

A new genus and species of raninoidian crab (Decapoda, Brachyura) from the Lower Cretaceous of Colombia, South America

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Key words – Aptian, new taxon, Neotropics, origin, Raninoidia.

A new raninoidian crab, *Bellcarcinus aptiensis* gen. nov., sp. nov., is described from the upper Aptian of Colombia. The new genus displays a combination of traits seen among some ancient species within the Necrocarcinidae and Orithopsidae, obscuring its family placement. This taxon represents the sixth known genus of pre-Albian raninoidians worldwide, and the fourth known from Colombia, in addition to *Joeranina*, *Planocarcinus* and *Colombicarcinus*. *Bellcarcinus* gen. nov., together with other Early Cretaceous finds from Colombia and Brazil, represents early stocks of stem-group frog crabs, which indicate that tropical South America might have played an important role in the early radiation of the group.

Palabras clave – Aptiano, nuevo taxón, Neotrópico, origen, Raninoidia.

Un nuevo cangrejo rana, *Bellcarcinus aptianicus* gen. et sp. nov., es descrito para el Aptiano superior de Colombia. El nuevo género exhibe una combinación de rasgos morfológicos presente en especies tempranas de Necrocarcinidae y Orithopsidae, dificultando su asignación familiar. Este taxón es el sexto género conocido de cangrejos rana a nivel mundial en rocas de edad pre-Aptiana, y el cuarto para Colombia junto con *Joeranina*, *Planocarcinus* y *Colombicarcinus*. *Bellcarcinus* gen. nov., junto con otros hallazgos del Cretácico Temprano de Colombia y Brasil, representan linajes tempranos de raninoidios, e indican que la Sur América tropical jugó un papel importante en la temprana radiación del grupo.

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Introduction

Our understanding of the evolution of raninoidian crabs through time has changed dramatically during the last decades, thanks to the discovery and restudy of several key fossil brachyurans, and the integration of novel approaches and techniques to test their phylogenetic relationships (e.g., Tucker, 1995, 1998; Schweitzer *et al.*, 2003; Guinot *et al.*, 2008, 2013; Karasawa *et al.*, 2011; Luque *et al.*, 2012; Van Bakel *et al.*, 2012; Van Bakel, 2013; Karasawa *et al.*, 2014; Luque, 2014). However, although Late Cretaceous and Cenozoic raninoidians are relatively abundant and well known worldwide, records

from the Lower Cretaceous are rather scarce, obscuring the evolutionary pathway of the earliest lineages. The discovery of *Bellcarcinus aptiensis* gen. nov., sp. nov., from upper Aptian (Paja Formation) near San Gil, Department of Santander (Colombia), increases the number of known pre-Albian genera of raninoidians to six, four of which are first known from Colombia, and three of them endemic, i.e., *Planocarcinus* Luque, Feldmann, Schweitzer, Jaramillo & Cameron, 2012, *Colombicarcinus* Karasawa, Schweitzer, Feldmann & Luque, 2014, and *Bellcarcinus* gen. nov. The new genus was found in association with the holotype of *Joeranina kerri* (Luque *et al.*, 2012), *Colombicarcinus*, and several other decapod remains which are currently under study. The presence of the gastropod *Turritella (Haustator) columbiana* Jaworski, 1938, and the ammonite *Acanthohoplites eleganteante* Etayo-Serna, 1979, stratigraphically below the decapod-rich interval containing *Bellcarcinus* gen. nov., and underlying upper Aptian limestones of the Tablazo Formation, indicates a late Aptian age (Kakabadze *et al.*, 2004; see Luque *et al.*, 2012, p. 406). Note that this late Aptian date cannot be confirmed for the holotype of *Planocarcinus olssoni* (Rathbun, 1937), discovered by A.A. Olsson nearly eight decades ago, and actually considered to be Barremian in age (Rathbun, 1937, p. 27).

The combination of dorsal traits seen in *Bellcarcinus* gen. nov. advocates affiliation with Necrocarcinidae Förster, 1968 or Orithopsidae Schweitzer *et al.*, 2003, the oldest families of raninoidian crabs. Its affinities to the necrocarcinid stock are discussed, as well as its spatio-temporal implications.

Systematic palaeontology

Decapoda Latreille, 1802

Brachyura Latreille, 1802

Raninoidia De Haan, 1839

?Orithopsidae Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003

***Bellcarcinus* gen. nov.**

Type species – *Bellcarcinus aptiensis* n. sp., by monotypy.

Etymology – The generic name honours Thomas Bell (1792-1880), for his vast contributions on fossil raninoidians.

Diagnosis – Carapace subhexagonal, slightly wider than long; maximum width at about mid-length; maximum length at about 80 per cent carapace width, measured from centre of posterior margin to base of rostrum. Fronto-orbital margin broad, about 55 per cent carapace width. Orbits wide, directed forwards, with two short, widely spaced orbital fissures; intra-orbital spine short, broad, truncated. Anterolateral margin with four small, triangular spines, excluding outer-orbital spine; posterolateral margins long, slightly convex, apparently lacking posterolateral spines; posterior margin wide, about 45 per cent carapace width, concave, nearly as wide as fronto-orbital margin. Postrostral slits absent; cervical and branchiocardiac grooves distinct, well developed, reaching anterolateral margins; postcervical groove absent. Dorsal carapace axially bearing row of tubercles; carapace axially keeled; protogastric regions ornamented with tubercles; branchial region with longitudinal ridge, with anterior half slightly concave, and posterior half slightly convex.

Stratigraphic range – Lower Cretaceous (upper Aptian).

Remarks – The carapace shape and proportions of *Bellcarcinus* gen. nov., the possession of anterolateral margins with multiple spines, the orbits with two fissures, the tuberculate anterior carapace, the longitudinal axial row of tubercles, and especially the distinctive branchial ridges, are diagnostic traits of the families Necrocarcinidae, Cenomanocarcinidae Guinot, Vega & Van Bakel, 2008 and Orithopsidae (see Karasawa *et al.*, 2011; Van Bakel *et al.*, 2012). Despite this, different traits vary considerably among the three families, obscuring the suprageneric placement of the new genus. For instance, *Bellcarcinus* gen. nov. shares with the Cenomanocarcinidae and Orithopsidae the presence of a faint transverse ridge over the cardiac region, but lacks (Pl. 1, figs. 1, 2) the conspicuous transverse epibranchial or hepatic ridges seen in the Cenomanocarcinidae (Guinot *et al.*, 2008; Karasawa *et al.*, 2011; Van Bakel *et al.*, 2012). The new genus has the wide horizontal orbits bearing truncated and flattened inner and intra-orbital spines, and the rather wide and open orbital fissures in common with orithopsids, but differs from members of that family in the highly deflected cervical groove (Pl. 1) that is diagnostic of the group (Schweitzer *et al.*, 2003; Van Bakel *et al.*, 2012) Similarly, *Bellcarcinus* gen. nov. shares with the Necrocarcinidae the apparently narrow rostrum and the smoothly deflected cervical groove, but markedly differs from necrocardinids in orbital and fronto-orbital configuration.

At this stage it is not possible to place the new genus at the family level with certainty, and more complete material, including appendicular and ventral remains will be necessary to substantiate or reject this affiliation.

***Bellcarcinus aptiensis* sp. nov.**

Pl. 1.

Diagnosis – As for genus.

Description – Dorsal carapace subhexagonal in outline, wider than long, with maximum width about at mid-length; maximum length at about 80 per cent carapace width, measured from centre of posterior margin to base of rostrum. Fronto-orbital margin broad, about 55 per cent carapace width; rostrum in holotype and paratype broken, but apparently narrow, subtriangular in holotype, extending beyond level of outer-orbital spine, wider at junction with intra-orbital spine, slightly less than 30 per cent fronto-orbital margin, with lateral sides straight and converging antero-mesially; lack of post-rostral slits. Orbits incompletely preserved, apparently wide, each one slightly more than 30 per cent of fronto-orbital margin, straight, directed forwards, bearing two short and widely spaced orbital fissures; intra-orbital spine short, truncated, squarish in appearance, intra-orbital spine short, truncated, nearly twice as broad as inner-orbital spine, rectangular in appearance, outer-orbital spine poorly preserved in holotype or paratype, but apparently short, subtriangular. Anterolateral margin shorter than posterolateral margin, convex, apparently bearing four short, triangular spines similar in size, excluding the outer-orbital spine; posterolateral margin long, slightly convex, apparently lacking posterolateral spines; posterior margin wide, concave, rimmed, about 45 per cent carapace width, nearly as wide as fronto-orbital margin.

Cervical groove distinct, well developed, sinuous, with smooth deflections, slightly interrupted axially, reaching anterolateral margin; postcervical groove absent; branchial grooves present; branchiocardiac groove distinct, well developed, sub-parallel to cervical groove. Epigastric region narrow, delimited laterally by subparallel postrostral grooves; protogastric region slightly inflated, bearing two tubercles, the most axial being roundish and lying posteriorly to the most distal, the most distal being somewhat reniform and lying posterior to intra-orbital spine; hepatic region wide, somewhat depressed, bearing one small tubercle posterior to outer-orbital spine; mesogastric region weakly defined anteriorly, more so posteriorly, bearing one axial tubercle anteriorly; metagastric region delimited laterally by branchial grooves, bearing one small axial tubercle anteriorly, bounded posteriorly by a shallow depression between metagastric and urogastric regions; urogastric region slightly depressed anteriorly, more inflated towards cardiac region, bearing one small axial tubercle; cardiac region well developed, wider anteriorly, laterally in contact with faint transverse ridges, interrupting the branchiocardiac groove, faint transverse ridges extending anterolaterally, connecting with anterior tubercles of branchial ridges, cardiac region bearing one tubercle posteriorly; mesogastric, metagastric, urogastric and cardiac axial tubercles nearly equidistant; intestinal region wide, not bounded by branchiocardiac groove; epibranchial region well developed, bounded by cervical and branchiocardiac grooves, bearing a boss; meso- and metagastric regions bearing two tubercles, connected by a sinuous longitudinal ridge, anterior tubercle in contact with faint transverse ridge, branchial longitudinal ridge slightly concave anteriorly, and slightly convex posteriorly. Cuticle apparently thin, dorsal carapace finely granulated; negative internal mould bearing muscle scars along branchiocardiac groove.

Etymology – The specific epithet refers to its Aptian age.

Material examined – The holotype (IGM p881107) and three paratypes (IGM p881154, IGM p881156 and IGM p881166), deposited in the palaeontological collections of the Colombian Geological Survey, formerly INGEOMINAS (acronym IGM), Bogotá, Colombia.

Measurements – Estimated measurements (in millimetres): holotype IGM p881107: CL=7.9; CW=10.2; FOM=5.7; PM=4.7; paratype IGM p881154: CL=13; CW=16.1; FOM=8.8; paratype IGM p881156: CL=9.1; CW=12; paratype IGM p881166: CL=6.6; CW=8. CL: carapace maximum length measured from posterior margin to base of rostrum; CW: carapace maximum width; FOM: fronto-orbital margin; PM: posterior margin.

Occurrence – Upper part of Paja Formation (upper Aptian), between the village of Curití and the town of San Gil, Cordillera Oriental, Department of Santander, Colombia (co-ordinates: 6.59621, -73.09146; compare Luque *et al.*, 2012).

Discussion – Based on previous and new palaeontological evidence, there is no doubt that the morphological diversity of early raninoidians is higher than previously envisioned (Luque *et al.*, 2012; Karasawa *et al.*, 2014). The earliest necrocarcinids, cenom-

anocarcinids and orithopsids might have had more traits in common with their most recent common ancestors than their later descendants, such as the possession of wider orbits and carapaces lacking posterolateral spines. This seems to be the case for *Bellcarcinus* gen. nov., which resembles both the Necrocarcinidae and Orithopsidae. Its overall dorsal ornament is more closely similar to *Orithopsis tricarinatus* (Bell, 1863) from the Albian of England, *Necrocarcinus woodwardi* Bell, 1863, from the Albian-Cenomanian of England and *N. texensis* Rathbun, 1935, from the Albian-Cenomanian of Texas, USA (see also Bishop & Williams, 1991, fig. 6A; Van Bakel *et al.*, 2012, fig. 22C), while the shape of the orbits and branchial ridges resembles that seen in *Silvacarcinus laurae* Collins & Smith, 1993, from the lower Eocene of Belgium (Van Bakel *et al.*, 2012, fig. 20B, E). Despite its uncertain familial placement, *Bellcarcinus* gen. nov. can be nested with certainty alongside other necrocarcinid-like taxa, including the contemporary *Planocarcinus olssoni* and *P. johnjagti* Bermúdez, Gómez-Cruz and Vega, 2013, from the upper Aptian of Colombia (Bermúdez *et al.*, 2013) and *Necrocarcinus undecimtuberculatus* Takeda & Fujiyama, 1983, from the Aptian of Japan. Together with *Paranecrocarcinus hexagonalis* Van Straelen, 1936, from the Hauterivian of France, these taxa are the oldest known raninoidians (Luque *et al.*, 2012). However, *Orithopsis tricarinatus* has also been suggested to be Aptian in age (Van Bakel *et al.*, 2012), although it might be of early Albian date (C.E. Schweitzer, pers. comm., September 2013). If *Bellcarcinus* gen. nov. turns out to be an orithopsid, it would further confirm the presence of the family during the Aptian, and especially, in the Neotropics.

In addition to *Bellcarcinus* gen. nov. (probably the oldest orithopsid), other early raninoidians also account for the oldest records of their families and lineages, namely *Planocarcinus* (two of the oldest necrocarcinids), *Cenomanocarcinus vanstraeleni* Stenzel, 1945 (apparently the oldest cenomanocarcinid) from the lower Albian of Colombia (Vega *et al.*, 2010), *Joeranina kerri* (Luque *et al.*, 2012) (the oldest palaeocorystid) and *Araripecarcinus ferreirai* Martins Neto, 1987 (an ancient lineage of necrocarcinid-like crabs) from the lower Albian of Brazil (Luque, 2014). Together, these occurrences indicate that many clades of brachyuran crabs previously considered to have originated at higher latitudes might have had their origins in the tropical South America, and that the equatorial Neotropics might have played an important role in the early radiation of the group.

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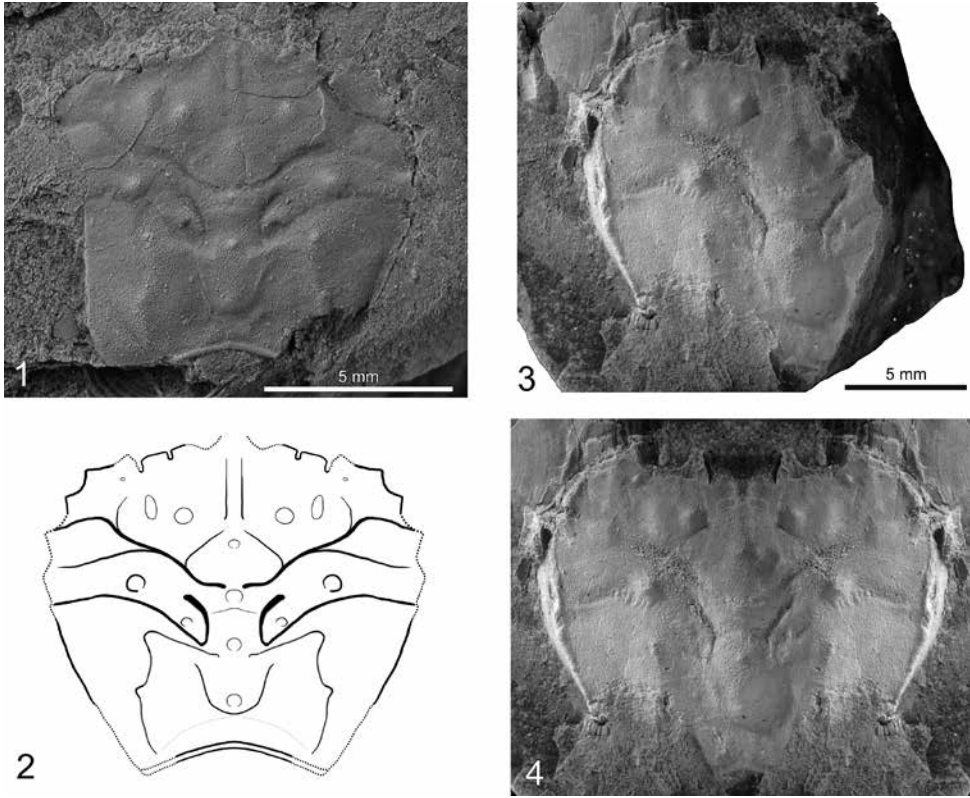


Plate 1

Bellcarcinus aptiensis gen. nov., sp. nov.

Fig. 1. Holotype (IGM p881107), dorsal carapace.

Fig. 2. Reconstruction of holotype (IGM p881107).

Fig. 3. Paratype (IGM p881154), left-hand side of dorsal carapace.

Fig. 4. Composite mirror image of left-hand side of dorsal carapace of paratype IGM p881154.