A puzzling frog crab (Crustacea: Decapoda: Brachyura) from the Early Cretaceous Santana Group of Brazil: frog first or crab first?

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The evolutionary origin of frog crabs (Raninoida) remains puzzling partly due to their astonishing morphological disparity, ranging from broad and heavily ornamented ‘crab-like’ extinct families (necrocarcinids and allies), to elongate and smoother ‘frog-like’ extant ones (raninids and allies). However, an ancient Cretaceous clade (Palaeocorystidae) displays a combination of plesiomorphic and apomorphic traits that might advocate for either evolutionary scenario: from ‘crab-like’ to ‘frog-like’, or vice versa. This lack of agreement is partly fuelled by the scarcity of Early Cretaceous fossils, a time from which the first raninoids are known. A close re-examination of an Early Cretaceous fossil from the Santana Group of Brazil, Araripecarcinus ferreirai Martins-Neto, 1987, combined with phylogenetic analysis including all main clades of podotreme crabs, reinforces its raninoidan condition, and rejects the initial hypothesis of a Portunoidea affinity. Furthermore, comparisons with other raninoids support the hypothesis that a more ‘crab-like’ body plan is the plesiomorphic condition for raninoidans, and that the ‘frog-like’ architecture of Palaeocorystidae, and perhaps the Raninoidea as a whole, reflects a derived condition related to a specialized burrowing lifestyle. Phylogenetic analyses are fundamental to evaluate the position of Palaeocorystidae with respect to raninoidean and necrocarcinid-like families, helping to better resolve the Raninoidea evolutionary tree of life, and to gain a broader understanding on their relatedness by common ancestry throughout geological time.

Keywords: Albian; evolution; Neotropics; Raninoida; Raninoidia; South America

Introduction

The particular body plan of extant frog crabs has puzzled scientists since the time of Linnaeus, resulting in multiple affiliations with ‘higher’ and ‘podotreme’ brachyuran crabs, anomurans, macrurans, and even apterous insects (Linnaeus 1758; Lamarck 1801; Latreille 1802; Milne Edwards 1837; Dana 1852; Ortmann 1892; Alcock 1896; Bourne 1922; Glaessner 1960; 1969; Števčić 1973; 1995; Martin & Davis 2001). They are a group of true crabs, or Brachyura, whose modern representatives are adapted for burrowing in soft to gravelly substrates. Their diagnostic traits, once considered to reflect an ancestral condition (e.g. elongate carapace, pleon exposed dorsally, narrow sternum and flattened legs), are now thought to be derived adaptations for their burrowing lifestyle, and therefore convergent between several non-related superfamilies of digging anomuran and brachyuran crabs (Borradaile 1903; Bourne 1922; Gordon 1966; Glaessner 1969; Števčić 1973; Williams 1974; Abele & Felgenhauer 1982; Gaten 1998; Dawson & Yaldwing 2000; Števčić 2005). The evolutionary origin of raninoids remains puzzling partly due their astonishing morphological disparity, ranging from broad and heavily ornamented ‘crab-like’ families (necrocarcinids and allies), to elongate and smoother ‘frog-like’ ones (raninids and allies). Furthermore, an intermediate group, the palaeocorystids, combines plesiomorphic and apomorphic traits seen in both clades, and their phylogenetic affinities are still debated. In addition, the Early Cretaceous has been deemed as the time where the main raninoidan lineages diversified (Karasawa et al. 2011; Luque et al. 2012; Van Bakel et al. 2012a), but their scarce fossil record compared to that in the Late Cretaceous biases our understanding of the polarity of change of certain traits, and thus our understanding of their relatedness by common ancestry throughout geological time.

The late Early Cretaceous Santana Group in Brazil, South America is an astonishing fossil-bearing deposit recognized worldwide for extraordinary preservation of marine and terrestrial invertebrates, vertebrates and plants (Maisey 1991). Despite the many arthropods found there, only one species of true crab or Brachyura, Araripecarcinus ferreirai, has been reported so far. Its holotype and sole specimen was originally described as a dorsal
carapace of a portunid crab, a group of higher brachyurans known for their ability to swim with paddle-like posterior legs (Martins-Neto 1987; Maisey 1991; Maisey & Carvalho 1995). However, a re-examination of this specimen has revealed that it is neither a portunid crab nor a dorsal carapace with a flattened last pair of legs. This was first noticed by Guinot & Breton (2006) who accurately proposed that Araripecarcinus belonged to Raninoidea, a group of crabs only distantly related to portunids (Guinot et al. 2013). Karasawa et al. (2008) discussed the ventral orientation of the Araripecarcinus type specimen, and based on the shared elongate buccal cavity, the narrow sternum and the posteriorly extended abdomen, allied it with Raninidae De Haan, 1839. Since then, Araripecarcinus has been regarded as a raninoid raninodidian, although with unclear affinities (Schweitzer et al. 2010; Luque et al. 2012; Van Bakel et al. 2012a; Guinot et al. 2013), which calls for re-examination of the type material, and discussion of the species’ systematic relationship with other raninoids.

This is the first attempt to place Araripecarcinus in synthetic and cladistic contexts, and discuss its implications for frog crab phylogenetic relationships.

**Institutional abbreviations**

AMNH: American Museum of Natural History, New York, United States; IMG: Museo Geológico Nacional José Royo y Gómez, Servicio Geológico Colombiano (formerly INGEOMINAS), Bogotá DC, Colombia; IRScNB: Institut royal des Sciences naturelles de Belgique, Brussels, Belgium; USNM: National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; UF: Invertebrate Paleontology Division, Florida Museum of Natural History, University of Florida; USP: Instituto de Geociências da Universidade São Paulo, São Paulo, Brazil.

**Anatomical abbreviations**

A6: sixth abdominal somite; Ca: carpus; Cg: cervical groove; Ch: cheliped; C1: consistency index; Cx2–Cx4: coxa of second to fourth pereiopods; Cx Ch: coxa of cheliped; Cx mpx3: coxa of third maxilliped; Da: dactylus; Ds: dorsal spine; E: compound eye; E4–E7: episternites four to seven; Ex mpx3: exopod of third maxilliped; Me: merus; Mxp3: third maxilliped; P2–P5: second to fifth pereiopods; Pr: propodus; ?Pr: ?propodus; Rs: rostral spine; S3–S8: sternites three to eight.

**Systematic palaeontology**

Decapoda Latreille, 1802
Brachyura Linnaeus, 1758

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Raninoidea De Haan, 1839
?Necrocarcinidae Förster, 1968

Genus *Araripecarcinus* Martins-Neto, 1987

**Type species.** *Araripecarcinus ferreirai* Martins-Neto, 1987, by monotypy.

**Emended diagnosis.** Carapace subcircular in outline, nearly as wide as long, as seen in Necrocarcinidae, Cenomanocarcinidae Guinot et al., 2008; Orthopsidae Schweitzer et al., 2003, and Camarocarcinidae Feldmann et al., 2007; maximum width near to midlength; pterygostome broad, vaulted, crest inconspicuous, surface granulated; anterolateral and posterolateral margins convex, both apparently lacking spines; cervical groove reaching ventral carapace; buccal cavity elongated, about half the carapace length. Thoracic sternum narrow; S3 distinct ventrally, wider than long; S4 flattened medially, lateral margins subparallel and slightly convex; E4 longer than wide, slightly ovate distally, forming with lateral margins of S4 an angle of ~120°; suture 4/5 incomplete; S5 similar in shape to S4; suture 5/6 incomplete; S6 separated in anterior and posterior plates by a weak, transverse break point; sterno-coxal depression absent; thoracic sexual openings absent; sternal pleon locking mechanisms on E5 absent in holotype. Chelipeds (Ch) isochelous; P2 and P3 the longest of all pereiopods, similar in size; P4 nearly half P2–P3; P5 the smallest, very reduced, apparently sub-dorsal.

**Occurrence.** Late Early Cretaceous (Albian) of the Araripe Basin, Brazil.

**Remarks.** The original assignment of *Araripecarcinus* within Portunoidea Rafinesque, 1815, was founded on the presumed possession of a P5 adapted for swimming as seen in most portunoids, and different enough from the ‘flattened and foliaceous’ pereiopods seen in extant members of Raninoidea (Martins-Neto 1987, p. 408). However, what was considered to be flattened sclerites of P5, actually correspond to the carpus and the apparently flat propodus of P4, whereas P5 is very reduced and apparently carried subdorsally (Figs 1B, 2A). In addition, the ‘portunid branchial lobes’ depicted by Martins-Neto (1987, fig. 2), are the arthrodial cavities of the chelipeds; the ‘epibranchial’ and ‘mesogastric’ regions are the pterygostome and the buccal cavity respectively; and the ‘urogastric’, ‘cardiac’ and ‘intestinal regions’ are part of the thoracic sternum (Figs 1A, B, 2A, B). Furthermore, Martins-Neto stated that *Araripecarcinus* “is clearly related to the torynommoid genus *Mithracites* from the Aptian of England” (Martins-Neto, in Maisey 1991, p. 411). Currently, *Mithracites* Gould 1859, is regarded as closer to homoloids than to torynommoimds (Guinot & Tavares 2001; Steväc 2005; Karasawa et al. 2011; Schweitzer & Feldmann 2011; Van Bakel et al. 2012b; Guinot et al. 2013), and based on the diagnostic traits seen in the type material of
Araripecarcinus, affiliation with portunoids, homoloids or torynommoids is untenable.

Among podotreme crabs, Araripecarcinus traits are reminiscent of those present in the raninoidan families Camarocarcinidae and Necrocarcinidae, especially the roundish carapace outline, the morphology of the thoracic sternum, and the cervical groove reaching ventrally (Fig. 1A, B). Araripecarcinus, however, lacks the grooved pterygostome seen in camarocarcinids, with a long blunt crest, the strongly concave thoracic sternum and the sterno-abdominal depression (Van Bakel et al. 2012a). Its episternites are more broadly spaced from each other than other palaeocorystoids, and the S4 has subparallel and slightly convex lateral margins and forms with the anterior margin of E4 an angle of nearly 120° (Fig. 2B). Moreover, its palaeogeographical and stratigraphical range contrast with those of typical camarocarcinids, exclusively known from Paleocene rocks of North Dakota, Greenland and Denmark (Holland & Cvancara 1958; Feldmann et al. 2007; Guinot et al. 2008; Van Bakel et al. 2012a), further casting doubts on any camarocarcinid relationship. This does not rule out that camarocarcinids might have Cretaceous representatives from low latitudes, but no such fossils have been found to date.

The thoracic configuration of Araripecarcinus is puzzling. Its sternite 3 is covered anteriorly by matrix, precluding the study of anterior sternites. The exposed part of sternite 3 is longer than in many other raninoidans.
However, sternal features vary considerably among families and genera, and a similar condition as in *Araripecarcinus* can be seen in specimens of *Necrocarcinus labeschei* (Eudes-Deslongchamps, 1835), as illustrated in Karasawa et al. (2011, fig. 10B), *Orithopsis tricarinata* (Bell, 1863) in Van Bakel et al. (2012a, fig. 22A, D), and *Planocarcinus johnjagti* in Bermudez et al. (2013, fig. 8I). The narrowness of *Araripecarcinus* sternite 4, particularly in the posterior portion, might be related with accommodation of a well-developed articular condyle of P1, and can be considered as an autapomorphy for *Araripecarcinus* among raninoids. Following the works of Karasawa et al. (2011) and Van Bakel et al. (2012a), the presence of a double protrusion mechanism on E5 for abdomen holding seen in Orithopsidae and Cenomanocarcinidae, their broad S4 with large and wide E4 (Fig. 3), their generally sub-hexagonal carapaces, and the cervical groove ending anterior to the spinose anterolateral...
margins, rule out affiliation with *Araripecarcinus*. *Araripecarcinus* ventral architecture is more reminiscent of some necrocarcinid-like taxa, especially that of *Planocarcinus* Luque et al. 2012. Both taxa have E4 and E5 separated from one another (Bermudez et al. 2013, fig. 8I). In some raninoids such as *Notopocorystes stokesii* (in Van Bakel et al. 2012, fig. 59A, B), the suture between sternites 6 and 7, at first, appears to be complete. However, that separation corresponds to a fracture zone related to a weak point in the thoracic sternum (Van Bakel, pers. comm. 2012), with its sutures only expressed laterally. Whether or not this is the case in *Araripecarcinus* is hard to tell since the specimen is likely a fragmented exuviae with disarticulated thoracic elements.

**Figure 3.** General sternal configuration in *Araripecarcinus* Martins-Neto, 1987, and representatives of the eight terminals of Raninoida (Figs 4, 5). A, *Araripecarcinus ferreirai* Martins-Neto, 1987 (Figs 1A, B, 2A, B). B, Camarocarcinidae, *Camarocarcinus arnesoni* Holland & Cvancara, 1958 (Fig. 2C). C, Necrocarcinidae, *Necrocarcinus labeschei* (Eudes-Deslongchamps, 1835) (after Karasawa et al. 2011, fig. 10B). D, Cenomanocarcinidae, *Cenomanocarcinus* sp. (Fig. 1D). E, Orthopsidae, *Silvacarcinus laurae* Collins & Smith, 1993 (Fig. 2D). F, Palaeocrystidae Lörenthey in Lörenthey & Beurlen, 1929, *Notopocorystes stokesii* (Mantell, 1844) (after Van Bakel et al. 2012, fig. 37A). G–I, Raninoida; G, Lyreididae, *Lyreidus tridentatus* de Haan, 1841 (after Feldmann & Schweitzer 2007, fig. 4B); H, Raninidae, *Raninoides* sp.; I, Symethidae, *Symethis* sp. Abbreviations: Ch, cheliped; P2, second pereiopod. The circles indicate the approximate location of coxae of Ch and P2.
Raninoids s.l. have diverse sternal morphologies, and *Araripecarcinus* appears not to be an exception. The overall sternal similarities with Sphaerodromiidae Guinot & Tavares, 2003 (see also Schweitzer & Feldmann 2010) and other podotremes would not be that surprising, if some early raninoid clades might have shared more plesiomorphies with other podotreme clades than more derived raninoids do. *Araripecarcinus* might well belong to the same stock as planocarcinids or paranecrocarcinids, but its unknown dorsal carapace, together with the poorly known sternal architecture of planocarcinids and paranecrocarcinids (Feldmann et al. 2007; Jäg et al. 2010; Luque et al. 2012; Van Bakel et al. 2012a), obscures its suprageneric placement.

*Araripecarcinus ferreirai* Martins-Neto 1987
(Figs 1A, B, 2A, B)

**Emended diagnosis.** As for genus.

**Material.** Series of photos and cast of the holotype and sole specimen USP (GP/1T 1477), deposited in the Instituto de Geociências da Universidade São Paulo, São Paulo, Brazil.

**Measurements.** Carapace maximum length: ~10.3 mm; width, ~10.4 mm.

**Occurrence.** Calcereous concretion from the upper unit of the Romualdo Formation, Fish Level, Santana Group, middle to upper Albian, exposed at the south-eastern flank of the Araripe Basin, near the city of Porteiras, Ceará, Brazil (Martins-Neto 1987, p. 407; Maisey 1991, p. 411; Maisey & Carvalho 1995, p. 9).

**Emended description.** The holotype is a ventral carapace of small size, subcircular in outline, approximately as wide as long (~10 mm width, ~10 mm length), and with maximum width slightly anterior to carapace midlength. Its pterygostome is broad, vaulted, finely granulated, and with a barely distinct blunt crest, and the cervical groove reaches the ventral carapace. The anterolateral margin is convex, slightly shorter than the posterolateral margin, and apparently lacking spines; the posterolateral margin is slightly convex, about as long as anterolateral margin, and lacks visible spines. The buccal cavity is elongated, at least three times as long as wide, about half the carapace length, and nearly as long as thoracic sternum, as in other necrocarcinid-like terminals.

The thoracic sternum is narrow, about half the carapace length, and with the sternites more or less flattened axially. Its episternites are directed posteriorly, and the external lobes of E4–E7 are sub-parallel to each other, lying oblique distally from the sternites (Figs 2A, B, 3A). The S1–S2 are unknown; but S3 is distinct ventrally, wider than long, with a subrectangular outline and lateral margins somewhat straight, and slightly diverging anteriorly.

Neither spermathecal apertures, nor sternal pleon locking mechanisms, are recognizable in the holotype. Its A6 is wider than long, with lateral margins convergent posteriorly, and posterior margin apparently concave. The Ch are isochelous; with the propodus longer than wide, bearing a manus moderately inflated, and with the pollex and dactylus poorly preserved; its merus is about twice as long as wide, wider anteriorly, and bearing a few tubercles externally. The P2 is partly preserved; its coxa is large, nearly as wide as long, and about the same width as S4; the merus is about six times as long as wide, nearly three-fourths of the carapace maximum length, somewhat slender, nearly straight, and with weakly convex external margins; no carpus, propodus or dactylus are known. As far as it can be recognized in the holotype, the P3 is very similar to P2 in shape and size; its coxa is about as long as wide, wider towards basis; the basis-ischium is subtrapezoidal and short; the merus is about five times as long as wide, nearly straight, with external margins weakly convex, and narrow distally at articulation with carpus; the carpus length is about one-third the length of merus and two-thirds as wide as merus, narrower at the articulation with the merus, and wider at articulation with propodus, with smoothly convex external margins and nearly straight internal margin; no propodus or dactylus are known. The P4 is partly preserved, with a reduced size about half the length of P3; its merus is sub-cylindrical, about three times as long as wide and with margins nearly straight; the carpus is short and longer than wide with a sub-trapezoidal outline, about half as long but nearly as wide as merus, narrower at the articulation with the merus, wider at articulation with propodus, and with its margins weakly convex; the propodus was not positively recognized on the material studied, except for the sculpted outline on the calcereous matrix (Figs 1A, B, 2A). In Maisey (1991, p. 432), however, a flattened and sub-ovate propodus seems to be present, about twice as long as carpus, and nearly one-third wider than carpus. The P5 is the
smallest of all pereiopods, very reduced in size, and apparently carried dorsally; its merus is slender and small, sub-cylindrical in shape, about five times as long as wide; it is about one-fourth as long but about one-fifth as wide as P3, and just slightly longer than half the length of P4 but about one-fourth its width; the carpus, propodus and dactylus are unknown.

Remarks. Among necrocarcinids and their allies, only the genera Corozzatocarcinus Larghi, 2004, and Cenomanocarcinus Van Straalen, 1936, have confirmed fossil representatives preserving the pereiopods, especially the distal articles of P2 and P3, and complete P4 and P5 (Roger 1846; Feldmann et al. 1999; Neumann & Jagt 2003; Larghi 2004; Vega et al. 2007; Guinot et al. 2008; Vega et al. 2010) (Fig. 1). A specimen described as Cenomanocarcinus renfronae (Stenzel, 1945) by Vega et al. (2010) from the late Albian Simiti Formation of Colombia, possesses similar P2 and P3 to those seen in specimens of C. vanstraeleni Stenzel 1945, while the P4 resemble those seen on Corozzatocarcinus hadjoulae (Roger, 1846) (Vega et al. 2010). Cenomanocarcinus renfronae, whose type series is known from the late Albian of Texas, was transferred by Van Bakel et al. (2012a) to Hasaracancer Jux 1971, the only other cenomanocarcinid genus known to date from the Cretaceous (Ossó-Morales et al. 2011; Van Bakel et al. 2012a). The Colombian specimen of ‘C. renfronae’ was re-examined, and its affiliation with Cenomanocarcinidae corroborated based on the subhexagonal carapace outline and the distinctive three longitudinal ridges, as accurately noted by Vega et al. (2010). Nevertheless, given its poor carapace preservation, and since pereiopods in the Texas specimens of H. renfronae are unknown, direct comparison between the materials is problematic, and therefore its generic identity is unwarranted until new material becomes available.

Despite the incomplete preservation of the pereiopods in Araripecarcinus, the taxon shares with Cenomanocarcinus, Corozzatocarcinus and the Albian cenomanocarcinid indet. from Colombia, slender P2 and P3 meri, similar in shape and size and larger than those on P4 and P5, and with the merus of P5 very reduced and carried in a subdorsal plane (Fig. 1). The size of P4 is variable among these taxa, from reduced in C. hadjoulae and the cenomanocarcinid indet., to moderately reduced in Araripecarcinus, and slightly reduced in C. vanstraeleni. In extant raninoid genera, shape and size of P4 may vary from noticeably reduced, nearly as much as P5, or just slightly shorter than P2–P3. Based on the illustration in Maisey (1991, p. 432), the apparently flattened, slender and sub-ovate P4 propodus of Araripecarcinus is similar to Corozzatocarcinus, and less so to cenomanocarcinid indet., while in Cenomanocarcinus it is broad, flat, ovate, and paddle-like (Feldmann et al. 1999; Vega et al. 2007, 2010; Guinot et al. 2008) (Fig. 1). In Araripecarcinus, A6 is wider than long as in Necrocarcinidae, Cenomanocarcinidae and Orithopsidae, but also as in several Paleocorystidae (Vega et al. 2007; Guinot et al. 2008; Vega et al. 2010; Karasawa et al. 2011; Van Bakel et al. 2012a).

Phylogenetic analysis
In order to test the phylogenetic relationships of Araripecarcinus with other brachyuran clades, two sets of analyses were performed. Analysis I was performed using the original dataset of Karasawa et al. (2011), constituted by 37 taxa and 74 adult morphological characters, and scoring Araripecarcinus following Karasawa et al. (2011) (Supplemental Table 1). Analysis II was performed using an updated dataset for raninoids after Karasawa et al. (2011) and Van Bakel et al. (2012a) containing 14 taxa and 44 adult morphological characters (Supplemental Tables 2, 3). Additional raninoidan taxa included in Analysis II are Lyreididae Guinot, 1993, and Orithopsidae, scored after Van Bakel et al. (2012a), plus the genus Araripecarcinus, and the eubrachyuran family Portunidae, to which Araripecarcinus was originally proposed to be related with (Martins-Neto 1987). For Analysis II, outgroup terminals were chosen and scored based on their phylogenetic positions after Karasawa et al. (2011), in order to explore the polarity of different plesiomorphic and apomorphic traits seen in Raninoida with respect to other ‘basal’ decapods. The rationale for scoring raninoidan taxa at the familial level is to convey the morphological diversity or disparity seen among raninoids, and therefore be able to examine the combination of plesiomorphic and apomorphic character states seen in Araripecarcinus. Ingroup terminals were chosen to test the hypothesis of affiliation of Araripecarcinus with Portunidea (Eubrachyura). The datasets were produced or modified in Mesquite (Maddison & Maddison 2011), and the phylogenetic analyses were conducted in TNT 1.1 (Goloboff et al. 2008). All characters were unordered and equally weighted. Branch supports were obtained in Mesquite. Traditional search for suboptimal trees included 1000 replicates, and Implicit enumeration search was performed without collapsing trees after the search. Both searches lead to the same topologies. Bootstrap and jackknife values were obtained after 1000 replicates each. Bremer support values for the traditional search were calculated under tree bisection reconnection (TBR), and retained trees suboptimal by 30 steps. Unknown character states were scored as ‘?’, and inapplicable ones as ‘–’. The following abbreviations are used: TL, tree length; CI, consistency index; RI, retention index.

Analysis I: tests the phylogenetic position of Araripecarcinus with respect to other podotreme and eubrachyuran clades. It yielded nine equally most parsimonious trees, with TL = 276 steps; CI = 0.48; and RI = 0.69 (Fig. 4). Given the incompleteness of Araripecarcinus, several of the characters in the dataset of Karasawa et al.
Figure 4. Strict consensus of nine equally most parsimonious trees for main podotreme terminals and *Araripecarcinus* Martins-Neto, 1987, following the work of Karasawa et al. (2011). Tree length (TL) = 276 steps; consistency index (CI) = 0.48; retention index (RI) = 0.69. Bremer support indicated above the branches, and bootstrap/jackknife values indicated below the branches, respectively. Terminal taxa indicated by † known only from fossil representatives.
cannot be scored for this terminal, resulting in a less resolved tree than the one obtained by the authors. In addition, the incompleteness of several other podotreme terminals (i.e. bucculentids, prosopids, tanidromitids, glaeisseropsids, konidromitids and lecythocarids) contributes to the overall low branch support and ambiguity for many clades. Despite this, in the strict consensus, Araripecarcinus is recovered in a soft polytomy with all higher raninoidan taxa (Fig. 4). This clade is united by the possession of an elongate buccal cavern, an mp3 lying in two planes, and flattened P2 to P4 (Karasawa et al. 2011; Van Bakel et al. 2012a). This group (Araripecarcinus + raninoidan terminals) lies in a trichotomy with Etyoida and the clade (Dakotocarcinoida (Cyclodorippoida + Eubrachyura)), providing further support to the hypothesis that Araripecarcinus might lie closer to Raninoida/Raninida than to any other podotreme or eubrachyuran clade.

Analysis II: tests the phylogenetic position of Araripecarcinus with respect to higher Raninoida terminals. It yielded one most parsimonious tree, with TL = 81 steps; CI = 0.85; and RI = 0.87 (Fig. 5A). Since the work by Karasawa et al. (2011), some additional raninoidan families have been recognized (e.g. Van Bakel et al. 2012a), and are therefore included in Analysis II. In this analysis the topology is better resolved, and the polytomies dissolved. The clade (Araripecarcinus (Camarocarcinus (Palaeocorystidae (Raninoidae)))) is united by the wide or flattened P2 to P4, and is recovered as sister to (Orthopсидae (Cenomanocarcioidae + Necrocarcioidae)). However, this trait is homoplasious since Cenomanocarcioidae also have wide or flattened P2 to P4. Araripecarcinus is recovered as sister taxon to the clade (Camarocarcinidae (Palaeocorystidae (Raninoidae))), which is united by the presence of an indistinct or faint cervical groove. This character is polymorphic on Cenomanocarcioidae and Palaeocorystidae, as it is in the sister group to Raninoidea. The clade (Palaeocorystidae (Raninoidae)) is united by the shared elongate carapace, which is an apomorphic condition among raninoids. It is possible that Symethidae Goeke, 1981 constitutes a subfamily within Raninidae, rather than its sister taxon, as initially envisioned by Goeke (1981) (see Guinot 1993; Ahyong et al. 2007; Van Bakel et al. 2012a; Guinot et al. 2013; Karasawa et al. 2014). Raninoidea is the clade stemming from the most recent common ancestor for lyreidids, raninids, and symethids, all of them known from fossil and extant taxa. They

**Figure 5.** A, strict consensus of seven equally most parsimonious trees for Raninoida terminals, following the works of Karasawa et al. (2011) and Van Bakel et al. (2012a). Tree length (TL) = 81 steps; consistency index (CI) = 0.85; retention index (RI) = 0.87. Bremer support indicated above the branches, and bootstrap/jackknife values indicated below the branches. Terminal taxa indicated by † known only from fossil representatives. B, cladogram showing the three main clades constituting the monophyletic Raninoida (white oval). The necrocarcinid-like clade (dark grey oval), embracing those raninoidan terminals with usually broad, highly ornamented carapaces with defined cervical and branchiocardiac grooves, and bearing branchial ridges or tubercles; i.e. Necrocarcioidae Förster, 1968, Cenomanocarcioidae Guinot et al., 2008 and Orthopсидae Schweitzer et al., 2003. Palaeocorystidae Lörenthey in Lörenthey & Beurlen, 1929 (grey oval), includes taxa with a somewhat ‘frog-like’ appearance, typically longer than wide, with carapaces varying from highly to poorly ornamented, and having well-defined to faint cervical and branchiocardiac grooves. Raninoidea De Haan, 1839 (light grey oval) embraces those raninoids with typical ‘frog-like’ longer carapaces, usually poorly ornamented to smooth, and with overall faint to incipient dorsal grooves. Camarocarcinidae Feldmann et al., 2007 and Araripecarcinus Martins-Neto, 1987 (dotted line) have dubious phylogenetic placement due their number of unknown character states, particularly Araripecarcinus. Main raninoidan apomorphies indicated by white bars and letters a to h. Terminal taxa indicated by a dagger (†) only known from fossil representatives.
seem to share a long carapace, with straight to convex posterior margins, bearing narrow to reduced posterior sternites, and a presumed united spermatheca (Karasawa et al. 2011). The palp of their mxp3 is carried in an inner mesial position, and they have partially exposed pleurites associated to sternopleural extensions (Van Bakel et al. 2012a). Necrocarcinid-like taxa are confined to the fossil record, ranging from the Early Cretaceous to the Palaeogene, and they differ from Raninoidea mainly, but not exclusively, in their broader carapaces, and the presence of branchial longitudinal ridges or rows of tubercles (Karasawa et al. 2011; Van Bakel et al. 2012a).

**Discussion**

Extant frog crabs are exclusively marine, ranging from very shallow subtidal bottoms to nearly 1400 m depth (Tucker 1995). Similarly, their fossils are known from marine rocks worldwide, and no taxon has been reported from freshwater settings. This suggests that *Araripecarcinus* was a marine dweller, as hypothesized by Martins-Neto (1987, p. 409). It was found in the same concretion with the aspidorhynchid fish *Vinctifer comptoni* (Agassiz, 1841), one of the most abundant fishes in the Romualdo Member, and considered to be a brackish to marine form (Martins-Neto 1987; Maisey 1991; Maisey & Carvalho 1995). Based on palynomorphs, a mid–late Albian age has been assigned to the *Vinctifer*-bearing horizons, and hence to the *Araripecarcinus* specimen (Pons et al. 1990; Moody & Maisey 1994). Although *Araripecarcinus* is the only adult brachyuran known from the Santana Group, and therefore the Romualdo Formation, a few brachyuran zoea larvae are known from stomach contents of the fish *Tharrhias araripis* Jordan & Branner, 1908; a presumed plankton feeder (Maisey 1994; Maisey & Carvalho 1995). One larva (Fig. 6) seemingly lacks lateral spines, and bears short rostral and dorsal spines – the latter apparently broken, that are shorter than the carapace length. This is the only fossil record of brachyuran protozoal larva known to date (Maisey & Carvalho 1995; Guinot et al. 2013). In the extant frog crab *Ranina ranina* (Linnaeus, 1758), instars I to VIII retain large rostral and dorsal spines, but lateral spines become faint to inconspicuous in late stages (Rice & Ingle 1977; Minagawa 1990). Whether the fossil larva belong to a raninoidan, and particularly to *Araripecarcinus*, remains uncertain, but it clearly indicates that brachyurans were present in the shallow marine to brackish waters of the Araripe Basin during the Albian, and that they might have played an important role as food items at different ontogenetic stages (Maisey & Carvalho 1995).

As in extant raninoidans, the flattened articles of P2 to P4 of *Araripecarcinus* might have assisted in burrowing, and even occasionally swimming (Guinot et al. 2008, p. 688). The shape and proportions of P4 in raninoidans can vary from a P4 slightly shorter than P2–P3 to nearly as reduced as P5, and scoring these characters in further phylogenetic analyses should reflect such variation in sizes. The clades including *Araripecarcinus* and Camarocarcinidae are poorly supported, and although both terminals were recovered as closer to Palaeocorystidae + Raninoidea, it is likely that it is an artefact of their number of unknown character states, being actually more closely related to the clade formed by the necrocarcinid-like terminals. Under either phylogenetic scenario, the superfamily Palaeocorystoidea is paraphyletic, and suggests that the plesiomorphic condition for raninoidans is to have broader carapaces, indicating that the innovation of an

**Figure 6.** A, fossil brachyuran crab zoea AMNH 80038, fossil invertebrates, recovered as stomach contents from the fish *Tharrhias araripis* Jordan & Branner, 1908; a presumed plankton feeder (Maisey 1994; Maisey & Carvalho 1995), from the Albian Romualdo Formation, late Early Cretaceous of the Araripe Basin, Brazil; B, close up of area shown in A. Abbreviations: Ds, dorsal spine; E, left compound eye bearing facets; Rs, rostral spine.
elongated carapace might have occurred only once in the evolutionary history of Raninoidea, and is likely to have been present in the last common ancestor for Palaeocorystidae, Lyreidae and Raninidae (including Symethinae). Due to the incompleteness of Araripecarcinus, it is impossible for me to warrant its familial or suprafamilial placement, although the general sternal configuration and carapace proportions are reminiscent of some necrocarcinids. Camarocarcinidae was recovered as the sister taxon to the clade (Palaeocorystidae (Raninoidea)), principally due its lack of branchial ridges or rows of tubercles, as seen among necrocarcinid-like families. This might imply that: (1) the lack of branchial ornamentation is the plesiomorphic condition for Raninoidea, and such innovation only evolved once in the most recent common ancestor for (Orthopsidae (Cenomanocarcinidae + Necrocarcinidae)); or (2) that Camarocarcinidae, if assuming it is closer to Orthopsidae + (Cenomanocarcinidae + Necrocarcinidae) than to Palaeocorystidae + Ranieoidea, might have secondarily lost them (reversal), or never had them (plesiomorphic). The evolution of Cretaceous brachyurans is complex, with many body plans restricted to this timeframe. Araripecarcinus might well belong to an ancient, early-branching lineage of Early Cretaceous stem-raninoidans endemic to Northern South America.

Although frog crabs sensu lato are considered as a monophyletic group, there is no agreement on whether they constitute a section (Raninoidea) alongside section Eubrachyura, or a subsection (Raninoidea) of section Podotremata, within the Infraorder Brachyura (Ahyong et al. 2007; Guinot et al. 2008; De Grave et al. 2009; Schweitzer et al. 2010; Karasawa et al. 2011; Ahyong et al. 2011; Van Bakel et al. 2012a). This is a non-trivial issue, since each rank underlies alternative hypotheses regarding the monophyly or paraphyly of Podotremata Guinot, 1977, and therefore the evolutionary relationships among the main brachyuran lineages (Tavares 2003; Ahyong et al. 2007; De Grave et al. 2009; Karasawa et al. 2011). Since both suprafamilial ranks convey the same taxa, either taxon would contain all the descendants from the most recent common ancestor for all frog crabs and allies. Although raninoidans families tend to be distinctive from each other, their phylogenetic relationships at the generic level remain unexplored (Karasawa et al. 2014).

Conclusions

Based on comparative anatomy and phylogenetic analyses, Araripecarcinus is included within Raninoidea, a higher clade of brachyuran crabs that embraces the same terminals included under the taxonomic ranks Raninoida and/or Raniniformes. Araripecarcinus, recovered as sister taxon to the clade uniting Camarocarcinidae, Palaeocorystidae and Raninoidea, supports the hypothesis that the plesiomorphic condition for raninoidans is to have broad rather than elongate carapaces. However, due its large number of unknown character states, its suprafamilial and familial placement are still uncertain, and based solely on the observed ventral traits, it is likely that Araripecarcinus was actually closer to the necrocarcinid-like stock than to Palaeocorystidae. The evolution of Cretaceous brachyurans is complex, with many body plans restricted to this timeframe. Araripecarcinus might well belong to an ancient, early-branching lineage of Aptian–Albian stem-raninoidans endemic to northern South America.

The clade containing the necrocarcinid-like taxa include some of the oldest raninoidans known to date (Hauterivian to late Aptian, ~132 to ~115 Ma), providing further evidence that a more ‘crab-like’ body plan was the ancestral condition for Raninoidea and raninoidan-like taxa. The key innovation of elongated carapaces, as seen in Palaeocorystidae, appears in the fossil record not long after some ancient necrocarcinid-like taxa (late Aptian, ~115 Ma), followed by the oldest raninoids (mid Albian, ~108 Ma), and should have been present in the most recent common ancestor for Palaeocorystidae and Raninoidea. Under this scenario, the earliest palaeocorystids must have derived from a necrocarcinoid-like ancestor, but once they occupied a new morphospace, they marked the evolutionary beginning of Raninoidea. Such transition from ‘crab-like’ to ‘frog-like’ carapaces could be related to their burrowing lifestyle, raising the question if all raninoidans were burrowers, or if some ancient necrocarcinoid lineages were mostly epibenthic.

Phylogenetic analyses at the generic level are needed in order to evaluate the position of Palaeocorystidae with respect to Necrocarcinidae and allies and Raninoidea, helping to better resolve the raninoidal evolutionary tree of life, and to gain a broader understanding on their relatedness by common ancestry throughout geological time.

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Supplemental data

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