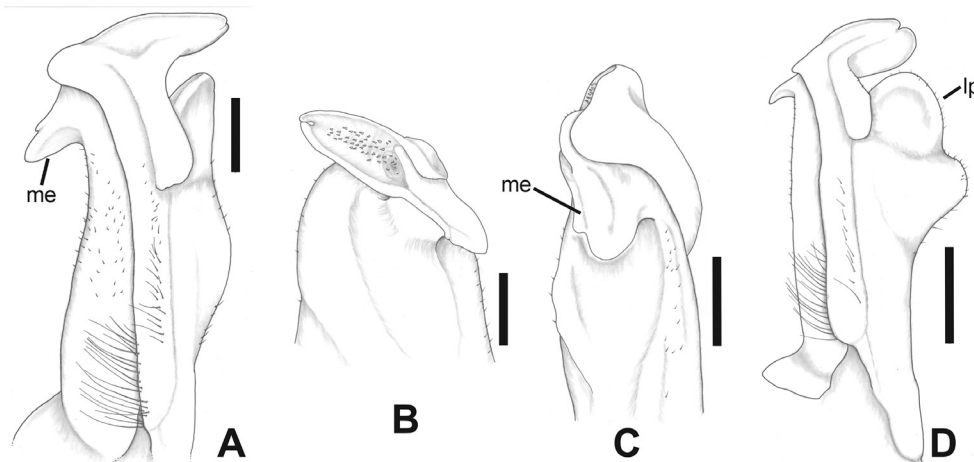
***Ptychophallus colombianus*** (Rathbun, 1893)

(Figs. 1A–C, 8)

*Material examined*: 1 male (37.0 × 22.7), ZRC 2015.0023, Panama, Chiriquí province, Boquete, Bajo Mono [~08°48'46"N 82°27'4"W], ~1,730 m above sea level (ASL), cloud forest, date and leg. unknown.

*Comparative material*: 1 male, 1 female, INPA 1654, Costa Rica, San José province, Pérez Zeledón canton, unnamed creek, tributary of Buena Vista River, drainage of Grande de Térraba River; 09°28'9.33"N 83°39'24.53"W, 1,200 m, 13.vi.2007, L.R. Lara leg.; 1 left G1, INPA 1659, same data locality and date; 4 males, INPA 1831, same data locality, 26.x.2009, L.R. Lara leg.

*Distribution*: Pacific drainage of southern Costa Rica and western Panama. In Panama, the species occurs in Chiriquí province (Fig. 8; Magalhães *et al.*, 2015: 307, fig. 79).



**Figure 1.** *Ptychophallus colombianus*, male (37.0 × 22.7 mm), ZRC 2015.0023, left G1. Complete structure, mesial view (A); distal part, lateral view (B); distal part, mesiocephalic view (C). *Ptychophallus tumimanus*, male (21.8 × 13.2), ZRC 2015.0017, left G1. Complete structure, mesial view (D). Scales: 1 mm. me, mesial process; lp, lateral process.

*Remarks*: The G1 of the specimen examined closely resembles those studied by Magalhães *et al.* (2015), except that the mesial process is slightly bilobed on its distal border (Fig. 1A, C). The species also resembles *P. bilobatus* sp. n., but the G1 morphology of the two species differs markedly in other characters (see Remarks of *P. bilobatus* sp. n. for a detailed morphological comparison).

***Ptychophallus tumimanus*** (Rathbun, 1898)

(Figs. 1D, 8)

*Material examined*: 1 male (21.8 × 13.2), ZRC 2015.0017, 1 male (23.5 × 14.5), INPA 2481 (from ZRC 2015.0018), Panama, Darién province, near Metetí, Reserva Hidrológica Filo del Tallo [~08°27'06"N 77°58'43"W], rainforest, ~163 m ASL, date and leg. unknown.

*Comparative material*: 1 male, USNM 230099, Panama, Coclé province, El Valle, date unknown, P. Allen leg.

*Distribution*: Atlantic and Pacific drainages of central and southeastern Costa Rica and Pacific drainage of Panama. In Panama, the species is known from the western and central portions of Pacific drainage (Magalhães *et al.*, 2015: 340, fig. 84); the present record extends its range towards the Darién province, eastern Panamá (Fig. 8).

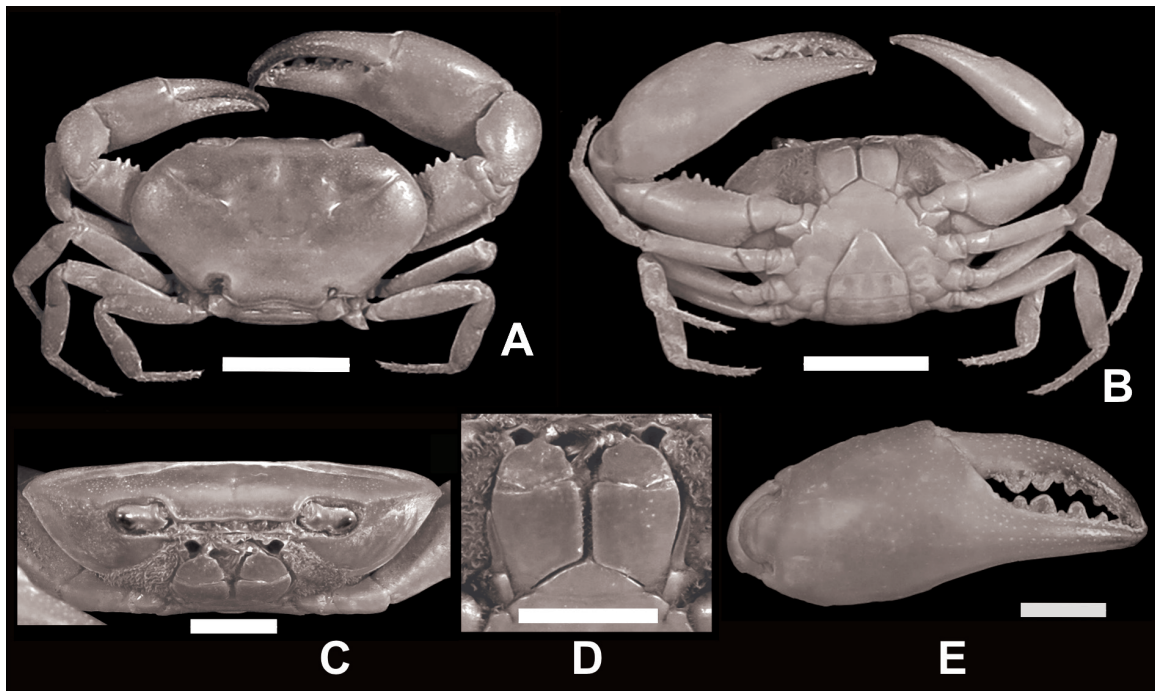
*Remarks*: The G1 of the specimen examined (Fig. 1D) is very similar to that described by Magalhães *et al.* (2015). In comparison with the specimen from El Valle (Coclé province) (USNM 230099) (Magalhães *et al.*, 2015: 319, fig. 58), the G1 of the specimen has a lateral process with a slightly smaller and more rounded proximal lobe, but such difference is subtle and can be considered as intraspecific variability.

***Ptychophallus bilobatus*** n. sp.

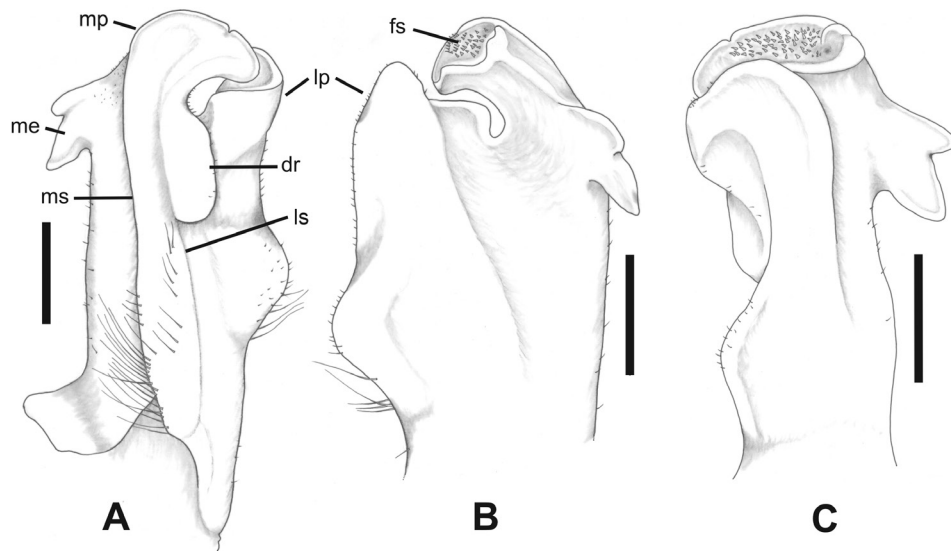
(Figs. 2, 3, 8)

*Type material*: Holotype: male (24.0 × 13.6), MZUSP 38799 (transferred from ZRC 2015.0022), Panama, Chiriquí province, Boquete, Bajo Mono [~08°48'N 82°28'W], ~1,730 m ASL, cloud forest, date and leg. unknown.

*Comparative material*: *Ptychophallus costaricensis* Villalobos, 1974: 1 male, paratype, INPA 1844, Costa Rica, San José province, Naranjo, Naranjo River, Guillermo Solís farm, 7.v.1972, R. Saenz,



**Figure 2.** *Ptychophallus bilobatus* n. sp., holotype male (24.0 × 13.6 mm), MZUSP 38799. Habitus, dorsal view (A); habitus, ventral view (B); frontal view of cephalothorax (C); mpx3 (D); outer view of right chela (larger) (E). Scales: A, B = 10 mm; C–E = 5 mm. Photograph CM.



**Figure 3.** *Ptychophallus bilobatus* n. sp., holotype male (24.0 × 13.6 mm), MZUSP 38799, left G1. Mesial view (A); cephalic view (B); lateral view (C). Scales: 1 mm. dr, caudal ridge; fs, field of apical spines; lp, lateral process; ls, lateral suture; me, mesial process; mp, marginal process; ms, marginal suture.

V. Ramírez & C. Villalobos leg. *P. uncinatus* Campos & Lemaitre, 1999: 1 male, INPA 2087, Costa Rica, Limón province, Limón municipality, Veragua Rainforest Research and Adventure Park, Ciccaba creek, 19.i.2013, A. Rodríguez & D. Hernández leg.; 1 male, INPA 1842, Costa Rica, Puntarenas province, Batambal creek, tributary of Camaronal River, Grande de Térraba River basin, 15.xi.2007, L.R. Lara leg.

**Diagnosis:** G1 with distinct subdistal ridge; marginal process indistinct, continuous with mesiocaudal margin of apex, not produced beyond this margin. Mesial process bilobed, slightly downturned, proximal lobe larger, subtriangular; distal lobe smaller. Lateral process long, encompassing approximately 75% of stem length (measured from proximal opening to caudal border of apex), with

distinct median concavity on caudal surface, moderately bilobed; proximal lobe rounded, as wide as distal lobe; distal lobe thicker distally, slightly wider than lateral end of apex, moderately swollen distally on cephalic surface.

**Description of holotype:** Carapace (Fig. 2A, B) outline ellipsoidal, widest medially (cw/cl 1.76), dorsal surface smooth, nearly flat, regions weakly defined. Two distinct gastric pits, close to each other, on metagastric region. Cervical grooves wide, deeper proximally, shallower distally, slightly arched, distal end not reaching anterolateral margin. Postfrontal lobules small, nearly indistinct; median groove barely visible. Surface of carapace between front, postfrontal lobules smooth, distinctly deflected anteroven- trally. Upper border of front (Fig. 2C) indistinct, median notch

absent (larger male paratype with upper border of front distinct, rounded, smooth, nearly straight in dorsal view); lower border carinate, slightly sinuous in dorsal view, nearly straight in frontal view. Upper orbital margin smooth towards inner side, lined with faint papillae towards outer side; lower orbital margin crenulate, lined with faint papillae; exorbital angle low, obtuse. Anterolateral margin of carapace with small notch just posterior to exorbital angle, followed by set of vestigial, rounded teeth decreasing in size from anterior to posterior portion; posterolateral margin smooth, marked by faint suture. Epistome narrow; epistomial tooth low, subtriangular, slightly deflected anteroventrally, carinate, smooth borders (Fig. 2C). Suborbital, subhepatic regions of carapace side-wall smooth; pterygostomial regions densely pilose (Fig. 2B, C).

Endopod of mxp3 (Fig. 2D) with ischium trapezoidal, inner margin nearly straight, outer margin slightly convex; merus subrectangular, outer margin with distolateral corner broadly rounded, inner surface of 3-articulated palp having setae; exopod of mxp3 long, narrow, 0.73 times length of outer margin of ischium. Aperture of efferent branchial channel wide, subquadrate, upper margin slightly rounded, smooth (Fig. 2C, D).

Chelipeds (Fig. 2A, B) distinctly heterochelous, similarly armed, right P1 larger. Larger cheliped with merus subtriangular in cross section; superior margin rounded, with irregular row of scaly, low tubercles, fainter distally; lower inner margin lined with longitudinal row of conical tubercles increasing in size distally; lower outer margin with single row of faint tubercles; distal upper margin arched, smooth, lower margin with oblique subdistal row of 3 faint tubercles. Carpus with inner margin with row of 4 faint tubercles, obtuse median spine, smooth distally; outer surface rounded, smooth. Palm moderately swollen (length/width 1.61), smooth on inner, outer, upper surfaces, lower margin proximally with few faint tubercles (Fig. 2E). Fingers of larger chela (Fig. 2E) slightly gaping, those of smaller chela not distinctly gaping, tips slightly crossing when closed; fixed finger with row of variable-sized subtriangular teeth, median ones larger. Dactylus moderately arched, slightly longer than palm (dactylus/palm 1.39, measured dorsally); upper, inner, outer surfaces of dactylus, pollex punctuated with rows of minute setae. P2–5 slender, ratios dactylus/propodus, dactylus/merus (left side measured; P5 right dissected for DNA analysis), respectively: P2 = 1.61, 0.76; P3 = 1.70, 0.66; P4 = 1.68, 0.85; P5 = 1.67, 0.87. P2–5 with 5 longitudinal rows of sharp, corneous spines, increasing in size distally.

Thoracic sternum slightly wider (~1.1 times) than long (Fig. 2B). Thoracic sternites of mxp3, first pereopods (sternites III, IV, respectively) completely fused, except for small notches at lateral edges of sternum; s4/s5, s5/s6 not reaching midline of thoracic sternum by short distance; s4/s5, s5/s6 shallow externally, deeper internally; s6/s7, s7/s8 reaching midline of thoracic sternum, s6/s7 internally shallower than preceding ones. Midline of thoracic sternum marked by distinct groove between sternites VII, VIII, deeper at sternite VII. Episternites 4–6 triangular posteriorly, episternite 7 posteriorly truncate. Sternopleonal cavity V-shaped, wide, with pubescence denser between sternites V–VII; tubercle of pleonal holding system small, placed near border of cavity, adjacent to s5/s6. Penis nearly straight, emerging from nearby coxo-sternal condyle articulation, located in shallow depression on sternite 8, proximally thick, abruptly tapering distally.

All pleonal somites free; somites with lateral margins fringed by rows of short setae; pleon with somite VI subrectangular, slightly longer than preceding ones, slightly shorter than telson (ratio length of somite VI/length telson = 0.81), lateral margins of somites V–VI nearly straight (Fig. 2B). Telson subtriangular, 1.71 times wider than long, lateral margins slightly concave, fringed by row of low tubercles, lined with short setae; tip rounded (Fig. 2B).

G1 (Fig. 3) straight in mesio-caudal view, cephalic margin nearly straight in mesial view, with scattered bristles; apex bent approximately 45° in laterocephalic direction. Marginal plate medially fused to caudal surface, forming distinct subdistal caudal ridge;

median, irregular row of setae present along proximal portion. Marginal suture on mesial side, nearly straight proximally medially, gently directed to caudal side distally, with row of long, short setae along proximal portion; marginal process indistinct, continuous with mesio-caudal margin of apex, not produced beyond this margin. Mesial process bilobed, slightly downturned, proximal lobe larger, subtriangular, distal lobe smaller. Lateral process lengthy, encompassing approximately 75% of stem length (measured from proximal opening to caudal border of apex), with distinct median concavity on caudal surface, moderately bilobed; proximal lobe rounded, with few short, long setae, some bristles, as wide as distal one; distal lobe thicker distally, slightly wider than lateral end of apex, distinctly swollen distally on cephalic surface, exceeding slightly cephalic margin of apex. Subdistal caudal ridge well developed, separated from distal border of lateral process by distinct depression. Apex oblong, open, obliquely directed towards laterocephalic side; caudal margin smooth, slightly convex, with small apical notch near lateral end, cephalic margin smooth, partially overlapped by terminal portion of distal lobe of lateral process in lateral view. Field of apical spines well developed, facing towards laterocephalic side. G2 nearly as long as G1, flagellum conspicuously slender, regularly tapering.

*Etymology:* The specific epithet refers to the bilobate mesial lobe of the G1.

*Type locality and distribution:* So far known only from Bajo Mono, in the municipality of Boquete, Chiriquí province, western Panama (Fig. 8).

*Remarks:* The new species clearly belongs to *Ptychophallus* Smalley, 1964 (cf. Smalley, 1964b) due to the length of the exopod of mxp3 and the morphology of the G1, particularly the apex being bent laterocephalically, presence of the subdistal caudal ridge, and the large, bilobed lateral process.

*Ptychophallus bilobatus* sp. n. resembles *P. colombianus* (Rathbun, 1893) with regards to some characters of the G1. In both species, the lateral process is quite long (approximately 70–80%) comparatively to the length of the whole stem, with the proximal and distal lobes separated by a shallow concavity. The bilobed mesial process is also a character shared by these two species. Although all specimens attributed to *P. colombianus* by Magalhães et al. (2015) have a G1 with unilobed mesial process, the G1 of the specimen examined possesses a slightly bilobed mesial process (Fig. 1A, C). *Ptychophallus bilobatus* sp. n. and *P. colombianus* can nevertheless be distinguished from each other by the following invariant G1 characters: 1) distal lobe of the lateral process is wider than the lateral end of the apex and is distinctly swollen distally, as well as slightly overlapping the cephalic margin of apex in *P. bilobatus* sp. n. (Fig. 3A, B) (only slightly narrower than the lateral end of the apex, moderately swollen distally and clearly shorter than the cephalic margin of apex in *P. colombianus*; Fig. 1A); 2) apical notch at the mesio-caudal margin of the apex in *P. bilobatus* sp. n. (Fig. 3A) (at the lateral end of the apex in *P. colombianus*; Fig. 1A); 3) distal portion of the marginal suture is directed to the caudal side in *P. bilobatus* sp. n. (Fig. 3A) (directed to the cephalic side in *P. colombianus*; Fig. 1A); and 4) marginal process is indistinct and continuous with the mesio-caudal margin of apex in *P. bilobatus* sp. n. (Fig. 1A) (short, rounded, slightly discontinuous from mesio-caudal margin of apex in *P. colombianus*; Fig. 1A).

A bilobed mesial process is also present in the G1 of *P. costaricensis* Villalobos, 1974, a species so far known only in central-southern Costa Rica (Magalhães et al., 2015), but its G1 differs from that of *P. bilobatus* sp. n. mainly by 1) the proximal and distal lobes of the lateral process are clearly divided by a deep median cleft and are subequal in length and width in *P. costaricensis* (cf. Magalhães et al., 2015: figs. 15, 16), whereas in *P. bilobatus* sp. n., the lobes are only separated by a shallow concavity and the distal lobe is

larger than the proximal one (Fig. 3A, B); 2) marginal process is more developed and slightly discontinuous with the caudal margin of the apex, reaching a little beyond this margin in *P. costaricensis* (cf. Magalhães *et al.*, 2015: fig. 16), whereas it is indistinct and continuous of the caudal margin of the apex in *P. bilobatus* **n. sp.** (Fig. 3A); and 3) presence of a short spine on the laterocephalic side of the mesial lobe (Magalhães *et al.*, 2015: fig. 15), which is absent in *P. bilobatus* **n. sp.** (Fig. 3B).

The thick, swollen distal lobe of the lateral process that can exceed the cephalic border of the apex is also seen in the G1 of *P. uncinatus* Campos & Lemaitre, 1999, but the lobes of the lateral process are clearly separated by a deep incision in this species, the mesial process is unilobed, and the distal portion of the marginal suture is directed to the cephalic side (Magalhães *et al.*, 2015: figs. 61–63).

The distribution of *P. bilobatus* **n. sp.** in Chiriquí province, Panama and the overall resemblance of its G1 with the one attributed to *P. colombianus* might raise some doubts about the validity of the new taxon. Magalhães *et al.* (2015) considered that the validity of *P. colombianus* might be questionable because it was based on two female syntypes from the Chiriquí province (David River), and because there are at least two other species of *Ptychophallus* (*P. paraxanthusi* (Bott, 1968) and *P. montanus* (Rathbun, 1898)) occurring in the same region of its type locality. Based on the morphological differences between the G1s of these three species, and to avoid nomenclatural instability, the authors recognized *P. colombianus* as a valid species. Similarly, the G1 of the specimens assigned to *P. colombianus* also show some differences in relation to that of *P. bilobatus* **sp. n.**, as discussed above. On this basis, we have therefore decided that it is best to describe the present new species. We nevertheless note the suggestion by Magalhães *et al.* (2015) that a thorough molecular and morphological study of the species from the region with a larger series of specimens from a wider geographical coverage could be useful.

*Nomenclatural statement:* A life science identifier (LSID) number was obtained for the new species: urn:lsid:zoobank.org:pub:urn:lsid:zoobank.org:pub:D25A4BDF-F9F2-4BB2-866A-430D61F87747.

### Tribe Potamocarcinini Ortmann, 1897

### Genus *Potamocarcinus* H. Milne Edwards, 1853

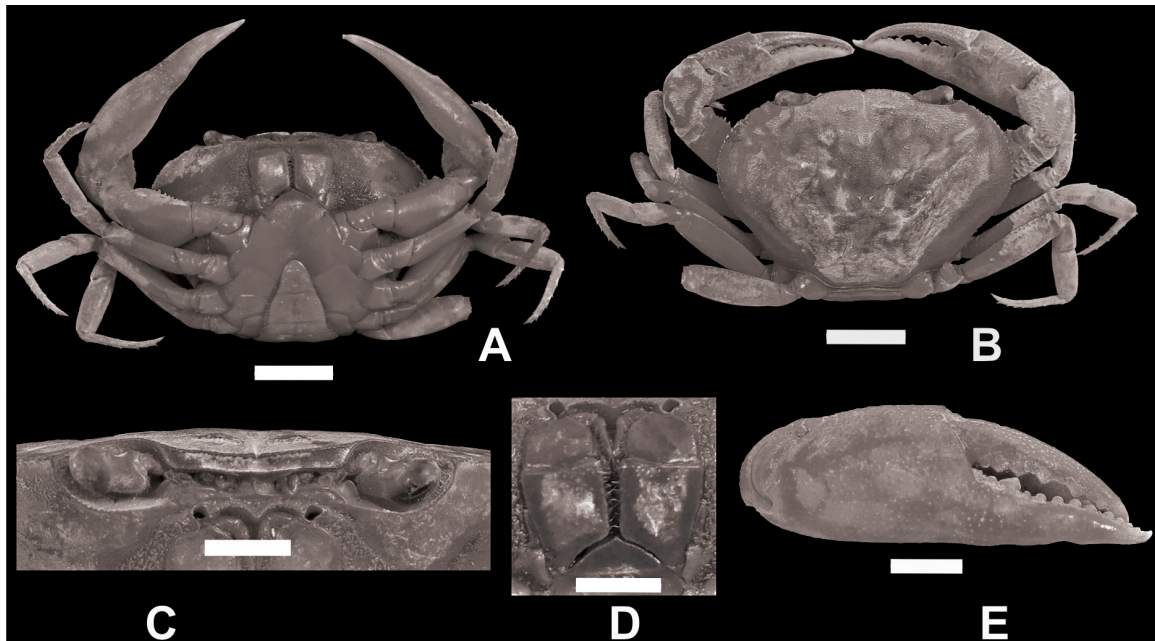
### *Potamocarcinus tapirrhynchus* **n. sp.**

(Figs. 4, 5, 8)

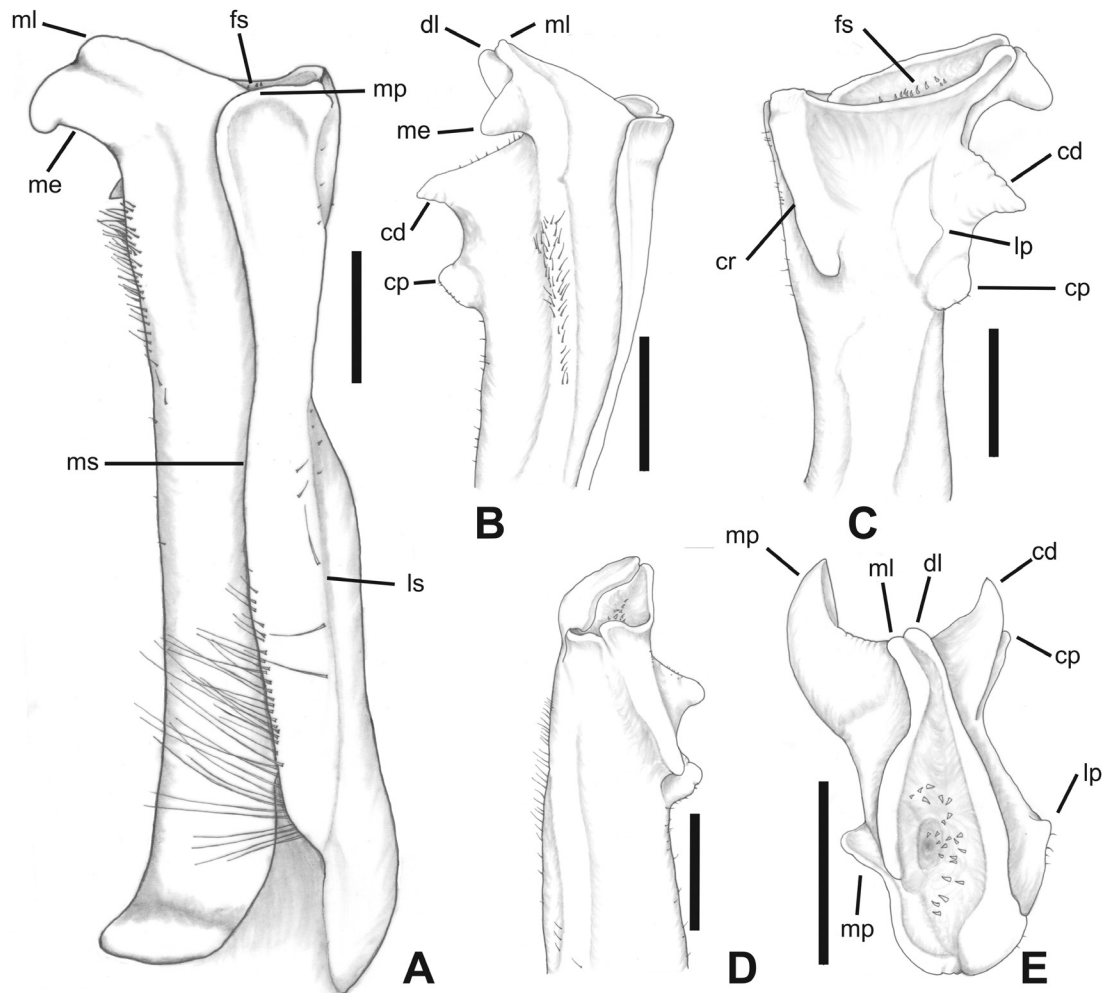
*Type material:* Holotype: male (36.5 × 24.2), MZUSP 38800 (from ZRC 2015.0019), Panama, Darién province, near Meteti, Reserva Hidrológica Filo del Tallo [~08°27'06''N 77°58'43''W], rainforest, ~163 m ASL, date and leg. unknown. Paratype: 1 immature male (20.5 × 14.2), ZRC 2015.0020, Panama, Darién province, near Meteti, Río El Balsal, [~08°28'16''N 77°59'50''W], rainforest, ~110 m ASL, date and leg. unknown; 1 male (31.9 × 22.2), CoZEM-CR 66, Panama, Darién province, Río Tuira, 08°01'08.11''N 77°44'06.83''W, 24 April 2014, leg. A. Cornejo, M. Molinar & A. Tuñon.

*Comparative material:* *P. magnus* (Rathbun, 1896): 1 male, INPA 1871, Costa Rica, Puntarenas province, Miramar, 24.iv.1977, C. Villalobos leg. *P. nicaraguensis* Rathbun, 1893: 1 male, INPA 1869, Costa Rica, Alajuela province, Atlantic drainage: Cantón San Carlos, San Carlos River, San Carlos estuary, 2.iii.2005, P. Gutierrez leg. *P. richmondi* (Rathbun, 1893): 1 male, INPA 1712, Panama City, Panama province, Capira River, 02.viii.2008, L. Torati leg.

*Diagnosis:* G1 straight in caudal, mesial views; marginal process shorter than mesial lobe on apical crest, situated at approximately same level of mesial process. Mesial process on distal portion of mesial border as stout, rounded projection overall obliquely directed apical-cephalically, only tip slightly curved downwards; mesial crest of apex produced into oblique, enlarged mesial lobe partially fused to mesial process in mesial view, slightly folded over apex cavity; cephalic surface with distal cephalic process as larger, conical tooth; proximal cephalic process as smaller, blunt tooth with few minute setae. Lateral process as subterminal low, blunt tooth. Distinct, short caudal ridge present on subterminal portion of caudal surface.



**Figure 4.** *Potamocarcinus tapirrhynchus* **n. sp.**, holotype male (36.5 × 24.2 mm), MZUSP 38800. Habitus, ventral view (A); habitus, dorsal view (B); frontal view of cephalothorax (C); mxp3 (D); outer view of right chela (larger) (E). Scales: A, B = 10 mm; C–E = 5 mm. Photograph CM.



**Figure 5.** *Potamocarcinus tapirrhynchus* n. sp., holotype male (36.5 × 24.2), MZUSP 38800, left G1. Mesial view (A); cephalic view (B); lateral view (C); caudal view (D); apical view (E). Scales: 1 mm. cd, distal cephalic process; cp, proximal cephalic process; cr, caudal ridge; dl, distocephalic lobe; fs, field of apical spines, lp, lateral process; ls, lateral suture; me, mesial process; ml, mesial lobe; mp, marginal process; ms, marginal suture.

*Description of holotype:* Carapace (Fig. 4A, B) outline ellipsoid, widest medially (cw/cl 1.51), dorsal surface smooth, nearly flat, regions weakly defined. Two barely visible gastric pits, close to each other, on metagastric region. Cervical grooves shallow, wide, nearly straight, distal end barely reaching anterolateral margin. Postfrontal lobules small, nearly indistinct; median groove distinct, shallow. Surface of carapace between front, postfrontal lobules smooth, slightly deflected anteroventrally in dorsal, frontal views. Upper border of front carinate, slightly convex, lined with faint papillae, median notch V-shaped, deep; lower border carinate, lined with faint papillae, nearly straight in frontal view, not projected beyond upper one in dorsal view. Upper, lower orbital margins carinate, lined with faint papillae; exorbital angle low, obtuse. Anterolateral margin of carapace with conspicuously shallow notch at level of distal portion of cervical groove, followed by row of minute, rounded teeth increasing in size from anterior to posterior portion; posterolateral margin smooth, marked by faint suture. Epistome narrow; epistomial tooth low, strongly deflected lateroventrally, with carinate, smooth borders, tip rounded (Fig. 4C). Suborbital, subhepatic regions of carapace with few scattered small setae, otherwise smooth; pterygostomial regions densely pilose (Fig. 4A).

Endopod of mxp3 with ischium subquadrate, inner margins straight, outer margin slightly convex; merus subretangular; outer margin with distolateral corner rounded, inner surface of

3-articulated palp with setae; exopod of mxp3 moderately long, narrow, 0.52 times length of outer margin of ischium (Fig. 4D). Aperture of efferent branchial channel wide, subretangular, outer margin somewhat sinuous, smooth (Fig. 4C, D).

Chelipeds (Fig. 4A, B) moderately heterochelous, similarly armed, right P1 largest. Larger cheliped with merus subtriangular in cross section; upper margin rounded, with irregular row of low, squamous teeth, slightly larger distally; inner lower margin lined by longitudinal row of conical tubercles increasing in size distally; outer lower margin with single row of small tubercles; distal upper margin arched, smooth, lower margin with subdistal row of small tubercles. Carpus with inner margin with prominent median spine, row of faint tubercles proximally, distally; outer surface rounded, smooth. Palm (Fig. 4E) slightly swollen (length/width 1.79); inner, outer surfaces, lower margin irregular mostly smooth, only few faint tubercles proximally. Fingers of both chelae (Fig. 4B) not noticeable gaping; tips slightly crossing on smaller chela; larger chela with large, subtriangular tooth proximally, followed by set of smaller, rounded ones. Dactylus of larger chela moderately arched, slightly shorter than polex, slightly longer than palm (dactylus/palm 1.3, measured dorsally); surfaces of dactylus, polex smooth, except for scattered punctuations with minute setae (Fig. 4E). P2–5 slender, ratios dactylus/propodus, dactylus/merus (left side measurements), respectively, as follows: P2 = 1.58, 0.85; P3 = 1.56, 0.79; P4 = 1.61, 0.85; P5 = 1.76, 0.94. P2–5

with dactyli having 5 longitudinal rows of sharp, corneous spines, increasing in size distally, 2 faint grooves on proximal external surface.

Thoracic sternum nearly as long as broad (Fig. 4A). Thoracic sternites of mxp3, first pereopods (sternites III, IV) completely fused, except for small notches at lateral edges of sternum; s4/s5, s5/s6, s6/s7 as shallow groove laterally, medially, deeper at level of reaching midline of thoracic sternum; s7/s8 complete, marked by shallow groove reaching midline of thoracic sternum. Midline of thoracic sternum flat, wide at somites V–VI, as deep groove between somites VII, VII, deeper at somite VII. Episternites 4–7 subtriangular posteriorly. Male sternopleonal cavity subtriangular; densely pilose in region around pleonal holding system. Tubercle of pleonal holding system small, placed near border of sternopleonal cavity, adjacent to s5/s6. Penis somewhat long, slender; hook-shaped distally, emerging from nearby coxo-sternal condyle articulation, located proximally on sternite 8.

All pleonal somites free; lateral margins of somites fringed by row of short setae; male pleon with somite VI trapezoidal, longest, slightly longer than telson (ration length somite VI / length telson = 1.1), lateral margins slightly concave (Fig. 4A). Male telson subtriangular, as long as wide, approximately as long as pleonal somite VI, lateral margins slightly concave medially, fringed by row of short setae become sparser distally; tip rounded (Fig. 4A).

G1 (Fig. 5) straight in caudal, mesial views, moderately compressed mesio-laterally, slightly narrower approximately medially. Mesial border nearly straight in mesial view; mesio-cephalic surface with dense subdistal longitudinal patch of short setae increasing size distally. Marginal plate medially fused to caudal surface, delimited by incomplete lateral suture marked by distinct sulcus on proximal half of stem, with few short, long setae. Marginal suture on mesial side, slightly sinuous, with dense row of short, long marginal setae proximally; marginal process broad, roughly subrectangular, shorter than mesial lobe of apical border, situated at approximately same level of mesial process. Mesial process on distal portion of mesial border as stout, subtriangular projection overall obliquely directed apical-cephalically, only with rounded tip slightly curved downwards. Apex moderately compressed in mesio-lateral direction; apical crests asymmetrical in height along median portion of apex, mesial crest slightly more produced distally than lateral one; mesial crest produced into oblique, enlarged mesial lobe towards cephalic side being slightly folded over apex cavity, partially fused to mesial process in mesial view; lateral crest produced into small, rounded distocephalic lobe; mesial lobe, distocephalic lobes ending symmetrically on cephalic side, separated by small depression. Spermatic channel opening situated apically, positioned closer to caudal end. Field of apical spines weakly developed, with small patch of few minute spines mostly around spermatic channel. Cephalic surface with distal cephalic process as larger, conical tooth with rounded tip; proximal cephalic process as smaller, blunt tooth with few minute setae. Lateral process as subterminal low, blunt tooth. Distinct, short caudal ridge present on subterminal portion of caudal surface.

Left G2 slightly shorter than G1, flagellum conspicuously slender, regularly tapering.

**Etymology:** The specific epithet is composed of *tapir*, the vernacular name of a South American mammal *Tapirus terrestris* (Linnaeus, 1758), which has a peculiar, large, curved snout, and *rhynchos*, Greek for snout or muzzle, in reference to the shape of the mesial process of the G1 that resembles a tapir's muzzle in mesial view (Fig. 5A). The name is used as a noun in apposition.

**Type locality and distribution:** Panama, Darién province, near Meteti, Reserva Hidrológica Filo del Tallo, rainforest, ~163 m ASL (Fig. 8).

**Remarks:** The new species is assigned to *Potamocarcinus* H. Milne Edwards, 1853 on account of exopod of mxp3 being

approximately half the length of the outer margin of the ischium; the mesial lobe of the G1 on the distal crest of the mesial surface extends beyond the apex; the G1 has a cephalically directed, well-developed mesial process; the cephalic process is composed of subdistal spines; and the field of apical spines is terminally located, positioned below or partially along the distal crests of the mesial and lateral surfaces (Magalhães *et al.*, 2015).

*Potamocarcinus tapirrhynchus* **n. sp.** can be readily distinguished from congeners by the upwardly directed mesial process of the G1, which is partially fused to the mesial lobe of the apical crest (Fig. 5A). Although the distal end is slightly recurved downwards, the overall position of the mesial process as a whole is obliquely directed upwards and towards the cephalic side relative to the main axis of the stem. Except for *P. nicaraguensis* Rathbun, 1893 and all other congeners, this process is positioned transversally (Pretzmann, 1975: pl. 6; Alvarez & Villalobos, 1998: fig. 4a, b; Campos & Lemaitre, 2002: fig. 2; Rodríguez & López, 2003: fig. 2; Campos, 2005: figs. 99, 100; Magalhães *et al.*, 2015: figs. 71–76) with regards to the stem axis. The mesial process of the new species is also slightly upwardly directed like in *P. nicaraguensis*, thus having a rounded distal end. Both species, however, can be easily distinguished because the mesial process is totally fused to the weakly developed mesial lobe in *P. nicaraguensis*, making their borders fully continuous (Magalhães *et al.*, 2015: figs. 73, 74), whereas the mesial process is only partially fused to the mesial lobe in *P. tapirrhynchus* **n. sp.**, making their borders slightly discontinuous (Fig. 5A). Their G1s also differ by the form of the marginal process, which is subtriangular and distinctly longer than the mesial lobe in *P. nicaraguensis* (Magalhães *et al.*, 2015: fig. 73), and subrectangular and shorter than mesial lobe in *P. tapirrhynchus* **n. sp.** (Fig. 5A).

In addition to the generic diagnostic characters, *P. tapirrhynchus* **n. sp.** resembles the other two species of the genus known to occur in Panama, *P. richmondi* (Rathbun, 1893) (Magalhães *et al.*, 2015: fig. 75) and *P. lobulatus* Campos & Lemaitre, 2002 (Campos & Lemaitre, 2002: fig. 2A) in having a G1 with a subrectangular marginal process, shorter than the mesial lobe and not produced apically beyond the apical cavity, and with a longitudinal patch of short setae along the subdistal portion of the mesio-cephalic surface (Fig. 5A, B). These species can be distinguished from each other mainly by characters of the mesial process, mesial lobe, and lateral process of the G1 (Table 1).

Judging from the published illustrations of *P. colombiensis* Prael & Ramos, 1987 (Prael & Ramos, 1987: fig. 1) and *P. pinzoni* Campos, 2003 (Campos, 2003: fig. 1A), the G1s of the two Colombian species of *Potamocarcinus* resemble that of the new species by having a marginal process that is shorter than the mesial lobe, and the cephalic surface with distal and proximal cephalic processes. *Potamocarcinus tapirrhynchus* **n. sp.** can nevertheless be distinguished from these species by the overall direction of the mesial process, the rounded distal end of the mesial process, and the lower mesial lobe.

**Nomenclatural statement:** A life science identifier (LSID) number was obtained for the new species: urn:lsid:zoobank.org:pub:8B41D3D2-7EA5-433D-8D69-7D513A759ED2.

### Emberacarcinus n. gen.

**Diagnosis:** Exopod of mxp3 approximately 0.5 times length outer margin of endopodal ischium. Orifice of efferent branchial channel open, with pyriform outline. G1 with lateral margin concave, with distinct rounded protuberance proximally, irregular row of minute spines along distal half; apex broadened by rounded protuberance with minute spines on caudolateral surface; apex cavity narrow, elongated caudocephalically, partially covered by folding of mesial lobe mesial lobe short, oblique to main axis of apex, folded in laterocephalic direction; mesial process triangular,

**Table 1.** Main morphological differences among the male first gonopod (G1) of the Panamanian species of *Potamocarcinus*.

	<i>P. tapirrhynchus</i> <b>sp. n.</b>	<i>P. richmondi</i> (Rathbun, 1893)	<i>P. lobulatus</i> Campos & Lemaitre, 2002
Mesial process:			
Direction relative to main axis	Obliquely directed upwards	Transversal	Transversal
Shape of distal end	Rounded	Acute	Acute
Mesial lobe:			
Position along mesial crest of apex	Displaced to cephalic side	Displaced to caudal side	Median
Position relative to marginal process	Slightly higher	Disctintly higher	Distinctly higher
Shape	Wide, mostly straight, rounded near cephalic end	Narrow, subquadrate	Wide, rounded
Lateral process	Low, blunt tooth	Indistinct	Low, blunt tooth

prominent, recurved cephalically, tip directed downwards; cephalic surface with small, conical cephalic process between mesial, lateral processes; lateral surface with large, prominent, subtriangular lateral process with minute spines scattered along rounded margins.

*Type species:* *Potamocarcinus darienensis* Magalhães, Campos & Türkay, 2013, by present designation and monotypy.

*Species included:* *Emberacarcinus darienensis* (Magalhães, Campos & Türkay, 2013) **n. comb.**

*Distribution:* Eastern Panama, Darién province (Fig. 8).

*Gender:* Masculine.

*Etymology:* The generic name is formed by the combination of *Emberá*, the Panamanian indigenous people, Emberá-Wounaan, who live in the Darién province, the region inhabited by the type species of the genus, and *carcinus*, from the Greek karkinus, in reference to the giant crab that, according to Greek mythology, helped Hydra in the battle against Herakles at the lake of Lerna.

*Material examined:* Male (20.5 × 12.7), paratype of *Emberacarcinus darienensis* **n. comb.**, INPA 1983, Panama, Darién province, Cerro Malí, Serranía de Darién, 1400 m, 18.i.1975, C.W. Myers.

*Remarks:* The morphology of the G1 of *E. darienensis* **n. comb.** shows some peculiarities that do not agree very well with the morphology of a typical *Potamocarcinus*-type G1. These differences became clear during our study to assess the affinities of the G1 of *P. tapirrhynchus* **n. sp.** with its congeners, leading to the decision of erecting a new genus to accommodate *Potamocarcinus darienensis*.

Several morphological features characterize the G1 of *Emberacarcinus* **n. gen.** (see Magalhães *et al.*, 2013: fig. 1C–F), which distinguishes it from the G1 of *Potamocarcinus* are as follows: 1) the lateral border bears a distinct rounded protuberance proximally (proximal portion of the lateral border is continuous and this protuberance is absent in *Potamocarcinus*); 2) the apex is narrow mesiolaterally and broadened on the caudolateral surface by a rounded protuberance with minute spines (apex is usually elongated mesiolaterally in *Potamocarcinus*, with its caudolateral surface narrower than in *Emberacarcinus* **n. gen.**); 3) the mesial lobe on the distal crest of the mesial surface is shorter than the marginal process in mesial view (mesial lobe is usually distinctly longer than the marginal process, except in *P. nicaraguensis*, in *Potamocarcinus*); 4) the mesial process is directed downwards regarding the main axis of the stem (transverse or slightly directed upwards relative to the main axis of the stem in *Potamocarcinus*); and most importantly, 5) a large, strong, subtriangular lateral process (proximal process

*sensu* Magalhães *et al.*, 2013) with minute spines scattered along its rounded margins (lateral process is reduced to a small, blunt tooth, sometimes vestigial or even absent in *Potamocarcinus*) (see Pretzmann, 1972, 1975; Rodríguez, 1982; 2001; Prah & Ramos, 1987; Campos & Lemaitre, 2002; Alvarez & Villalobos, 1998; Campos, 2003; Rodríguez & López, 2003; Magalhães *et al.*, 2015). The diagnosis of *E. darienensis* **n. comb.** offered by Magalhães *et al.* (2013) reflects these generic differences and can be used to distinguish the species from *P. tapirrhynchus*.

*Nomenclatural statement:* A life science identifier (LSID) number was obtained for the new genus: urn:lsid:zoobank.org:pub:37310C50-FF39-4828-BC37-5487D921BEC9.

### Trichodactylidae Latreille, 1828

#### Subfamily Trichodactylinae H. Milne Edwards, 1853

#### *Trichodactylus quinquedentatus* Rathbun, 1893

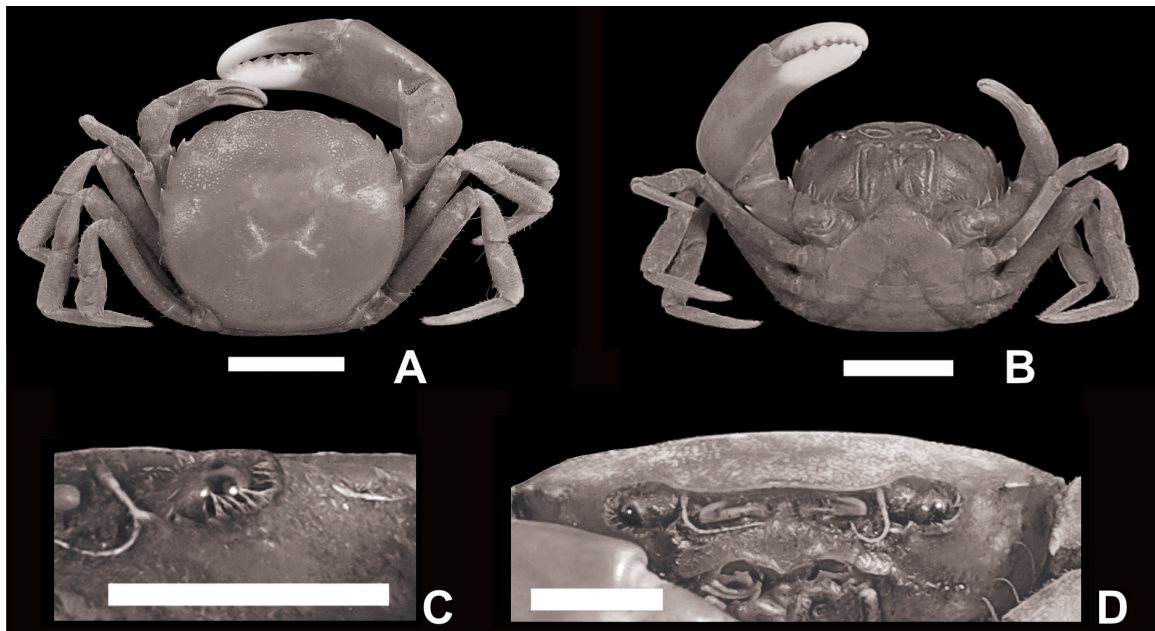
(Figs. 6, 7, 9)

*Material examined:* 1 male (21.8 × 17.9), USNM 285035, Honduras, Gracias a Dios department, Río Patuca [~15°41'N 84°22'W], near the town of Brus Laguna, 05.viii.1975, leg. R.R. Miller, F.H. Miller, R.K. Johnson, G.K. Gloder, D.W. & T. Greenfield; 1 male (21.2 × 18.9), ZRC 2015.0021, Panama, Darién province, near Meteti, Quebrada El Loro [~08°28'26"N 77°59'23"W], rainforest, ~30 m ASL, date and leg. unknown.

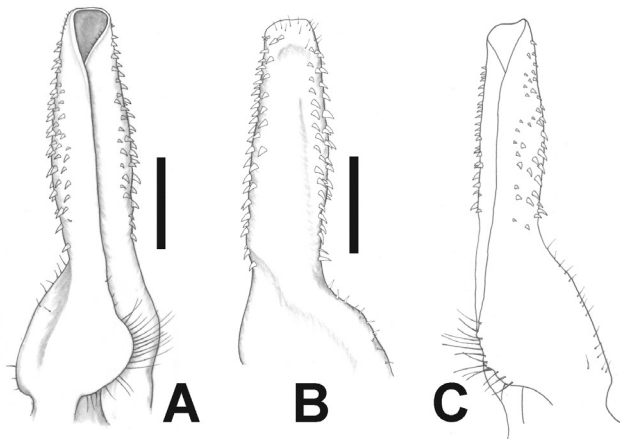
*Comparative material:* 2 males (15.4 × 12.7; 19.8 × 17.2), 2 females (16.9 × 14.6; 21.5 × 18.2), INPA 311, Colombia, Magdalena Department, Sevilla River [~10°52'02"N 74°18'04"W], tributary of the Ciénaga Grande de Santa Marta, 24.x.1978, leg. M. Türkay.

*Description:* Carapace (Fig. 6A, B) subcircular, smooth, convex longitudinally; lateral margin with 5 low, sharp teeth decreasing in size posteriorly. Orbit with lower margin smooth, interrupted by distinct sinus about ¾ distance from lateral angle of orbit, with sharp, medially curved tooth (Fig. 6C, D). Pleonal somites free, lateral margins slightly concave. Telson (Fig. 6B) subtriangular; lateral margins discontinuous with those of pleonal somite VI. G1 (Fig. 7) straight, with median constriction; proximal portion wider than distal portion; distal portion tubular, with dorsal, ventral margins subparallel, slightly convex in mesial view, with field of subterminal spines divided into caudal, cephalic patches. Marginal suture straight, situated along mesial surface. Apex nearly symmetrical, distal margin nearly straight; distal opening subtriangular; wide, directed mesially; few apical setae situated subdistally on dorsal side, distally on lateral side, as well as in inner side of distal opening.





**Figure 6.** *Trichodactylus quinquedentatus*, male (21.2 × 18.9), ZRC 2015.0021. Habitus, dorsal view (A); habitus, ventral view (B); detail of the left orbit (C); frontal view of cephalothorax (D). Scales: A, B = 10 mm; C, D = 5 mm. Photograph CM.



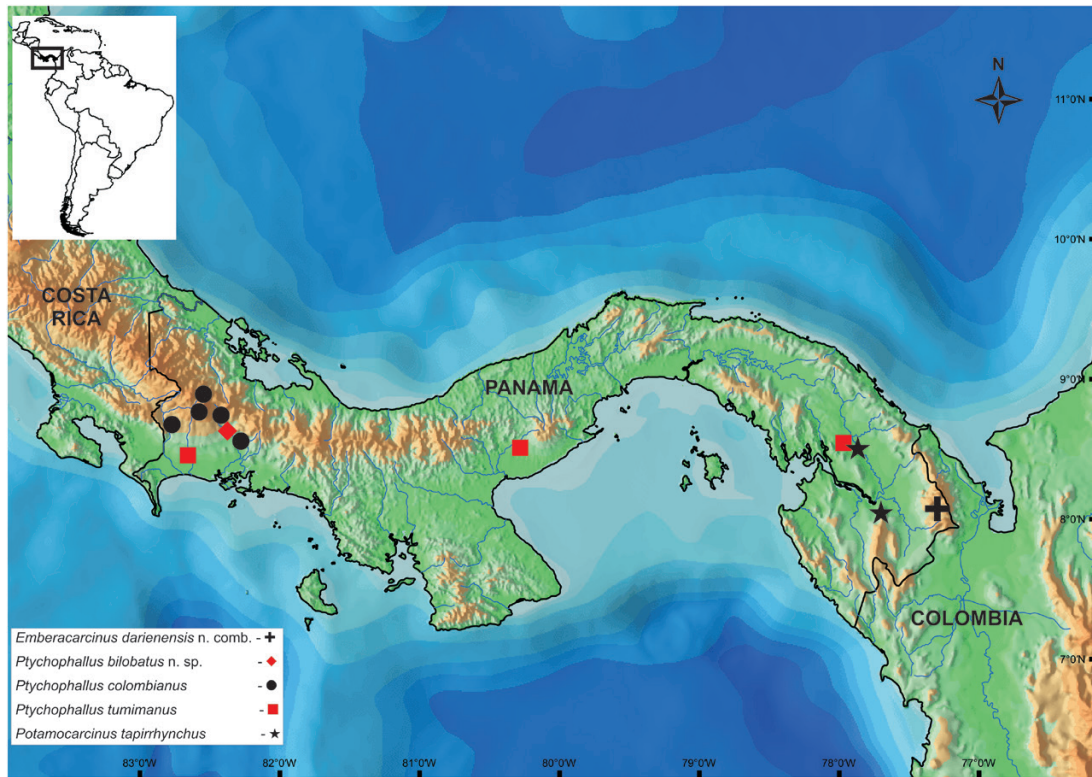
**Figure 7.** *Trichodactylus quinquedentatus*. Male (21.2 × 18.9 mm), ZRC 2015.0021, Panama. Right G1, complete structure, mesial view (A); right G1, distal part, ventral view (B). Male (21.8 × 17.9 mm), USNM 285035, Honduras. Left G1, complete structure, mesiocaudal view (reproduced from an unpublished manuscript by A.E. Smalley) (C). Scales: A, B = 1 mm; C = scale not known.

**Distribution:** Eastern Honduras and Nicaragua (Caribbean slope), western Panama (Pacific slope), and central, northern, and north-western Colombia (Caribbean slope) (Rathbun, 1893; Rodríguez, 1992; Campos, 2005, 2014; herein) (Fig. 9).

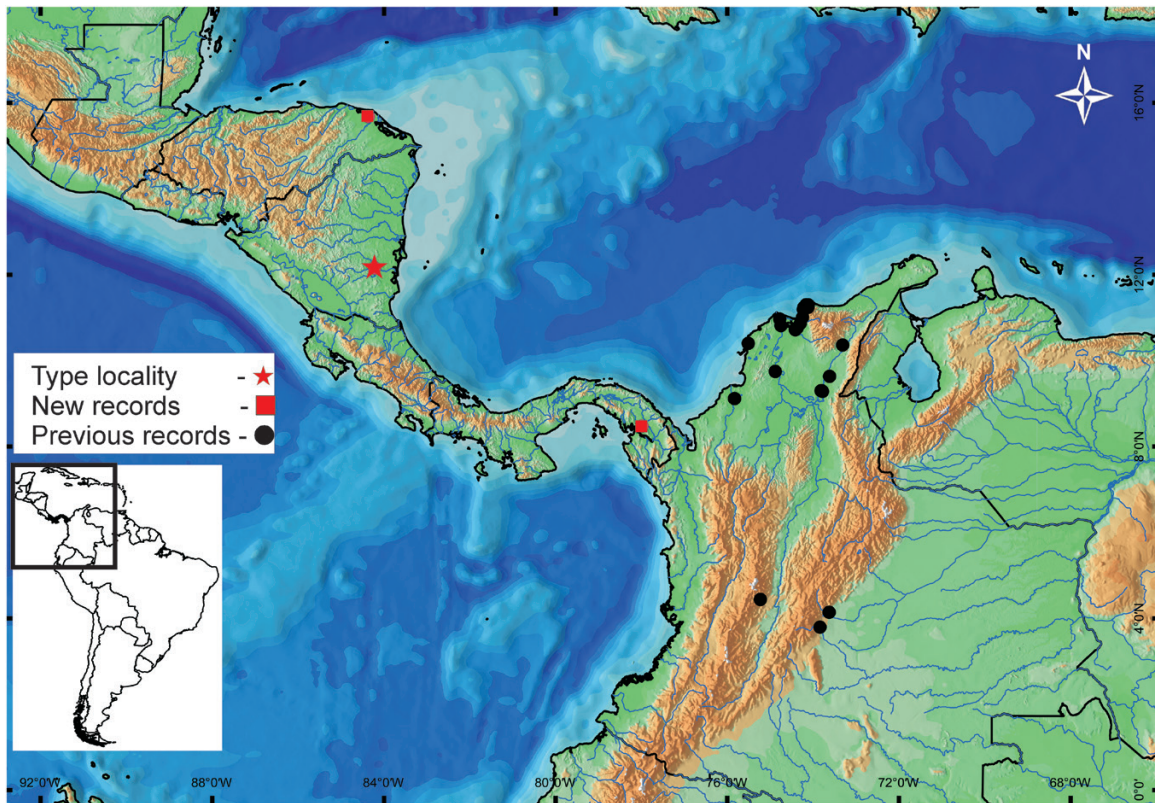
**Remarks:** The examined specimens exhibit some variation on the lateral teeth of the carapace. The specimens from Colombia and Honduras have all five teeth distinct and sharp (the specimen from Honduras has an additional vestigial tooth after the posterior-most tooth on the right side), whereas the fifth tooth is vestigial in the Panamanian specimen. Otherwise, their carapacial and gonopodal characters are very similar, including the shape of the suborbital margin and its resemblance with that of the holotype. According to Smalley & Rodríguez (1972) and Rodríguez (1992), the morphology of the suborbital margin is very distinctive in this species and the similarity among the specimens examined would be sufficient to consider them as conspecific.

The species has a disjunct distribution in Central (Honduras, Nicaragua, and Panama) and South America (central, north-north-western Colombia) (Smalley & Rodríguez, 1972; Rodríguez, 1992; herein) (Fig. 9). It was described on the basis of a single female from Bluefield, on the Atlantic coast of Nicaragua (Rathbun, 1893), and subsequently found in several localities in the Magdalena, Sinú, and Meta rivers basins in Colombia (Campos, 1985, 2005, 2009, 2010, 2014; Smalley & Rodríguez, 1972). These first records of *T. quinquedentatus* in Honduras and Panama could indicate that its distribution could be nearly continuous throughout the whole range, and its absence in some areas might be the consequence of poor collecting efforts. It should be noted, however, that the species has not yet been found in well-explored regions of central and western Panama (Abele & Kim, 1989; Ábrego & Cornejo, 2015), as well as in Costa Rica, where recent intensive surveys of the freshwater crab fauna yielded no trichodactylids (Magalhães *et al.*, 2010, 2015; Lara *et al.*, 2013). As such, the disjunct distribution of this species may well be real. It is also intriguing that no additional specimens of *T. quinquedentatus* have been found in Central America in nearly a century following its description by Rathbun (1893), although it inhabits lowland areas of relatively easy access.

The disjunct, transbasin distribution of *T. quinquedentatus* in Honduras, Nicaragua, Panama, and Colombia raises some taxonomic, evolutionary, and biogeographical issues. Do the populations from Honduras to central Colombia belong to the same species? Is the genetic distance between these populations greater than what could be considered interspecific variability? Regardless of whether these populations represent one or more than one closely related taxon, how did these populations reach their current distribution, which vicariant event (or events) could have caused this divergence and posterior dispersion, where has this lineage originated and evolved, what was its dispersal route (from South America to Central America or vice versa), and which would be their closest phylogenetic affinities, South American or Mesoamerican Trichodactylinae? These are questions that may impact our understanding of the complex geological, ecological, and biogeographical history of Central America and north-western South America (see Hoorn *et al.*, 1995, 2010; Lundberg *et al.*, 1998; Iturralde-Vinent & MacPhee, 1999; Albert *et al.*, 2006; Kirby *et al.*, 2008; Hoorn & Wesselingh, 2010; Albert & Reis, 2011; Farris *et al.*, 2011; Montes *et al.*, 2012, 2015; Leigh *et al.*, 2014; Bacon *et al.*, 2015; Hoorn & Flantua, 2015; Rodríguez Tribaldos *et al.*, 2017).



**Figure 8.** Occurrence of *Emberacarcinus darienensis* Magalhães, Campos & Türkay, 2013, **n. comb.** (cross), *Ptychophallus bilobatus* **n. sp.** (red diamond), *P. colombianus* (circle), *P. tumimanus* (square), and *Potamocarcinus tapirrhynchus* **n. sp.** (star) in Panama (previous records according to Magalhães *et al.*, 2013, 2015). This figure is available in color at *Journal of Crustacean Biology* online.



**Figure 9.** Distribution of *Trichodactylus quinquedentatus* (red star: type locality; red square: new records; black circle: previous records according to Smalley & Rodriguez, 1972; Campos, 1985, 2005, 2009, 2010, 2014). This figure is available in color at *Journal of Crustacean Biology* online.

The current transbasin distribution of *T. quinquentatus* in Colombia (Campos, 2014) suggests that it should have been present in the proto-Orinoco-Amazonas system, a large northwesterly directed fluvio-lacustrine system flowing towards the Caribbean and extending south to north along the foreland basins of the emerging Central Andes, a landscape that dominated much of northern South America, with the northwestern lowlands alternating between freshwater environments and brackish marine embayments due to episodic marine transgressions, from the middle Eocene to Oligocene (43–24 mya) (see Hoorn *et al.*, 1995, 2010; Lundberg *et al.*, 1998; Albert *et al.*, 2006; Wesselingh *et al.*, 2010; Albert & Reis, 2011; Wesselingh & Hoorn, 2011; Rodríguez Tribaldos *et al.*, 2017, and references therein for details on the paleogeomorphology and landscape evolution of South America). When the present-day Río Magdalena basin was isolated from this system by the uplift of the Eastern Andean Cordillera during the early-middle Miocene (24–11 mya), the distribution of *T. quinquentatus* was split into two areas: central Colombia, restricted to the upper tributaries of Río Meta (Río Orinoco basin), and a larger area in the Magdalena and Sinú river basins in north-northwestern Colombia (Campos, 2005, 2014) (Fig. 9). The origin of the species could thus be extended back at least to the Oligocene (34–24 mya). Assuming that the species was distributed in northwestern South America at that period, it could have reached eastern Panama and Mesoamerica after the complete closure of the Central American Seaway in the middle Miocene (~13–15 mya) (Hoorn & Flantua, 2015; Montes *et al.*, 2015). Such event, however, could have taken place even earlier. Molecular biology studies involving several taxa indicate that cross-Isthmian migrations occurred in incremental pulses over an extended period and were probably correlated with the gradual formation and emergence of the Isthmus of Panama (Bacon *et al.*, 2015). Although their study did not include crustaceans, the rates of dispersal estimated by Bacon *et al.* (2015) for groups with similar limited dispersal abilities, such as freshwater fishes and amphibians, showed a cross-Isthmian migration occurring since the early-middle Eocene, with two statistically significant migration rate shifts at around 6.5 and 24 mya. The length of time involved, however, has not resulted in any obvious morphological differences between the two populations.

Answers to these questions and a consistent hypothesis to explain the historical biogeography of the Mesoamerican trichodactylids should only be available after comprehensive molecular and morphological studies based on a more abundant series of specimens from the complete distributional range of the species.

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#### REFERENCES

Abele, L.G. & Kim, W. 1989. The decapod crustaceans of the Panama Canal. *Smithsonian Contribution to Zoology*, **482**: 1–50.  
 Ábrego, T. & Cornejo, A. 2015. Listado de especies de decápodos dulceacuáticos de Panamá. *Puente Biológico*, **7**: 15–35.

Albert, J.S., Lovejoy, N.R. & Crampton, W.G.R. 2006. Miocene tectonism and the separation of sis- and trans-Andean river basins: Evidence from Neotropical fishes. *Journal of South American Earth Sciences*, **21**: 14–27.  
 Albert, J.S. & Reis, R.E. (eds.). 2011. *Historical biogeography of Neotropical freshwater fishes*. University of California Press, Berkeley, CA, USA.  
 Alvarez, F. & Villalobos, J.A. 1998. Six new species of fresh-water crabs (Brachyura: Pseudothelphusidae) from Chiapas, Mexico. *Journal of Crustacean Biology*, **18**: 187–198.  
 Bacon, C.D., Silvestro, D., Jaramillo, C., Smith, B.T., Chakrabarty, P. & Antonelli, A. 2015. Biological evidence supports an early and complex emergence of the Isthmus of Panama. *Proceedings of the National Academy of Sciences of the United States of America*, **112**: 6110–6115.  
 Bott, R., 1968. Fluß-Krabben aus dem östlichen Mittel-Amerika und den Großen Antillen. *Senckenbergiana biologica*, **49**: 39–49.  
 Campos, M.R. 1985. Decápodos de agua dulce del suborden Brachyura reportados para Colombia. *Caldasia*, **14**: 265–284.  
 Campos, M.R. 2003. A new species of freshwater crab of the genus *Potamocarcinus* H. Milne Edwards, 1853 (Crustacea: Brachyura: Pseudothelphusidae) from Colombia. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales*, **27**: 283–286.  
 Campos, M. 2005. *Freshwater crabs from Colombia: a taxonomic and distributional study*. Academia Colombiana de Ciencias Exactas, Físicas y Naturales, Bogotá, Colombia.  
 Campos, M.R. 2009. Crustáceos decápodos de la serranía de Perijá. In: *Colombia diversidad biótica VIII. Media y baja montaña de la serranía de Perijá* (O. Rangel Ch., ed.), pp. 561–566. Universidad Nacional de Colombia, Instituto de Ciencias Naturales, Bogotá, Colombia.  
 Campos, M.R. 2010. Crustáceos. In: *Colombia Diversidad Biotica IX. Ciénagas de Córdoba: Biodiversidad-ecología y manejo ambiental* (O. Rangel Ch., ed.), pp. 491–497. Universidad Nacional de Colombia, Instituto de Ciencias Naturales, Bogotá, Colombia.  
 Campos, M.R. 2014. *Crustáceos decápodos de agua dulce de Colombia*. Universidad Nacional de Colombia, Instituto de Ciencias Naturales, Bogotá, Colombia.  
 Campos, M.R. & Lemaitre, R. 1999. Two new freshwater crabs of the genus *Ptychophallus* Smalley, 1964 (Crustacea: Decapoda: Brachyura: Pseudothelphusidae) from Panamá. *Proceedings of the Biological Society of Washington*, **112**: 553–561.  
 Campos, M.R. & Lemaitre, R. 2002. A new species of freshwater crab of the genus *Potamocarcinus* H. Milne Edwards, 1853 (Crustacea: Decapoda: Brachyura: Pseudothelphusidae) from Panamá. *Proceedings of the Biological Society of Washington*, **115**: 600–604.  
 Farris, D.W., Jaramillo, C.A., Bayona, G.A., Restrepo-Moreno, S.A., Montes, C., Cardona, A., Mora, A., Speakman, R.J., Glasscock, M.D., Reiners, P. & Valencia, V. 2011. Fracturing of the Panamanian isthmus during initial collision with South America. *Geology*, **39**: 1007–1010.  
 Hoorn, C. & Flantua, S. 2015. An early start for the Panama land bridge. *Science*, **348**: 186–187.  
 Hoorn, C. & Wesselingh, F. (eds.). 2010. *Amazonia, landscape and species evolution: A look into the past*. Wiley-Blackwell, Oxford.  
 Hoorn, C., Guerrero, J., Sarmiento, G.A. & Lorente, M.A. 1995. Andean tectonics as a cause for changing drainage patterns in Miocene northern South America. *Geology*, **23**: 237–240.  
 Hoorn, C., Wesselingh, F.P., Ter Steege, H., Bermudez, M.A., Mora, A., Sevink, J., Sanmartín, I., Sanchez-Meseguer, A., Anderson, C.L., Figueiredo, J.P., Jaramillo, C., Riff, D., Negri, F.R., Hooghiemstra, H., Lundberg, J., Stadler, T., Särkinen, T. & Antonelli, A. 2010. Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. *Science*, **330**: 927–931.  
 Iturralde-Vinent, M.A. & MacPhee, R.D.E. 1999. Paleogeography of the Caribbean region: implications for Cenozoic biogeography. *Bulletin of the American Museum of Natural History*, **238**: 1–95.  
 Kirby, M.X., Jones, D.S. & MacFadden, B.J. 2008. Lower Miocene stratigraphy along the Panama Canal and its bearing on the Central American Peninsula. *PLoS ONE*, **3**: e2291 [doi: 10.1371/journal.pone.0002791].  
 Lara, L.R., Wehrmann, I.S., Magalhães, C. & Mantelatto, F.L. 2013. Species diversity and distribution of freshwater crabs (Decapoda: Pseudothelphusidae) inhabiting the basin of the Río Grande de Térraba, Pacific slope of Costa Rica, Central America. *Latin American Journal of Aquatic Research*, **41** (special issue): 685–695.  
 Leigh, E.G., O’Dea, A. & Vermeij, G.J. 2014. Historical biogeography of the Isthmus of Panama. *Biological Reviews*, **89**: 148–172.

- Linnaeus, C. 1758. *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*. Vol. 1, Edn. 10. Reformata. Laurentii Salvii, Holmiae [= Stockholm].
- Lundberg, J.G., Marshall, L.G., Guerrero, J., Horton, B., Malabarba, M.C.S.L. & Wesselingh, F. 1998. The stage for Neotropical fish diversification: A history of tropical South American rivers. In: *Phylogeny and classification of Neotropical fishes* (L.R. Malabarba, R.E. Reis, R.P. Vari, Z.M.S. Lucena & C.A.S. Lucena, eds.), pp. 13–48. EDIPUCRS, Porto Alegre, Brazil.
- Magalhães, C., Campos, M.R. & Türkay, M. 2013. Freshwater crabs from eastern Panamá: a new species of *Potamocarcinus* H. Milne Edwards, 1853, and new records of two little-known species (Crustacea: Decapoda: Pseudothelphusidae, Trichodactylidae). *Zootaxa*, **3702**: 348–356.
- Magalhães, C., Lara, L.R. & Wehrmann, I.S. 2010. A new species of freshwater crab of the genus *Allacanthos* (Crustacea, Decapoda, Pseudothelphusidae) from southern Costa Rica, Central America. *Zootaxa*, **2604**: 52–60.
- Magalhães, C., Wehrmann, I.S., Lara, L.R. & Mantelatto, F.L. 2015. Freshwater crabs from Costa Rica, with a taxonomic revision of the genus *Ptychophallus* Smalley, 1964 (Crustacea: Decapoda: Pseudothelphusidae). *Zootaxa*, **3905**: 301–344.
- Milne Edwards, H. 1853. Mémoire sur la famille des Ocypodiens. *Annales des Sciences naturelles (Zoologie)*, **20**: 163–228.
- Montes, C., Cardona, A., MacFadden, R., Morón, S.E., Silva, C.A., Restrepo-Moreno, S., Ramírez, D.A., Hoyos, N., Wilson, J., Farris, D., Bayona, G.A., Jaramillo, C.A., Valencia, V., Bryan, J. & Flores, J.A. 2012. Evidence for middle Eocene and younger land emergence in central Panama: implications for Isthmus closure. *GSA Bulletin*, **124**: 780–799.
- Montes, C., Cardona, A., Jaramillo, C., Pardo, A., Silva, J.C., Valencia, V., Ayala, C., Pérez-Angel, L.C., Rodríguez-Parra, L.A., Ramirez, V. & Niño, H. 2015. Middle Miocene closure of the Central American Seaway. *Science*, **348**: 226–229.
- Ng, P.K.L. & Castro, P. 2016. Revision of the family Chasmocarcinidae Serène, 1964 (Crustacea, Brachyura, Goneplacoidea). *Zootaxa*, **4209**: 1–182.
- Ng, P.K.L. & Guinot, D. 2001. On the land crabs of the genus *Discoplax* A. Milne Edwards, 1867 (Crustacea: Decapoda: Brachyura: Gecarcinidae), with description of a new cavernicolous species from the Philippines. *Raffles Bulletin of Zoology*, **49**: 311–338.
- Prahl, H. von & Ramos, G. 1987. *Potamocarcinus colombiensis* sp. nov.: Un nuevo cangrejo de agua dulce (Decapoda: Brachyura: Pseudothelphusidae) de la Serranía Costera del Baudo, Colombia. *Revista de Biología Tropical*, **35**: 131–133.
- Pretzmann, G. 1965. Vorläufiger Bericht über die Familie Pseudothelphusidae. *Anzeiger der Österreichischen Akademie der Wissenschaften Mathematische Naturwissenschaftliche Klasse*, **1**: 1–10.
- Pretzmann, G. 1968a. Neue südamerikanische Süßwasserkrabben (Vorläufige Mitteilung). *Entomologisches Nachrichtenblatt*, **15** (Supplement 1): 1–15.
- Pretzmann, G. 1968b. Weitere neue südamerikanische Süßwasserkrabben (Vorläufige Mitteilung). *Entomologisches Nachrichtenblatt*, **15**(2): 1–6.
- Pretzmann, G. 1971. Fortschritte in der Klassifizierung der Pseudothelphusidae. *Sitzungsberichte der Österreichischen Akademie der Wissenschaften, Mathematisch Naturwissenschaftliche Klasse* (Abteilung 1), **179**: 15–24.
- Pretzmann, G. 1972. Die Pseudothelphusidae (Crustacea Brachyura). *Zoologica*, **120**: 1–182.
- Pretzmann, G. 1975. Die bedornten Arten der Gattung *Potamocarcinus* Milne Edwards, 1853. *Annalen des Naturhistorisches Museum Wien*, **79**: 615–621.
- Pretzmann, G. 1978. Neue Potamocarcinini, Poglayen-Neuwall leg. 1975 (vorläufige Mitteilung). *Sitzungsberichte der Österreichischen Akademie der Wissenschaften, Mathematisch Naturwissenschaftliche Klasse*, Series 1, **1978**: 51–54.
- Rathbun, M.J. 1893. Descriptions of new species of American fresh-water crabs. *Proceedings of the United States National Museum*, **16**: 649–661, pls. 73–77.
- Rathbun, M.J. 1896. Descriptions of two new species of fresh-water crabs from Costa Rica. *Proceedings of the United States National Museum*, **18**: 377–379, pls. 19–30.
- Rathbun, M.J. 1898. A contribution to a knowledge of the fresh-water crabs of America. The Pseudothelphusinae. *Proceedings of the United States National Museum*, **21**: 507–537.
- Rodríguez, G. 1982. *Les crabes d'eau douce d'Amérique. Famille des Pseudothelphusidae*. Faune Tropicale **22**. ORSTOM, Paris.
- Rodríguez, G. 1992. *The freshwater crabs of America. Family Trichodactylidae and supplement to the family Pseudothelphusidae*. Faune Tropicale **31**. ORSTOM, Paris.
- Rodríguez, G. 1994. A revision of the type material of some species of *Hypolobocera* and *Ptychophallus* (Crustacea: Decapoda: Pseudothelphusidae) in the National Museum of Natural History, Washington, D.C., with descriptions of a new species and a new subspecies. *Proceedings of the Biological Society of Washington*, **107**: 296–307.
- Rodríguez, G. 2001. New species and records of pseudothelphusid crabs (Crustacea: Brachyura) from Central America in the Museum of Natural History of Tulane University. *Proceedings of the Biological Society of Washington*, **114**: 435–443.
- Rodríguez, G. & López, B. 2003. Insular species of Neotropical freshwater crabs (Crustacea: Brachyura). *Journal of Natural History*, **37**: 2599–2614.
- Rodríguez Tribaldos, V., White, N.J., Roberts, G.G. & Hoggard, M.J. 2017. Spatial and temporal uplift history of South America from calibrated drainage analysis. *Geochemistry, Geophysics, Geosystems*, **18**: 2321–2353.
- Shih, H.-T., Ng, P.K.L. & Christy, J.H. 2015. *Uca (Petruca)*, a new subgenus for the rock fiddler crab *Uca panamensis* (Stimpson, 1859) from Central America, with comments on some species of American broad-fronted subgenera. *Zootaxa*, **4034**: 471–494.
- Smalley, A. 1964a. A terminology for the gonopods of the American river crabs. *Systematic Zoology*, **13**: 28–31.
- Smalley, A.E. 1964b. The river crabs of Costa Rica, and the subfamilies of the Pseudothelphusidae. *Tulane Studies in Zoology*, **12**: 5–13.
- Smalley, A.E. & Rodríguez, G. 1972. Trichodactylidae from Venezuela, Colombia, and Ecuador (Crustacea: Brachyura). *Tulane Studies in Zoology and Botany*, **14**: 41–55.
- Villalobos, C.R. 1974. *Ptychophallus costaricensis*, a new freshwater crab from Costa Rica. *Revista de Biología Tropical*, **21**: 197–203.
- Villalobos, J.L. & Álvarez, F. 2010. Phylogenetic analysis of the Mexican freshwater crabs of the tribe Pseudothelphusini (Decapoda: Brachyura: Pseudothelphusidae). *Zoological Journal of the Linnean Society*, **160**: 457–481.
- Wehrmann, I.S., Magalhães, C. & Orozco, M.N. 2016. The primary freshwater crabs of Guatemala (Decapoda: Brachyura: Pseudothelphusidae), with comments on their conservation status. *Journal of Crustacean Biology*, **36**: 776–784.
- Wesselingh, F.P. & Hoorn, C. 2011. Geological development of Amazon and Orinoco basins. In: *Historical biogeography of Neotropical freshwater fishes* (J.S. Albert & R.E. Reis, eds.), pp. 59–67. University of California Press, Berkeley, CA, USA.
- Wesselingh, F.P., Hoorn, C., Kroonenberg, S.B., Antonelli, A., Lundberg, J.G., Vonhof, H.B. & Hooghiemstra, H. 2010. On the origin of the Amazonian landscapes and biodiversity: a synthesis. In: *Amazonia, landscape and species evolution* (C. Hoorn & F. Wesselingh, eds.), pp. 421–432. Wiley-Blackwell, Oxford.