New brachyuran crabs from the Aptian–Albian Romualdo Formation, Santana Group of Brazil: Evidence for a Tethyan connection to the Araripe Basin

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Despite the exceptional palaeontological richness of the renowned Santana Group from the Early Cretaceous Araripe Basin of Brazil, only one specimen of true crabs (Brachyura) has been discovered to date. Here we present two new genera and species of brachyuran crabs from the upper Aptian–lower Albian Romualdo Formation of the Santana Group, represented by 30 specimens from several localities across the Araripe Basin in the state of Pernambuco, Brazil. One taxon, *Exucarcinus gonzagai* Prado and Luque gen. et sp. nov., is similar to several endemic stem raninoidans (Orithopsidae) from the late Aptian and early Albian of Colombia and the USA, respectively, while *Romualdocarcinus salesi* Prado and Luque gen. et sp. nov., seems to be closer to "higher" true crabs (Eubrachyura) from the Cenomanian of Spain. The presence of taxa similar to those from the mid-Cretaceous of northern South America, southern North America, and western Europe, reinforces the view of a Tethyan marine influence in Araripe during the breakup of South America and Africa, and adds to the growing data that suggest a generic and specific degree of endemism of true crabs in tropical South America during the mid-Cretaceous.

Key words: Decapoda, Eubrachyura, Raninoida, *Exucarcinus*, *Romualdocarcinus*, Cretaceous, South America.

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Introduction

Our understanding of the diversity and geographic distributions of fossil crabs in the tropical Americas has grown considerably in the last decades, especially regarding Late Cretaceous and Cenozoic occurrences (Luque et al. 2017). Yet, little is known about the fossil record of true crabs (Brachyura) from the Early Cretaceous in South America, with only a handful of taxa reported so far. In Brazil, several fossil decapod crustaceans have been discovered in Aptian–Albian rocks of the Santana Group, Araripe Basin (mostly shrimps, see Table 1), but so far only one crab specimen has yet been reported and described as *Araripecarcinus ferreirai* Martins-Neto, 1987. Although only ventral and appendicular features are preserved in the holotype of *A. ferreirai*, its phylogenetic position and overall anatomical characteristics suggest affinities to stem raninoidans of the superfamily Necrocarcinoidea, yet with uncertain familial affinities (Luque 2015a; Schweitzer et al. 2016b; Luque et al. 2017).

Several other Early Cretaceous necrocarcinoids are known from South America, such as the orithopsid crabs *Bellcarcinus* Luque, 2014; *Colombicarcinus* Karasawa, Schweitzer, Feldmann, and Luque, 2014; and *Planocarcinus* Luque, Feldmann, Schweitzer, Jaramillo, and Cameron, 2012; all of them from the upper Aptian and lower Albian of Colombia (Luque et al. 2012, 2017; Bermúdez et al. 2013; Karasawa et al. 2014; Schweitzer et al. 2016b; Fig. 1).

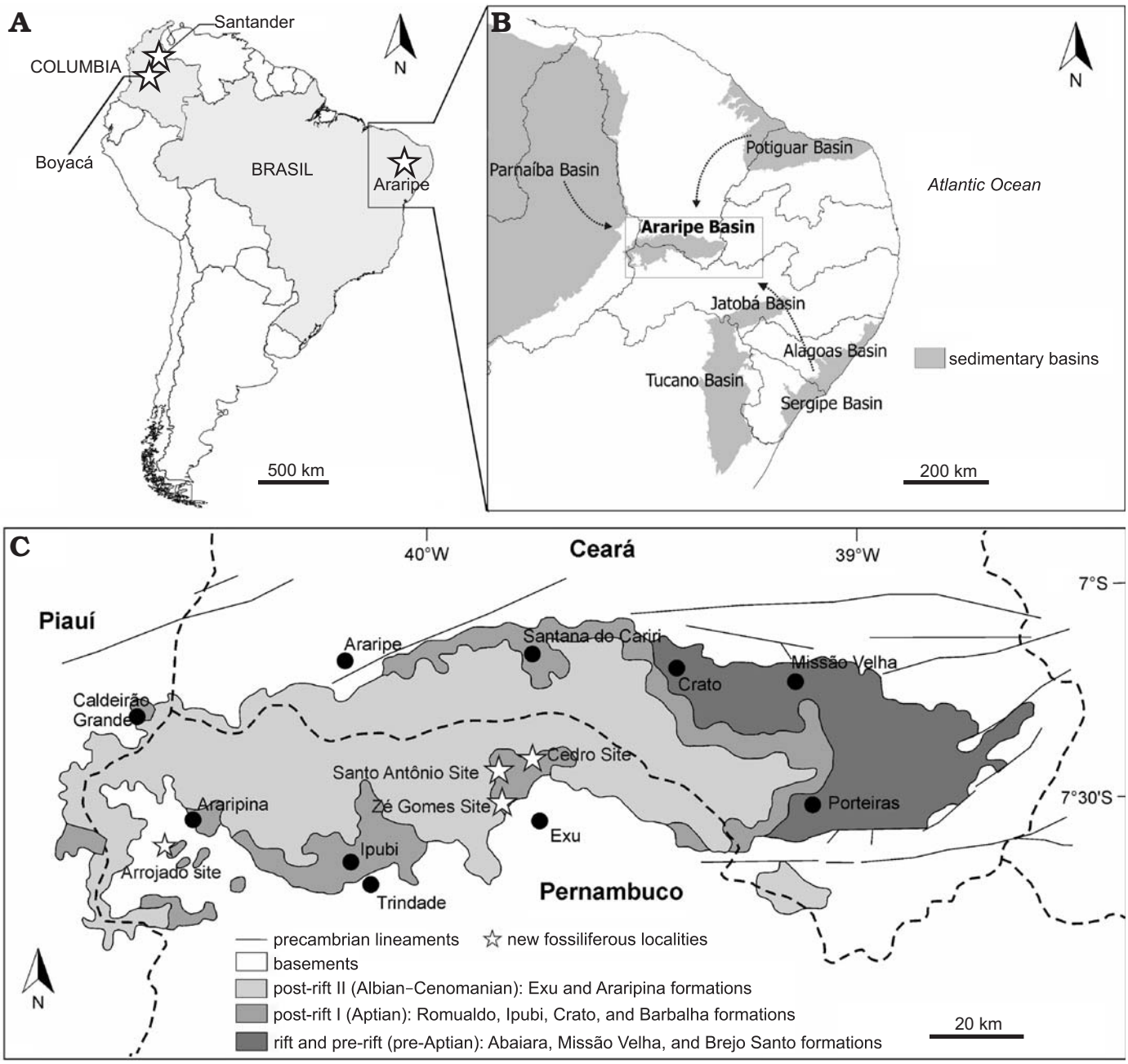


Fig. 1. **A**. Map showing the known occurrences (stars) of orithopsid and eubrachyuran genera in the Early Cretaceous of South America: upper Aptian–lower Albian San Gil Inferior Formation, Boyacá and upper Aptian Paja Formation, Santander, Colombia and upper Aptian–lower Albian Romualdo Formation, Araripe Basin, Brazil. **B**. Sedimentary basins of northeast Brazil; arrows show the three possible routes of Cretaceous marine ingression into the Araripe Basin. **C**. New fossiliferous localities (asterisked) with brachyuran crabs from upper Aptian–lower Albian Romualdo Formation, Araripe Basin, Pernambuco, Brazil (base map modified from Assine 2007).

Similarly, only a handful of Early Cretaceous eubrachyurans, or "higher" true crabs, have been discovered worldwide (Klompmaker 2013; Luque 2015b), with *Telamonocarcinus antiquus* Luque, 2015b, from the late Aptian–early Albian of Colombia representing the oldest crown eubrachyuran (Luque et al. 2017). Here we describe two new genera and species of brachyuran crabs, *Exucarcinus gonzagai* gen. et sp. nov. (Raninoida: Necrocarcinoidea: Orithopsidae) and *Romualdocarcinus salesi* gen. et sp. nov. (Eubrachyura: ?Portunoidea: ?Eogeryonidae), from upper Aptian–lower Albian rocks of the fossiliferous Romualdo Formation, Santana Group, near the municipality of Exu in the state of Pernambuco, and discuss aspects of their systematic affinities, taphonomy, palaeoenvironment, and their palaeogeographical implications.

Institutional abbreviations.—DGEO-CTG-UFPE, Palaeontology Collection of the Geology Department, Centre of Technology and Geosciences, Federal University of Pernambuco, Brazil.

Table 1. List of decapods described from the Santana Group in the Araripe Basin.

Taxon	Stratigraphy	Locality	References
Araripecarcinus ferreirai Martins-Neto, 1987 (brachyuran crab)	Romualdo Formation (upper Aptian–lower Albian): calcareous concretions with fish	near the municipality of Porteiras, state of Ceará	Martins-Neto 1987; Luque 2015a
Beurlenia araripensis Martins-Neto and Mezzarila, 1991 (palaemonid shrimp)	Crato Formation (upper Aptian): laminated limestone	uncertain	Martins-Neto and Mezzarila 1991; Saraiva et al. 2009
Paleomattea deliciosa Maisey and Carvalho, 1995 (sergestid shrimp)	Romualdo Formation (upper Aptian–lower Albian): shales and calcareous concretions with fish	municipalities of Santana do Cariri and Missão Velha, state of Ceará, and Trindade, state of Pernambuco	Viana and Agostinho 1995; Saraiva et al. 2009; Pinheiro et al. 2016
Brachyuran crab zoeae indet. (brachyuran crab)	Romualdo Formation (upper Aptian–lower Albian): calcareous concretions with fish	uncertain	Maisey and Carvalho 1995; Luque 2015a
Kellnerius jamacaruensis Santana, Pinheiro, Silva, and Saraiva, 2013 (palaemonid shrimp)	Romualdo Formation (upper Aptian–lower Albian): calcareous concretions	municipalities of Missão Velha and Jardim, state of Ceará	Santana et al. 2013; Pinheiro et al. 2014
Araripenaeus timidus Pinheiro, Saraiva, and Santana, 2014 (penaeid shrimp)	Romualdo Formation (upper Aptian–lower Albian): calcareous concretions	municipality of Jardim, state of Ceará	Pinheiro et al. 2014
Sume marcosi Saraiva, Pinheiro, and Santana, 2018 (luciferid shrimp)	Romualdo Formation (upper Aptian–lower Albian): shale	municipality of Trindade, state of Pernambuco	Saraiva et al. 2018
Exucarcinus gonzagai gen. et sp. nov. Prado and Luque, 2018 (orithpsid crab)	Romualdo Formation (upper Aptian–lower Albian): coquina	municipality of Exu, state of Pernambuco	this paper
Romualdocarcinus salesi gen. et sp. nov. Prado and Luque, 2018 (eubrachyuran? / eogeryonid? crab)	Romualdo Formation (upper Aptian–lower Albian): coquina	municipality of Exu, state of Pernambuco	this paper

Geographic and geological setting

During the late Early Cretaceous, rapid changes in plate tectonic reconfigurations occurred leading to the separation of South America and Africa. As a result, several small basins were formed in the interior of northeastern Brazil due to the opening of the central Atlantic Ocean (Matos 1992; Assine 1994). Among them, the Araripe Basin stands out, known internationally for the fossiliferous Lagerstätten of the Crato and Romualdo formations (Maisey 1991). The Araripe Basin, located between the states of Pernambuco, Piauí, and Ceará, is formed by five sequences: Paleozoic, Cariri Formation (upper Ordovician–lower Devonian), pre-rift Brejo Santo and Missão Velha formations (Upper Jurassic), rift Abaiara Formation (Neocomian), post-rift I Barbalha, Crato, Ipubi, and Romualdo formations (upper Aptian–lower Albian) and post-rift II Araripina and Exu formations (Albian–Cenomanian) (Assine 1992, 2007; Assine et al. 2014; Fig. 1). The Romualdo Formation is constituted by a sequence of shale intercalated with sandstone at the base, followed by black shale with usually fossiliferous calcareous nodules, and layers of calcareous sandstone with macroinvertebrates, respectively (Assine et al. 2014). At the top, fine sandstone can be found with intercalations of siltstone and shale bearing freshwater fossils such as conchostracans and molluscs (Beurlen 1971; Assine 2007).

The Romualdo Formation contains bony and cartilaginous fish, dinosaurs, pterosaurs, molluscs, echinoids, crustaceans, foraminifera, dinoflagellates, gymnosperms, and angiosperms, that suggest sedimentation in a shallow marine to transitional palaeoenvironment (Silva-Santos and Valença 1968; Mabessone and Tinoco 1973; Arai and Coimbra 1990; Berthou et al. 1990; Kellner 2002; Bruno and Hessel 2006; Lima et al. 2012; Pinheiro et al. 2014; Pereira et al. 2017). However, the palaeogeographic reconstruction of the marine transgression in the Araripe Basin is still controversial, and three directions of ingression are suggested: (i) from the Parnaíba Basin (W-NW) (Beurlen 1963, 1966, 1971; Arai et al. 1994; Arai 2014; Prado et al. 2015; Pereira et al. 2017); (ii) from the Potiguar Basin (N-NE) (Lima 1978; Petri 1987); or (iii) from de Recôncavo–Tucano–Jatobá basins (S-SE), crossing the limits of Sergipe-Alagoas Basin (Assine et al. 2014; Custódio et al. 2017; see Fig. 1 and Table 2).

Two new brachyuran crabs, *Exucarcinus gonzagai* Prado and Luque gen. et sp. nov. and *Romualdocarcinus salesi* Prado and Luque gen. et sp. nov., were collected from marine rocks of the Romualdo Formation cropping out at Cedro (39°35’32”N 7°29’35”E), Santo Antônio (39°32’51”N 7°30’31”E), and Zé Gomes (7°31’16”S 39°34’18”W) in the municipality of Exu in the State of Pernambuco (Fig. 1). All of these outcrops include calcareous sandstone layers between shale layers with calcareous nodules of the Romualdo Formation, differing from each other by the thickness of the layers and their faunistic composition (Fig. 2). From the calcareous sandstone in the municipality of Exu were collected bivalves (e.g., *Corbula* sp., *Brachidontes araripensis* Pereira, Cassab, Barreto, and Almeida, 2016b, and *Aguileria dissita* White, 1887), gastro-

Table 2. Key evidence advanced for three proposed marine ingression into the Araripe Basin.

Proposed directions of marine transgression into the Araripe Basin	Evidence
Parnaíba Basin	The presence of autochthonous echinoids restricted to the western portion of the Araripe Basin (Beurlen 1963, 1966, 1971; Prado et al. 2015). The marine molluscs (e.g., *Tylostoma rancharienses* Pereira, Cassab, Barreto, and Almeida, 2016b, and *Gymnentome* (*Craginia*) *beurleni*) Pereira, Cassab, and Barreto, 2016a and fishes (e.g., *Araripichthys castilhoi* Silva Santos, 1985) of Tethyan affinity in the Araripe Basil (Maisey 1991, 2000; Maisey and Moody 2001; Alvarado-Ortega and Brito 2011; Pereira et al. 2016a, 2017). Dinoflagellates of the genus *Subtilisphaera*, which represents a ecozone of Tethyan affinity more prominent in the basins of northeastern Brazil located to the west (Arai et al. 1994; Arai 2014)
Recôncavo–Tucano–Jatobá basins	Fluvial palaeocurrents measured in the Barbalha (Aptian, Santana Group) and Marizal formations (Aptian, Tucano Basin), indicating south and southeast paleoflows. As the marine transgressions normally occur in the opposite direction to the continental palaeodrainage, the transgression during the Aptian–Albian in Araripe would have occurred from south-southeast to north-northwest (Assine 1994; Assine et al. 2014, 2016; Custódio et al. 2017). Tucano (Serra do Tonã) and Jatobá (Serra Negra) basins with the same stratigraphic succession of the Araripe Basin (Varejão et al. 2016).
Potiguar Basin	Faults with SW directions that could connect the Araripe and Potiguar basins (Lima 1978). The subsiding area extended farther toward the southwest of Potiguar Basin that probably connected it to the Araripe Basin (Petri 1987).

pods (e.g., undetermined cassiopids, *Tylostoma rancharienses* Pereira, Cassab, Barreto, and Almeida, 2016b, and *Cerithium sergipensis* Maury, 1936), echinoids (e.g., *Bothryopneustes araripensis* Manso and Hessel, 2007) (Pereira et al. 2017), and the two new genera and species of true crabs described herein. In the calcareous sandstone at the Arrojado site (7°41'12"S 40°33'48"W) in the municipality of Araripina, also in the state of Pernambuco, no molluscs or echinoids have been found, but fish predominate. In one of these layers we found a crab claw associated with fossil fish (Fig. 2).

Material and methods

A total of 30 crab specimens, represented only by dorsal carapaces plus a single isolated cheliped, were collected in situ and ex situ from calcareous sandstone of the upper Aptian–lower Albian Romualdo Formation. The specimens were prepared mechanically and examined under a stereoscopic microscope. For a complete analysis of the material, more complete specimens (DGEO-CTG-UFPE-7747, 8109, 8116, 8122, 8127, 8137, and 8144) were imaged with a Zeiss Sigma 300 VP-FESEM scanning electron microscope at the University of Alberta, Edmonton, Canada. The type series of *Exucarcinus gonzagai* gen. et sp. nov. and *Romualdocarcinus salesi* gen. et sp. nov. are deposited in DGEO-CTG-UFPE.

Systematic palaeontology

Order Decapoda Latreille, 1802

Infraorder Brachyura Latreille, 1802

Section Raninoida Ahyong, Lai, Sharkey, Colgan, and Ng, 2007

Family Orithopsidae Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg, and Ross, 2003

Included genera: *Aetocarcinus* Schweitzer, Feldmann, Rader, and Frantescu, 2016; *Bellcarcinus* Luque, 2014; *Cherpiocarcinus* Marangon and De Angeli, 1997; *Colombicarcinus* Karasawa, Schweitzer, Feldmann, and Luque, 2014; *Cristella* Collins and Rasmussen, 1992; *Exucarcinus* Prado and Luque, gen. nov.; *Marycarcinus* Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg, and Ross, 2003; *Orithopsis* Carter, 1872; *Paradoxilissopsa* Schweitzer, Dworschak, and Martin, 2011 (= *Lissopsis* Frič and Kafka, 1887); *Paradoxicarcinus* Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg, and Ross, 2003; *Planocarcinus* Luque, Feldmann, Schweitzer, Jaramillo, and Cameron, 2012; *Shazella* Collins and Williams, 2004; *Silvacarcinus* Collins and Smith, 1993; *Texicancer* Franţescu, Feldmann, and Schweitzer, 2016.

Genus *Exucarcinus* Prado and Luque nov.

ZooBank LSID: urn:lsid:zoobank.org:act:1E8FAB5B-5466-4D4C-B382-99EDFE2B4E3D

Type species: *Exucarcinus gonzagai* Prado and Luque sp. nov.; by monotypy, see below.

Etymology: From the municipality of Exu where the material was collected, and the Greek *carcinus* (= *karkinos*), crab; gender masculine.

Diagnosis.—As for the type species by monotypy.

Exucarcinus gonzagai Prado and Luque sp. nov.

Fig. 3.

ZooBank LSID: urn:lsid:zoobank.org:act:B206279B-DB4B-4221-AB34-E8AE0D90E1E1

Etymology: In honour of Luiz Gonzaga do Nascimento (1912–1989) "the king of baião", a singer, composer, and one of the most influential musicians of Brazilian popular music of the twentieth century, born in the Exu municipality, Pernambuco, Brazil.

Type material: Holotype (carapace): DGEO-CTG-UFPE-8114. Paratypes (carapaces): DGEO-CTG-UFPE-7745, 7748, 7749, 7751, 8103, 8105, 8107, 8109, 8115, 8116, 8133, 8106; all from the type locality.

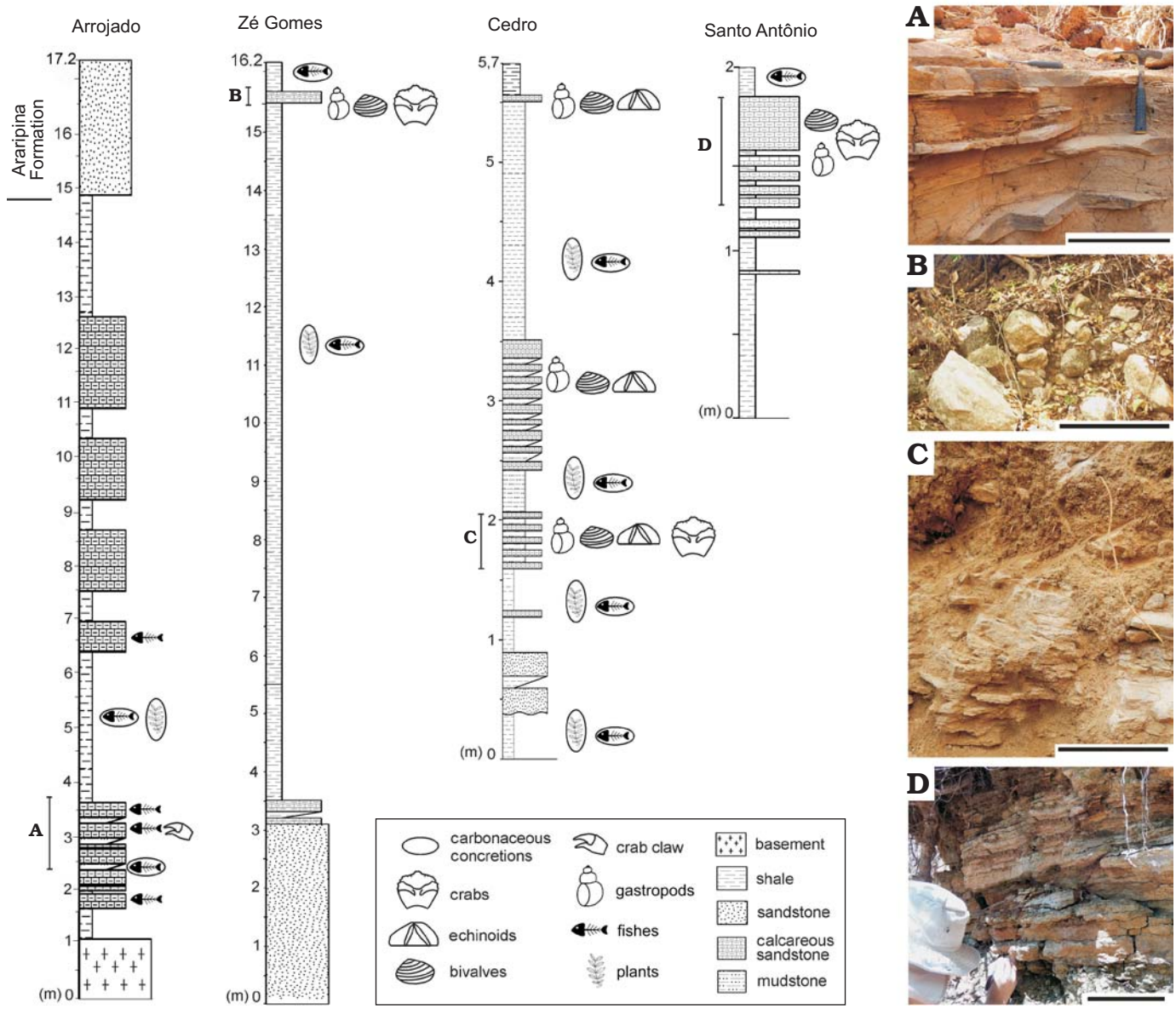


Fig. 2. Stratigraphic sections (A_1–D_1) and field photographs (A_2–D_2) of the upper Lower Cretaceous Romualdo Formation, Pernambuco, Brazil, where the new brachyuran crabs were discovered: Arrojado site (**A**), municipality of Araripina, Zé Gomes (**B**), Cedro (**C**), and Santo Antônio (**D**) sites, municipality of Exu. Scale bars 25 cm.

Type locality: Zé Gomes, Santo Antônio, and Cedro sites, Araripe Basin, municipality of Exu, Pernambuco, Brazil.

Type horizon: Romualdo Formation (upper Aptian–lower Albian).

Diagnosis.—Carapace sub-hexagonal, nearly equidimensional, weakly vaulted to flattened, widest at carapace mid-length at level of epibranchial spine, finely granulated, lacking tubercles, bosses, ridges, or reniform swellings. Fronto-orbital margin slightly wider than half the carapace maximum width; rostrum long, extending beyond outer-orbital spine, sulcate axially, bifid distally, with a short lateral spine on each side of the rostrum; post-rostral slits absent. Orbits wide, horizontal, upturned, with two relatively narrow orbital fissures; innermost fissure the shortest; intra-orbital lobe short, truncated, squarish; outer orbital spine well-developed, simple, triangular, shorter than rostrum, directed anteriorly. Anterolateral margin nearly as long as posterolateral margin, with 5–7 spines excluding outer orbital spine, acute, unequal, directed anterolaterally; epibranchial spine short. Posterolateral margin slightly convex to straight, lacking spines, denticles, or tubercles. Posterior margin concave, slightly narrower than fronto-orbital margin. Cervical and branchiocardiac grooves distinct, shallow, sub-parallel to each other; cervical groove reaching anterolateral margin; secondary groove not defined; post-cervical groove absent. Dorsal regions without tubercles, bosses, reniform swellings, or ridges; intestinal region wide, depressed laterally, delimited by swollen metabranchial regions; epibranchial region swollen proximally near contact with branchial groove; meso- and metabranchial regions not

differentiated, lacking conspicuous spines or tubercles, but bearing an incipient oblique ridge.

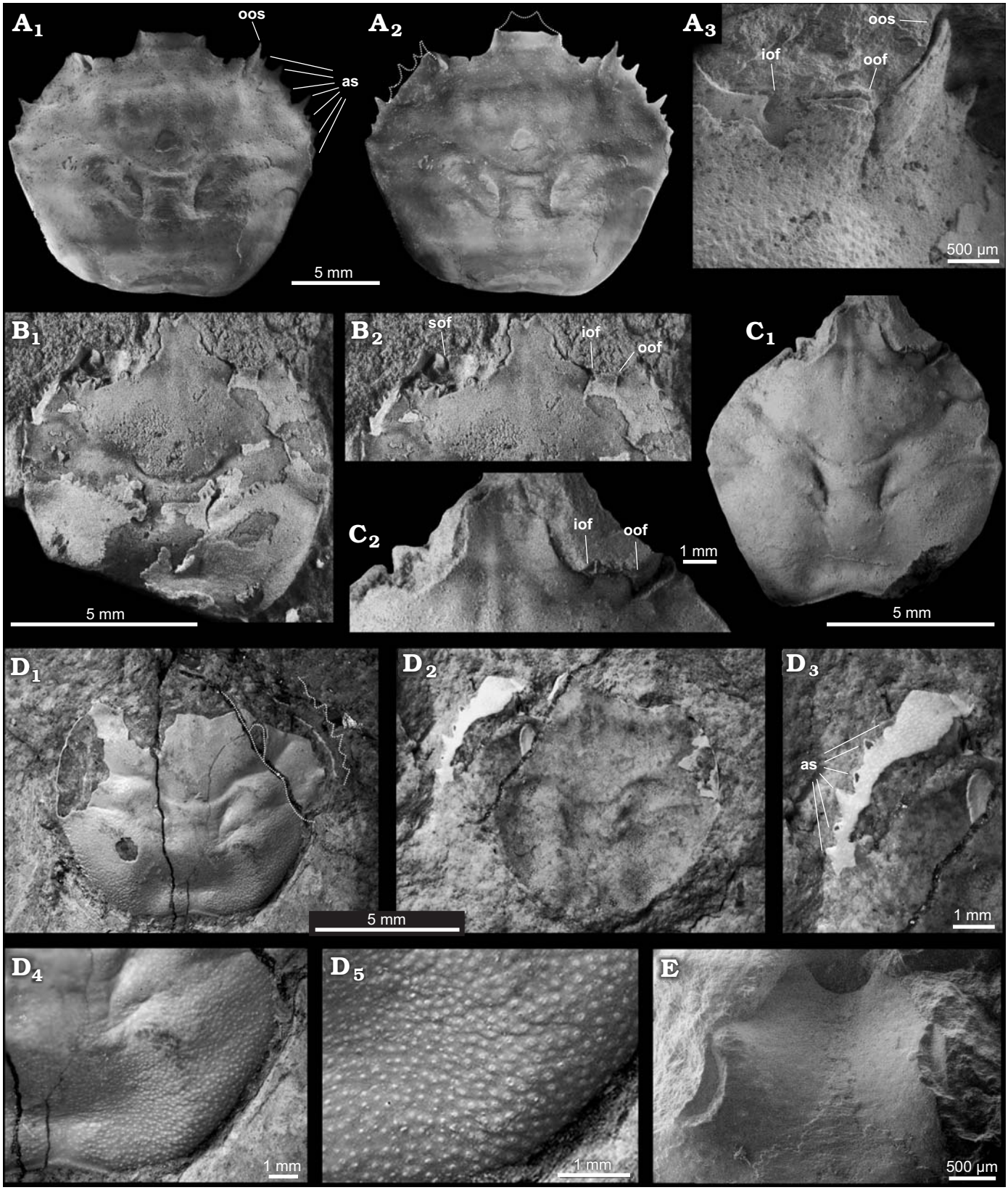
Description.—Carapace sub-hexagonal, about as long as wide in smaller specimens and slightly wider in larger specimens; dorsal carapace weakly vaulted to flattened, widest at carapace mid-length at the level of epibranchial spine. Dorsal carapace smooth, lacking conspicuous tubercles, bosses, ridges, or reniform swellings, covered with fine granulations. Fronto-orbital margin broad, slightly wider than half the carapace maximum width, and wider than posterior margin. Rostrum well-developed, long, extending well beyond outer-orbital spine, nearly one-third of fronto-orbital margin width, wider at base, with straight lateral margins converging antero-medially, bearing a pair of short but well-developed lateral spines positioned at mid-length, and a pair of distal spines forming a weakly downturned bifid rostrum; rostrum sulcate axially, with posterolateral margins at higher level than orbits; post-rostral slits absent. Orbits wide, upturned, directed forward, each orbit about one-third of fronto-orbital margin; supra-orbital margin straight, horizontal, with two relatively narrow orbital fissures parallel to each other, innermost orbital fissure shorter than outermost fissure; inner orbital lobe short, moderately developed, grading from lower margin of rostrum; intra-orbital lobe short, truncated, squarish in outline, separated from inner and outer lobes by the orbital fissures; outer orbital spine well-developed, simple, triangular, shorter than rostrum, with outer margin slightly converging anteriorly; sub-orbital margin visible in dorsal view, with one short, narrow suborbital fissure. Anterolateral margin slightly convex in smaller specimens, less so in larger specimens, nearly as long as posterolateral margin, bearing five to seven acute spines excluding outer orbital spine, of different sizes, and directed anterolaterally; epibranchial spine short, weakly to moderately developed, directed laterally. Posterolateral margin slightly convex in smaller specimens, nearly straight in larger specimen, without spines, denticles, or tubercles. Posterior margin wide, concave, slightly rimmed, much shorter than half of carapace maximum width, and slightly shorter than fronto-orbital margin. Cervical groove distinct, shallow, sinuous, arcuate, with smooth deflections, axially interrupted, distally reaching anterolateral margin; secondary groove not defined; post-cervical groove absent; branchial grooves distinct, well-developed, crescent-shaped; branchiocardic groove present, well-developed, sub-parallel to cervical groove. Epigastric region narrow, barely defined laterally by faint sub-parallel grooves; protogastric and mesogastric regions faintly tumid; hepatic region wide, depressed, without transverse ridge; epigastric, protogastric, mesogastric, and hepatic regions poorly delimited, without tubercles or bosses; metagastric and urogastric lacking tubercles or longitudinal ridge, faintly separated by a shallow depression, both regions defined laterally by crescent-shaped branchial grooves; urogastric region narrow; cardiac region well-developed, tumid, broader than meta- and urogastric regions, wider anteriorly lacking tubercles, without transverse or longitudinal ridges; intestinal region wide, depressed anteriorly by contact with posterior cardiac region, depressed laterally and delimited by swollen metabranchial regions; epibranchial region moderately defined, limited by cervical and branchiocardic grooves, swollen proximally near contact with branchial groove; meso- and metabranchial regions not differentiated, lacking conspicuous spines or tubercles, but bearing an incipient oblique ridge extending towards the posterolateral corner.

Dimensions.—For a list of measurements see Table 3.

Table 3. Measurements (in mm) of the fossil crabs *Exucarcinus gonzagai* gen. et sp. nov. and *Romualdocarcinus salesi* gen. et sp. nov. Abbreviations: AL, anterolateral length; CL, carapace length; CW, carapace width; FW, fronto-orbital width; PL, posterolateral length; PW, posterior width; RW, rostrum width.

Species	DGEO-CTG-UFPE-	Occurrence	CL	CW	RW	FW	AL	PL	PW
Exucarcinus gonzagai	7745	Zé Gomes	7	8	–	5	3	4	4
	7749		7.5	9	–	–	3.5	4	3
	8114		13	15	3	9	6	7	8
	8116		10	11	2.5	7.5	4	5	6
	7748	Santo Antônio	6	7	1.5	4.5	2.5	3.5	4
	7751		8.5	10	–	6	4	4.5	5
	8103	Cedro	6	6	–	4.5	2.5	3.5	4
	8104		6.5	8	–	6	3	3.5	4
	8105		6.5	7	2	6	3	3.5	5
	8106		6	7	–	5	2.5	3.5	4
	8107		4.5	5.5	–	3.5	2.5	3	2.5
	8109		9	8	2	6	3.5	5	5
	8115		9	10	–	6	4	5	5
	8133		7	8	2	6	3	4	5
Romualdocarcinus salesi	8108	Cedro	4.5	6.5	2	5	2	2.5	4
	8110		4.5	6	1	3	2	2.5	2
	8111		–	–	2	–	–	–	–
	8119		3.5	4	1	3	2	1.5	2
	8122		5.5	6.5	2	6	1.5	2.5	3
	8123		4.5	6	1.5	5	2	2.5	3.5
	8124		6.5	7	2	6	3	3.5	4
	8125		–	8	2	6	4	5	–
	8126		5	7	6	2	2	3	3
	8127		10	9	3	9	4	3	4.5
	8128		5	7	6	2	2	3	–
	8129		–	–	2	–	–	–	–
	8131		5	6	1.5	4.5	2	3	3
	8132		6	7	2	6	2.5	3.5	4
	8135		–	9	2.5	7.5	–	–	–
	8137		7	8	2	6	4	3	4

Fig. 3. Orithopsid brachyuran *Exucarcinus gonzagai* Prado and Luque gen. et sp. nov. from the upper Aptian–lower Albian Romualdo Formation of the Santana Group, Araripe Basin, Pernambuco, Brazil. **A**. Holotype DGEO-CTG-UFPE-8114; A_1, SEM image of dorsal carapace; A_2, negative colour image of A_1; A_3, close-up of right orbit, orbital fissures, and outer orbital spine. **B**. Paratype DGEO-CTG-UFPE-8133; B_1, dorsal carapace; B_2, sub-orbital margin visible in dorsal view with one short and narrow suborbital fissure. **C**. Paratype DGEO-CTG-UFPE-8109; C_1, dorsal carapace; C_2, orbit and bifid rostrum extending well beyond the outer-orbital →



spine. **D**. Paratype DGEO-CTG-UFPE-8115; D_1, dorsal carapace; D_2, counterpart; D_3, close-up of ventral view of right anterolateral margin bearing multiple anterolateral spines; D_4, close-up of posterolateral and posterior margins lacking spines; D_5, close-up of dorsal carapace cuticle with fine granulations. **E**. Paratype DGEO-CTG-UFPE-8116, SEM image of bifid rostrum. Abbreviations: as, anterolateral spines; ios, inner orbital spine; iof, innermost orbital fissure; its, intra-orbital spine; oof, outermost orbital fissure; oos, outer orbital spine; sof, sub-orbital fissure. All specimens photographed dry and uncoated, except B, C, which are coated with ammonium chloride.

Remarks.—*Exucarcinus* Prado and Luque gen. nov. strongly differs from Camarocarcinidae Feldmann, Li, and Schweitzer, 2007, Necrocarcinidae Förster, 1968, and several Cenomanocarcinidae Guinot, Vega, and Van Bakel, 2008, in its slightly vaulted to flattened dorsal carapace, the lack of posterolateral spines (Fig. 3A_1, A_2, B_1, C_1, D_1, D_4), and the absence of transverse or branchial ridges, contrasting with the strongly vaulted and ornamented carapaces seen in these families. Also, it lacks the deep cervical and branchiocardic grooves and short rostrum seen in Necrocarcinidae (Fig. 3A_1, A_2, B, C, E). Among stem raninoidans, the presence of a well-defined longitudinal mesial ridge, absent in *Exucarcinus*, is mostly seen among Palaeocorystidae Lőrenthey in Lőrenthey and Beurlen, 1929, Cenomanocarcinidae, Necrocarcinidae in part (i.e., *Elektrocarcinus* Schweitzer, Karasawa, Luque, and Feldmann, 2016, and *Hadrocarcinus* Schweitzer, Feldmann, and Lamanna, 2012), and most of the non-American Orithopsidae genera (see below). *Exucarcinus* Prado and Luque gen. nov. differs from Paranecrocarcinidae Fraaije, Van Bakel, Jagt, and Artal, 2008, in its flattened mesogastric region, the spinose anterolateral margin (5–7 spines) (Fig. 3A_1, A_2, D_1–D_3), and the lack of post-rostral slits, so distinctive of paranecrocarcinids. The new genus also differs from Paranecrocarcinidae and several Orithopsidae in the lack of protogastric swellings, but shares with them the wide, somewhat spatulate bifid rostrum extending well beyond the outer-orbital spine, the overall sub-hexagonal carapace with wide fronto-orbital margins, and the lack of posterolateral spines.

Exucarcinus Prado and Luque gen. nov. differs from other orithopsids (e.g., *Bellcarcinus*, *Cherpiocarcinus*, *Marycarcinus*, *Orithopsis*, *Paradoxilissopsa*, *Silvacarcinus*, *Texicancer*) in the lack of dorsal tubercles, reniform swellings, keels, or ridges (Fig. 3A_1, A_2, B_1, C_1, D_1, D_2). Other genera like *Cristella* and *Shazella* have pronounced epibranchial spines or pustulose dorsal carapaces with conspicuous dorsal grooves, none of which are apparent in the new genus. In fact, among orithopsids, *Exucarcinus* Prado and Luque gen. nov. seems to be more similar to some genera endemic to the Americas, like *Aetocarcinus*, *Colombicarcinus,* and *Planocarcinus* based on the lack of posterolateral spines, the smooth dorsal carapace lacking conspicuous dorsal ridges, keels, or tubercles, and the broad spatulate and bifid rostrum extending beyond the outer-orbital spine. However, these genera lack the numerous well-developed and acute anterolateral spines diagnostic of *Exucarcinus* Prado and Luque gen. nov. (Fig. 3A_1, A_2, D_1–D_3).

Stratigraphic and geographic range.—Type locality and horizon only.

Section Eubrachyura Saint Laurent, 1980

Clade Heterotremata Guinot, 1977

Family ?Eogeryonidae Ossó, 2016

Type genus: *Eogeryon* Ossó, 2016.

Included genera: Type genus and tentatively *Romualdocarcinus* Prado and Luque gen. nov.

Genus *Romualdocarcinus* Prado and Luque nov.

ZooBank LSID: urn:lsid:zoobank.org:act:DA947443-E1A9-485B-B1C0-F1C058DC1A6D

Type species: *Romualdocarcinus salesi* Prado and Luque sp. nov.; by monotypy, see below.

Etymology: From the Romualdo Formation, Santana Group; a Konservat-Lagerstätte in northeast Brazil where the material was collected, and the Greek *carcinus* (= *karkinos*), crab; gender masculine.

Diagnosis.—As for the type species by monotypy.

Romualdocarcinus salesi Prado and Luque sp. nov.

Fig. 4.

ZooBank LSID: urn:lsid:zoobank.org:act:86A8591D-A6D8-436B-AD02-8A29B36E3CF6

Etymology: In honour of the late Professor Alexandre Magno Feitosa Sales (1969–2016), an important figure in the paleontological scenario of Brazilian Northeast, mainly the Araripe Basin.

Type material: Holotype (carapace): DGEO-CTG-UFPE-8122. Paratypes (carapaces): DGEO-CTG-UFPE-8110, 8111, 8119, 8123, 8124, 8125, 8126, 8127, 8128, 8129, 8131; all from the type locality.

Type locality: Cedro site, Araripe Basin, municipality of Exu, Pernambuco, Brazil.

Type horizon: Romualdo Formation (upper Aptian–lower Albian).

Diagnosis.—Carapace sub-hexagonal to sub-square, nearly equidimensional, weakly vaulted transversely and longitudinally, widest anterior to carapace mid-length and to epibranchial spine, finely granulated, lacking ridges, bosses, tubercles, or reniform swellings. Fronto-orbital margin nearly as wide as carapace maximum width; rostrum well-developed, elongated, bifid, somewhat spatulate, axially sulcate, extending well beyond outer orbital spine, bearing a pair of short lateral spines at anterior third; post-rostral slits absent. Orbits wide, directed forward, faintly upturned; supra-orbital margin straight, sub-horizontal to slightly diverging postero-laterally, with two very short but wide orbital fissures somewhat oblique to each other; inner orbital lobe short; intra-orbital lobe short, roundish in outline; outer orbital spine well-developed, relatively long, simple, triangular, shorter than rostrum, with outer margin directed anteriorly or slightly diverging antero-laterally. Anterolateral margin shorter than posterolateral margin, with three short, broad, well-developed triangular spines excluding the outer orbital spine, first two spines the largest; epibranchial spine weakly developed, directed laterally. Posterolateral margin entire, slightly convex to nearly straight. Posterior margin slightly concave to straight, rimmed, narrower than front-orbital margin. Cervical groove moderately defined, shallow, sinuous, distally reaching anterolateral margins; secondary groove faint; postcervical groove absent. Branchiocardic groove shallower than cervical groove. Epigastric region narrow, protogastric and mesogastric regions slightly tumid; hepatic region wide, slightly tumid; intestinal region wide; epibranchial region with two swellings near contact with branchial groove; meso- and metabranchial regions not differentiated.

Description.—Carapace sub-hexagonal to sub-square, as long as wide; dorsal carapace weakly vaulted to flattened,

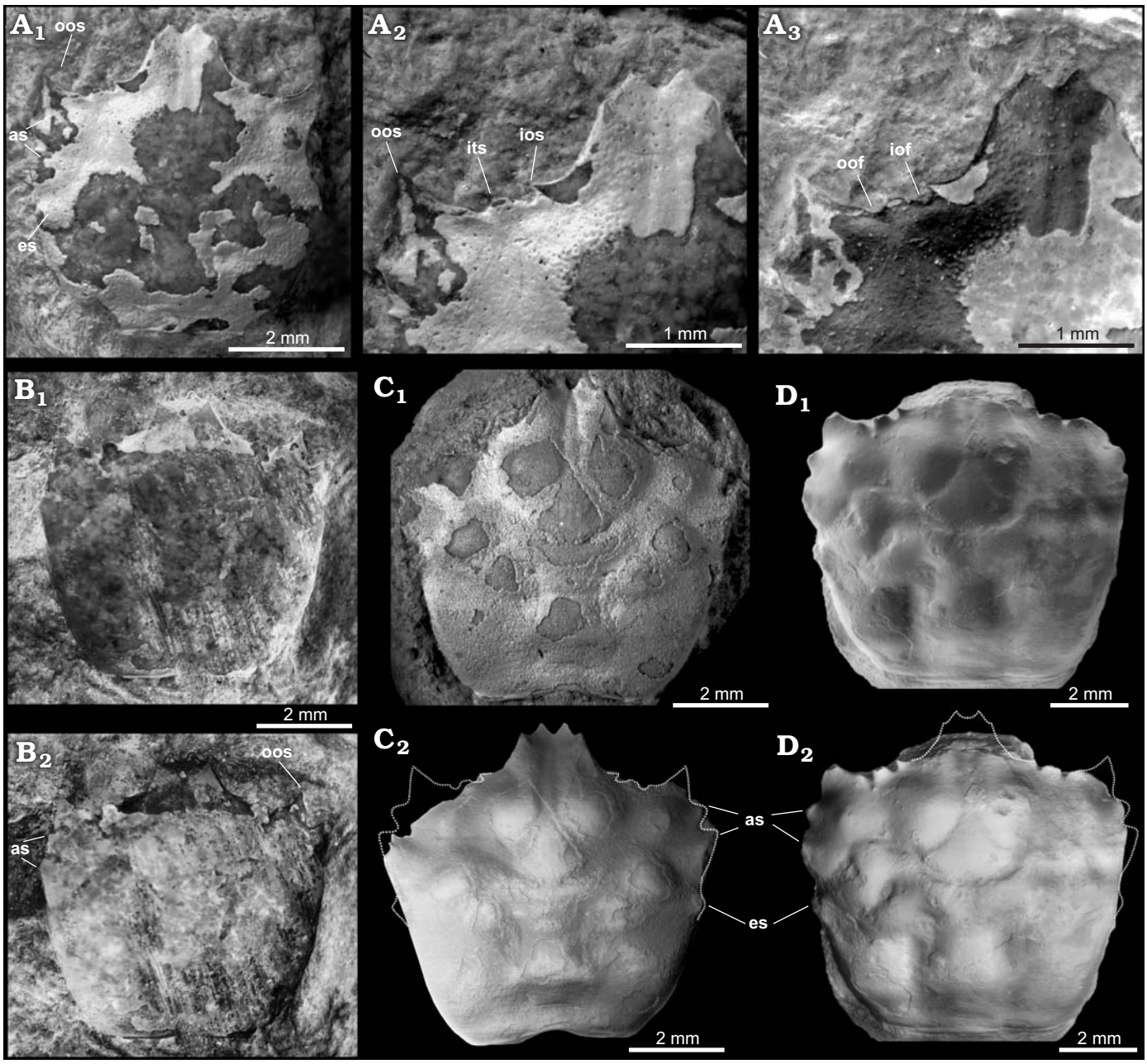


Fig. 4. ?Eogeryonid brachyuran *Romualdocarcinus salesi* Prado and Luque gen. et sp. nov. from the upper Aptian–lower Albian Romualdo Formation of the Santana Group, Araripe Basin, Pernambuco, Brazil. **A**. Holotype DGEO-CTG-UFPE-8122; A_1, dorsal view showing the two anterolateral spines, the epibranchial spine, and the outer orbital spine; A_2, close-up of rostrum and left orbit showing the inner-, intra-, and outer- orbital spines; A_3, inverted colour image of A_2, showing the short and wide inner and outer orbital fissures. **B**. Paratype DGEO-CTG-UFPE-8119; B_1, dorsal carapace; B_2, inverted colour image of B_1 showing the outer orbital spine and the two anterolateral spines. **C**. Paratype DGEO-CTG-UFPE-8137; C_1, dorsal carapace; C_2, inverted colour image of C_1, showing the anterolateral spines and the short epibranchial spine. **D**. Paratype DGEO-CTG-UFPE- 8127; D_1, SEM image of dorsal carapace; D_2, inverted colour image of D_1, showing the anterolateral spines and the short epibranchial spine. Abbreviations: as, anterolateral spines; ios, inner orbital spine; iof, innermost orbital fissure; its, intra-orbital spine; oof, outermost orbital fissure; oos, outer orbital spine. All specimens photographed dry and uncoated, except for C_1, which was coated with ammonium chloride.

widest anterior to carapace mid-length at level of second anterolateral spine; dorsal carapace smooth, finely granulated, with well-defined regions lacking ridges, tubercles, or reniform swellings. Fronto-orbital margin broad, nearly as wide as carapace maximum width and wider than posterior margin. Rostrum well-developed, broad, long, somewhat spatulate, extending well beyond outer orbital spine, nearly one-third of fronto-orbital margin width, wider at the base, with straight lateral margins converging antero-medially, bearing a pair of short lateral spines at anterior third, and a pair of distal spines forming a weakly downturned bifid rostrum; rostrum sulcate axially, with posterolateral margins at level of supraorbital margin; post-rostral slits absent. Orbits wide, faintly upturned, directed forward, each or-

bit slightly over one-third of fronto-orbital margin; supra-orbital margin straight, sub-horizontal to slightly diverging postero-laterally, with two very short but wide orbital fissures somewhat oblique to each other; innermost orbital fissure slightly wider than outermost fissure; inner orbital lobe short, moderately developed, grading from lower margin of rostrum; intra-orbital lobe short, roundish in outline, separated from inner and outer lobes by orbital fissures; outer orbital spine well-developed, simple, triangular, shorter than rostrum, with outer margin directed anteriorly or slightly diverging antero-laterally. Anterolateral margin slightly convex to straight, slightly shorter than posterolateral margin, bearing three triangular, short, well-developed spines excluding outer orbital spine; first two spines the largest, directed antero-laterally, second antero-lateral spine wider than adjacent spines; third antero-lateral spine representing the epibranchial spine, weakly developed, directed laterally. Posterolateral margin slightly convex to nearly straight, without spines, denticles, or tubercles. Posterior margin wide, slightly concave, rimmed, shorter than fronto-orbital margin and slightly wider than half of carapace maximum width. Cervical groove distinct but moderately defined, shallow, sinuous, arcuate, with smooth deflections, axially interrupted, distally reaching anterolateral margins; secondary groove present but faint; post-cervical groove absent; branchial grooves distinct, moderately developed, crescent-shaped; branchiocardic groove present, weakly developed, sub-parallel to cervical groove. Epigastric region narrow, well-defined laterally by sub-parallel grooves; protogastric and mesogastric regions slightly inflated; hepatic region wide, without transverse ridge but slightly tumid; epigastric, protogastric, mesogastric, and hepatic regions without tubercles or bosses; metagastric and urogastric regions lacking tubercles or longitudinal ridges, faintly separated by a shallow depression, both regions defined laterally by crescent-shaped branchial grooves; urogastric region narrow; cardiac region well-developed, inflated, broader than meta- and urogastric regions, wider anteriorly, lacking tubercles, without transverse or longitudinal ridges; intestinal region wide, depressed anteriorly by contact with posterior cardiac region; epibranchial region well-defined, limited by cervical and branchiocardic grooves, with two swellings near contact with branchial groove; meso- and metabranchial regions not differentiated, lacking spines, tubercles, or conspicuous ridges, but with posterior metagastric region inflated.

Dimensions.—For a list of measurements see Table 3.

Remarks.—The systematic affinities of *Romualdocarcinus* Prado and Luque gen. nov. are puzzling, in part due to its incompleteness (only known from dorsal carapaces), and its superficial resemblance to brachyuran crabs from different groups. For instance, *Romualdocarcinus* shares a sub-hexagonal carapace outline with Paranecrocarcinidae, Cenomanocarcinidae, and Orithopsidae, although *Romualdocarcinus* is more sub-squarish than most orithopsids, and lacks the posterolateral spines and weakly projected rostrum of Cenomanocarcinidae, or the postrostral slits seen in most Paranecrocarcinidae. *Romualdocarcinus* also shares with Orithopsidae, Necrocarcinidae, and Paranecrocarcinidae a fronto-orbital margin that is wider than half the carapace maximum width, but differs from Necrocarcinidae, Paranecrocarcinidae, or any other necrocarcinoid-like raninoidan, in its fronto-orbital margin being almost as wide as the carapace (Fig. 4A$_1$, B, C, D). The subspatulate bifid rostrum that extends beyond the outer-orbital spine seen in several Paranecrocarcinidae and Orithopsidae, and the smooth dorsal carapace lacking ridges or rows of tubercles distinctive of orithopsids like *Planocarcinus*, *Colombicarcinus*, and *Aetocarcinus*, would advocate for affinities with the group.

Romualdocarcinus Prado and Luque gen. nov. and the orithopsid *Exucarcinus* Prado and Luque gen. nov., are known from the same strata and localities in the Araripe basin, yet both taxa differ in several features. In *Romualdocarcinus* the carapace outline is squarish, its dorsal regions are more tumid, and the posterior margin nearly straight, while in *Exucarcinus* the carapace is more hexagonal, has less marked dorsal regions, and the posterior margin is concave. Also, *Romualdocarcinus* has a shorter anterolateral margin, only three anterolateral spines (Fig. 4A$_1$, B$_2$, C$_2$, D$_2$), and a maximum width anterior to its mid-length, whereas *Exucarcinus* has anterolateral and posterolateral margins about the same length, has six to seven anterolateral spines, and is wider at its mid-length. Furthermore, in *Romualdocarcinus* the supra-orbital margins are weakly upturned and slightly divergent postero-laterally, and bear two short and wide orbital fissures faintly oblique to each other (Fig. 4A$_2$, A$_3$, C$_2$, D$_2$), which differ from the sub-horizontal margins with two narrower and sub-parallel orbital fissures seen in *Exucarcinus*.

Despite the superficial similarities between *Romualdocarcinus* and several necrocarcinoid-like raninoidans, the new genus seems to fit better within Eubrachyura, in particular Eogeryonidae, known from the Cenomanian of Spain (Ossó 2016). Both taxa share a sub-hexagonal to sub-square carapace outline, they have anterolateral margins with three spines (excluding the outer orbital spine), wide orbits with two open fissures, and a broad bifid rostrum with secondary lateral spines (Ossó 2016). However, in Eogeryonidae the rostrum is short and four tipped, while in *Romualdocarcinus* it is elongated and bifid (Fig. 4A, C). Other early eubrachyurans like Marocarcinidae Guinot, De Angeli, and Garassino, 2008, from the Cenomanian of Morocco, also share with *Romualdocarcinus* the bifid rostrum with secondary lateral spines, and the presence of three spines in the anterolateral margin, but it has smaller orbits than those of *Romualdocarcinus*, it lacks orbital fissures, and has cervical and branchiocardial grooves marked only towards the lateral margin. Another family from the Upper Cretaceous of the Americas, Longusorbiidae Karasawa, Schweitzer, and Feldmann, 2008, shares with *Romualdocarcinus* a fronto-orbital margin nearly as wide as the carapace maximum width,

the broad orbits, and a rostrum elongated and axially sulcate. However, Longusorbiidae has a considerably narrower downturned rostrum and well-defined dorsal carapace regions, both absent in *Romualdocarcinus.*

Although most eubrachyuran families have their earliest fossil representatives in Upper Cretaceous or Cenozoic rocks, only a handful of eubrachyuran-like families are currently known from Lower Cretaceous units, i.e., Telamonocarcinidae Larghi, 2014, from the lower Albian of Colombia; Tepexicarcinidae Luque, 2015b, from the lower Albian of Mexico; and Componocancridae Feldmann, Schweitzer, and Green, 2008, from the lower Albian of USA (see summary in Luque 2015b). A fourth family of eubrachyurans, Priscinachidae Breton, 2009, is known from the upper Albian and Cenomanian of Spain and France (Breton 2009; Klompmaker 2013). Although only two of these families, i.e., Telamonocarcinidae and Priscinachidae, can be placed within crown superfamilies such as Dorippoidea and Majoidea, respectively, all four taxa belong to basal eubrachyuran branches, whereas *Romualdocarcinus* is more reminiscent of modern-looking eubrachyurans like Eogeryonidae. If *Romualdocarcinus* is indeed an eogeryonid, it will extend the temporal distribution of the family into the Early Cretaceous, and represents one of the oldest "higher" true crab yet known.

Stratigraphic and geographic range.—Type locality and horizon only.

Concluding remarks

Early Cretaceous crabs of the family Orithopsidae are known from the Aptian–Albian of North America, South America, and Europe (Van Bakel et al. 2012; Schweitzer et al. 2016b; Luque et al. 2017, and references therein). *Exucarcinus* Prado and Luque gen. nov., from the Aptian–Albian of Brazil, is very similar to other endemic South American taxa of nearly the same age such as *Planocarcinus*, *Bellcarcinus*, and *Colombicarcinus.*

The only brachyuran crab previously known from the Romualdo Formation and the Santana Group as a whole is *Araripecarcinus ferreirai*, represented by a single ventral carapace with appendages associated (Maisey 1991; Luque 2015a). In contrast, *Exucarcinus gonzagai* Prado and Luque gen. et sp. nov. and *Romualdocarcinus salesi* Prado and Luque gen. et sp. nov. are so far known exclusively from dozens of dorsal carapaces. It is possible that *E. gonzagai* Prado and Luque gen. et sp. nov. might correspond to the dorsal carapace of *A. ferrerai*, but without conclusive evidence and dorso-ventral material associated, this is just a possibility and both taxa so far cannot be compared directly or assumed as conspecific. In addition, *A. ferreirai* comes from a different stratigraphic interval, facies, and taphocoenosis than *E. gonzagai*, further suggesting a possible independent systematic placement. An isolated right brachyuran claw found in the site Arrojado (Fig. 5) was collected from

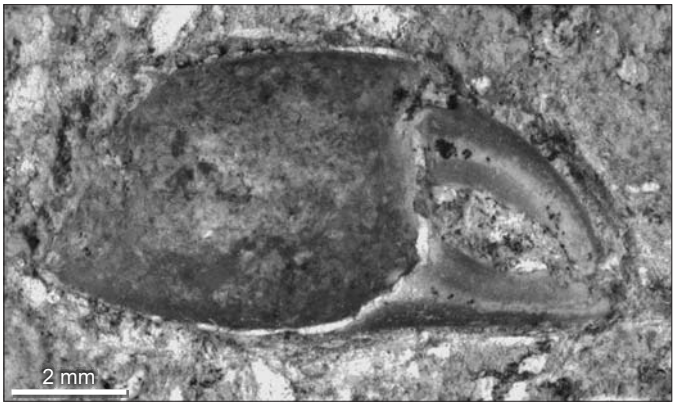


Fig. 5. Brachyura indet. (right cheliped) from the upper Aptian–lower Albian Romualdo Formation of the Santana Group, Araripe Basin, Pernambuco. DGEO-CTG-UFPE-7743, possibly akin to *Araripecarcinus ferreirai* Martins-Neto, 1987.

the concretionary fish level from which *Araripecarcinus* comes (Fig. 2), and is similar to the chelipeds of *A. ferreirai*, suggesting that it could belong to this species. To date, all fossil and extant raninoidans, i.e., Necrocarcinoidea, Palaeocorystoidea, and Raninoidea, are exclusively known from marine subtidal settings, and there are no fossil or extant raninoidans known from brackish or freshwater habitats (Luque 2015a). Therefore, the occurrences of *Exucarcinus* Prado and Luque gen. nov. associated with echinoids in the municipality of Exu, Pernambuco, suggest shallow marine sedimentation in the western portion of the Araripe Basin rather than brackish depositional settings.

As previously indicated, the eubrachyuran-like *Romualdocarcinus salesi* Prado and Luque gen. et sp. nov. might be an eubrachyuran related to *Eogeryon*, a genus whose sternal anatomy clearly indicates an eubrachyuran affinity (Ossó 2016: fig. 5). As such, *Romualdocarcinus* would be expected to have a sternal construction closer to eubrachyurans and unlike that of *Araripecarcinus* (Luque 2015a).

Molluscs and echinoids from the same stratigraphic levels of the Romualdo Formation where the new crab faunule occurs have been interpreted as transported clasts in deposits generated by storms at different water depths (Sales 2005; Prado et al. 2015, 2016). The occurrence of mostly dorsal carapaces of crabs lacking any preferential position within the matrix of coquinas, limited at the base by abrupt contacts which exhibit fragmented bioclasts without signs of abrasion or rounding, suggest deposition under storm events where the energy was not sufficient to transport the remains over long distances. Some specimens show local fragmentation due to compaction, as the carapaces are complete but broken, and some of the fragments are only slightly displaced from the rest of the carapace. The crab carapaces here reported most likely would have been transported over short distances or remobilized within their own environment (parautochthonus sensu Kidwell et al. 1986).

To date, the genera *Planocarcinus*, *Bellcarcinus*, *Colombicarcinus, Exucarcinus* Prado and Luque gen. nov., and *Romualdocarcinus* Prado and Luque gen. nov. are restricted

to northern South America, and are quite different from closer relatives in North America and Europe (Van Bakel et al. 2012; Schweitzer et al. 2016a, b; Luque et al. 2017). Our new findings indicate that the tropical Americas might have been inhabited by several early brachyuran lineages, with several endemic genera and species during the Cretaceous.

The Lower Cretaceous rocks of northeastern Brazil, including those in the Araripe Basin, record the transition from continental to marine facies (rift and post-rift sequences) linked to the separation of South America and Africa, and the birth of the Central Atlantic that connected the water masses of both hemispheres. According to Arai (2014), the Tethyan influence on these basins during the upper Aptian–lower Albian is suggested by the presence of several Tethyan faunas, such as the isopod *Codoisopus brejensis* in the Parnaíba Basin (Codó Formation) (Lindoso et al. 2013), the pithonellid calcispheres (calcareous dinoflagellates) in the Potiguar and Sergipe-Alagoas basins (Dias-Brito 1985a, b, 2002), bivalve *Neithea* (*Neithea*) *coquandi* (Péron, 1877) (Monteiro et al. 2010), planktonic foraminifera (e.g., *Globigerinelloides aptiensis*, *G. barri*, *G. blowi*, *G. ferreolensis*, *G. maridalensis*, *Hedbergella labocaensis*, *H. maslakovae*, *H.semielongata*, *H. similis*), and ammonoids (*Epicheloniceras* cf. *martinioides*, *Vectisites simplex*, and *V.* cf. *cruzi*) (Bengtson and Koutsoukos 1992; Bengtson et al. 2007) in the Sergipe-Alagoas Basin (Riachuelo Formation), and the molluscs and fishes in the Araripe Basin (see Table 2). Therefore, the marine ingression would have reached the Araripe either from the north through the Parnaíba Basin (Arai 2014) or from the northeast through the Potiguar Basin (Lima 1978) (Table 2), but not from the south (Recôncavo–Tucano–Jatobá basins).

Although the fragmentary and sparse record of fossil raninoidans and eubrachyurans from the Early Cretaceous does not help resolve this issue, the presence of taxa similar to those from the Aptian–Albian of Colombia, and the Albian–Cenomanian of USA, England, and Spain, confirm the broad distribution of these groups in the Tethys Ocean during the Early Cretaceous, and reinforces the view of a Tethyan influence in Araripe at the time.

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