

## THE OLDEST FROG CRABS (DECAPODA: BRACHYURA: RANINOIDA) FROM THE APTIAN OF NORTHERN SOUTH AMERICA

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### ABSTRACT

Raninoidea, also known as “frog crabs,” is a clade of extant true crabs (Brachyura) characterized by a fusiform carapace (raninid-type), narrow thoracic sternum, pleon partially exposed dorsally, and paddle-like limbs, all of which are well suited to their cryptic burrowing lifestyle. However, the most basal raninoids from the Cretaceous were morphologically different, with ornamented carapaces that were wider than long (necrocarcinid-type), a broader thoracic sternum, and the pleon fitting between the legs assisted by pleonal locking mechanisms. During Albian times (~112 to 99.6 Ma.) both body plans flourished worldwide. In contrast, pre-Albian (older than ~112 Ma.) fusiform families have not yet been reported. The discovery of *Notopocorystes kerri* n. sp., a fusiform crab from the upper Aptian (~115 Ma.) of Colombia, South America, and the re-examination of *Planocarcinus olssoni* (Rathbun, 1937) n. comb., a necrocarcinid-like crab from the same age and locality, extend the record of the two body plans back into the Aptian of the equatorial Neotropics. *Notopocorystes kerri* is the oldest fusiform raninoid known to date, revealing that the morphological innovation of a fusiform carapace was already evolved in Raninoidea before the rapid radiation experienced during Albian times. Our findings are suggestive of a still unresolved Palaeocorystidae, containing the rootstock for the post-Aptian Raninidae/Symethidae clade, with the most basal palaeocorystids lying in proximity to, and possibly derived from, a necrocarcinid-like ancestor.

**KEY WORDS:** Albian, Aptian, body plan, Brachyura, Cretaceous, Neotropics, raninoid crabs

DOI: 10.1163/193724012X626539

### INTRODUCTION

The monophyletic Raninoidea constitute one of the five major clades of extant true crabs within the Infraorder Brachyura Linnaeus, 1758 (Karasawa et al., 2011). They are a group of marine crabs adapted for inhabiting soft and sandy bottoms across a wide bathymetric range, and are distributed throughout the tropical to low-latitude temperate regions of the world. Superfamily Raninoidea De Haan, 1839, is comprised of six families ranging in age from the Early Cretaceous to the present. Only two families, Raninidae De Haan, 1839 and Symethidae Goeke, 1981, have living representatives. Palaeocorystidae Lörenthey (in Lörenthey and Beurlen, 1929), is the only family restricted to the Cretaceous, and shares with raninids and symethids the characteristic ‘frog-like’ body plan, with an elongated, fusiform carapace and the lack of pleonal locking mechanisms (Karasawa et al., 2011). In contrast, Camarocarcinidae Feldmann, Li, and Schweitzer, 2007; Cenomanocarcinidae Guinot, Vega, and Van Bakel, 2008; and Necrocarcinidae Förster, 1968, known from the Cretaceous and Paleogene, possess a very different body plan with rounded to wide hexagonally shaped carapaces, usually very ornamented dorsally and laterally, and most having pleonal locking mechanisms. Despite this strong difference in cara-

pace configuration, the similarities seen among some palaeocorystids, cenomanocarcinids, and necrocarcinids are remarkable: the possession of a dorsal longitudinal ridge, the well-differentiated anterolateral margins bearing multiple spines, the distinct cervical groove, the bifid rostrum, and the very similar configuration of the sternal plates. These similarities have led to the formulation of three phylogenetic hypotheses of the palaeocorystids: 1) Palaeocorystidae closer to the ‘necrocarcinid-like’ stock due to their shared dorsal and ventral features (Guinot et al., 2008, in Karasawa et al., 2011, p. 533) (Fig. 1A), 2) Palaeocorystidae allied with the ‘raninid-like’ families based on the shape of the carapace and the lack of pleonal locking mechanisms (Karasawa et al., 2011) (Fig. 1B), or 3) an unresolved polytomy within Palaeocorystidae, whereby the common ancestor of Raninidae/Symethidae might lie within Palaeocorystidae ‘pro parte,’ but the most basal palaeocorystids (*Notopocorystes* McCoy, 1849) lying in proximity to, and possibly derived from, the clade of Cenomanocarcinidae/Necrocarcinidae (Glaessner, 1960; Förster, 1970; Guinot et al., 2008) (Fig. 1C).

During the Albian (~112-99.6 Ma.), the two major raninoid morphological groups diversified and spread worldwide, with representatives of four families, ten genera,

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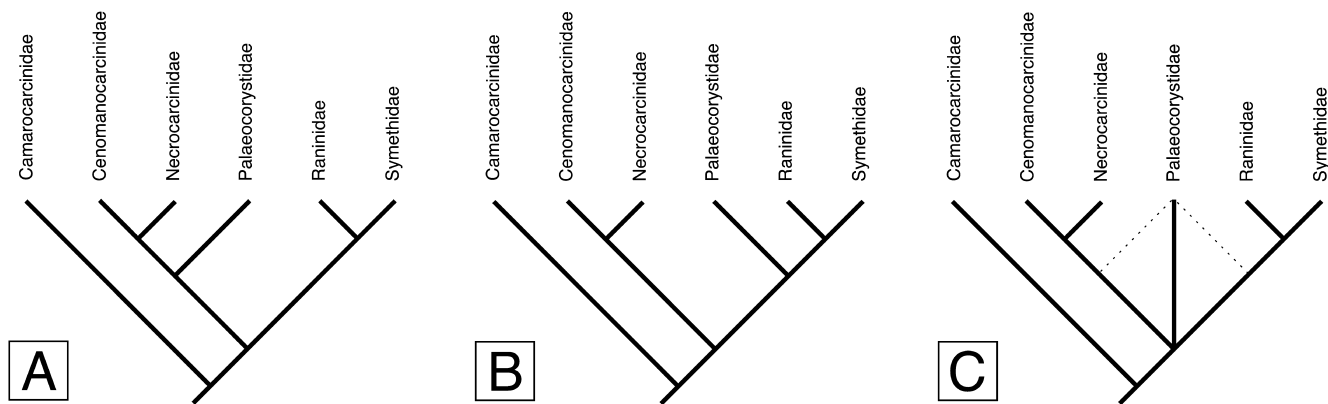


Fig. 1. Schematic cladistic trees for the Section Raninoidea, showing the different hypotheses regarding the affiliation of the family Palaeocorystidae. A, Palaeocorystidae allied to the Cenomanocarcinidae/Necrocarcinidae clade; B, Palaeocorystidae allied to the Raninidae/Symethidae clade; C, Palaeocorystidae in an unresolved polytomy between the Cenomanocarcinidae/Necrocarcinidae and the Raninidae/Symethidae clades. Base tree topology for the Raninoidea clade after Karasawa et al. (2011: fig. 3).

and 31 species known from North America, northern Central America, northern South America, Europe, the Middle East, China, Japan, New Zealand, and Madagascar (Table 1). Although Early Cretaceous raninoids are well known from high latitudes, records from low latitudes are scarcely known, precluding a global understanding of its biogeographic distribution prior to their Albian diversification. Here we re-examine the type material of *Dakoticancer olssoni* Rathbun, 1937, from the upper Aptian (~115 Ma.) Paja Formation of Colombia, northern South America, and describe *Notopocorystes kerri* n. sp. from the same unit and age, extending considerably the geological and paleobiogeographic ranges of the two raninoid body plans into the Aptian of the Neotropics. Based on the new information, we address different hypotheses for the systematic placement of the oldest members of Palaeocorystidae, and discuss their plausible relationships with the ancient necrocarcinid-type taxa and the more derived raninoid-like clade.

#### LOCALITY AND STRATIGRAPHY

The specimens of *Planocarcinus olssoni* n. comb. and *Notopocorystes kerri* n. sp. were discovered in Lower Cretaceous rocks of the Aptian Paja Formation, cropping out between the town of San Gil and the village of Curití, Department of Santander, Cordillera Oriental, Colombia, about 60 km south of the city of Bucaramanga, and approximately 125 km northeast of the city of Tunja (Fig. 2A). The Paja Formation was originally named by Wheeler (in Morales et al., 1958) to describe the packages of gray fossiliferous shales, with intercalations of yellow-grayish fine-grained sandstones, gray fossiliferous limestones, and calcareous concretions exposed along La Paja Creek between Bucaramanga and San Vicente de Chucurí, and overlain by the gray fossiliferous limestones and gray shales of the upper Aptian-lower Albian Tablazo Formation (Julivert, 1968; Etayo-Serna, 1979; Pulido, 1979, 1995; Royero and Clavijo, 2001; Vega et al., 2010). In the area of study, the Paja Formation is largely covered by vegetation and agricultural crops, with poor and patchy exposure of rocks.

The holotype of *Notopocorystes kerri* was recovered from shales of the upper portion of the Paja Formation along the

San Gil/Bucaramanga main road, highway 45A, approximately 300 meters southwest of the junction with the road leading to Curití (Latitude 6.59621, Longitude -73.09146) (Fig. 2B), in association with abundant bivalves and gastropods of small size (~4 mm to 50 mm) such as *Corbula* sp., *Astarte* sp., *Crassatella aequalis* Gerhardt, 1897, *Chenopus (Tessarolax) bicarinata* var. *evolutior* Jaworski, 1938, *Liopista (Psilomya) gigantea* (Sowerby, 1818) in Woods, 1909, and *Clementia ricordeana* Orbigny, 1845, in Woods, 1909 (Etayo-Serna, personal communication, 2011). The gastropod *Turritella (Haustator) columbiana* Jaworski, 1938, and the ammonite *Acanthohoplites elegantante* Etayo-Serna, 1979, were recovered stratigraphically below the level bearing decapod remains, and indicate an upper Aptian age in Colombia (Etayo, 1979; Kakabadze et al., 2004; Cortés et al., 2006; Etayo-Serna, personal communication, 2011). In the case of *P. olssoni*, the exact stratigraphic position is not certain, since the only historical mention of its geographic provenance is "...near junction of branch road leading to the village of Curití, Eastern Cordillera, from the main auto road from San Gil to Bucaramanga" (Rathbun, 1937: p. 27) (Vega et al., 2010). Nevertheless, the only rock outcroppings near this junction are middle to upper Aptian shales of the upper Paja Formation, and upper Aptian limestones of the lower Tablazo Formation (Fig. 2B), suggesting a middle to late Aptian age for *P. olssoni*.

#### SYSTEMATICS

Illustrated specimens are deposited in the collection of INGEOMINAS, Museo Geológico José Royo y Gómez, Bogotá DC, Colombia, under the acronym IGM; the National Museum of Natural History, Smithsonian Institution, Washington, D.C., United States, under the acronym USNM; Natural History Museum, London, England, under the acronym BMNH; National Museum of Nature and Science, Tokyo, Japan (formerly National Science Museum, Tokyo), under the acronym NSM-PA; and Sedgwick Museum, Cambridge University, UK, under the acronym SM.

Table 1. Updated list of Early Cretaceous families, genera and species within the Section Raninoidea Ahyong et al., 2007 (modified after Schweitzer et al., 2010; Karasawa et al., 2011). Taxa arranged alphabetically. Ber: Berriasian (~145 to 140 My.); Val: Valanginian (~140 to 136 My.); Hau: Hauterivian (~136 to 130 My.); Bar: Barremian (~130 to 125 My.); Apt: Aptian (~125 to 112 My.); Alb: Albian (~112 to 99.6 My.). X: taxon stratigraphic range known for the Early Cretaceous. X?: taxon stratigraphic range uncertain.

Family	Genus	Species	Locality	Ber	Val	Hau	Bar	Apt	Alb		
Cenomanocarcinidae	<i>Cenomanocarcinus</i> Guinot, Vega, and Van Bakel, 2008	<i>C. armatus</i> (Rathbun, 1935)	Texas, USA						X		
		<i>C. oklahomensis</i> (Rathbun, 1935)	Oklahoma, USA						X		
		<i>C. renfroae</i> (Stenzel, 1945)	Texas, USA; Colombia						X		
		<i>C. vanstraeleni</i> Stenzel, 1945	Texas and New Mexico, USA; Mexico; Colombia						X		
Necrocarcinidae Förster, 1968	<i>Araripecarcinus</i> Martins-Neto, 1987	<i>A. ferreirai</i> Martins-Neto, 1987	Brazil						X		
		<i>Necrocarcinus</i> Bell, 1863	<i>N. bedrakensis</i> Levitski, 1974 <i>N. labeschei</i> (Eudes-Deslongchamps, 1835) <i>N. tauricus</i> Ilyin and Alekseev, 1998 <i>N. texensis</i> Rathbun, 1935 <i>N. undecimtuberculatus</i> Takeda and Fujiyama, 1983 <i>N. woodwardi</i> Bell, 1863	Crimea Great Britain; France Crimea Texas, USA Japan					X X X X		
	<i>Paranecrocarcinus</i> Van Straelen, 1936a	<i>P. graysonensis</i> (Rathbun, 1935)	Texas, USA							X	
		<i>P. hexagonalis</i> Van Straelen, 1936	France		X?	X?	X?			X	
		<i>P. kennedyi</i> Wright, 1997	South Africa					X			
		<i>P. moseleyi</i> (Stenzel, 1945)	Texas, USA							X	
	<i>Planocarcinus</i> n. gen. <i>Pseudonecrocarcinus</i> Förster, 1968	<i>P. olssoni</i> (Rathbun, 1937)	Colombia						X		
		<i>P. scotti</i> (Stenzel, 1945)	Texas, USA							X	
		<i>P. stenzeli</i> Bishop, 1983	Texas, USA							X	
	Palaeocorystidae Lőrenthey, in Lőrenthey and Beurlen, 1929	<i>Cretacorantina</i> Mertin, 1941	<i>C. punctata</i> (Rathbun, 1935a)	Texas, USA						X	
			<i>Eucorystes</i> Bell, 1863	<i>E. broderipii</i> (Mantell, 1844) <i>E. carteri</i> (McCoy, 1854) <i>E. mangyshlakensis</i> Ilyin and Pistshikova in Ilyin, 2005 <i>E. oxtedensis</i> Wright and Collins, 1972 <i>E. platys</i> Schweitzer and Feldmann, 2001	England; France; Swiss Jura England Kazakhstan England Oregon, USA; British Columbia, Canada					X X X X X	
		<i>Notopocorystes</i> McCoy, 1849	<i>N. bituberculatus</i> Secretan, 1964	Madagascar							X
			<i>N. kerri</i> n. sp.	Colombia						X	
<i>N. parvus</i> Rathbun, 1935a			Texas, USA							X	
<i>N. stokesii</i> (Mantell, 1844)			England							X	
<i>N. xizangensis</i> Wang, 1981			Lhasa, China; Iran							X	
Raninidae De Haan, 1839 [in De Haan, 1833-1850]		<i>Hemioon</i> Bell, 1863	<i>H. cunningtoni</i> Bell, 1863	England						X	
			<i>H. elongatum</i> (A. Milne- Edwards, 1862)	England; France; Czech; Germany; UK						X	
			<i>H. novozelandicum</i> Glaessner, 1980	New Zealand						X	
	<i>H. yanini</i> Ilyin and Alekseev, 1997		Crimea						X		
	<i>Raninella</i> A. Milne- Edwards, 1862	<i>R. armata</i> Rathbun, 1935	Texas, USA							X	
		<i>R. atava</i> Carter, 1898	England							X	
		<i>R. mucronata</i> Rathbun, 1935	Texas, USA						X		

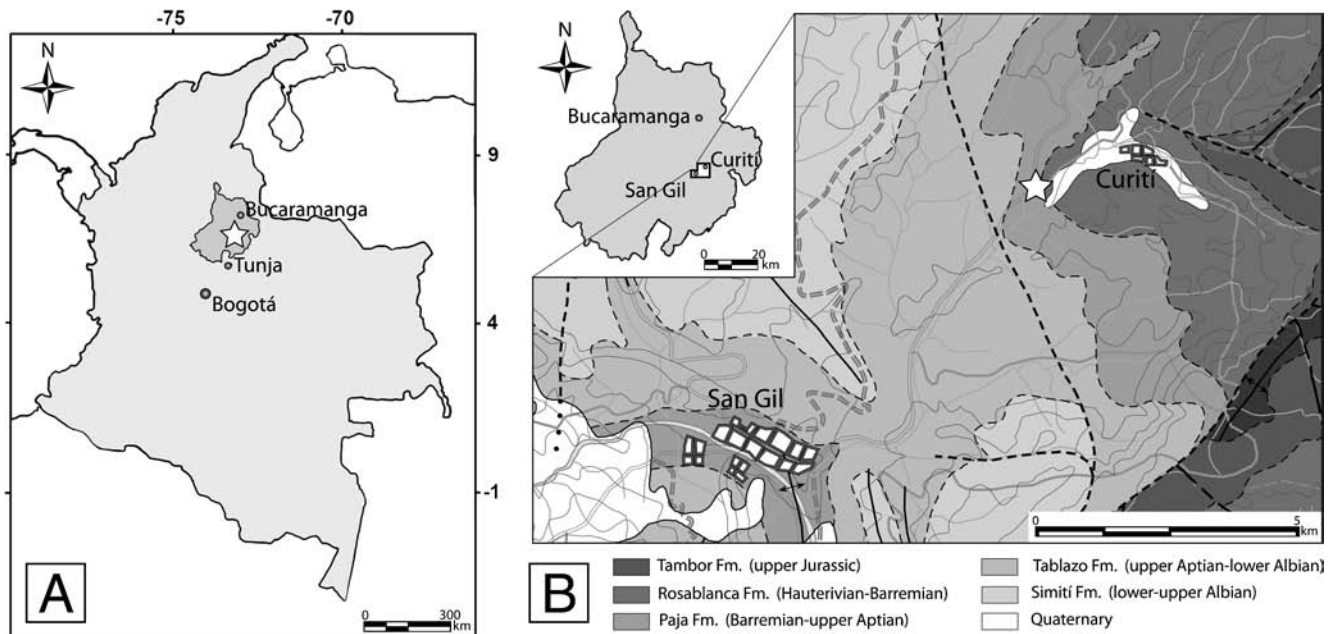


Fig. 2. Locality maps. A, Generalized map of Colombia, South America, showing the location of the study area (white star) in the Department of Santander, Cordillera Oriental, where *Planocarcinus olssoni* n. comb., and *Notopocorystes kerri* n. sp. were recovered; B, Geological map of the study area between San Gil and Curití, Department of Santander, Cordillera Oriental, Colombia, where *P. olssoni* and *N. kerri* were found (white star). Base map modified from INGEOMINAS Plancha 135 San Gil (after Pulido, 1985).

Order Decapoda Latreille, 1802  
 Infraorder Brachyura Linnaeus, 1758  
 Section Raninoidea De Haan, 1839  
 [in De Haan, 1833-1850]  
 Raninoidea De Haan, 1839  
 [in De Haan, 1833-1850]  
 Necrocarcinidae Förster, 1968  
*Planocarcinus* n. gen.

Type Species.—*Dakoticancer olssoni* Rathbun, 1937, by monotypy.

Diagnosis.—Carapace subcircular in outline, slightly wider than long, with distinct cervical, postcervical, and branchio-cardiac grooves; fronto-orbital margin as long as posterior margin; rostrum bilobate, spatulate, wider than long; orbits somewhat narrow, upturned, bearing two short orbital fissures; anterolateral margin concave, bearing at least five spines; posterolateral margin convex, lacking spines; posterior margin straight; hepatic region depressed; metabranchial region swollen, lacking nodules or ridges.

Etymology.—The generic name is derived from the Latin word 'planus' (plane, flat), given its dorso-ventrally flattened carapace, and the Greek word 'karkinos' (crab).

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.

Remarks.—The specimen named by Rathbun (1937) as *Dakoticancer olssoni*, is herein ascribed to *Planocarcinus* n. gen., as it strongly contrasts from any known dakoticancroid crab in the general configuration of the rostrum and orbits, the carapace regions and dorsal grooves, the protogastric tubercles anterior to the cervical groove, and the presence

of anterolateral spines (Weller, 1905, 1907; Rathbun, 1917, 1935; Kesling and Reimann, 1957; Glaessner, 1969; Bishop, 1972, 1974, 1983b, 1986, 1988; Vega and Feldmann, 1991; Vega et al., 1995; Bishop et al., 1998; Artal et al., 2008; Karasawa et al., 2011) (Fig. 3A-C). Any affinity with the dakoticancroids, contrary to Rathbun (1937), is ruled out.

Assignment of *Planocarcinus* to Necrocarcinidae is supported by exhibiting a carapace that is about as long as wide, with regions and grooves well defined, bearing tubercles on the protogastric region, the rostrum relatively narrow, sulcate, bilobate, and with small orbits (Schweitzer and Feldmann, 2000; Schweitzer et al., 2003; Karasawa et al., 2011). *Planocarcinus* shares with *Necrocarcinus* Bell, 1863, and its type species *Necrocarcinus labeschei* (Eudes-Deslongchamps, 1835) (Fig. 3D), the generally circular carapace nearly as wide as long, bearing complete and somewhat parallel cervical and branchio-cardiac grooves, the relatively small, round, and upturned orbits directed forward, provided with two orbital fissures and small orbital spines (Bell, 1858; Carter, 1898; Förster, 1968; Wright and Collins, 1972; Schweitzer et al., 2003). Such similarities suggest affinity to *Necrocarcinus*, as previously noticed by Feldmann et al. (1999). However, *Planocarcinus* strongly differs from *Necrocarcinus* in the flattened and smooth dorsal carapace, devoid of well-developed axial and metabranchial rows of tubercles or ridges, the shape, size, and width of the spinose and spatulate rostrum, and the straight posterior margin. *Planocarcinus* also differs from necrocarcinid genera as *Corazzatocarcinus* Larghi, 2004, *Shazella* Collins and Williams, 2004, *Polycnemidium* Reuss, 1845, and most *Paranecrocarcinus* Van Straelen, 1936, and *Pseudonecrocarcinus* Förster, 1968, in the roundish, convex nature of the anterolateral and posterolateral margins rather than con-

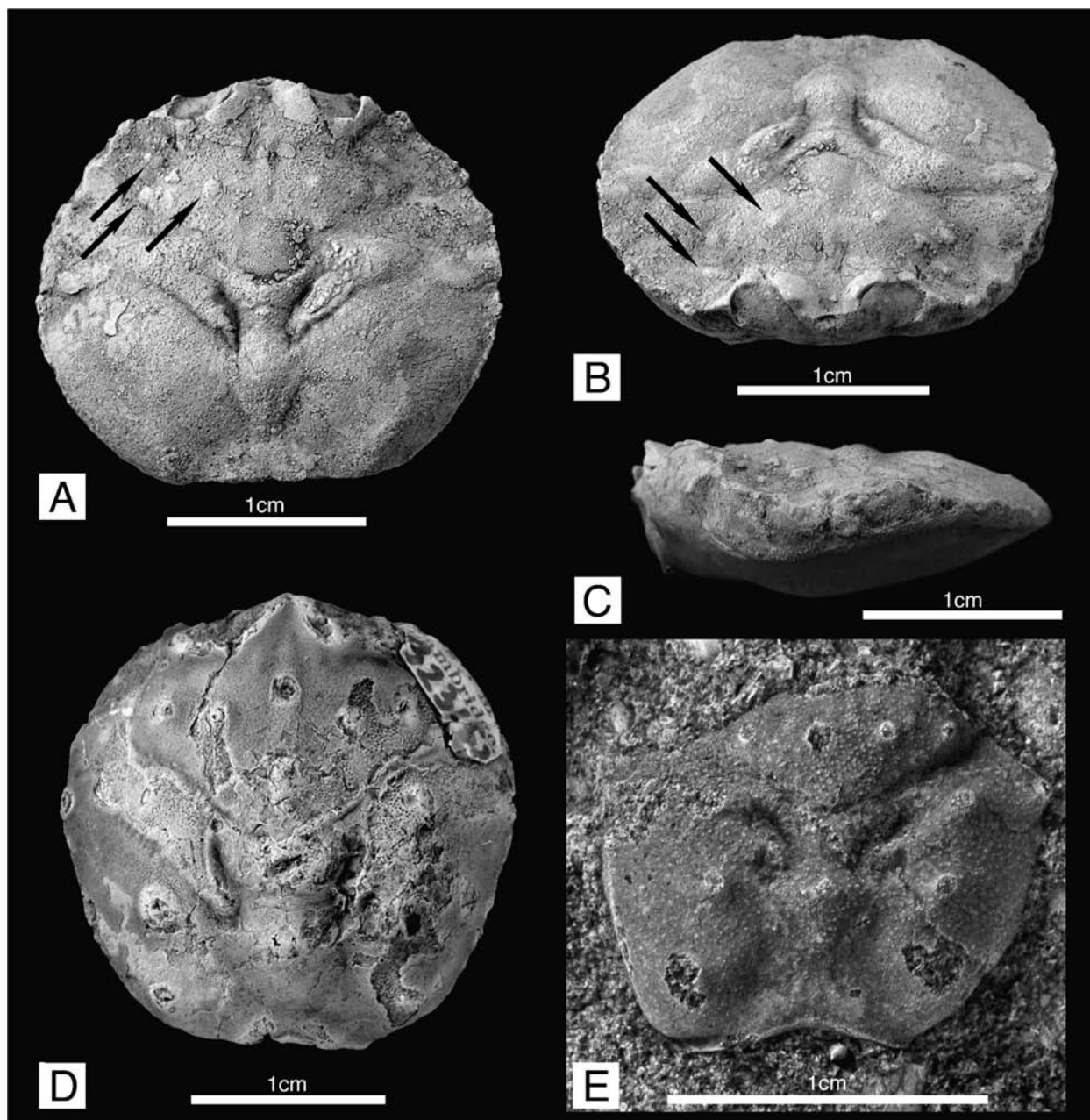


Fig. 3. Raninoidea, Necrocarcinidae. A-C, *Planocarcinus olssoni* (Rathbun, 1937) n. comb., holotype USNM 495104, upper Aptian, Colombia. A, Carapace in dorsal view, showing the general roundish outline and dorsal carapace regions. Arrows indicate the three small tubercles on protogastric region; B, Frontal view, showing the orbitofrontal margin, and depressed intestinal region. Arrows indicate the three small tubercles on protogastric region; C, Lateral view. Specimen coated with ammonium chloride; D, *Necrocarcinus labeschei* (Eudes-Deslongchamps, 1835), hypotype SM B 23152, dorsal carapace, lower Albian, England; E, *Necrocarcinus undecimtuberculatus* Takeda and Fujiyama, 1983, holotype NSM-PA 12223, dorsal posterior carapace, upper Aptian, Japan.

cave or nearly straight, the dorsal carapace depleted of ridges or rows of tubercles, the lack of pustulose ornamentation, and the carapace flattened dorso-ventrally (Fritsch and Kafka, 1887; Van Straelen, 1936; Stenzel, 1945; Roberts, 1962; Wright and Collins, 1972; Bishop, 1983a; Collins and Williams, 2004; Larghi, 2004; Collins, 2010; Jagt et al., 2010; Breton and Collins, 2011). *Planocarcinus* also can be differentiated from *Cristella* Collins and Rasmussen, 1992, based on the subhexagonal outline, the rostrum narrow and

pointed, and the strongly produced epibranchial spine that characterize the latter.

Vega et al. (2010) synonymized *Necrocarcinus olssoni* with *Orithopsis tricarinata* Bell, 1863, but the distinctive metabranchial longitudinal ridges, the wider than long hexagonal carapace (Schweitzer et al., 2003; Števíć, 2005), with 'concave' anterolateral and straight posterolateral margins (Vega et al., 2010), and the long, distinctive rostral and orbital spines (Schweitzer and Feldmann, 2000; Guinot et

al., 2008) present in the monotypic Orithopsidae are not seen in the sole specimen of *P. olssoni*, precluding kinship with this family at this point. The systematic position of Orithopsidae is still unresolved, and has been traditionally associated with either the eubranchyuran Superfamily Dorippoidea MacLeay, 1838 (Glaessner, 1969; Schweitzer et al., 2003, 2010; De Grave et al., 2009); or the podotreme Superfamily Raninoidea, particularly Necrocarcinidae and Cenomanocarcinidae stocks (Schweitzer and Feldmann, 2000; Schweitzer et al., 2003; Guinot et al., 2008; Vega et al., 2010). Despite this, the well-preserved sterna referred to '*Orithopsis tricarinata*' by Guinot et al. (2008), from the upper Albian Greensand of England, and Vega et al. (2010), from the upper Albian Hudspeth Formation of Oregon, USA, are certainly reminiscent of the sterna seen in some camarocarcinids, cenomanocarcinids and necrocarcinids, advocating for a raninoid affinity.

*Planocarcinus olssoni* (Rathbun, 1937) n. comb.

Fig. 3A-C

*Dakoticancer olssoni* Rathbun, 1937: p. 26, pl. 5, fig. 6.

*Necrocarcinus olssoni* (Rathbun, 1937); Feldmann, Villamil, and Kauffman, 1999: p. 91.

*Necrocarcinus olssoni* (Rathbun, 1937); Schweitzer, Feldmann, Garassino, and Schweigert, 2010: p. 81.

*Necrocarcinus? olssoni* (Rathbun, 1937); Schweitzer, Feldmann, González-Barba, and Vega, 2002: p. 37.

*Necrocarcinus? olssoni* (Rathbun, 1937); Guinot and Breton, 2006: p. 615.

*Orithopsis tricarinata* (Bell, 1863); Vega, Nyborg, Kovalchuck, Etayo-Serna, Luque, Rojas-Briceño, Patarroyo, Porrás-Múzquiz, Armstrong, Bermúdez, and Garibay, 2010: p. 275, fig. 8.23.

Emended Diagnosis.—As for genus.

Emended Description.—Carapace small, subcircular in outline, slightly wider than long, with maximum length about four-fifths maximum width, measured approximately at midlength. Cervical groove distinct, complete, more pronounced axially, and less distinct laterally, concave posterior to mesobranchial region, and gently convex posterior to protogastric region until reaching lateral margin. Postcervical groove well developed, deep, posteriorly in contact with branchiocardiac groove, and diverging anteriorly, flanking the metagastric and urogastric regions. Branchiocardiac groove well developed, deeper mesially, and shallowing toward lateral margin, subparallel to cervical groove, flanking the cardiac and branchial regions. Fronto-orbital margin as long as posterior margin, about two-fifths maximum carapace width. Rostrum well developed, bilobate spatulate, wider than long, less than one-fifth carapace width, sulcate axially, distally downturned, tip broken, rostrum sides diverging posteriorly and forming the inner margin of the orbit, bearing one upraised and anteriorly directed spine. Orbits somewhat narrow, upturned, each orbit about one-fourth carapace maximum width, concave, roundish, bearing two very small, narrow orbital fissures; orbital fissure about the same length; outer orbital spine single, small, well produced, subtriangular, shorter than rostrum, with outer margins nearly straight, converging anteriorly; lower orbital margin visible in dorsal view. Anterolateral margin smoothly convex, approximately as long as posterolateral

margin, about half the carapace maximum length, bearing five eroded spines, excluding outer orbital spine. Anterior-most spine small, subtriangular in shape, directed anteriorly. Posterolateral margin smoothly convex, as long as nearly half carapace length, lacking spines. Posterior margin nearly as long as fronto-orbital margin, two-fifths carapace width, straight, horizontal.

Regions defined by grooves; protogastric region slightly inflated, bearing three small, very short, round nodules behind the orbital rim (Fig. 3A, C, arrows); the two posterior tubercles positioned anterior of cervical groove, approximately at mid position of protogastric region, the most distal tubercle positioned near boundary between protogastric and hepatic regions; the most anterior tubercle smaller than the other two, positioned behind outer orbital spine. Mesogastric region narrow, weakly defined anteriorly and swollen, well defined posteriorly, lacking tubercles or spines. Metagastric region V-shaped, swollen, bounded anteriorly by cervical groove, and laterally by postcervical groove. Urogastric region short, narrow, depressed, delimited laterally by postcervical groove. Cardiac region narrow, elongated, lacking tubercles or spines, wider anteriorly, delimited laterally and posteriorly by deep branchiocardiac groove. Intestinal region narrow, very depressed, lacking tubercles or spines. Hepatic regions depressed. Epibranchial region very inflated proximally, and subtly laterally, bounded by cervical and postcervical grooves, bearing a boss. Mesobranchial and metabranchial regions undifferentiated, bearing a faint, oblique ridge lacking nodules or tubercles.

Material Examined.—The holotype and sole specimen USNM 495104, deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C., United States.

Measurements.—Carapace maximum length: 20.5 mm; width, 24.0 mm; frontal-orbital margin: 9.8 mm.

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.

Remarks.—Among Necrocarcinidae, *Planocarcinus* appears closer to *Necrocarcinus* than to any of the other genera. The configuration of the protogastric tubercles, with a small node anterior to the other tubercles and posterior to the orbital region, near the protogastric/hepatic boundary (Fig. 3A-B), is also visible on other necrocarcinid species such as *Necrocarcinus labeschei*, *N. pierrensis* Rathbun, 1917, *N. davisi* Bishop, 1985, and *N. rathbunae* Roberts, 1962 (Rathbun, 1917; Förster, 1970; Bishop, 1985; Bishop and Williams, 1991; Guinot et al., 2008). *Necrocarcinus undecimtuberculatus* (Fig. 3E), from the upper Aptian of Japan (Takeda and Fujiyama, 1983; Fraaye, 1994; Schweitzer et al., 2003; Guinot et al., 2008), also suggested as possibly related to the genus *Paranecrocarcinus* Van Straelen, 1936 (Takeda and Fujiyama, 1983; Guinot et al., 2008), differs from *P. olssoni* n. comb. in the concave posterior margin, the less convex posterolateral margin, the branchial regions bearing three longitudinally spaced tubercles, and the developed eleven tubercles (Takeda and Fujiyama, 1983).

*Planocarcinus olssoni*, together with *Necrocarcinus inornatus* Breton and Collins, 2011, from the lower Cenoma-

nian of France, and *Paranecrocarcinus libanoticus* Förster, 1968, from the Cenomanian of Lebanon and France (Breton and Collins, 2011), are the least ornamented necrocarcinids. *Planocarcinus olssoni* differs from both taxa in lacking a vaulted carapace bearing faint dorsal grooves, the absence of well-developed protuberances along the axial ridge, the narrower metagastric and urogastric regions, and the posterolateral margin deprived of granules.

The specimens illustrated in Vega et al. (2010: fig. 8.18-20) as '*Orithopsis tricarinata*' differ from *P. olssoni* on the sub-hexagonal nature of the carapace, with straight to slightly concave posterolateral margins, the narrow and relatively long bifid rostrum with sub-parallel lateral margins, the orbits wider than the rostrum, and the broader metagastric, urogastric, and cardiac regions. One dorsal specimen (Vega et al., 2010: fig. 8.22) appears neither to be conspecific with *O. tricarinata*, nor congeneric with *Orithopsis*. Based solely on the preserved right carapace, a resemblance to *Planocarcinus* appears more plausible given the convex nature of the posterolateral margin and the nearly straight posterior margin. Unfortunately, the anterior half of the carapace and the fronto-orbital margin are eroded, precluding an accurate comparison with *P. olssoni*. Under the hypothetical scenario of a taxonomic relationship with *Planocarcinus*, the spatial and temporal range of the genus would be marked by its first appearance in the upper Aptian of Colombia, and its last appearance in the late Albian of Oregon.

Palaeocorystidae Lőrenthey,  
in Lőrenthey and Beurlen, 1929  
*Notopocorystes* McCoy, 1849

*Notopocorystes* McCoy, 1849: p. 169.

*Palaeocorystes* Bell, 1863: p. 11, pl. II, figs. 8-13.

Type Species.—*Palaeocorystes stokesii* Mantell, 1844, by original designation.

Included Species.—*Notopocorystes australis* Secretan, 1964; *N. bituberculatus* Secretan, 1964; *N. callianassarum* (Fritsch and Kafka, 1887); *N. denisae* Secretan, 1964; *N. exiguus* Glaessner, 1980; *N. fritschi* Glaessner, 1929; *N. japonicus* (Jimbó, 1894); *N. normani* (Bell, 1863); *N. parvus* Rathbun, 1935; *N. ripleysensis* Rathbun, 1935; *N. stokesii* (Mantell, 1844) (type); *N. xizangensis* Wang, 1981; *N. kerri* n. sp.

Geologic Range.—Early Cretaceous (late Aptian) to Late Cretaceous (Campanian?).

*Notopocorystes kerri* n. sp.  
Fig. 4A-B

Diagnosis.—Carapace small, moderately elongate, ovate, wider at anterior third; dorsal carapace finely granulated; cervical groove complete, well developed; mesial longitudinal ridge present, not ornamented, narrow and shallow; two small and rounded tubercles on protogastric region; fronto-orbital region wide, slightly more than two-thirds carapace maximum width, two shallow orbital fissures; anterolateral margin bearing three short, weakly pronounced spines; posterior margin as wide as half carapace greatest width, and about two-thirds the fronto-orbital region.

Description.—Carapace small, elongate, ovate in outline, moderately vaulted transversely, less so longitudinally, with

maximum width about four-fifths maximum length, located approximately at anterior third. Cervical groove well developed, deep, complete from side to side, only slightly interrupted axially by incipient mesial longitudinal ridge between mesogastric and metagastric regions, extending obliquely anterolaterally from axis, concave posterior to mesogastric region, less so posterior to protogastric region, and deflecting posterolaterally posterior to hepatic region. Postcervical grooves well developed, short, deep, arcuate, located at approximately medial portion of carapace, flanking the metagastric and urogastric regions. Branchiocardiac grooves shallow, faint, with muscle scars gently developed anterior to branchiocardiac and posterior to postcervical grooves. Mesial longitudinal ridge present, narrow, smooth, very shallow anteriorly, and slightly better developed posteriorly, non-tuberculate, excepting for a very small tubercle at metagastric region. Postfrontal region slightly lobate, gently sulcate postrostrally; dorsal carapace finely granulated; two small, distinct, rounded tubercles on protogastric region, located posterior to orbital rim and anterior to cervical groove.

Rostrum tip missing; fronto-orbital region wide, slightly more than two-thirds carapace maximum width; orbits transverse, nearly one-third the fronto-orbital region width, bearing two shallow, closed orbital fissures; inner orbital margin missing; medial orbital spine small, truncated, straight, sloping posterolaterally, nearly as large as postorbital spine; postorbital spine single, small, weakly produced, truncated, straight, sloping posteromesially, outer postorbital margin straight, converging anteriorly.

Anterolateral margin slightly convex, positioned in carapace anterior third, bearing three short, weakly pronounced spines; anteriormost spine subtriangular, well developed, placed at the level of lateralmost orbital fissure, with outer margin diverging anteriorly; median spine the smallest, weakly developed, subrounded; posteriormost spine subtriangular, well developed, immediately above cervical groove, with outer margin diverging anteriorly. Posterolateral margin long, three times as long as anterolateral margin, gently convex, bearing at least two very small, faint, smooth spines anteriorly. Posterior margin incomplete, apparently concave, as wide as half carapace greatest width, and about two-thirds the fronto-orbital region.

Etymology.—The trivial name honors Kecia Kerr, who greatly contributed in the discovery of the holotype.

Material Examined.—The holotype and sole specimen IGM p881128, deposited in the Geological and Paleontological Museum José Royo y Gómez, INGEOMINAS, Bogotá-Colombia.

Measurements.—Carapace maximum length: 11.2 mm; estimated width, 10.1 mm; estimated frontal-orbital margin: 7.0 mm.

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. Latitude 6.59621, Longitude -73.09146.

Remarks.—The palaeocorystid affiliation of *Notopocorystes kerri* is supported based on the possession of a fusiform, ovate carapace, covered with fine granules, with



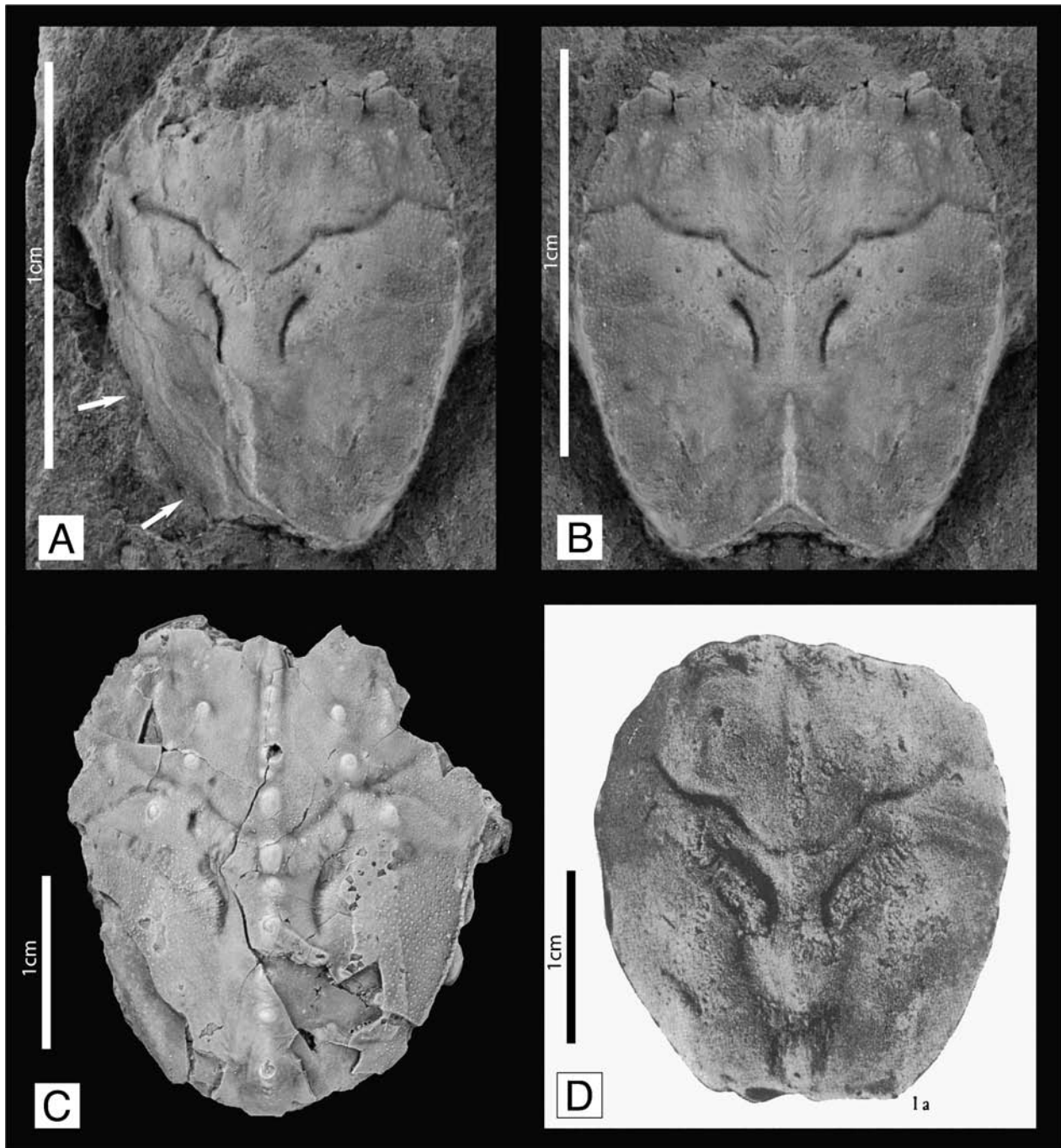


Fig. 4. Raninoidea, Palaeocorystidae. A-B, *Notopocorystes kerri* n. sp. holotype IGM p881128, upper Aptian, Colombia. A, Carapace in dorsal view, with arrows indicating the distorted left posterolateral and posterior carapace margins; B, Mirror image of the well preserved right half of the dorsal carapace; C, *Notopocorystes stokesii* (Mantell, 1844), hypotype (BMNH) In. 39366, dorsal carapace, lower Albian, England; D, *Notopocorystes xizangensis*, digital image from Wang (1981, pl. 2, fig. 1a), Albian, Xizang, China.

a distinctive cervical groove, bearing a mesial longitudinal ridge, and with more than three anterolateral spines. The genera *Notopocorystes*, *Eucorystes* Bell, 1863, and *Cretacoranina* Mertin, 1941, ranging in age from early Albian to Campanian, have been typically included within Palaeocorystidae. The genus *Heus* Bishop and Williams, 2000, was included in Palaeocorystidae by De Grave et al. (2009), and Schweitzer et al. (2010). Nevertheless, based on the illus-

trations and description by Bishop and Williams (2000), the holotype and sole specimen of *Heus* appears to lack diagnostic palaeocorystid features, such as an anterolateral margin bearing multiple spines and the broad fronto-orbital margin, plus the different dorsal ornamentation and carapace groove development, therefore suggesting removal from Palaeocorystidae, and rather placement within Raninidae as originally proposed by Bishop and Williams (2000). *Cenoco-*



*rystes* Collins and Breton, 2009, originally considered a palaeocorystid, has been recently allied with Raninoidinae Lörenthey (in Lörenthey and Beurlen, 1929) (De Grave et al., 2009; Schweitzer et al., 2010).

Schweitzer and Feldmann (2001) highlighted the different degree of ornamentation on the dorsal carapace among palaeocorystid genera. A mesial ridge is present in all genera, appearing more developed in some *Notopocorystes*, and less in most *Eucorystes* and *Cretacorantina*. In *Notopocorystes*, the cervical groove is deep, the anterior dorsal ornamentation consists of nodes and tubercles. In *Eucorystes*, the cervical groove is shallow and the anterior dorsal ornamentation is constituted by a unique strap-like sculpted pattern of flattened vermiform ridges separated by grooves (McCoy, 1854; Bell, 1863; Tucker, 1998). *Cretacorantina* has an incipient or barely perceptible cervical groove, a smoother dorsal surface, and lacks nodes, tubercles, or strap-like ornamentation (Mertin, 1941; Tucker, 1998). The presence in *Notopocorystes kerri* of a deep cervical groove, a distinctive mesial longitudinal ridge, and two tubercle-like protuberances on the protogastric region, supports affiliation with the genus *Notopocorystes* within Palaeocorystidae.

*Notopocorystes kerri* differs from Albian notopocorystids in exhibiting a broader posterior third of the carapace, smaller anterolateral spines, lack of a postfrontal axial ridge or well developed lines of tubercles, and a subtle, non-tuberculate longitudinal ridge (Fig. 4A-B). In *N. stokesii* (Mantell, 1844), from the Albian of England (Fig. 4C), the posterior third of the carapace is narrower than in *N. kerri*, the spines on the anterolateral margin are better developed, the protogastric region possesses multiple tubercles, and the dorsal longitudinal ridge is well-developed and tuberculate, extending from the mesogastric to the urogastric region (McCoy, 1849; Glaessner, 1969; Collins, 1996; Tucker, 1998; Karasawa et al., 2011). *Notopocorystes bituberculatus* Secretan, 1964, from the Albian of Madagascar, possesses a characteristic axial row of paired tubercles, and a more

elongated carapace than *N. kerri*, whereas *N. xizangensis* Wang, 1981, from the Albian of China and Iran (Yazdi et al., 2009) (Fig. 4D), shares with *N. kerri* the smooth longitudinal ridge lacking tubercles and with the postfrontal lobe ornamented only by two small protuberances on the protogastric region. However, the general carapace outline, the configuration of the orbital region and anterolateral and posterolateral margins, are different enough to warrant independent species assignment.

## DISCUSSION

### Paleobiogeography

*Planocarcinus olssoni* (Fig. 5A) and *N. undecimtuberculatus* (Fig. 5E), from the upper Aptian of Colombia and Japan, *Paranecrocarcinus? kennedyi* Wright, 1997, from the Barremian of South Africa, and *P. hexagonalis* Van Straelen, 1936, from the Neocomian of France (Table 1; Fig. 6A), are the oldest known raninoids and suggest that the earliest frog crabs belong to the necrocarcinid-type. It must be noted that the affiliation of *P? kennedyi* to Necrocarcinidae has been questioned (Guinot et al., 2008; Collins, 2010), and that more precise chronostratigraphic information of the sole specimen of *P. hexagonalis* is still needed, since the Neocomian in France embraces from Berriasian, ~145.5 Ma., to Hauterivian, ~130 Ma., although a Hauterivian age has been suggested for the species (Wright and Collins, 1972; Guinot et al., 2008). Notwithstanding the age uncertainty, *P. hexagonalis* stands as the oldest raninoid known to date. The appearance of a fusiform carapace is not documented until the upper Aptian, as represented by the palaeocorystid *Notopocorystes kerri* n. sp. (Figs. 5B, 7A). Given the scarce representation of pre-Albian raninoid taxa (2 fam., 4 gen., 5 spp.) few interpretations of their early paleobiogeographic patterns can be made, except that Raninoida was already distributed worldwide (Figs. 6A, 7A). In sharp contrast, the morphological diversity (4 fam., 10 gen., 31 spp.)

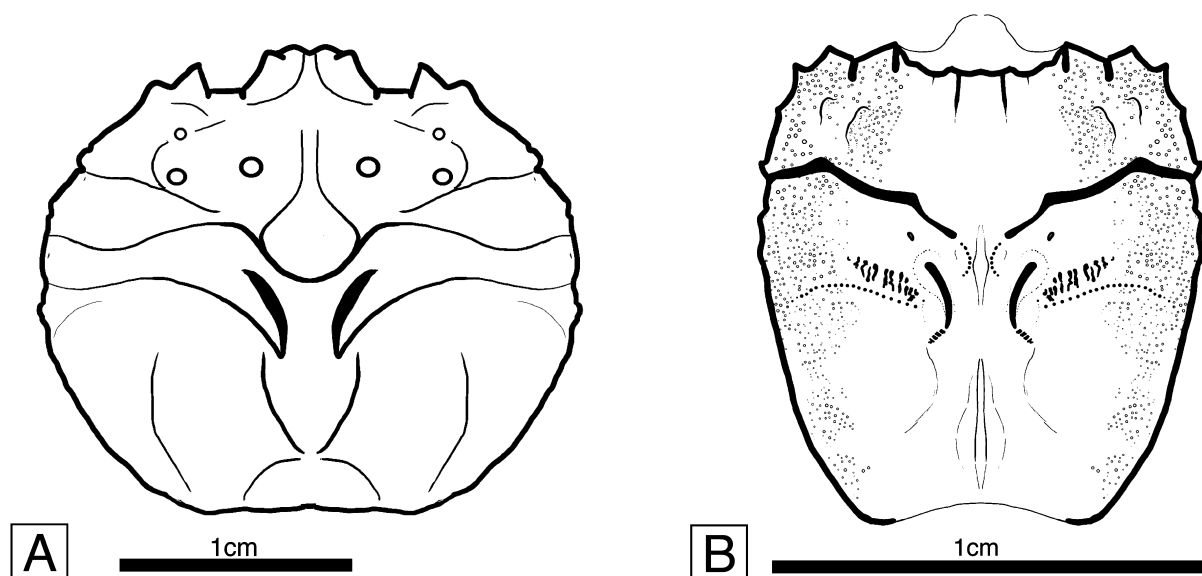


Fig. 5. Camera lucida line drawings of upper Aptian raninoids from Colombia, illustrated in Figs. 3A and 4A-B. A, *Planocarcinus olssoni* n. comb., dorsal carapace; B, *Notopocorystes kerri* n. sp. Mirror drawing of well preserved right half of dorsal carapace (Fig. 4A).

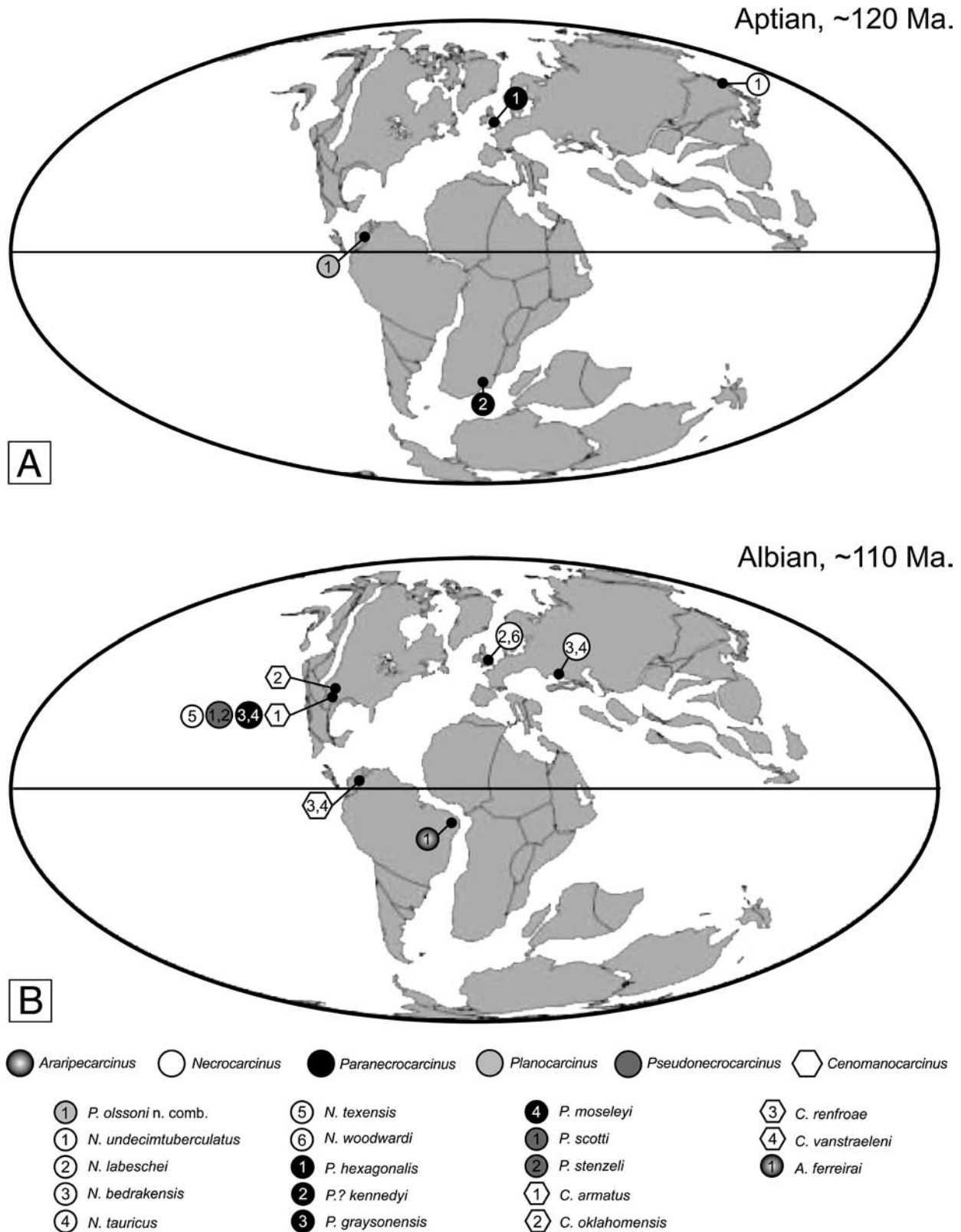


Fig. 6. Paleobiogeographic distribution of the early Cretaceous raninoids with 'necrocarcinid-like' body plan, wider than long or about as wide as long. A, Aptian, ~120 Ma.; B, Albian, ~110 Ma. Necrocarcinidae?: *Araripecarcinus* Martins-Neto, 1987 (gradient circle). Necrocarcinidae: *Necrocarcinus* Bell, 1863 (white circle); *Paranecrocarcinus* Van Straelen, 1936 (black circle); *Planocarcinus* n. gen. (light gray circle); *Pseudonecrocarcinus* Förster, 1968 (dark gray circle). Cenomanocarinidae: *Cenomanocarcinus* Van Straelen, 1936 (white hexagon). Taxa listed in Table 1. Base maps modified after Scotese (2004).

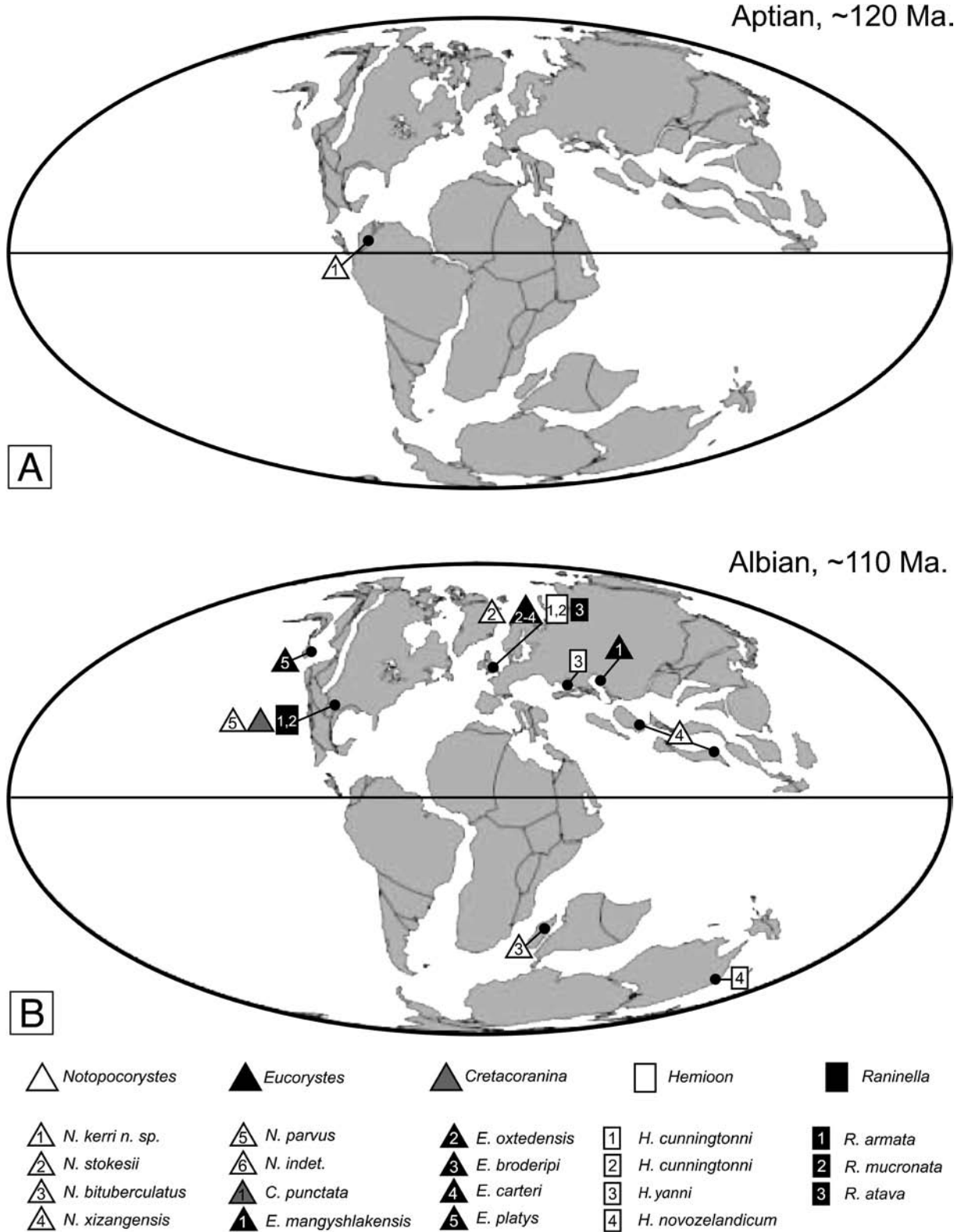


Fig. 7. Paleobiogeographic distribution of the early Cretaceous raninoids with ‘raninid-like’ body plan, longer than wide. A, Aptian, ~120 Ma.; B, Albian, ~110 Ma. Palaeocorystidae: *Cretacorantina* Mertin, 1941 (gray triangle); *Eucorystes* Bell, 1863 (black triangle); *Notopocorystes* McCoy, 1849 (white triangle). Raninidae: Lyreidinae: *Hemioon* Bell, 1863 (white rectangle). Ranininae: *Raninella* A. Milne-Edwards, 1962 (black rectangle). Taxa listed in Table 1. Base maps modified after Scotese, 2004.

(Table 1) and cosmopolitan distribution reached during the Albian (Figs. 6B, 7B), suggest the hypothesis of a rapid radiation of both body plans.

During the mid-Cretaceous, the world was characterized by much warmer global temperatures than today, with a low equatorial-pole temperature gradient, high concentrations of greenhouse gases including CO<sub>2</sub>, and CH<sub>4</sub> release from dissociation of methane clathrates (Barron, 1985; Barron and Washington, 1985; Berner, 1990; Wilson and Norris, 2001; Beerling et al., 2002; Jenkyns, 2003; Méhay et al., 2009). The production of oceanic crust and emplacement of Large Igneous Provinces (Mahoney et al., 1993; Larson and Kincaid, 1996; Tejada et al., 1996; Larson, 1997; Larson and Erba, 1999), together with an ice-free greenhouse world led to high global sea level, producing extensive large epicontinental seas (Herman and Spicer, 1996; Bice et al., 2003; Jenkyns et al., 2004; Hay, 2008; in Hay, 2011). The separation of North America from northern South America led to the widening of the Caribbean Tethys, connecting to the Mediterranean Tethys to the east and the Central Pacific to the west (Figs. 6-7). A Tethian Circumglobal Current (TCC), which separated northern from southern landmasses (Stanley, 1995; Poulsen et al., 1998), allowed the mixture of waters from different oceanic basins. Although the strength, stability, uniformity and direction of the Cretaceous TCC have been debated, there is evidence for a complicated circulation pattern (Poulsen et al., 1998) characterized by a westbound flow (Luyendyk et al., 1972; Gordon, 1973; Berggren and Hollister, 1974; Lloyd, 1982; Föllmi and Delamette, 1991; Bush, 1997), but also an eastward gyre along the northern margin of the Tethys (Barron and Peterson, 1989, 1990). The wide latitudinal distribution of mid-Cretaceous raninoid crabs may be the product of a shallow latitudinal temperature gradient combined with a system of oceanic currents connecting polar regions with the tropics (Hay, 2011). The Tethys Ocean is known to have acted as an important dispersal pathway for many groups of decapod crustaceans (Feldmann and Schweitzer, 2006), and Raninoida appears to follow this pattern.

In addition to the occurrence of *Planocarcinus* and *Notopocorystes* in the Aptian of Colombia, *Cenomanocarcinus* Van Straelen, 1936 (Vega et al., 2010), from the Upper Albian of Colombia, and *Araripearcinus* Martins-Neto, 1987, from the lower-middle Albian of Brazil (Karasawa et al., 2008; Luque et al., under study), suggest that Raninoida were well established in the Neotropics during the Early Cretaceous, and warrants considering the possible role of the Neotropics in the origin and diversification of frog crabs.

#### Systematic Issues

The six families comprising Raninoida are united by two synapomorphies: an elongated buccal cavity, and the mxp3 lying in two planes (Karasawa et al., 2011). Therefore, these characteristics are expected to be present in the earliest common ancestor for the raninoidan body plans, which might have had its origins in the earliest Cretaceous, or even, the Late Jurassic (Wright and Collins, 1972; Collins, 1996). Still, the question of what body plan is the ancestral condition is still poorly understood. The hypothesis advanced by Glaessner (1960) and Guinot et al. (2008) envisions Palaeocorystidae proximate to Necrocarcinidae stock

(Fig. 1A), and is supported by such synapomorphies as a distinct cervical groove, a longitudinal ridge or row of tubercles, an anterolateral margin provided with multiple spines, similar configuration of the thoracic sternum, and particularly the coxae of the last pereopods separated enough to allow the pleon to be pressed against the sternum (Stenzel, 1945; Wright and Collins, 1972; Collins, 1996; Tucker, 1998; Karasawa et al., 2011). Under this scenario, Guinot et al. (2008) shared Glaessner's (1960) point of view, which stated that the earliest palaeocorystid representatives (referring to *Notopocorystes*) "are closer to *Necrocarcinus* than to their living typical raninid descendants" (Glaessner, 1960: p. 46; Collins, 1996: p. 75; Guinot et al., 2008: p. 700). For the clade Palaeocorystidae + (Cenomanocarcinidae + Necrocarcinidae) to be monophyletic, it must contain all the descendants of their latest common ancestor, and therefore Raninidae cannot be derived from Palaeocorystidae, contrary to what has been previously suggested (Bourne, 1922; Glaessner, 1960; Tucker, 1998; Guinot et al., 2008). Since Raninidae + Symethidae is a monophyletic clade (Karasawa et al., 2011), the innovation of a fusiform carapace must have evolved twice within Raninoida. However, no current paleontological evidence supports such a scenario, and therefore the hypothesis of a monophyletic Palaeocorystidae + (Cenomanocarcinidae + Necrocarcinidae) clade is rejected. Nevertheless, if considering the inverse scenario, where the fusiform anatomy would be the primitive condition for Raninoida, then the necrocarcinid-type body plan would have appeared once in the Camarocarcinidae + (Cenomanocarcinidae + Necrocarcinidae) clade, and probably derived from a palaeocorystid ancestor. This hypothesis, although plausible, is also not supported by any known paleontological evidence; therefore it is rejected.

The hypothesis of a monophyletic Palaeocorystidae + (Raninidae + Symethidae) clade (Fig. 1B) has been supported based on the shared fusiform carapace and the lack of pleonal locking mechanisms (Karasawa et al., 2011). Under the premise that the necrocarcinid-type body plan is the primitive condition for Raninoida, as suggested by its earliest fossil representatives, the later innovation of the fusiform carapace is expected to have occurred once (Fig. 8). Regarding the pleonal locking mechanisms, none has been reported in the necrocarcinid-like Camarocarcinidae to date, and conversely, locking mechanisms are present in the raninid subfamily Lyreidinae Guinot, 1993 (*Lyreidus* De Haan, 1841, and *Lysirude* Goeke, 1985) (Guinot, 1993; Guinot and Bouchard, 1998), typical frog crabs with living representatives, casting uncertainty on the trait as an informative character to unite Palaeocorystidae with the modern raninoids.

Although the hypothesis of a fusiform carapace appearing only once within Raninoida seems to be most parsimonious, given the unclear relationship among the principal body arrangements, plus the fragmentary fossil record of pre-Aptian raninoids, an unresolved polytomy is proposed (Fig. 1C) placing Palaeocorystidae in between the (Cenomanocarcinidae + Necrocarcinidae) and the (Raninidae + Symethidae) clades, until new paleontological material and phylogenetic analysis are available. The most basal palaeocorystids (*Notopocorystes*) would be expected to be closer to a hypothetical necrocarcinid-like ancestor rather than to their

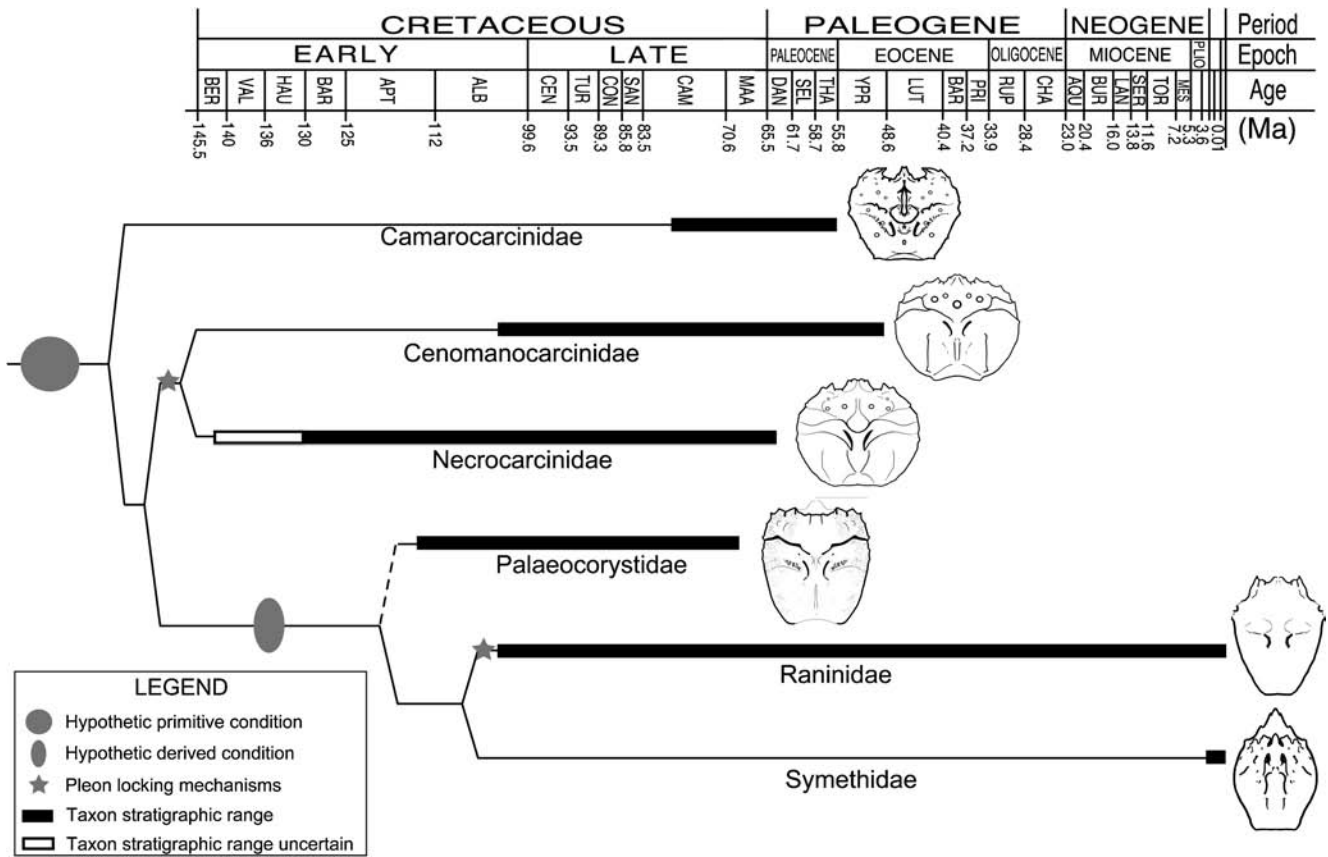


Fig. 8. Chronostratigraphic distribution of the six known fossil and extant families within the Section Raninoida, as indicated by their current First Appearance Datum (FAD) and Last Appearance Datum (LAD). Camarocarcinidae: *Cretacocarcinus smithi* Feldmann, Li, and Schweitzer, 2007, Campanian, US (line drawing); *Camarocarcinus obtusus* Jakobsen and Collins, 1979, Paleocene (Danian?), Denmark. Cenomanocarcinidae: *Cenomanocarcinus armatus* (Rathbun, 1935), upper Albian, Texas; *C. oklahomensis* (Rathbun, 1935), upper Albian, Oklahoma; *C. renfroae* (Stenzel, 1945), upper Albian, Colombia; *C. vanstraeleni* Stenzel, 1945, upper Albian, Colombia (line drawing). Necrocarcinidae: *Paranecrocarcinus hexagonalis* Van Straelen 1936, Neocomian, France; *Planocarcinus olssoni* n. comb., upper Aptian, Colombia (line drawing); *Necrocarcinus bispinus* Segerberg, 1900, lower Paleocene, Antarctica; *N. insignis* Segerberg, 1900, Paleocene (Danian), Sweden and Denmark. Palaeocorystidae: *Notopocorystes kerri* n. sp., upper Aptian, Colombia (line drawing); *Eucorystes eichhorni* Bishop, 1983b, upper Campanian?, Montana. Raninidae: Lyreidinae: *Hemioon cunningtonni* Bell, 1863, upper Albian, England; *H. elongatum* (A. Milne-Edwards, 1862), upper Albian, England, France, Czech, Germany, UK; *H. novozelandicum* Glaessner, 1980, upper Albian, New Zealand; *H. yanini* Ilyin and Alekseev, 1998 upper Albian, Crimea. Ranininae: *Raninella armata* Rathbun, 1935, upper Albian, Texas; *R. atava* Carter, 1898, upper Albian, England; *R. mucronata* Rathbun, 1935, upper Albian, Texas (line drawing from specimen of *R. trigeri* A. Milne-Edwards, 1862, illustrated in Waugh et al. (2009, fig. 5.3)). Symethidae: *Symethis coraliica* Davie, 1989, recent; *S. garthi* Goeke, 1981, recent (line drawing modified after Hendrickx, 1997, fig. 49a); *S. variolosa* (Fabricius, 1793), recent. Base tree modified after Karasawa et al. (2011, fig. 3). Dotted line indicates the uncertain phylogenetic affiliation of Palaeocorystidae with the clade Raninidae + Symethidae.

living relatives, whereas the rootstock of Raninidae may lie closer to the most derived Palaeocorystidae, e.g., *Cretacoranina*.

ACKNOWLEDGEMENTS

We thank the Smithsonian Tropical Research Institute (STRI), and the Lerner Gray Memorial Fund of the American Museum of Natural History (AMNH) for providing (to JL) facilities and funds to allow the development of the present research. Kecia Kerr (McGill University) for the valuable field assistance and improvements to the manuscript, and Fernando Etayo-Serna (INGEOMINAS) for intellectual support. Danièle Guinot (MHNH), Matatsune Takeda (Teikyo Heisei University), Francisco Vega (UNAM), Angel Aguirre and the staff of the STRI Library provided literature items. Jose Arenas (INGEOMINAS, Colombia) supplied export permits. Tomoki Kase (National Museum of Nature and Science, Tokyo) provided a photo of one specimen from Japan. Julia Figueroa and family provided kind hospitality and permission to collect on their property. Two anonymous reviewers are gratefully acknowledged for their constructive comments. Partial funding for this project was provided by an NSERC grant to CBC.

REFERENCES

Artal, P., D. Guinot, B. van Bakel, and J. Castillo. 2008. Ibericancridae, a new dakoticancrid family (Decapoda, Brachyura, Podotremata) from the upper Campanian (Upper Cretaceous) of Spain. *Zootaxa* 1907: 1-27.

Barron, E. J., and W. H. Peterson. 1989. Model simulation of the Cretaceous ocean circulation. *Science* 244: 684-686.

\_\_\_\_\_, and \_\_\_\_\_. 1990. Mid-Cretaceous ocean circulation: results from model sensitivity studies. *Paleoceanography* 5: 319-337.

\_\_\_\_\_, and W. M. Washington. 1985. Warm Cretaceous climates: high atmospheric CO<sub>2</sub> as a plausible mechanism, pp. 546-553. In E. T. Sundquist and W. S. Broecker (eds.), *The Carbon Cycle and Atmospheric CO<sub>2</sub>: Natural Variations Archaeal to Present*. American Geophysical Union Geophysical Monograph. Vol. 32.

Beerling, D. J., M. R. Lomas, and D. R. Gröcke. 2002. On the nature of methane gas-hydrate dissociation during the Toarcian and Aptian Oceanic Anoxic Events. *American Journal of Science* 302: 28-49.

Bell, T. 1858. A monograph of the fossil malacostracous Crustacea of Great Britain, Pt. I, Crustacea of the London Clay. *Monograph of the Palaeontographical Society*, London 10[1856]: i-viii, 1-44, 11 pls.

- . 1863. A monograph of the fossil malacostracous Crustacea of Great Britain, Pt. II, Crustacea of the Gault and Greensand. Palaeontographical Society Monograph, London: 1-40, 11 pls.
- Berggren, W. A., and C. D. Hollister. 1974. Paleogeography, paleobiogeography, and the history of circulation in the Atlantic Ocean, pp. 126-186. In: W. W. Hay (ed.), *Studies in Paleooceanography*. Society of Economic Paleontologists and Mineralogists Special Publication. Vol. 20.
- Berner, R. A. 1990. Atmospheric carbon dioxide levels over phanerozoic time. *Science* 249: 1382-1386.
- Bice, K. L., B. T. Huber, and R. D. Norris. 2003. Extreme polar warmth during the Cretaceous Greenhouse? Paradox of the late Turonian  $\delta^{18}O$  record at Deep Sea Drilling Project Site 511. *Paleoceanography* 18(2): 1031.
- Bishop, G. A. 1972. Moults of *Dakoticancer overanus*: an Upper Cretaceous crab from the Pierre Shale of South Dakota. *Palaeontology* 15: 631-636.
- . 1983a. Fossil decapod crustaceans from the Lower Cretaceous, Glen Rose Limestone of central Texas. *Transactions of the San Diego Society of Natural History* 20: 27-55.
- . 1983b. Fossil decapod Crustacea from the Late Cretaceous Coon Creek Formation, Union County, Mississippi. *Journal of Crustacean Biology* 3: 417-430.
- . 1985. Fossil decapod crustaceans from the Gammon Ferruginous Member, Pierre Shale (Early Campanian), Black Hills, South Dakota. *Journal of Paleontology* 59: 605-624.
- . 1986. Taphonomy of the North American decapods. *Journal of Crustacean Biology* 6: 326-355.
- . 1988. A new crab, *Seorsus wadei*, from the Late Cretaceous Coon Creek Formation, Union County, Mississippi. *Proceedings of the Biological Society of Washington* 101: 72-78.
- , and A. B. Williams. 1991. *Necrocarcinus olsonorum*, new species, a crab (Decapoda, Calappidae) from the Cretaceous Carlisle Shale (Turonian), Western Interior United States. *Journal of Crustacean Biology* 11(3): 451-459.
- , and ———. 2000. Fossil crabs from Tepee Buttes, submarine seeps of the late Cretaceous Pierre Shale, South Dakota and Colorado, U.S.A. *Journal of Crustacean Biology* 20(2)(special number): 285-300.
- , R. M. Feldmann, and F. J. Vega. 1998. The Dakoticancridae (Decapoda, Brachyura) from the Late Cretaceous of North America and Mexico. *Contributions to Zoology* 67: 237-255.
- Breton, G., and J. H. Collins. 2011. New and rare Cenomanian crabs (Crustacea, Decapoda, Brachyura) from the Paris Basin (France), and a comparison with necrocarcinids, etyids and dynomenids from Devon (England). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 260(2): 141-156.
- Bush, A. B. G. 1997. Numerical simulation of the Cretaceous Tethys Circumglobal Current. *Science* 275: 807-810.
- Carter, J. 1898. A Contribution to the Palaeontology of the Decapod Crustacea of England. *Quarterly Journal of the Geological Society, London* 54: 15-44.
- Collins, J. S. H. 1996. A systematic survey of the genus *Notopocorystes* McCoy, 1849 (Crustacea, Decapoda, Raninidae). *Bulletin of the Mizunami Fossil Museum* 23: 75-87.
- . 2010. New species of crabs (Crustacea, Decapoda), one from the Middle Danian of Denmark, and three new species from the Upper Cretaceous of Nigeria. *Bulletin of the Mizunami Fossil Museum* 36: 13-19.
- , and G. Breton. 2009. New crabs (Crustacea, Decapoda) from the Cenomanian stratotype (Western Paris Basin, France). *Bulletin of the Mizunami Fossil Museum* 35: 43-50.
- , and H. W. Rasmussen. 1992. Upper Cretaceous-Lower Tertiary decapod crustaceans from west Greenland. *Grønlands Geologiske Undersøgelse Bulletin* 162: 1-46.
- , and R. J. Williams. 2004. A new genus and species of necrocarcinid crab (Crustacea, Brachyura) from the Upper Cretaceous of England. *Bulletin of the Mizunami Fossil Museum* 31: 33-35.
- Cortés, M., B. Colleta, and J. Angelier. 2006. Structure and tectonics of the central segment of the Eastern Cordillera of Colombia. *Journal of South American Earth Sciences* 21: 437-465.
- Davie, P. J. F. 1989. *Symethis corallica* sp. nov. (Crustacea, Brachyura, Raninidae), the first member of the Symethinae to be recorded from the Indo-West Pacific region. *Bulletin du Muséum National d'Histoire Naturelle, Paris (A)* (4) 14: 501-561.
- De Grave, S., N. D. Pentcheff, S. T. Ah Yong, T.-Y. Chan, K. A. Crandall, P. C. Dworschak, D. L. Felder, R. M. Feldmann, C. H. J. M. Fransen, L. Y. D. Goulding, R. Lemaitre, M. L. Low, J. W. Martin, P. K. L. Ng, C. E. Schweitzer, S. H. Tan, D. Tshudy, and R. Wetzer. 2009. A classification of recent and fossil genera of decapod crustaceans. *Raffles Bulletin of Zoology Supplement* 21: 1-109.
- De Haan, W. 1833-1850. Crustacea. In: P. F. von Siebold (ed.), *Fauna Japonica sive Descriptio Animalium, quae in Itinere per Japoniam, Jussu et Auspiciis Superiorum, qui summum in India Batava Imperium Tenent, Suscepto, Annis 1823-1830 Collegit, Notis, Observationibus et Adumbrationibus Illustravit: i-xvii, i-xxxi, ix-xvi, 1-243, pls. A-J, L-Q, 1-55, circ. tab. 2*. J. Müller et Co., Lugduni Batavorum [Leyden].
- Etao-Serna, F. 1979. Zonation of the Cretaceous of Central Colombia by ammonites. *INGEOMINAS, Bogotá*, 186 pp.
- Eudes-Deslongchamps, J. A. 1835. Mémoire pour servir à l'histoire naturelle des Crustacés fossils. *Mémoire de la Société Linnéenne de Normandie* 5: 37-46, pl. 1.
- Fabricius, J. C. 1793. *Entomologiae systematica emendata et aucta, secundum Classes, Ordines, Genera, Species, adjectis Synonymis, Locis, Observationibus, Descriptionibus: 1-519*. C. G. Profet Storch, Hafniae [Copenhagen].
- Feldmann, R. M., and C. E. Schweitzer. 2006. Paleobiology of southern hemisphere decapod Crustacea. *Journal of Paleontology* 80(1): 83-103.
- , R.-Y. Li, and C. E. Schweitzer. 2007. A new family, genus, and species of crab (Crustacea, Decapoda, Brachyura) from the Upper Cretaceous (Campanian) of Manitoba, Canada. *Canadian Journal of Earth Science* 44: 1741-1752.
- , T. Villamil, and E. G. Kauffman. 1999. Decapod and stomatopod crustaceans from mass mortality Lagerstätten: Turonian (Cretaceous) of Colombia. *Journal of Paleontology* 73: 91-101.
- Föllmi, K. H., and M. Delamette. 1991. Model simulation of mid-Cretaceous ocean circulation. *Science* 251(4989): 94-95.
- Förster, R. 1968. *Paranecrocarcinus libanoticus* n. sp. (Decapoda) und die Entwicklung der Calappidae in der Kreide. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie* 8: 167-195.
- . 1970. Neue Dekapoden-Reste aus der Oberkreide von Mocambique, Norddeutschland und den bayerischen Alpen. *Paläontologische Zeitschrift* 44(3/4): 134-144.
- Fraaye, R. H. B. 1994. Early Paleocene crabs (Crustacea, Decapoda) from the Middle Vistula Valley, Central Poland. *Acta Geologica Polonica* 44(3-4): 261-266.
- Fritsch, A., and J. Kafka. 1887. Die Crustaceen der böhmischen Kreideformation: 1-53, 10 pls. Selbstverlag in Commission von F. Rivnác, Prag.
- Gerhardt, K. 1897. Beiträge zur Kenntniss der Kreideformation in Columbien. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie* 11: 118-208, 5 pl.
- Glaessner, M. F. 1929. Crustacea Decapoda. In: F. J. Pompeckj (ed.), *Fossilium catalogus, 1: Animalium, Part 41: 1-464*. W. Junk, Berlin.
- . 1960. New Cretaceous and Tertiary crabs (Crustacea: Brachyura) from Australia and New Zealand. *Transactions of the Royal Society of South Australia* 104: 171-192.
- . 1969. Decapoda, pp. R400-R533, R626-R628. In: R. C. Moore (ed.), *Treatise on Invertebrate Paleontology, Part R: Arthropoda 4. Vol. 1*. Geological Society of America, Boulder, Colorado, and University of Kansas Press, Lawrence, Kansas.
- . 1980. New Cretaceous and Tertiary crabs (Crustacea: Brachyura) from Australia and New Zealand. *Transactions of the Royal Society of South Australia* 104: 171-192.
- Goeke, G. D. 1981. Symethinae, new subfamily, and *Symethis garthi*, new species, and the transfer of *Raninoides ecuadorensis* to *Notosceles* (Raninidae: Brachyura: Gymnopleura). *Proceedings of the Biological Society of Washington* 93: 971-981.
- . 1985. Decapod Crustacea: Raninidae, pp. 205-228. In: *Résultats des Campagnes MUSORSTOM I et II - Philippines (1976, 1980)*. Vol. 2. Mémoires du Muséum national d'Histoire naturelle. Nouvelle Série. Série A, Zoologie. Vol. 133 [for 1985]. Éditions du Muséum, Paris.
- Gordon, W. A. 1973. Marine life and ocean surface currents in the Cretaceous. *Journal of Geology* 81: 269-284.
- Guinot, D. 1993. Données nouvelles sur les Raninoidea De Haan, 1841 (Crustacea Decapoda Brachyura Podotremata). *Comptes Rendus Académie des Sciences, Paris (Sciences de la Vie)* 316: 1324-1331.
- , and J. M. Bouchard. 1998. Evolution of the abdominal holding systems of brachyuran crabs (Crustacea, Decapoda, Brachyura). *Zoosystema* 20: 613-694.

- , and G. Breton. 2006. *Lithophylax trigeri* A. Milne-Edwards and Brocci, 1879, from the French Cretaceous (Cenomanian) and placement of the family Lithophylacidae Van Straelen, 1936 (Crustacea, Decapoda, Brachyura). *Geodiversitas* 28(4): 591-633.
- , F. J. Vega, and B. W. M. van Bakel. 2008. Cenomanocarcinidae n. fam., a new Cretaceous podotreme family (Crustacea, Decapoda, Brachyura, Raninoidea), with comments on related families. *Geodiversitas* 30(4): 681-719.
- Hay, W. W. 2008. Evolving ideas about the Cretaceous climate and ocean. *Cretaceous Research* 29: 725-753.
- . 2011. Can humans force a return to a 'Cretaceous' climate? *Sedimentary Geology* 235: 5-26.
- Hendricks, M. E. 1997. Los Cangrejos Braquiuros (Crustacea: Brachyura: Dromiidae hasta Leucosiidae) del Pacifico Mexicano. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. Instituto de Ciencias del Mar y Limnología, UNAM, México, 178 pp.
- Herman, A. B., and R. A. Spicer. 1996. Paleobotanical evidence for a warm Cretaceous Arctic Ocean. *Nature* 380: 330-333.
- Ilyin, I. V. 2005. Cretaceous and Paleogene Decapod Crustaceans of the Western Part of Northern Eurasia: 1-296. State University Press, Moscow. [In Russian.]
- , and A. S. Alekseev. 1998. New crab species (Decapoda, Brachyura) from the Lower Cretaceous of south-west Crimea. *Paleontological Journal* 32: 592-595. [Translated from *Paleontologicheskii Zhurnal*.]
- Jagt, J. W. M., R. H. B. Fraaije, B. W. M. van Bakel, and P. Artal. 2010. *Necrocarcinus ornatisimus* Forst., 1887, and *Prehepatus wernerii* Fraaye and Collins, 1987 (Upper Maastrichtian, The Netherlands) revisited, with notes on other Cretaceous dromenid crabs (Decapoda, Brachyura), pp. 48-125. In P. Castro, P. Davie, P. Ng, and B. Richer de Forges (eds.), *Studies in Brachyura: a Homage to Danièle Guinot*.
- Jakobsen, S. L., and J. S. H. Collins. 1979. Decapod Crustacea from the Palaeocene of Zealand, Denmark. *Proceedings of the Geologists Association* 90(2): 61-64.
- Jaworski, E. 1938. Gasterópodos del Cretácico inferior de Colombia. *Estudios geológicos y Paleontológicos sobre la Cordillera Oriental de Colombia, Parte 3*: 109-121, pl. 23.
- Jenkyns, H. C. 2003. Evidence for rapid climate change in the Mesozoic-Paleogene greenhouse world. *Philosophical Transactions of the Royal Society London A* 361: 1885-1916.
- , A. Forster, S. Schouten, and J. S. Sinninghe Damsté. 2004. High temperatures in the Late Cretaceous Arctic Ocean. *Nature* 432: 888-892.
- Jimbô, K. 1894. Beiträge zur Kenntnis der Fauna der Kreideformation von Hokkaidô. *Paläontologische Abhandlungen, N. F.* 2(3): 149-194, pls. 17-25.
- Julivert, M. 1968. *Lexique Stratigraphique International*. Vol. 5(4a): Amérique Latine, Colombie (première partie) – Précambrien, Paléozoïque, Mésozoïque et intrusions d'âge Mésozoïque-Tertiaire. Centre National de la Recherche Scientifique, France, 651 pp.
- Kakabadze, M. V., P. J. Hoedemaeker, T. N. Bogdanova, and M. Z. Sharikadze. 2004. On the Barremian-Early Albian biogeography (by ammonites) of Colombia. *Scripta Geologica* 128: 515-558.
- Karasawa, H., C. E. Schweitzer, and R. M. Feldmann. 2011. Phylogenetic analysis and revised classification of podotrematous Brachyura (Decapoda) including extinct and extant families. *Journal of Crustacean Biology* 31(3): 523-565.
- Kesling, R. V., and I. G. Reimann. 1957. An Upper Cretaceous crab, *Avitelmessus grapsoides* Rathbun. *Contributions from the Museum of Paleontology* 14(1): 1-15, 4 pls. (University of Michigan).
- Larghi, C. 2004. Brachyuran decapod Crustacea from the Upper Cretaceous of Lebanon. *Journal of Paleontology* 78(3): 528-541.
- Larson, R. L. 1997. Superplumes and ridge interactions between Ontong Java and Manihiki Plateaus and the Nova-Canton Trough. *Geology* 25: 779-782.
- , and E. Erba. 1999. Onset of the Mid-Cretaceous greenhouse in the Barremian-Aptian: igneous events and the biological, sedimentary, and geochemical responses. *Paleoceanography* 14: 663-678.
- , and C. Kincaid. 1996. Onset of mid-Cretaceous volcanism by elevation of the 670 km thermal boundary layer. *Geology* 24: 551-554.
- Latreille, P. A. 1802-1803. *Histoire naturelle, générale et particulière, des Crustacés et des Insectes* 3: 1-468. F. Dufart, Paris.
- Linnaeus, C. 1758. *Systema Naturae per Regna tria Naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis* (ed. 10) 1: 1-824. Laurentii Salvii, Holmiae [Stockholm].
- Lloyd, C. R. 1982. The Mid-Cretaceous earth: palaeogeography, ocean circulation and temperature, atmospheric circulation. *Journal of Geology* 90: 393-413.
- Lórenthey, E., and K. Beurlen. 1929. Die fossilen Decapoden der Länder der Ungarischen Krone. *Geologica Hungarica (Palaeontologica)* 3: 1-421, 12 tabs., 16 pls.
- Luyendyk, B., D. Forsyth, and J. D. Phillips. 1972. Experimental approach to the paleocirculation of the oceanic surface waters. *Geological Society of America Bulletin* 83: 2649-2664.
- MacLeay, W. S. 1838. On the brachyurous decapod Crustacea brought from the Cape by Dr. Smith, pp. 53-71, 2 pls. In A. Smith, *Illustrations and Descriptions of the Objects of Natural History Collected During an Expedition into the Interior of South Africa, in the Years 1834, 1835, and 1836: Fitted out by "The Cape of Good Hope Association for Exploring Central Africa."* Smith, Elder and Company, London.
- Mahoney, J. J., M. Storey, R. A. Duncan, K. J. Spencer, and M. Pringle. 1993. Geochemistry and age of the Ontong Java Plateau, pp. 233-261. In M. Pringle, W. Sager, W. Sliter, and S. Stein (eds.), *The Mesozoic Pacific: Geology, Tectonics, and Volcanism*. Geophysical Monograph. Vol. 77. American Geophysical Union, Washington, DC.
- Mantell, G. A. 1844. *Medals of Creation* 1-2: 1-1016, 6 pls. H. G. Bohn, London.
- Martins-Neto, R. G. 1987. Primeiro registro de decápode na Formação Santana, bacia do Araripe (Cretáceo Inferior), Brasil. *Ciência e Cultura* 39: 406-410.
- McCoy, F. 1849. On the classification of some British fossil Crustacea with notices of new forms in the university collection at Cambridge. *Annals and Magazine of Natural History* (2) 4: 161-179, 330-335.
- . 1854. On some new Cretaceous Crustacea. *Annals and Magazine of Natural History* (2) 44: 116-122.
- Méhay, S., C. Keller, S. M. Bernasconi, H. Weissert, E. Erba, C. Bottini, and P. A. Hochuli. 2009. A volcanic CO<sub>2</sub> pulse triggered the Cretaceous Oceanic Anoxic Event 1a and a biocalcification crisis. *Geology* 37: 819-822.
- Mertin, H. 1941. Decapode Krebse aus dem subhercynen und Braunschweiger Emscher und Untersenon sowie Bemerkungen über verwandte Formen in der Oberkreide. *Nova Acta Leopoldina* 10(68): 149-264, pls. 1-8.
- Milne-Edwards, A. 1862. Sur l'existence de Crustacés de la famille des Raniniens pendant la période crétacée. *Comptes Rendus de l'Académie des Sciences de Paris* 55: 492-494.
- Morales, L. G., D. J. Podesta, W. C. Hatfield, H. Tanner, S. H. Jones, M. H. Barker, D. J. O'Donoghue, C. E. Mohler, E. P. Dubois, C. Jacobs, and C. R. Goss. 1958. General geology and oil occurrence of the Middle Magdalena Valley, Colombia, pp. 641-695. In L. G. Weeks (ed.), *Habitat of Oil a Symposium*. American Association of Petroleum Geologists, Tulsa, Oklahoma, USA.
- Poulsen, C. J., D. Seidov, E. J. Barron, and W. H. Peterson. 1998. The impact of paleogeographic evolution on the surface oceanic circulation and the marine environment within the Mid-Cretaceous Tethys. *Paleoceanography* 13: 546-559.
- Pulido, O. 1979. *Geología de las Planchas 135 San Gil y 151 Charalá*; Departamento de Santander. *Boletín Geológico del Ministerio de Minas y Energía*, Instituto Nacional Investigaciones Geológicas y Minerales 23(2).
- . 1985. *Geología de la Plancha 135 San Gil*, Escala 1: 100.000. Instituto Colombiano de Geología y Minería INGEOMINAS, Bogotá. Versión digital 2009.
- Rathbun, M. J. 1917. New species of South Dakota Cretaceous crabs. *Contributions to Zoology* 67: 237-255.
- . 1935. Fossil Crustacea of the Atlantic and Gulf Coastal Plain. *Geological Society of America (Special Paper)* 2: i-viii, 1-160.
- . 1937. Cretaceous and Tertiary crabs from Panama and Colombia. *Journal of Paleontology* 11: 26-28, pl. 5.
- Reuss, A. E. 1845. *Die Versteinerungen der böhmischen Kreideformation*. Stuttgart.
- Roberts, H. B. 1962. The Upper Cretaceous decapod crustaceans of New Jersey and Delaware, pp. 163-192. In H. G. Richards (ed.), *The Cretaceous fossils of New Jersey*. Bulletin of the New Jersey Division of Geology. Vol. 61.
- Royero, J. M., and J. Clavijo. 2001. *Mapa Geológico del Departamento de Santander*, Escala 1: 400.000. INGEOMINAS, Bucaramanga, Colombia, 1 map with text, 92 pp.



- Schweitzer, C. E., and R. M. Feldmann. 2000. New species of calappid crabs from western North America and reconsideration of the Calappidae De Haan sensu lato. *Journal of Paleontology* 74: 230-246.
- , and ———. 2001. New Cretaceous and Tertiary decapod crustaceans from western North America. *Bulletin of the Mizunami Fossil Museum* 28: 173-210.
- , ———, G. Gonzáles-Barba, and F. J. Vega. 2002. New crabs from the Eocene and Oligocene of Baja California Sur, Mexico and an assessment of the evolutionary and paleobiogeographic implications of Mexican fossil decapods. *Paleontological Society Memoir* 76: 1-43.
- , J. Fam, W. A. Hessin, S. W. Hetrick, T. G. Nyborg, and R. L. M. Ross. 2003. Cretaceous and Eocene Decapod Crustaceans from the Georgia Basin, British Columbia, Canada. *National Research Council of Canada Memoir Series*, 66 pp.
- Scotese, C. R. 2004. A continental drift flipbook. *Journal of Geology* 112: 729-741.
- Secretan, S. 1964. Les Crustacés du Jurassique supérieur et Crétacé de Madagascar. *Mémoires du Muséum National d'Histoire Naturelle*, Paris 156: 1-223.
- Segerberg, K. O. 1900. De Anomura och Brachyura dekapoderna inom Skandinavien Yngre krita. *Geologiska Föreningens i Stockholm Förhandlingar* 22: 347-388, pls. 7-9.
- Stanley, S. M. 1995. New horizons for paleontology, with two examples: the rise and fall of the Cretaceous Supertethys and the cause of the modern ice age. *Journal of Paleontology* 69(6): 999-1007.
- Stenzel, H. B. 1945. Decapod crustaceans from the Cretaceous of Texas. Texas University, Publication 4401: 401-476.
- Števíč, Z. 2005. The reclassification of brachyuran crabs (Crustacea: Decapoda: Brachyura). *Natura Croatica* 14(suppl.)(1): 1-159.
- Takeda, M., and I. Fujiyama. 1983. Three decapod crustaceans from the Lower Cretaceous Miyako Group, northern Japan. *Bulletin of the National Science Museum, Tokyo (C, Geology and Paleontology)* 9(4): 129-136, pls. 1, 2.
- Tejada, M. L. G., J. J. Mahoney, R. A. Duncan, and M. P. Hawkins. 1996. Age and geochemistry of basement and alkalic rocks of Malaita and Santa Isabel, Solomon Islands, southern margin of Ontong Java Plateau. *Journal of Petrology* 37: 361-394.
- Tucker, A. B. 1998. Systematics of the Raninidae (Crustacea: Decapoda: Brachyura), with accounts of three new genera and two new species. *Proceedings of the Biological Society of Washington* 111: 320-371.
- Van Straelen, V. 1936. Crustacés Décapodes nouveaux ou peu connus de l'époque Crétacique. *Bulletin du Musée Royal d'Histoire Naturelle de Belgique* 12(45): 1-49.
- Vega, F. J., and R. M. Feldmann. 1991. Fossil crabs (Crustacea: Decapoda) from the Maastrichtian Difunta Group, Northeastern Mexico. *Annals of Carnegie Museum* 60(2): 163-177.
- , ———, and F. Sour-Tovar. 1995. Fossil crabs (Crustacea: Decapoda) from the Late Cretaceous Cárdenas Formation, East-Central Mexico. *Journal of Paleontology* 69(2): 340-350.
- , T. Nyborg, G. Kovalchuck, F. Etayo-Serna, J. Luque, A. Rojas-Briceño, P. C. Patarroyo, H. Porras-Múzquiz, A. Armstrong, and L. Garibay. 2010. On some Panamerican Cretaceous crabs (Decapoda: Raninoidea). *Boletín de la Sociedad Geológica Mexicana* 62(2): 263-279.
- Wang, Y. 1981. Late Lower Cretaceous fossil Decapoda from Lhasa Region, Xizang, pp. 349-354. In, *The Scientific Expedition to the Qinghai-Xizang Plateau (compiler)*. Vol. 198. *Palaeontology of Xizang*. Vol. 3. Science Press, Beijing.
- Waugh, D. A., R. M. Feldmann, and C. E. Schweitzer. 2009. Systematic evaluation of raninid cuticle microstructure. *Bulletin of the Mizunami Fossil Museum* 35: 15-41.
- Weller, S. 1905. The fauna of the Cliffwood (N. J.) Clays. *Journal of Geology* 13: 324-337.
- . 1907. A report on the Cretaceous paleontology of New Jersey. *Geological Survey of New Jersey, Paleontological Survey IV*: 846-853.
- Wilson, P. A., and R. D. Norris. 2001. Warm tropical ocean surface and global anoxia during the Mid-Cretaceous period. *Nature* 412: 425-429.
- Woods, H. 1909. A monograph of the Cretaceous Lamellibranchia of England, parts 5 and 6. *Paleontographical Society*: 181-260, pl. 28-44.
- Wright, C. W. 1997. New information on Cretaceous crabs. *Bulletin of the Natural History Museum, London* 53: 135-138.
- , and J. S. H. Collins. 1972. British Cretaceous crabs. *Palaeontographical Society Monographs* 126(533): 1-113.
- Yazdi, M., A. Bahrami, and F. J. Vega. 2009. Albian decapod Crustacea from Southeast Isfahan, Central Iran-Kolah-Qazi area. *Bulletin of the Mizunami Fossil Museum* 35: 71-77, 2 pls., 3 figs.

RECEIVED: 2 October 2011.

ACCEPTED: 3 November 2011.