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Taxonomy, Biogeography and Phylogeny of Cretaceous Frog Crabs (Crustacea: Decapoda: Brachyura) from the Neotropics

par

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Ce mémoire intitulé :

Taxonomy, Biogeography and Phylogeny of Cretaceous Frog Crabs (Crustacea: Decapoda: Brachyura) from the Neotropics

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Résumé

Le but du présent travail est d'apporter la preuve paléontologique mettant en évidence que le clade Raninoida était bien établi dans le Néotropique durant la période Crétacée, où il était représenté par les plus anciennes familles ou par quelques-uns des plus anciens membres des plus anciennes familles. Je décris des taxa raninoïdiens ou similaires, incluant Archaeochimaeridae n. fam. et *Archaeochimaera macrophthalma* n. gen. n. sp., du Cénomanien supérieur (~95 Ma.) de Colombie (Chapitre 3), *Planocarcinus* n. gen., *Planocarcinus olssoni* (Rathbun, 1937) n. comb. et *Notopocorystes kerri* n. sp., de l'Aptien supérieur (~115 Ma.) de Colombie (Luque et al., accepté) (Chapitre 2). Ces taxa nouveaux, plus la présence de *Cenomanocarcinus vanstraeleni* Stenzel, 1945, dans l'Albien supérieur de Colombie (Vega et al., 2010), et d'*Araripecarcinus ferreirai* Martins-Neto, 1987, dans l'Albien du Brésil (Luque et al., en cours) (Chapitre 4), représentent certains des plus anciens signalements de quatre des sept familles raninoïdiennes, au moins, connues à ce jour. La nouvelle famile Archaeochimaeridae se présente comme le groupe frère du clade Raninidae + clade Symethidae. Cependant, la combinaison unique de caractères primitifs, dérivés et homoplasiques est inégalable chez les Raninoida, et, en fait, chez les autres sections de crabes podotrèmes. Alors que les taxa raninoïdiens du Crétacé sont bien connus aux latitudes élevées, les signalements en Amérique du Sud tropicale sont rares et épars, avec pour résultat de considérables distorsions pour traiter des importantes questions biogéographiques et phylogénétiques. Sur la base de données taxonomiques, paléobiogéographiques et cladistiques, une ré-appréciation des toute premières distributions spatio-temporelle des “crabes grenouilles” est proposée, avec pour objet de contribuer à une plus large compréhension de la diversité, phylogénie et évolution des premiers brachyoures au cours des âges.

Mots-clés : Raninoida, phylogénie, taxonomie, paléobiogéographie, Néotropique.

Abstract

The aim of the present work is to present new paleontological evidence that depicts the clade Raninoida well established in the Neotropics during Cretaceous times, as represented by the oldest, or some of the oldest members of its earliest families. I describe raninoid and raninoidid-like taxa including Archaeochimaeridae n. fam., and *Archaeochimaera macrophthalma* n. gen. n. sp., from the upper Cenomanian (~95 Ma.) of Boyacá, *Planocarcinus* n. gen., *Planocarcinus olssoni* (Rathbun, 1937) n. comb., and *Notopocorystes kerri* n. sp., from the upper Aptian (~115 Ma.) of Santander. These newly described taxa, plus the occurrence of *Cenomanocarcinus vanstraeleni* Stenzel, 1945, in the upper Albian of Boyacá (Vega et al., 2010), and *Araripecarcinus ferreirai* Martins-Neto, 1987, in the lower Albian of Brazil (Luque et al., in progress), represent the oldest records of, at least, four out of seven raninoidid families known to date. The new family Archaeochimaeridae, stands as the sister taxon to Raninidae + Symethidae clade. However, its unique combination of primitive, advanced, and homoplasic traits is matchless within Raninoida, and in fact, with the remaining podotreme sections. While Cretaceous raninoid taxa from higher latitudes are well known, records from the tropical South America are scarce and sparse, resulting in considerable biases when attempting to address major biogeographic and phylogenetic questions. Based on taxonomic, paleobiogeographic and cladistic information, some reconsideration of the early spatio-temporal distributions of frog crabs are proposed, with the aim of contributing to a broader understanding of the diversity, phylogeny, and evolution of early brachyuran crabs throughout time.

Keywords : Raninoida, phylogeny, taxonomy, paleobiogeography, Neotropics.

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A1	Antennula
A2	Antenna
Ba	Basis
Bcg	Branchiocardiac groove
Blr	Branchial longitudinal ridge
Br	Branchial ridge
Ca	Carpus
cd	Crista dentata
Cg	Cervical groove
CI	Consistency Index
cxP1-cxP3	Coxa of cheliped to pereiopod 3
Da	Dactylus
Es5-Es6	episternites 5 to 6
Exg	Exognath
Gp	Gonopod
Is	Ischium
Le	Left eye
lm	Linea media
Lr	Mesial longitudinal ridge
Ma	Mandibula
mn	Manus, or palm
Me	Merus
Mlr	Mesial longitudinal ridge
Mtg	Metagastric/urogastric pits
Mxp2-Mxp3	Second and third maxillipeds
OAE	Oceanic Anoxic Event
Or	Orbital ridge
P1	Cheliped, or claw
P2-P5	Pereiopods, or walking legs, 2 to 5
Pcr	Pre-cervical ridge
Pfr	Post-frontal ridge
Pl	Pleon
Pl1-Pl6	Pleonites, or abdominal somites, 1 to 6
Por	Post-orbital ridge
Pr	Propodus
Px	Pollex, or fixed finger
R	Rostrum
RC	Rescaled Consistency Index
Re	Right eye
RI	Retention Index
S1-S7	Sternite 1 to 7
S5r	Sternite 5 longitudinal ridge
st	Spermatheca
Sc	Sternal crown
Sf	Sternal furrow
T	Telson

TCC	Tethyan Circumtropical Current
Tf-I	Taphofacies I: crustacean-rich surface
Tf-II	Taphofacies II: appendage-rich surface
Tf-III	Taphofacies III: scattered debris surface
TL	Treelength

To Kecia and Livia, my source of inspiration,
strength, encouragement and perseverance.
To them, my eternal thanks, my eternal love.

1. INTRODUCTION

Raninoid crabs, also called “frog crabs”, are an unusual clade within the Infraorder Brachyura (true crabs). This group of fully marine podotreme crabs has been studied since Linnean times, but their particular body plan has merited them different systematic affiliations with different eubrachyuran groups (calappids, leucosiods), other podotreme sections (cyclodorippoids and dromiaceans), anomurans and macrurans, and even apterous insects (Linnaeus, 1758; Lamarck 1801; 1837; Latreille, 1806; Milne Edwards, 1837; Dana, 1852; Ortmann, 1892; Alcock, 1896; Bourne, 1922; Glaessner, 1960, 1969; Števčić, 1973, 1995, 1998). Their morphology is characterized by a fusiform and poorly ornamented body, a narrow sternum, and an exposed (rather than concealed beneath the carapace) abdomen (Fig. I). The legs are often flattened, and the fifth pair of walking legs is generally reduced and carried sub-dorsally (Bourne, 1922; Goeke, 1981; Poore, 2004; Števčić, 2005; Dawson and Yaldwing, 2000) (Figure 1.1). Once considered to be primitive traits, these features in raninoids have also been purported to be adaptations to a burrowing lifestyle, convergent between several non-related superfamilies of anomurans and brachyuran crabs (Glaessner, 1969; Števčić, 1973; Williams, 1984; Tucker, 1995; Gaten, 1998; Dawson and Yaldwin, 2000).

Currently, five fossil and extant subfamilies are recognized within the family Raninidae De Haan, 1839: 1) Cyrtorhininae Guinot, 1993; 2) Lyreidinae Guinot, 1993; 3) Notopoidinae Serene and Umali, 1972; 4) Ranininae De Haan, 1841; and 5) Raninoidinae Lörenthey, 1929 in Lörenthey and Beurlen, 1929 (Guinot, 1993; Tucker, 1995; Števčić, 2005; Ng et al., 2008; De Grave et al., 2009). Symethidae Goeke, 1981, and Palaeocorystidae Lőrenthey, 1929 in Lőrenthey and Beurlen, 1929, once considered as subfamilies within Raninidae, have been granted full family status based on their considerably different morphologies (Goeke, 1981; Guinot, 1993; Tucker, 1998; Guinot et al., 2008; Karasawa et al., 2011).

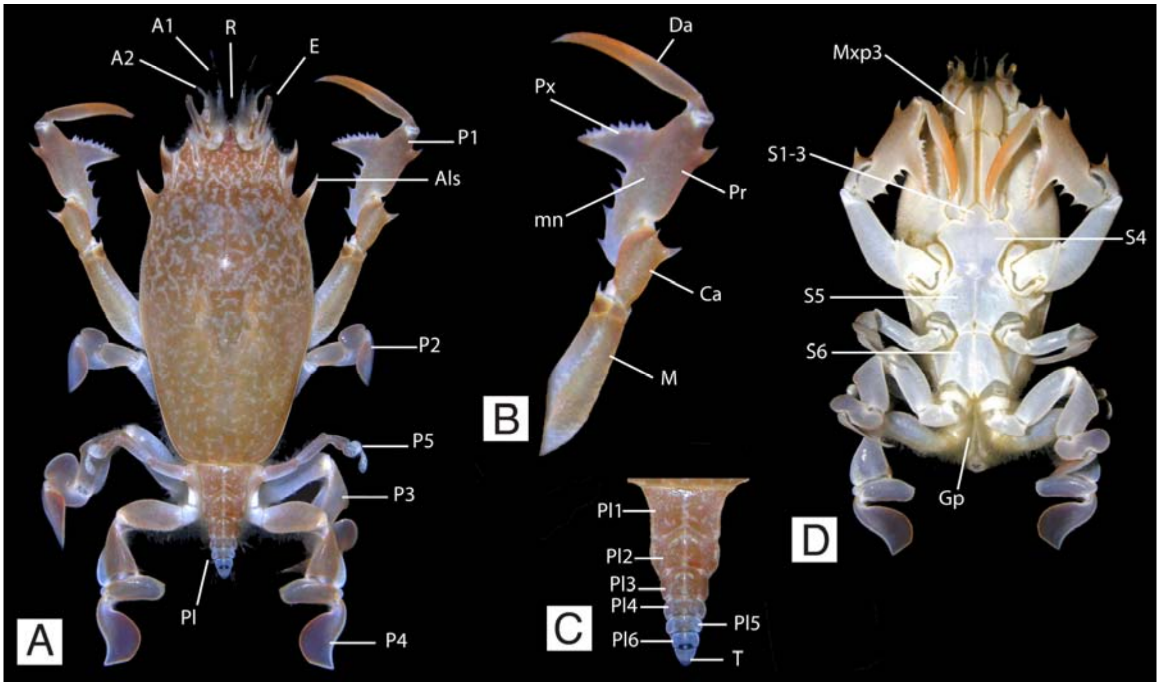

Figure 1.1. General morphology of a frog crab. A-D, Brachyura, Raninoidea, Raninidae, *Raninoides benedicti* (Rathbun, 1935), Panama (photos by Arthur Anker), male. A, dorsal view, showing the smooth and unornamented dorsal carapace, the fronto-orbital margin, the chelipeds and pereiopods 2-5. B, close-up of right cheliped showing the main parts. C, pleon showing the unfused pleonites and the lack of uropods or uropodal plates. D, ventral view showing the thoracic sternum, the third maxillipeds, and the gonopods. A1: antennula; A2: antenna; Als: anterolateral spine; Ca: carpus; Da: dactulus; E: eye; Gp: gonopods; Me: merus; mn: manus; P1: cheliped or claw; P2-P5: pereiopods 2 to 5; Pl: pleon; Pl1-6: pleonites 1 to 6; Pr: propodus; Px: pollex; R: rostrum; S1-6: sternites 1 to 6; T: telson.

Palaeocorystidae is exclusively known from the Cretaceous, and has been typically regarded as the rootstock of the clade Raninidae + Symethidae (Bourne 1922; Glaessner 1960; Tucker 1998; Guinot et al., 2008). However, the most ancient raninoid families (Camarocarcinidae Feldmann, Li, and Schweitzer, 2007, Cenomanocarcinidae Guinot, Vega, and Van Bakel, 2008, and Necrocarcinidae Förster, 1968) are morphologically very different from their fusiform relatives. They are instead more reminiscent of other true crab body plans with very ornamented, wide carapaces, a wider thoracic sterna, and the abdomen pressed against the chest, usually assisted by locking mechanisms.

The scarce, sparse, and often fragmentary fossil record of ancient raninoids complicates our understanding of the phylogenetic and morphological relationships between the two principal raninoidid architectures. Herein, based on new paleontological material from the Cretaceous of Colombia, South America, and the re-examination of some ancient raninoids from the equatorial Neotropics, I attempt to provide a comprehensive analysis of the morphologic diversity, the phylogenetic affiliations, and evolutionary trends of raninoid lineages throughout time.

A comparison of stratigraphic data with phylogenetic and biogeographic data indicates that: 1) some of the oldest frog crabs (Chapter 2), including a new monotypic family of frog-like crabs (Chapter 3), have their oldest fossil records in the Neotropics; 2) there is a general trend of loss of carapace ornamentation and carapace elongation through time, from broad, heavily ornamented and sculpted carapaces during the Cretaceous, to fusiform, weakly ornamented and smooth carapaces in the Tertiary and modern times; and 3) contrary to what might be expected from an 'incomplete' fossil record, extant raninoids are underrepresented in modern oceans, with only 2 families and 12 genera known from living species.

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2. Article: The oldest Frog Crabs (Decapoda: Brachyura: Raninoida) from the Aptian of Northern South America

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

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Abstract

Raninoida, 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 Raninoida 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.

Introduction

The monophyletic Raninoida 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 Lőrenthey (in Lőrenthey 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 carapace 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) (Figure 2.1A), 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) (Figure 2.1B), 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) (Figure 2.1C).

During the Albian (~112-99.6 Ma), the two major raninoid morphological groups diversified and spread worldwide, with representatives of four families, ten genera, and 31 species known from North America, northern Central America, northern South America, Europe, the Middle East, China, Japan, New Zealand, and Madagascar (Appendix: Table I) 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 (Figure 2.2A). 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) (Figure 2.2B), 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 eleganteante* 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,

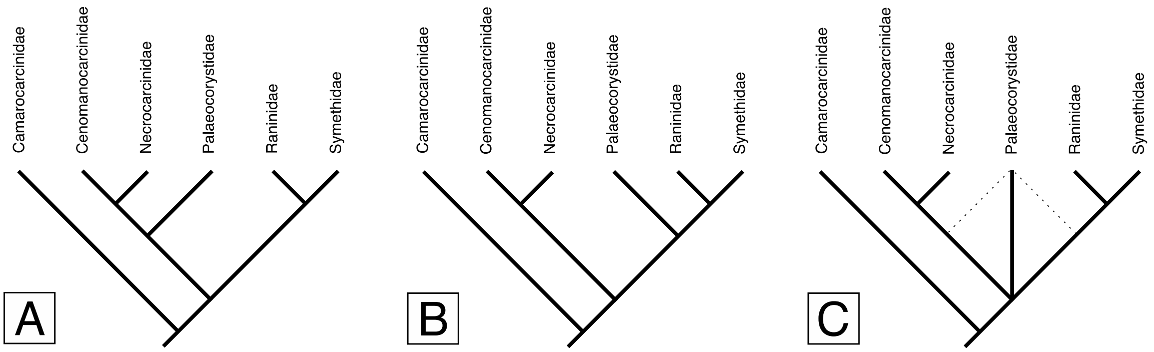

Figure 2.1. Schematic cladistic trees for the Section Raninoida, showing the different hypotheses regarding the affiliation of the family Palaeocorystidae. A, Palaeocorystidae allied to the Cenomanocarcinidae + Necrocarcinidae clade; B, Palaeocorystidae allied to the Raninidae + Symethidae clade; C, Palaeocorystidae in an unresolved polytomy between the Cenomanocarcinidae + Necrocarcinidae and the Raninidae + Symethidae clades. Base tree topology for the Raninoida clade after Karasawa et al. (2011: fig. 3).

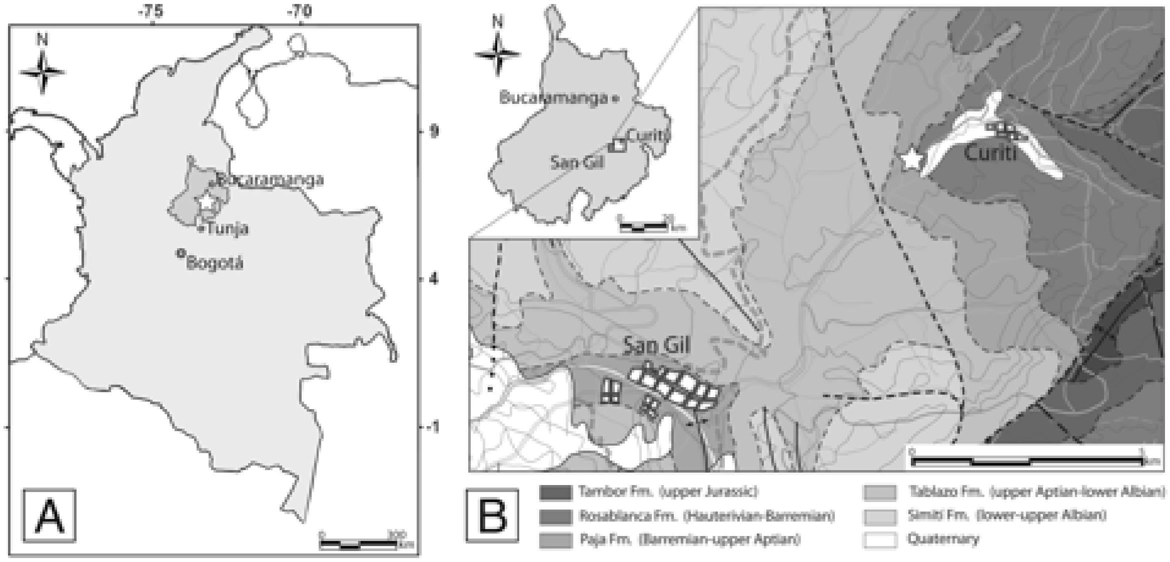

Figure 2.2. Locality maps. A, generalized map of Colombia, South America, showing the location of the study area (white star) in the Department of Santander, Cordillera Oriental, where Planocarcinus olssoni n. comb., and Notopocorystes kerri n. sp. were recovered; B, geological map of the study area 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).

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 (Figure 2.2B), 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.

Order Decapoda Latreille, 1802
Infraorder Brachyura Linnaeus, 1758
Section Raninoida De Haan, 1839
[in De Haan, 1833-1850]
Superfamily Raninoidea De Haan, 1839
[in De Haan, 1833-1850]
Family 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 branchiocardiac 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) (Figure 2.3A-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

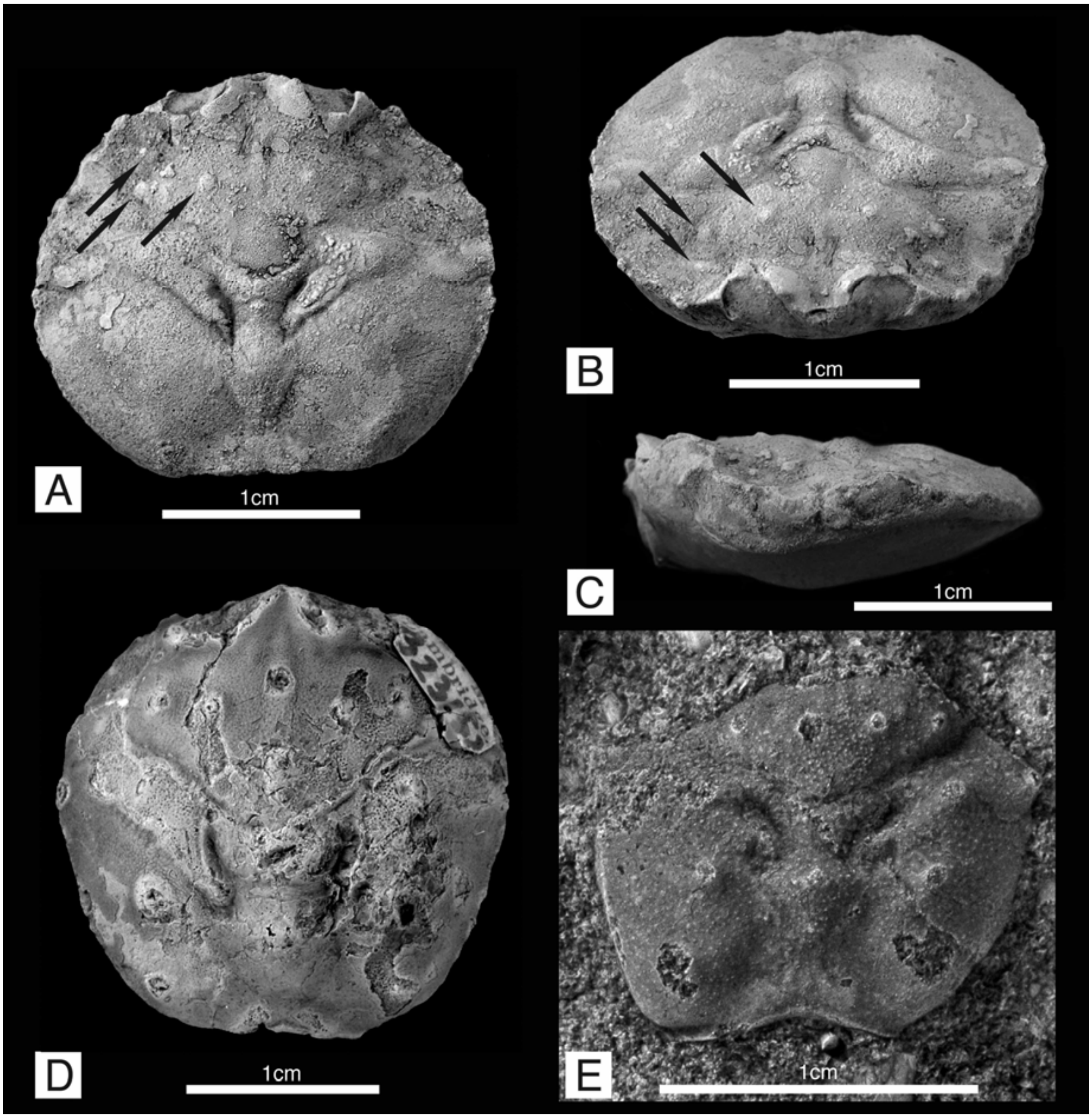

Figure 2.3. Raninoidea, Necrocarcinidae. A-C, *Planocarcinus olssoni* (Rathbun, 1937) n. comb., holotype USNM 495104, upper Aptian, Colombia; A, carapace in dorsal view, showing the general roundish outline and dorsal carapace regions. Arrows indicate the three small tubercles on protogastric region; 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.

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) (Figure 2.3D), the generally circular carapace nearly as wide as long, bearing complete and somewhat parallel cervical and branchiocardiac 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 concave 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; Larghi, 2004; Van Straelen, 1936; Stenzel, 1945; Roberts, 1962; Wright and Collins, 1972; Bishop, 1983a; Collins and Williams, 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; Števčić, 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 eubrachyuran 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.**

Figure 2.3A-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, Porras-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. Anteriormost 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 (Figure 2.3A, 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 (Figure 2.3A-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* (Figure 2.3E), 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 Cenomanian 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.

Family 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. bituberculatu*s 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. ripleyensis* 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.**

Figure 2.4 A-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.

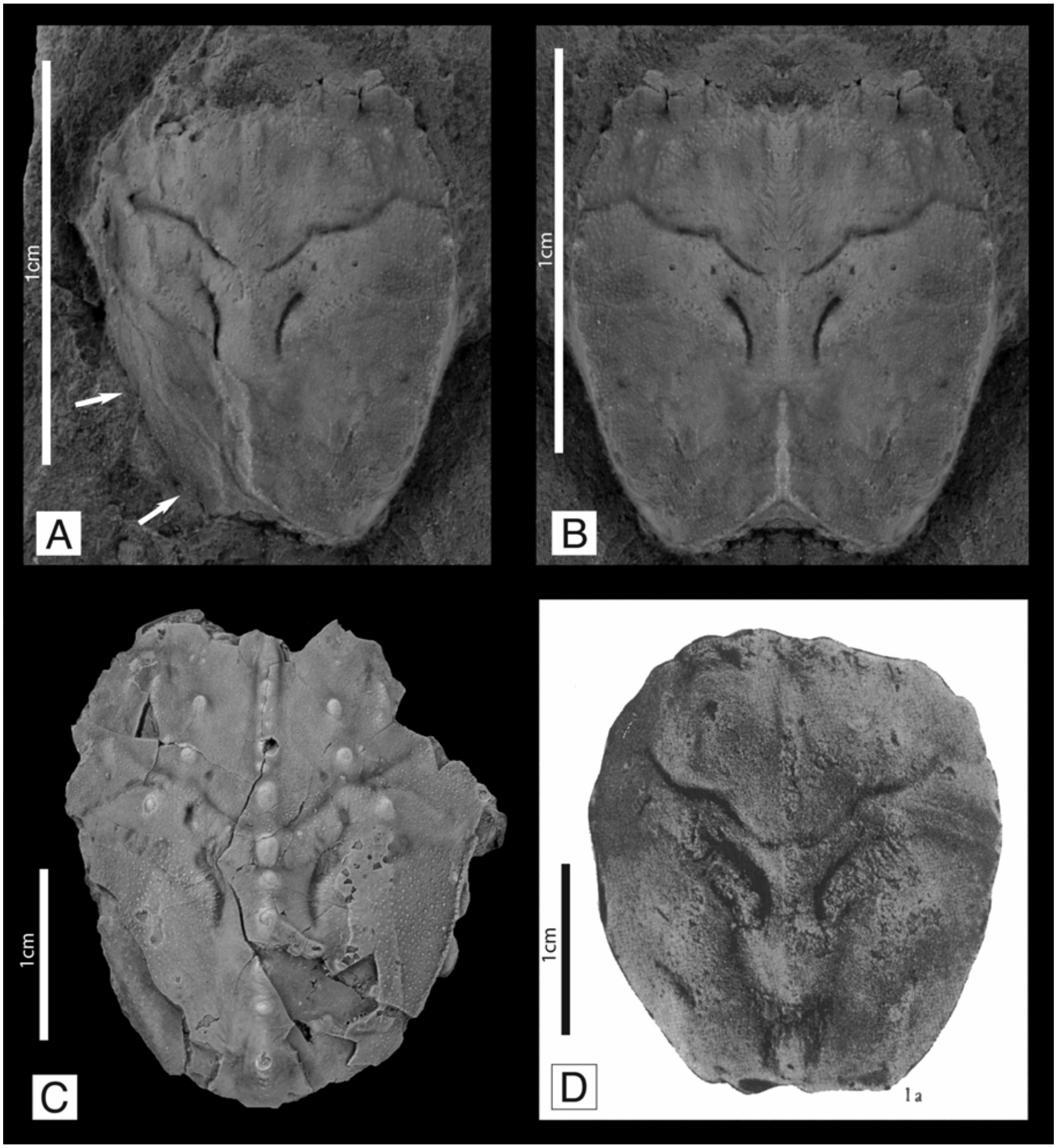

Figure 2.4. Raninoidea, Palaeocorystidae. A-B, *Notopocorystes kerri* n. sp. holotype IGM p881128, upper Aptian, Colombia; A, carapace in dorsal view, with arrows indicating the distorted left posterolateral and posterior carapace margins; B, mirror image of the well preserved right half of the dorsal carapace. C, *Notopocorystes stokesii* (Mantell, 1844), hypotype (BMNH) In. 39366, dorsal carapace, lower Albian, England. 4: *Notopocorystes xizangensis*, digital image from Wang (1981, pl. 2, fig. 1a), Albian, Xizang, China.

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 to 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 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 illustrations 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). *Cenocorystes* Collins and Breton, 2009, originally considered a palaeocorystid, has been recently allied with Raninoidinae Lőrenthey (in Lőrenthey 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 *Cretacoranina.* 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). *Cretacoranina* 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 (Figure 2.4A-B). In *N. stokesii* (Mantell, 1844), from the Albian of England (Figure 2.4C), 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) (Figure 2.4D), 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 assignation.

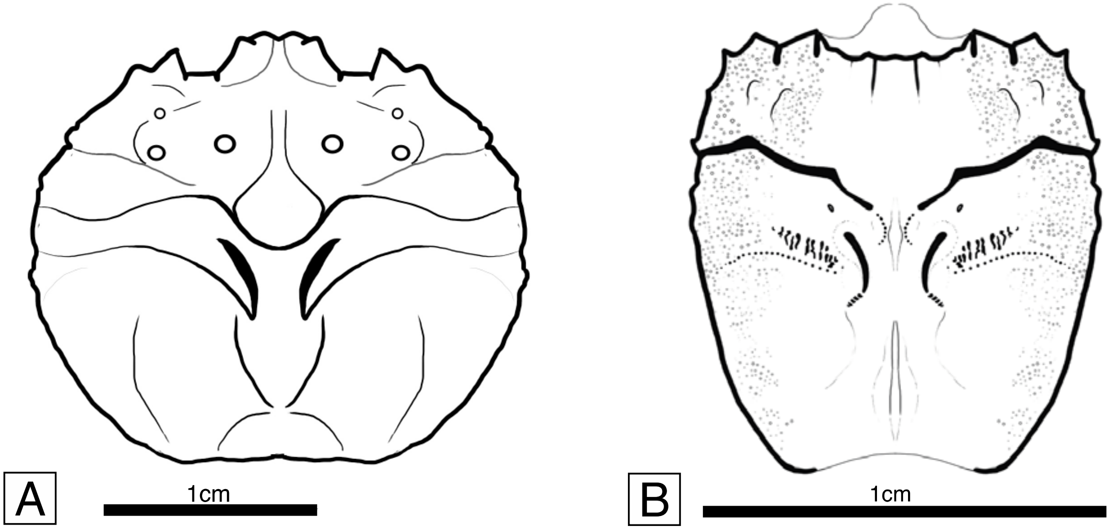

Figure 2.5. Camera lucida line drawings of upper Aptian raninoids from Colombia, illustrated in figs. 3A and 4A-B. A, *Planocarcinus olssoni* n. comb., dorsal carapace. B, *Notopocorystes kerri* n. sp. Mirror drawing of well preserved right half of dorsal carapace (fig. 4A).

Discussion

Paleobiogeography

Planocarcinus olssoni (Figure 2.5A) and *Necrocarcinus undecimtuberculatus* (Figure 2.3E), 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 (Appendix Table I; Figure 2.6A), 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. (Figures 2.5B, 2.7A). 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 (Figure 2.6A, Figure 2.7A). In sharp contrast, the morphological diversity (4 fam., 10 gen., 31 spp.) (Appendix Table I) and cosmopolitan distribution reached during the Albian (Figures 2.6B, 2.7B), 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_2, and CH_4 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 (Tejada et al., 1996; Mahoney et al., 1993; Larson, 1997; Larson and Erba, 1999; Larson and Kincaid, 1996), 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 (Figure 2.6, Figure 2.7). 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; Berggren and Hollister, 1974; Gordon, 1973; 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 *Araripecarcinus* 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.

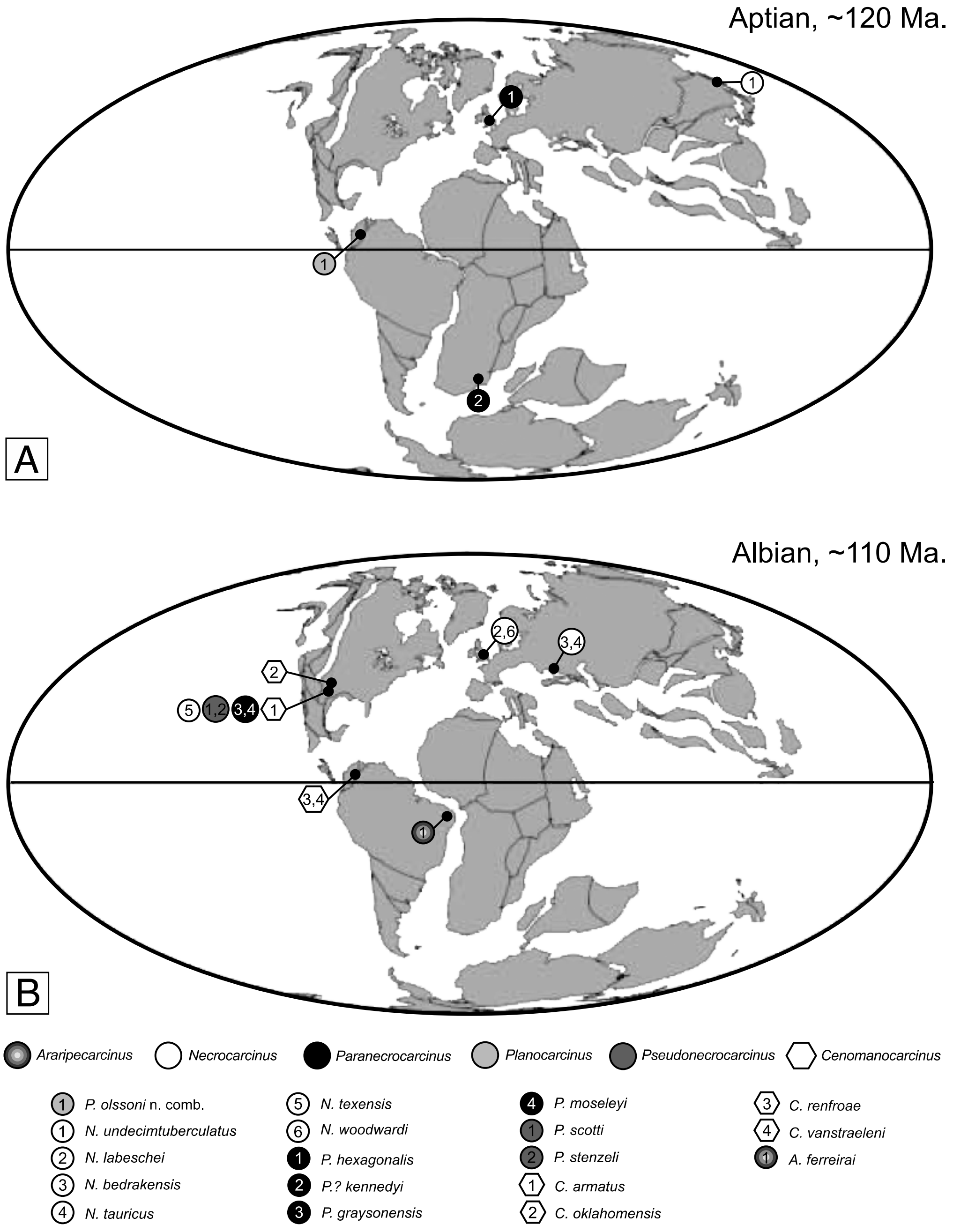

Figure 2.6. Paleobiogeographic distribution of the early Cretaceous raninoids with ‘necrocarcinid-like’ body plan, wider than long or about as wide as long. A, Aptian, ~120 Ma; B, Albian, ~110 Ma. ?Necrocarcinidae: *Araripecarcinus* Martins-Neto, 1987 (gradient circle). Necrocarcinidae: *Necrocarcinus* Bell, 1863 (white circle); *Paranecrocarcinus* Van Straelen, 1936 (black circle); *Planocarcinus* n. gen. (light gray circle); *Pseudonecrocarcinus* Förster, 1968 (dark gray circle). Cenomanocarcinidae: *Cenomanocarcinus* Van Straelen, 1936 (white hexagon). Taxa listed in Table I. Base maps modified after Scotese (2004).

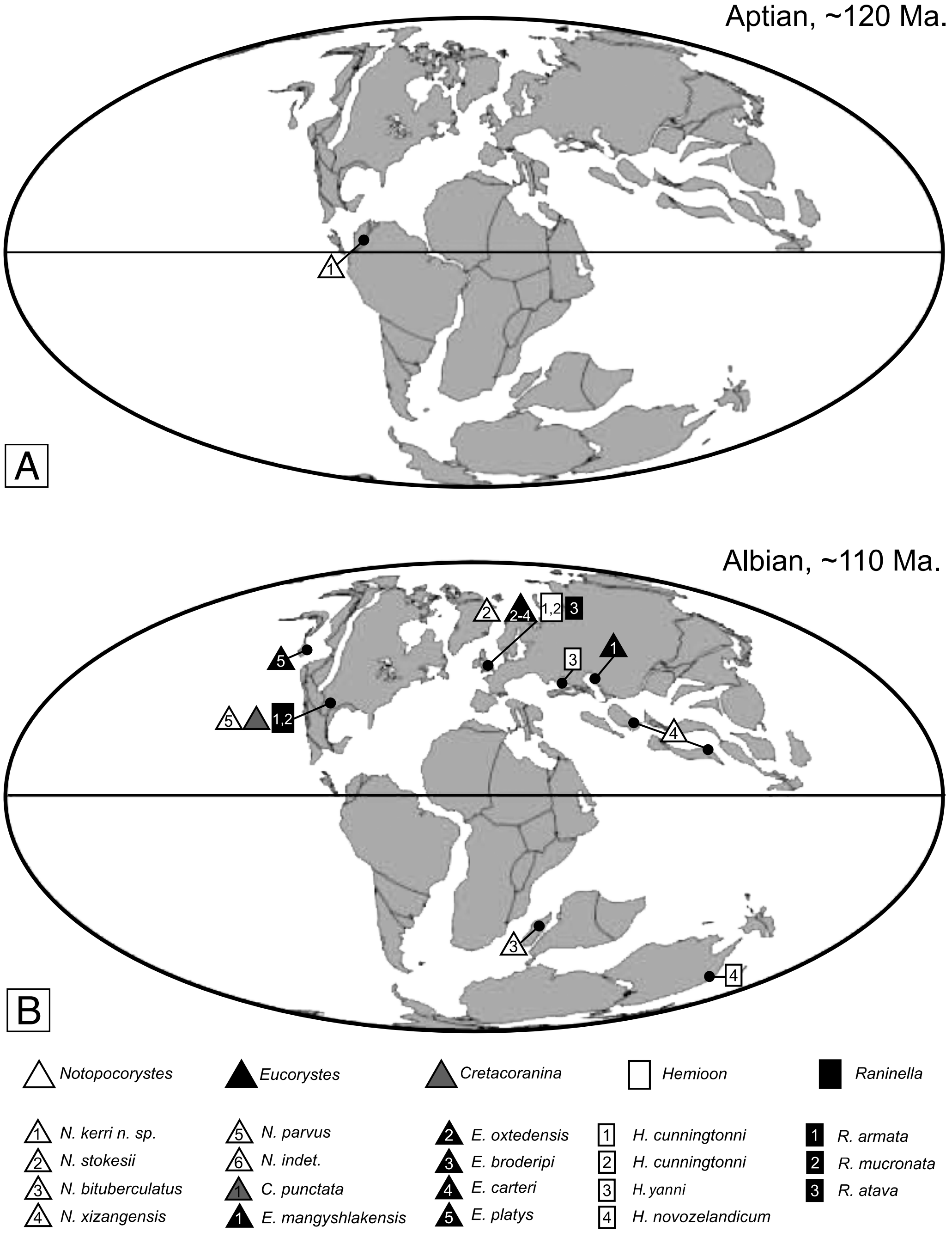

Figure 2.7. Paleobiogeographic distribution of the early Cretaceous raninoids with 'raninid-like' body plan, longer than wide. A, Aptian, ~120 Ma; B, Albian, ~110 Ma. Palaeocorystidae: *Cretacoranina* Mertin, 1941 (gray triangle); *Eucorystes* Bell, 1863 (black triangle); *Notopocorystes* McCoy, 1849 (white triangle). Raninidae: Lyreidinae: *Hemioon* Bell, 1863 (white rectangle). Ranininae: *Raninella* A. Milne Edwards, 1962 (black rectangle). Taxa listed in Table I. Base maps modified after Scotese, 2004.

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 (Figure 2.1A), 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 pereiopods 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 (Figure 2.1B) 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 (Figure 2.8). 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 (Figure 2.1C) 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 living relatives, whereas the rootstock of Raninidae may lie closer to the most derived Palaeocorystidae, e.g., *Cretacoranina*.

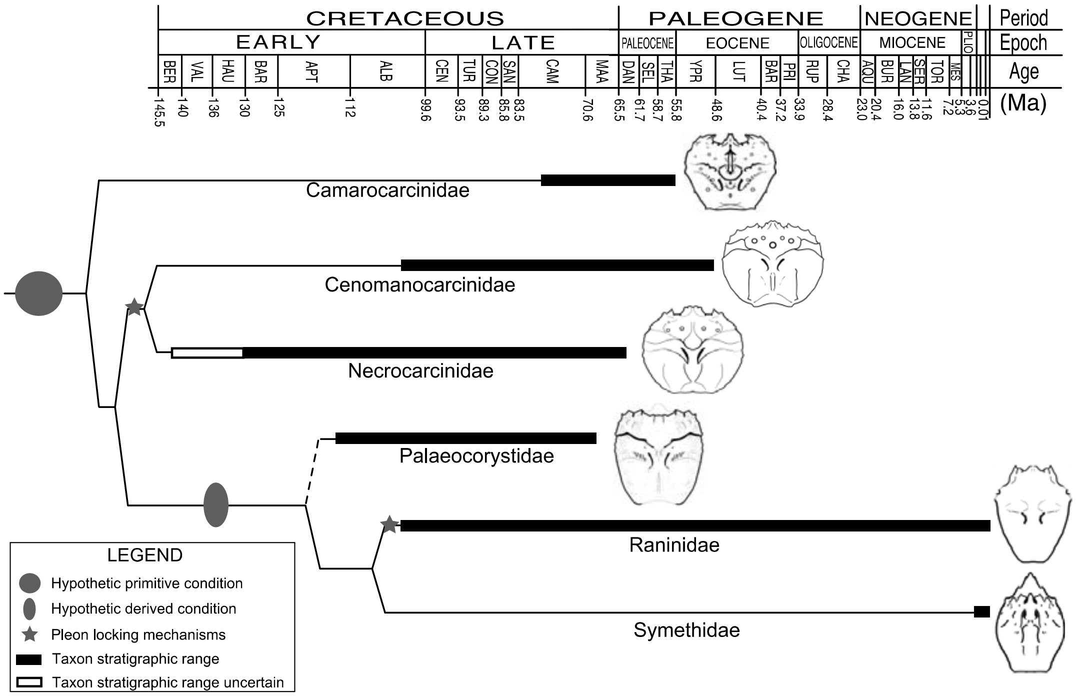

Figure 2.8. Chronostratigraphic distribution of the six known fossil and extant families within the Section Raninoida, as indicated by their current First Appearance Datum (FAD) and Last Appearance Datum (LAD). Camarocarcinidae: *Cretacocarcinus smithi* Feldmann, Li and Schweitzer, 2007, Campanian, US (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 bispinous* 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.
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3. Article: Archaeochimaeridae: a new Family of Enigmatic Crabs (Crustacea: Decapoda: Brachyura) from the Cretaceous of Colombia

Javier Luque, Rodney M. Feldmann, Christopher B. Cameron and Carlos Jaramillo

Article in progress

Abstract

A new family of enigmatic crabs, Archaeochimaeridae, is erected based on forty-two specimens collected from crustacean-rich surfaces from the Cenomanian (~94 million years ago) Churuvita Group at the Nocuatá Section, Department of Boyacá, Colombia. The exceptional degree of preservation of *Archaeochimaera macrophthalma* n. gen. n. sp., permits the description of complete dorsal and ventral features, claws, all walking legs, muscular tissue, antennae, sexually dimorphic pleon and pleopods, mouthparts, and large compound eyes bearing facets, thus allowing comparison with fossil and extant decapods. A brachyuran affinity is supported by the possession of a folding symmetric pleon, an absence of articulated rings, short antennae and antennulae located between the eyes, only one pair of chelae, therefore pereiopods 2-5, or walking legs, are achelate, and the last pereiopod visible dorsally. However, the unusual body plan, including a unique sternal configuration, postfrontal ornamentation, aberrant optical characters, and a combination of primitive and advanced traits, is matchless among any known fossil or extant superfamily of true crabs, obscuring the animal's phylogenetic position. Affiliation of Archaeochimaeridae with the Section Raninoida, particularly the Raninidae + Symethidae clade, is suggested by the elongated carapace, and a telson lying behind the base of the third pereiopods. However, similar fusiform body plans have evolved independently at least five times in burrowing Anomura and Brachyura, and many of the diagnostic traits of Archaeochimaeridae present a high degree of homoplasy within Brachyura. Functionally, its dorsal and ventral carapace, mouthparts, limbs and eyes, suggest an agile marine burrower and swimmer, well suited for predation and scavenging. *Archaeochimaera macrophthalma* is one of the most, if not the most, complete fossil brachyuran crabs discovered to date, enhancing our understanding of the role of the Neotropics in the origin and diversification of primitive crab lineages during Cretaceous times.

Keywords: *Archaeochimaera*, body plan, Brachyura, Cretaceous, Neotropics, podotreme.

Introduction

The Order Decapoda is one of the most diverse and widespread animal groups, exhibiting unmatched morphological disparity (e.g., Martin and Davis, 2001; Dixon et al., 2003; Feldmann, 2003; Števčić, 2005). Decapod crustaceans account for more than 14,600 extant species, and more than 3,200 known as fossils (De Grave et al., 2009; Feldmann and Schweitzer, 2010; Schweitzer et al., 2010). Among decapods, brachyuran crabs, also called 'true' crabs, are the most derived clade, originating during the Early to Middle Jurassic (Schweitzer and Feldmann, 2010a), and rapidly diversifying during the Late Jurassic and Cretaceous (~161 to 65 M.y.) (Feldmann and Schweitzer, 2006), leading to a burst of morphological diversification and broader niche occupation than previously expected (Schweitzer and Feldmann, 2010b, 2011a; Karasawa et al., 2011). Unfortunately, while Jurassic and Cretaceous brachyurans and their distributions are well known for the northern Tethys and higher hemispheres, reported occurrences in the southern Tethys, especially in the tropical South America are few.

The general lack of knowledge of crustacean paleontology from the equatorial Neotropics may result in considerable biases when attempting to address the origin, evolution and paleobiogeography of the group. This scarcity of reports could be related to the small number of researchers working on fossil decapods from tropical regions, the relatively low abundance of well-exposed outcrops in tropical areas, and the asymmetry of landmasses between the Northern and Southern hemispheres, restricting the area for potential outcrops with fossil crustaceans in the latter (Feldmann and Schweitzer, 2006). Such is the case of Colombia, South America, a tropical country with complex tectonic settings and outcrops that are usually poorly exposed. Despite this, Colombia has a very high paleontological richness but with a rather poor representation of fossil crustaceans. In particular, for podotreme crabs (i.e. those true crabs with sexual openings at the base of legs in both male and female), the only two genera recognized so far are: *Cenomanocarcinus* Van Straelen, 1936, and *Planocarcinus* Luque, Feldmann, Schweitzer, Jaramillo and

Cameron, in press, (Rathbun, 1937; Feldmann et al., 1999; Vega et al., 2007; 2010; Guinot et al., 2008; Luque et al., in press).

An upper Cenomanian, middle Turonian fossiliferous locality, with excellent preservation of marine arthropod fauna from crustacean-rich surfaces, has been discovered in Central Colombia (Figure 3.1). This assemblage includes the first Cretaceous cumaceans (Gerken and Luque, in progress), a few penaeid and ?caridean shrimps, thalassinids, *Cenomanocarcinus*, and the enigmatic brachyuran crab *Archaeochimaera macrophthalma* n. gen. n. sp. (Figure 3.2). The preservation of the *Archaeochimaera* specimens is exceptional, permitting the description of virtually the entire organism, from complete dorsal and ventral features, to extraordinary large compound eyes bearing facets. The degree of preservation of these specimens allows for comparison with fossil and extant decapods, which supports a brachyuran podotreme affinity based on diagnostic traits. Functionally, its dorsal and ventral carapace, mouthparts, limbs and eyes, suggest an agile marine burrower and swimmer, well suited for predation and scavenging. Despite its small size (~7 mm to ~16 mm) *Archaeochimaera* is the largest macrofaunal element in the assemblage. The relatively high abundance of well-preserved archaeochimaerid crabs and cumaceans might be related to a combination of conditions which would increase the chance of preservation of remains, such as: high availability of food, sporadic mass mortality events, low scavenging and minimal bacterial decay of corpses and exuviae, and a benthic burrowing lifestyle.

Among podotremes, affiliation of Archaeochimaeridae n. fam. with the Section Raninoida, particularly the Raninidae + Symethidae clade, is suggested based on the elongated carapace, principally. Nevertheless, the innovation of elongated carapaces is highly homoplasic, having evolved independently multiple times within Anomura and Brachyura, and cannot be used as a synapomorphy to unite Archaeochimaeridae with other fusiform crabs. In addition, Archaeochimaeridae lacks the two synapomorphies that unite members within the clade Raninoida; i.e. the triangular buccal cavity and the mxp3 with two planes. Furthermore, the complex set of diagnostic traits seen in *Archaeochimaera*'s body plan is matchless among any know fossil or extant presumed monophyletic clade of true crabs, but still shares synapomorphies and homoplasies with different brachyuran clades, profoundly obscuring its phylogenetic affiliation.

The mid-Cretaceous age of the monotypic Archaeochimaeridae, and its 'chimaeric' phenotype, raises the question of whether the taxon represents a primitive podotreme lineage, basal to the non-dromiacean/homoloidean clades, or conversely, a very derived, highly specialized taxon endemic to the Neotropics. Therefore, different hypotheses regarding its phylogenetic affiliation are examined, and evidence for an independent origin of the fusiform body plan within the Cretaceous podotremes is discussed.

Materials and Methods

The type series of *Archaeochimaera macrophthalma* n. gen. n. sp. was collected from carapace-rich, appendage-rich, and scattered remains surfaces in light gray, micaceous fossiliferous claystones. Specimens are generally preserved compacted dorso-ventrally, however, the thoracic sternites, pleonites, dorsal carapaces, mandibles, and even internal optical structures often show tridimensionality. Given the softness of the rocks embedding the delicate remains, the specimens were exposed using fine tungsten carbide needles and pin vises, dissecting scalpel blades, and fine pneumatic pencils, under a Nikon Eclipse 80i microscope with camera lucida, and a Leica microscope with Spotflex digital camera. Broken or fragile samples were consolidated with the cyanoacrylate adhesive Paleo Bond™ PB40, and/or stabilized with Paraloid™ B72 and EtOH 95% as the solvent. Given the very small size (microns) of the external and internal optical features, specimens preserving fine-detailed eyes were studied under Zeiss Scanning Electron Microscope (SEM) Evo 40vp under variable pressure, and Back-scattered Electron Detector (BSED) with acceleration voltages of 15 and 20kV. For regular photography, most specimens were coated with sublimated NH_4Cl prior to photographing, in order to enhance relief and fine ornaments. Sets of photographs at different focal points were taken with a Nikon Eclipse 80i + Nikon Digital Camera Dxm 1200f, Olympus SZX16® Research Stereomicroscope with a digital camera Qimaging Retiga 2000R Fast 1394, Leica with Spotflex digital camera, and a Nikon D3100 with MicroNikkor 60 mm lens. The resulting multi-layered stacks of photos were merged using the image stacking software Helicon Focus, in order to generate high-definition. The photo editing was completed in Adobe® Photoshop CS5, and figure editing in Adobe® Illustrator CS5.

Given the small size of the specimens, measurements of carapace and sclerites lengths/widths were taken in the open source software ImageJ64 1.46a, using a scale with tenths of a millimeter. In order to generate morphological reconstructions of *Archaeochimaera*, camera lucida line drawings were digitized using a Wacom® Intuos4 Pen Tablet. Digital reconstructions and animations were performed using standard polygon and UV layout techniques with the software Autodesk Maya 2009. The structure, rendering and topology of the base mesh were edited in Pixologic's Zbrush 4.0 for digital sculpting and high frequency detailing of the carapace.

A character-taxon matrix for 38 taxa and 74 dorsal and ventral characters was constructed and manipulated using the free source softwares MacClade 4.08 and Mesquite 2.75 (Maddison and Maddison, 2005; 2007), and was modified directly from the phylogenetic analysis by Karasawa et al. (2011), which stands as the most complete and up-to-date phylogenetic analysis incorporating all of the known superfamilies and families of fossil and extant podotreme crabs. The phylogenetic analysis was conducted using the softwares PAUP* 4.0b10 (Swofford, 1999), and TNT (Goloboff et al., 2003). The analysis was performed following the same parameters utilized in Karasawa et al. (2011). Bremer support was calculated under traditional search, tree bisection reconnection (TBR) on the strict consensus retained in the software, and absolute support using all trees. All characters were equally weighted and unordered.

Locality and Stratigraphy

The crustaceans were collected in the locality of Nocuatá, Pesca, Department of Boyacá, Eastern Cordillera of Colombia, 150 km northeast of Bogotá, 50 km southeast of Villa de Leiva, 5.58102° N, 73.05266° W (Figure 3.1). The Nocuatá Section is 95 m thick, and includes the uppermost part of the Churuvita Formation at the base (Segments A and B) and the lowermost part of the San Rafael Formation at the top (Segment C) (Figure 3.2). The lowermost Segment A (28 m) is composed at the base of 15.5 m of gray shales, and light gray, micaceous, fossiliferous claystones. Abundant cumaceans, some shrimps, and *Archaeochimaera macrophthalma* n. gen. n. sp. constitute the dominant macrofaunal elements in this segment (Figure 3.3). Occasional scattered fish remains are also present. The uppermost portion of Section A (12.5 m) is covered/weathered. The overlying Segment B is composed of 11 m of silty sandstones, and thick beds of white-yellowish, micaceous sandstones, representing the last occurrence of coarse-grained deposits along the section.

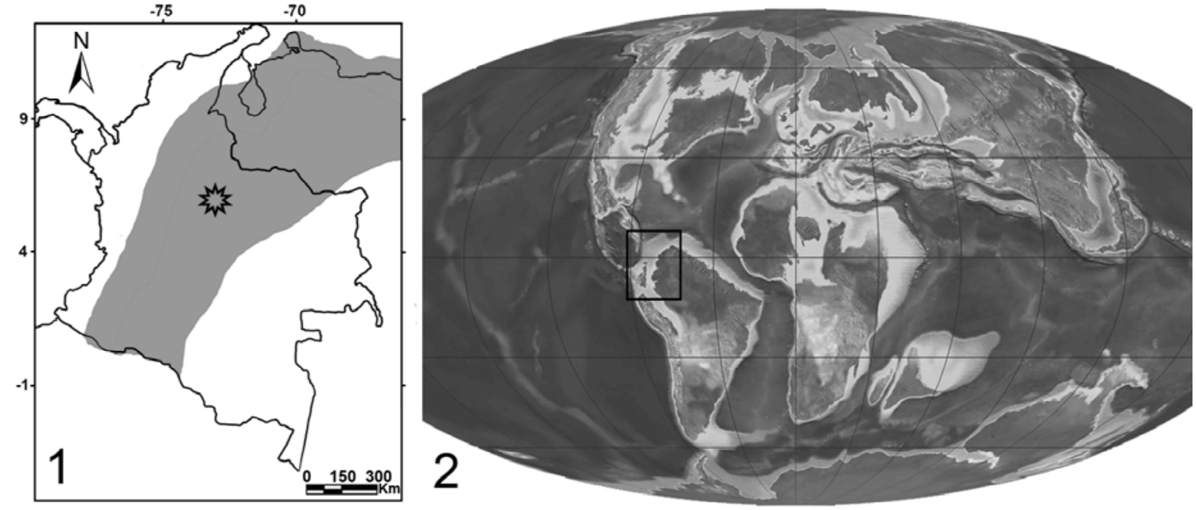

Figure 3.1.—A, Paleogeographic map of Colombia during the upper Cenomanian (~94 M.y.), showing the NNE-SSW facing epicontinental sea where the sediments containing *Archaeochimaera macrophthalma* n. gen. n. sp., at Nocuatá Section, Pesca, Department of Boyacá, were deposited (base map modified after Villamil and Arango, 1998). The black star indicates the location of the stratigraphic section. B, paleogeographic map showing the tropical setting of Colombia during Cenomanian times (base map modified after Blakey, 2006).

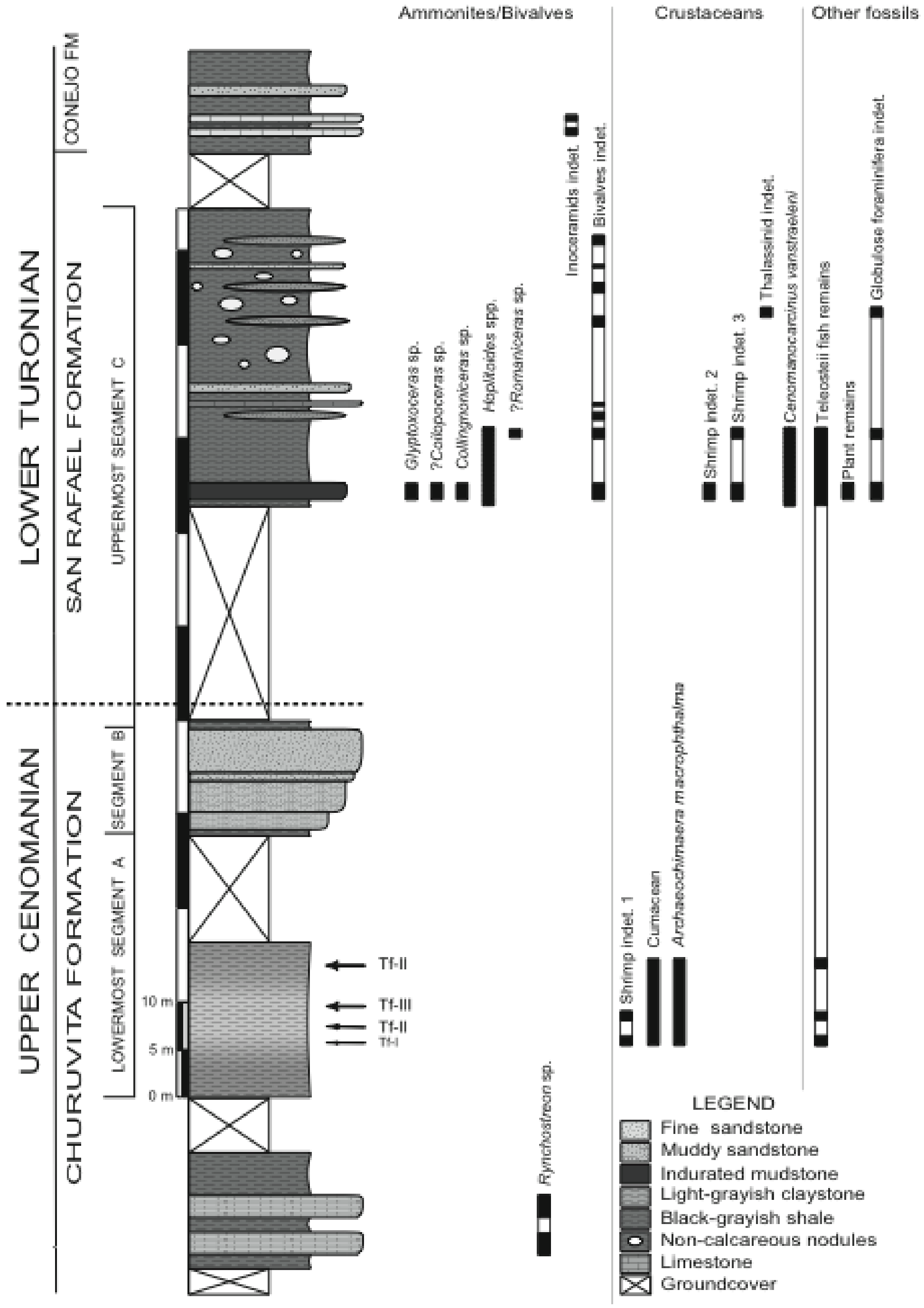

Figure 3.2. Stratigraphic column of the Cenomanian-Turonian Churuvita Group cropping out at the Nocuatá Section, Department of Boyacá, Colombian Eastern Cordillera. For each taxon, black and white columns indicate where macrofossils were recovered or not along the section, respectively. Dashed line indicates the tentative Cenomanian-Turonian boundary. Arrows denote horizons in which crustacean-rich surfaces (Tf-I), appendage-rich surfaces (Tf-II), and scattered debris surfaces (Tf-III) were found along the lowermost portion of Segment A.

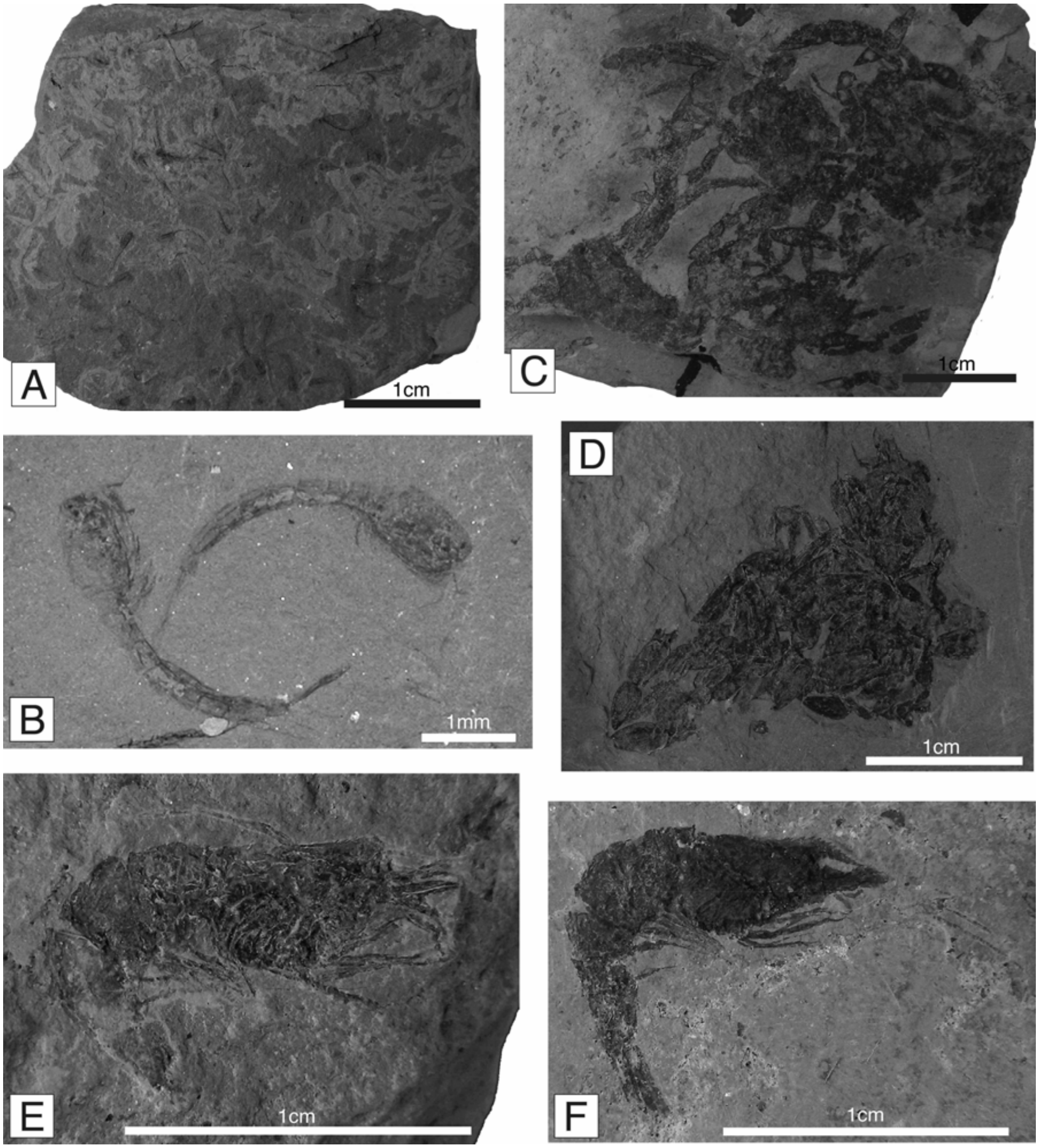

Figure 3.3. Crustacean-dominated faunule at the Nocuatá Section. A, *Archaeochimaera macrophthalma* n. gen. n. sp. A, cumaceans-rich surface (Tf-I), sample IGM p881226, showing the high density and random orientation of the specimens. B, sample IGM p881224, cumacean specimens showing details of the thoracopods and the pleon. C, *Archaeochimaera*-rich surfaces, sample IGM p881212, showing several specimens randomly orientated, mostly with the pereiopods attached. D, Appendage-rich surface, sample IGM p881192, showing the concentration of pereiopods 2 and 3, and a few cheliped remains. One disarticulated ventral carapace bearing the left eye is associated with the abundant appendages. E-F, shrimps indeterminate.

Segment C lies above these thick layers of sandstone and is composed of 56 m of gray fossiliferous shales with occasional indurated, gray, fossiliferous shale beds in the lower portion, interbedded at the top with a fine-grained, silty sandstone lens and non-calcareous nodules (Figure 3.2). The lowermost portion of Segment C (25 m) is not exposed. The uppermost Segment C (31 m) contains invertebrate assemblages typical of the lower-middle Turonian San Rafael and La Frontera formations in Colombia (Villamil and Arango, 1998; Feldmann et al., 1999; Vega et al., 2007) and of the Eagle Ford Group equivalent strata in Coahuila, Mexico (Vega et al., 2007; Guinot et al., 2008). Abundant globulose foraminifera, teleosteii fish remains, *Hoplitoides* spp., *Glyptoxoceras* sp., *Collingnoniceras* sp., ?*Coilopoceras* sp., and ?*Romaniceras* sp. (Etayo-Serna, personal communication, 2011), diverse and abundant decapod crustaceans such as *Cenomanocarcinus vanstraeleni* Stenzel, 1945 (Vega et al., 2007; Guinot et al., 2008; Vega et al., 2010), and several shrimp and thalassinid remains, also occur within Section C. The San Rafael Formation has been dated as lower to middle Turonian and the Churuvita Formation as Cenomanian in age using ammonites (Etayo-Serna, 1968b, 1979), and foraminifera (Sánchez-Quiñonez and Tchegliakova, 2005). A regional transgressive surface separates the Churuvita and San Rafael formations, indicating the end of a relatively shallow-water, coarse clastic sedimentation during the Cenomanian and the initiation of a deeper-water, fine-grained sedimentation at the beginning of the Turonian (Etayo-Serna, 1968a; Villamil and Arango, 1998; Feldmann et al*.,* 1999).

Systematic Paleontology

Illustrated specimens of the type series are deposited in the collection of INGEOMINAS, Museo Geológico José Royo y Gómez, Bogotá DC, Colombia, under the acronym IGM.

Order Decapoda Latreille, 1802

Infraorder Brachyura Linnaeus, 1758

Section ?Raninoida De Haan, 1839
[in De Haan, 1833-1850]
Superfamily ?Raninoida De Haan, 1839
[in De Haan, 1833-1850]

Archaeochimaeridae n. fam.

Included genera.—*Archaeochimaera* new genus.

Diagnosis.—Crabs with carapace longer than wide, fusiform; cervical groove and branchiocardiac groove distinct; mesial longitudinal ridge and postfrontal ridges present. Sternites 1 to 4 fused axially, forming a large and narrow sternal crown; sternites 4 to 7 unfused, sulcate axially by linea media; sternite 5 very wide; all sternites very different in shape and size; suture 5/6 complete, irregular, sinuous, rather defined by a deep groove; lack of true sterno-pleonal cavity; absence of evident thoracic sexual openings in both male and female; female spermatheca paired in sternite 7, positioned posterior to pereiopod 3 coxa; broad episternites 5-6. Pleon symmetrical, sexually dimorphic, pleonites unfused, lacking articulated rings and uropods, bearing dorsal median tubercle, with pleonites 1 to 4 exposed subdorsally; absence of pleonal, sternal, or appendicular pleon locking mechanisms. Antennae and antennulae small, between the eyes; eyes very large, nearly as wide as long, bearing short eyestalk, lack of orbits and orbital fissures; mxp3 pediform, elongate, bearing a crista dentata; length of ischio + merus slightly longer than length of palp, mxp3 merus positioned far from anterior ventral carapace or basal antennal segments. P2-P3 large, wide, with propodus and dactylus paddle-like; coxa of P2-P3 small; P4-P5 short, narrow, with a longitudinal keel, not subchelate or modified to carry objects, neither flattened or paddle-like; pereiopod 5 the smallest, carried dorsally.

Etymology.—The family and generic name are derived from the Greek 'arkhaios' (ancient), and 'khimaira' (chimaera), the mythological creature composed of parts of different animals, alluding to the unique combination of primitive and derived traits present in many brachyuran clades seen in the described organism.

Remarks.—The affiliation of Archaeochimaeridae with the Infraorder Brachyura, rather than the Anomura MacLeay, 1838, is supported by the possession of a symmetric folding pleon lacking uropods, the absence of articulated rings between pleonites, the short antennae and antennulae located between the eyes, the possession of only one pair of chelae (P1), therefore P2-P5 achelate; and P5 invariably visible (Figure 3.4-7). However, this taxon displays a unique combination of primitive and derived morphological characters that, if considered independently, may advocate for different systematic affiliations within the known podotreme clades. Dromiacea is the oldest and most primitive brachyuran section, with fossil records extending back to the Early to Middle Jurassic (Schweitzer and Feldmann, 2010a). The superfamilies Homolodromioidea Alcock, 1900, Koniodromitoidea Karasawa, Schweitzer and Feldmann, 2011, and Glaessneropsoidea Patrulius, 1959, differs from Archaeochimaeridae in the possession of subchelate P4 and P5, eyes protected by well-defined orbits and an augenrest (except in Glaessneropsoidea), a subhepatic region that is usually inflated, the postcervical groove usually present, the pleon retaining the uropods or uropodal plates, and pleon in males close to the coxae (Alcock, 1900; Števčić, 2005; Schweitzer and Feldmann, 2009; Schweitzer and Feldmann, 2010c; Karasawa et al., 2011).

Similarly, the superfamily Dromioidea De Haan, 1833, is distinguished by its well-developed orbits, the inflated subhepatic regions, usually developed postcervical groove, a narrow sternum bearing sternal projections, the presence of a sterno-coxal depression, pleonite 6 usually bearing triangular epimeres, the possession of uropodal plates, and last pair of pereiopods usually prehensile, carried subdorsally (Ortmann, 1892; Wright and Collins, 1972; McLay, 1993; 1999; Guinot, 2008; Guinot and Tavares, 2003; Schweitzer and Feldmann, 2010c; Karasawa et al., 2011). Furthermore, the possession of small mxp3 coxae that never touch, sternites 1-3 distinct ventrally, and the absence of a postcervical

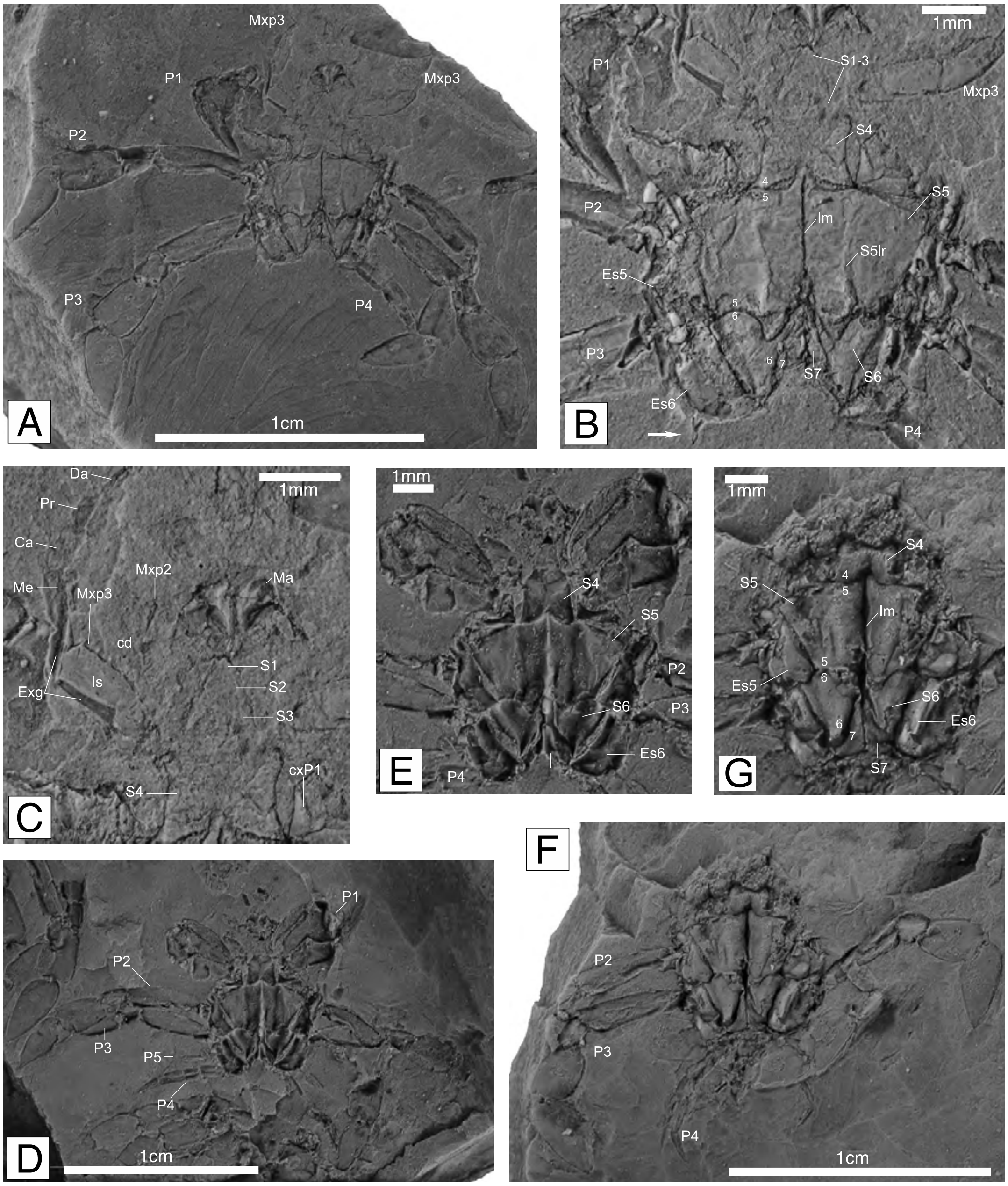

Figure 3.4. *Archaeochimaera macrophthalma* n. gen. n. sp. Specimens coated with ammonium chloride. A-C, holotype IGM p881215, ventral view: A, thoracic sternum, limbs and mouthparts. B, close-up of the thoracic sternum showing sternites, sternal sutures, and episternites; arrow pointing to the posterior spine. C, close-up of sternal crown and mouthparts. D-E, paratype IGM p881196, ventral view: D, thoracic sternum and limbs. E, close-up of thoracic sternum, showing sternites, episternites, sternal sutures, and sternal-episternal sutures. F-G, paratype IGM p881206, ventral view: F, thoracic sternum and limbs. G, close-up of thoracic sternum showing sternites, episternites, sternal sutures and sternal-episternal sutures. Ca: carpus; cd: crista dentata; cxP1: coxa cheliped; Da: dactylus; Es5-Es6: episternites 5 to 6; Exg: exognath; Is: ischium; lm: linea media; Ma: mandibula; Me: merus; Mxp2-Mxp3: maxillipeds 2 to 3; P1: cheliped or claw; P2-P5: pereiopods or walking legs 2 to 5; Pr: propodus; S1-S7: sternites 1 to 7.

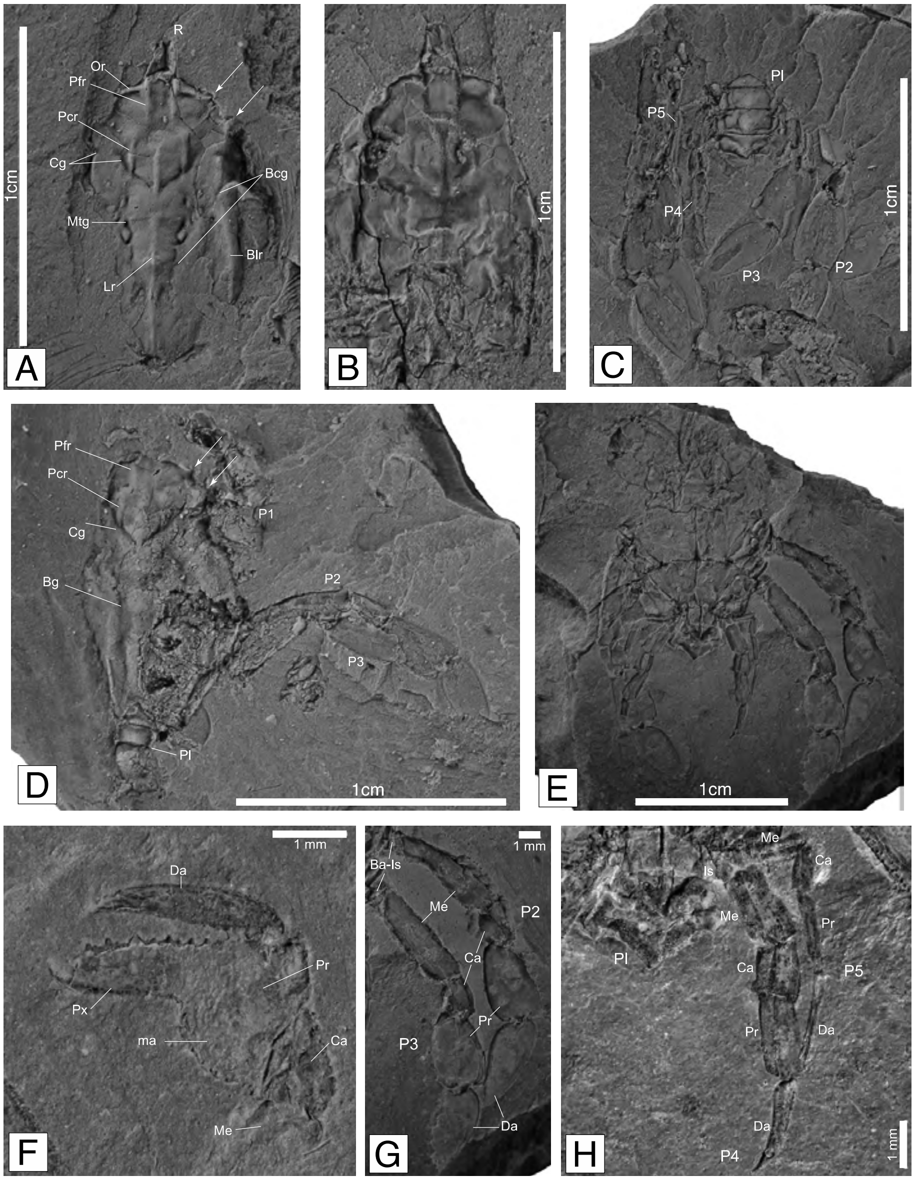

Figure 3.5. *Archaeochimaera macrophthalma* n. gen. n. sp. Specimens coated with ammonium chloride. A, paratype IMG p881203, dorsal view. Note the distinct dorsal grooves and the mesial, branchial, and postfrontal ridges. White arrows point to the position of the two protrusions that might correspond to orbital and/or anterolateral spines. B, paratype IGM p881204, dorsal counterpart showing the fine granulation at the median portion of the carapace. C, paratype IMG p881217, dorsal view showing the limbs and the pleonites bearing dorsal tubercles. D, paratype IMG p881218, moderately preserved dorsal view showing the limbs, a narrow pleon, cervical and branchiocardiac grooves, and the postfrontal ridges. E, G-H, paratype IGM p881214, ventral view: E, thoracic sternum, limbs and pleon. G, P2-P3. Note the similar shape and size, and the paddle-like condition of distal sclerites. H, P4-P5. Note the similar shape, P5 shorter, both legs keeled mesially, and the narrow and slender condition of distal sclerites. G, paratype IGM p881185, showing the strong angle formed between the palm and the pollex or immovable finger. Note the multiple teeth restricted to the occlusal surface of the pollex. Ba: basis; Bcg, branchio-cardiac groove; Blr, branchial longitudinal ridge; Ca: carpus; Cg, cervical groove; Da: dactylus; Is: ischium; Lr, mesial longitudinal ridge; mn: manus, or palm; Me: merus; Mtg, metagastric/urogastric pits; Or, orbital ridge; P1: cheliped or claw; P2-P5: pereiopods or walking legs 2 to 5; Pcr, pre-cervical ridge; Pfr, post-frontal ridge; Pr: propodus; Px: pollex.

groove (except for Diaulacidae Wright and Collins, 1972, and Xandarocarcinidae Karasawa et al., 2011), ensures separate phylogenetical affiliation from the most primitive brachyurans. Archaeochimaeridae can also be differentiated from members within the Section Homoloida by the lack of an evident 'linea', the 'homolid press-button', a telson projecting between the coxae of maxillipeds, the absence of an augenrest (except in Latreillidae Stimpson, 1858), and the lack of sterno-coxal and sterno-pleonal depressions (Guinot, 1991; Števčić, 2005; Scholtz and McLay, 2009; Karasawa et al., 2011).

Two synapomorphies unite *Archaeochimaera* with the remaining podotreme and eubrachyuran ingroup: the well developed sutures 4/5 and 5/6 (Figure 3.4). Despite the resemblance of the *Archaeochimaera* carapace to that of some corystids, and of the sternal architecture to that of some dorippids (Ng et al., 2000; Feldmann et al., 2007; Ng et al., 2008), the absence of male-female thoracic sexual openings excludes any eubrachyuran (Heterotremata + Thoracotremata) affinity. Among the remaining podotremes, kinship with the Section Torynommoida Karasawa et al., 2011, is ruled out based on the lack of broad and forward-directed orbits bearing a short intraorbital spine, the presence of a crista dentata in mxp3, and the telson never reaching the coxae of P1 (Glaessner, 1980; Feldmann, 1993; Karasawa et al., 2011; Schweitzer and Feldmann, 2011b). The elongated carapace bearing a bifid rostrum, the lack of sterno-pleonal depression, the pediform mxp3, and P4 and P5 carried subdorsally, prevent affiliation to the Section Etyoida Karasawa et al., 2011 (Bell, 1863; Guinot and Tavares, 2001; Karasawa et al., 2011) (Figures 4-6). *Archaeochimaera* contrast with the Section Dakoticancroida (Karasawa, Schweitzer and Feldmann, 2011), based on their subquadrate to nearly circular carapaces, narrow and bilobate rostra, the retractable eyes protected by well-developed orbits, with sternites relatively similar in shape, the wide pleon of the males, and the presence of pleon locking mechanisms (Rathbun, 1917; Glaessner, 1969; Artal et al., 2008; Karasawa et al., 2011).

The affiliation of Archaeochimaeridae to the sections Raninoida and Cyclodorippoida is more complicated to interpret, since different traits demonstrate either affinity with one, both, or neither of the sections. Affiliation with Cyclodorippoida appears to be supported by the possession of short coxae of pereiopods, the absence of a sterno-pleonal depression, the wide thoracic sterna lacking pleonal locking mechanisms, and the inner orbital angle not defined. However, Archaeochimaeridae differs from any cyclodorippoid family based on the fusiform carapace, the dorsal longitudinal ridges, and the reduced posterior sternites (Ortmann, 1892; Bouvier, 1897; Tavares, 1998; Karasawa et al., 2011). Similarly, Archaeochimaeridae possesses a complete suture 6/7, a fusiform carapace, reduced posterior sternites (or at least smaller than the others), and the location of the anterior end of the telson behind coxa of P3. All of these traits are shared with most raninoid families, giving phylogenetic support to the affiliation of Archaeochimaeridae with the clade Raninidae + Symethidae. Notwithstanding, kinship with Raninoida is uncertain since the two synapomorphies that unite the clade; the triangular buccal cavity and the mxp3 with two planes, are unknown or inconclusively preserved in the new family.

Archaeochimaeridae is provisionally included within the Section Raninoida, as suggested by the phylogenetic analyses, albeit with strong reservation given the inconclusively recognized synapomorphies that unite the clade Raninoida, the high degree of homoplasy seen in some of its diagnostic characters, especially the fusiform nature of the carapace, and the few tree-steps that separate Archaeochimaeridae from the Cyclodorippoida. For these reasons, different evolutive scenarios for this unusual body plan, as well as the phylogenetic implications for an assumed raninoid affiliation, are presented and discussed below.

***Archaeochimaera* n. gen.**

Included species.—*Archaeochimaera macrophthalma* new species, by monotypy.

Diagnosis.—As for family.

Archaeochimaera macrophthalma n. sp.

Figure 3.4 - Figure 3.8

Raninidae 1 indet; Vega, Nyborg, Rojas, Patarroyo, Luque, Porras-Múzquiz and Stinnesbeck, 2007, p. 418-419, figs. 9.9, 9.11.

Diagnosis.—As for family.

Description.—Carapace relatively small (~0.7 to ~1.6 cm maximum length), elongate, fusiform, longitudinally sub-ovate in outline, with maximum width two-thirds maximum length of carapace, widest at posterior two-fifths carapace length, at level of sternite 5; cervical groove well developed, shallow anteriorly, and more pronounced posteriorly at medial portion, interrupted axially by mesial longitudinal ridge, and ending at anterolateral margin; branchiocardiac groove developed, shallow at middle portion of carapace, and more pronounced toward the anterolateral margin; dorsal carapace finely granulated; two short, postero-orbital ridges arise at base of rostrum and deflect posterodistally, apparently continuing longitudinally as pre-cervical ridges, apparently delimiting protogastric and mesogastric region; main mesial longitudinal ridge prominent, more or less continuous, extending from mesogastric region, approximately at first anterior quarter of carapace length, to cardio-intestinal regions, interrupting axially the cervical groove, and bearing a row of few low-relief tubercles along its length; lateral branchial ridges present, unornamented (Figure 3.5A-B, D).

Rostrum semi-rectangular, bifurcated, depressed axially, slightly longer than wide, broader at the base, with sides almost parallel, represents one-tenth the maximum carapace length; fronto-orbital margin short, about one-third maximum carapace length; absence of true orbits, and lack of orbital fissures, bearing only one short, blunt spine-like protuberance, presumably homologous to a postorbital spine. Anterolateral margin sinuous, slightly concave anteriorly and convex posteriorly, sloping posterolaterally from the

?postorbital spine, bearing one short, blunt spine-like protuberance approximately at mid-length of postfrontal margin, then deflecting posterior until reaching anterolateral expression of branchiocardiac groove, and extending convexly posterolaterally at level of metagastric region; posterolateral margin convex at middle portion of carapace and straight posteriorly, with a small, slender and acute posterior distal spine, generally obscured by P4-P5; posterior margin concave, slightly less than half the maximum carapace width.

Thoracic sternum wide anteriorly, narrow posteriorly; sternites 1 to 4 forming an elongated sternal crown (Figure 3.4A-E); sternites 1 to 3 distinctive ventrally, fused, forming a triangle, with straight, convergent anterior lateral margins, nearly as long as sternite 4; sutures 1/2 and 2/3 not clear; sternite 4 semi-rectangular, slightly wider than long, width one-fourth carapace width, length one-eighth carapace length, not mesially depressed or furrowed, lateral margins smoothly concave, anterior portion nearly equal to posterior, strongly concave posterior margin mesially; suture 3/4 distinct only on the sides; sternite 5 the broadest, maximum width at anterior portion, approximately two-thirds maximum carapace width, maximum length near sternum axis, one-fourth the maximum carapace length, depressed mesially by linea media, with lateral margins straight, convergent posteriorly, and bearing long and prominent longitudinal ridge on each side, extending along maximum length portion, parallel to main axis; suture 4/5 complete, rather well defined by a deep sinuous groove, with anterior mesial portion of sternite 5 articulating into sternite 4 posterior margin concavity (Figure 3.4); episternite 5 semi-rectangular in outline, articulating laterally with sternite 5; sternite 6 very different in shape and size to sternites 5 and 7, maximum width at anterior portion, approximately half as wide as maximum carapace width, maximum length approximately one-sixth as long as carapace length, strongly depressed mesially by a deep cleft, occasionally bearing a subtle ridge on each side, almost parallel to main axis, with anterior margin irregular, extending obliquely posterior from main axis, producing a sinuous concavity posteriorly near where sternite 5 longitudinal ridge ends (Figure 3.4A-B, D-G), and describing a convex, arcuate loop ending at lateral margin, which is straight, converging posteriorly, suture 5/6 complete, rather well defined by a deep groove; episternite 6 semi-rectangular in outline, articulating laterally with sternite 6; sternite 7 reduced, very different in shape and size to sternites 5 and 6, maximum width at posterior portion, nearly parallel to carapace posterior margin, approximately one-sixth maximum carapace width, maximum length near carapace axis, approximately one-seventh carapace maximum length, inverted V-shaped, strongly depressed mesially, with margins non-parallel, diverging posteriorly, suture 6/7 complete, rather well defined by a deep groove; sternite 7 in one female specimen (Figure 3.6A-B) bearing a paired spermatheca axially; sternite 8 not seen. Thoracic sexual openings not recognized.

Male and female pleon symmetrical, short, lacking articulated rings and uropodal plates, sexually dimorphic; female pleonites sub-rectangular in outline, pleonites 1 to 3 exposed dorsally, pleonite 1 reduced, pleonites 2 to 5 similar in shape and size, epimeres with a longitudinal depression, separate from the tergum; each pleonite bearing dorsal axial tubercle, that may be distinctly spiniform in small specimens; in one specimen (Figure 3.5C), pleonite 4 tergum bearing a notch, extending antero-laterally to postero-mesial portion; pleonites 5-6 and telson ventrally exposed in one specimen (Figure 3.6A-B), pleonite 5 similar in shape to pleonites 2-4 but smaller; pleonite 6 the smallest, with a concave posterior margin articulating with telson; telson short, wider than long, strongly convex anteriorly. Male pleonites narrower than in females, pleonite 6 and telson ventrally exposed in one male specimen (Figure 3.6E-F); pleonite 6 longer than wide, semi-rectangular in outline, posteriorly arcuate, concave, articulating with telson; telson small, lanceolate, longer than wide, approximately two-thirds as long as pleonite 6 length.

Eyes extremely large, approximately as long as wide, round to semi-ovate in outline; length one-fifth the maximum carapace length in small specimens to one-seventh in large specimens, always exposed and lacking any protective structure; compound eye facets predominantly hexagonal in hexagonal arrangements, through most of the outer-

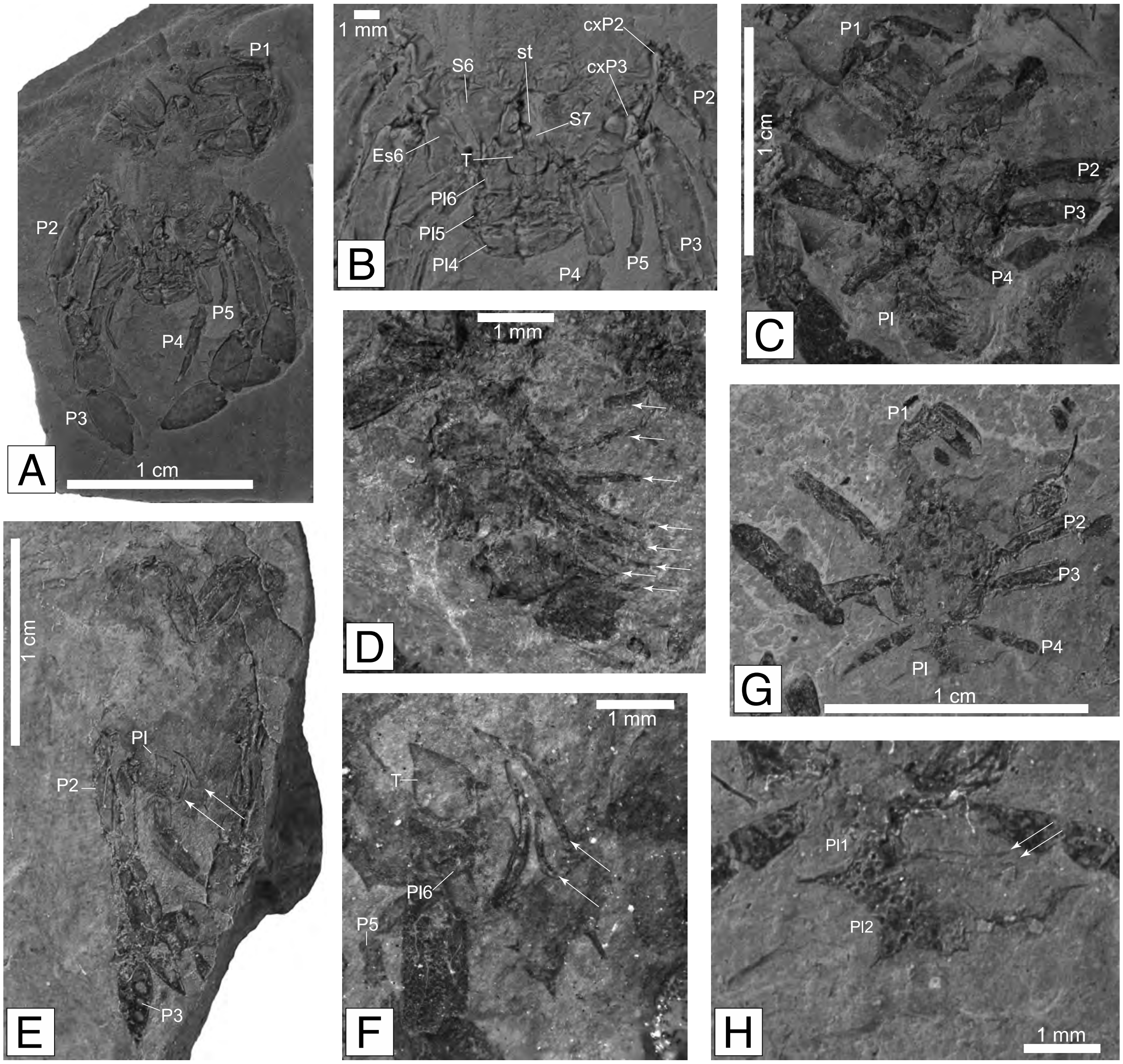

Figure 3.6. *Archaeochimaera macrophthalma* n. gen. n. sp. Specimens coated with ammonium chloride. A-B, paratype IGM p881206, female: A, ventral view showing the limbs, posterior sternites and pleon. B, close-up, showing pleonites and telson, coxae of P2-P3, and paired spermatheca positioned in S7. C-D, paratype IGM p881209b, female, ventral view: C, specimen showing the unfolded pleon and limbs. D, close-up of female pleon. Arrows indicating the pleopods. E-F, paratype IGM p881202, male, ventral view: E, specimen showing the limbs and pleon. F, close-up showing the male's last pleonal somites and telson. Arrows indicate sclerotized gonopods. G-H, paratype IGM p881217, male, ventral view: G, specimen of small size showing limbs and pleon bearing gonopods. H, close-up showing the first pleonites bearing an acute protuberance dorso-mesially. Arrows indicate sclerotized gonopods. cxP2-cxP3: coxae of P2 and P3; P1: cheliped or claw; P2-P5: pereiopods or walking legs 2 to 5; Pl: pleon; Pl1-Pl6: pleonites 1 to 6; S6-S7: sternites 6 to 7; st: spermatheca; T: telson.

middle portion; squarish facets in square-like arrangement at anterior portion are present in one specimen with well-preserved eyes (Figure 3.7B); three retinal layers are recognizable in one specimen (Figure 3.7E-G); eyestalk short and stout, one-third eye length; antennae and antennulae short and slender, between the eyes, antenna as long as eye maximum length, first segment broad, one-fourth the length of rostrum.

Third maxillipeds pediform-like, articulating with postero-distal portion of sternite 3; endognath ischium elongate, semirectangular in outline, as long as sternite 4 width, two-fifths as wide as long, bearing a crista dentata armored with four to five small, acute, evenly spaced spines on internal margin; merus elongate, semi-rectangular in outline, slender, somewhat shorter than ischium, more than twice as long as broad; palp (carpus-dactylus) slightly shorter than ischium + merus, directed forward; merus of endognath never reaching anterior carapace, ischium + merus length approximately one-fifth carapace maximum length; exognath slender, nearly as long as endognath ischium, as wide as one-third endognath ischium width, with nearly straight outer margin; mxp2 endognath very small, pediform; mandibulae as long as half the endognath ischium length, robust, slightly asymmetrical, left mandible describing a different curvature on occlusal surface than right.

Chelipeds (P1) isochelous, ischio-merus semi-rectangular, about one-fourth as long as carapace length; carpus sub-trapezoidal, as long as two-thirds the length of merus; propodus-carpus articulation subparallel to merus long axis; propodus height as long as ischio-merus length, with a blunt tooth-like projection at outer distal corner, close to articulation with dactylus; manus stout and inflated, maximum width two times carpus width in large specimens, often tuberculate; fixed finger deflected ~90°, three times longer than carpus length, broad, with 10 to 15 small, sharp, and irregular, well-developed denticles on occlusal surface, distal denticle upturned; dactylus slender, with distal denticle downturned, slightly shorter than fixed finger, smooth edentulous occlusal surface, except occasional one or two small, fine denticles near junction with propodus; P2 the longest of all pereiopods, usually as long as, or slightly longer than maximum carapace length; ischio-merus subrectangular, slightly convex forward, bearing a small spine at upper distal margin, close to articulation with carpus; carpus length one-third the length of ischio-merus, trapezoidal in outline, narrow at articulation with merus, may bear small spines on outer margin; propodus elongate, ovoid, twice the length of carpus, or two-thirds as long as ischio-merus length, may be serrated, sometimes with one to three small, acute, spiniform projections at anterior edge close to articulation with dactylus, narrow at articulation with carpus; dactylus broadly lanceolate, as long as propodus length, narrow at articulation with propodus; P2 segments bearing a fine rim of evenly spaced setal pits; P3 almost identical in shape and size to P2, but slightly shorter; P4 slender, half the length of P2-P3, with a median carina along all sclerites; ischio-merus subrectangular, often finely granulated, broader posteriorly; carpus half the size of ischio-merus, subquadrate, narrow at articulation with merus; propodus subrectangular, one-third longer than carpus length, and similar in size to ischio-merus; dactylus sharp, slender and acute, similar in length to propodus, but two-thirds the width, weakly serrate, narrow at articulation with propodus; P5 the smallest pereiopod, one-third length of P3, slender, with median carina along all the segments, very different in shape and size from P2 and P3, more similar to P4, but considerably smaller and carried subdorsally, without paddle-like dactylus; ischio-merus fused, sub-perpendicular to main carapace axis, as long as P4 dactylus; carpus length half the ischio-merus length, narrow at junction with ischio-merus; propodus as long as ischio-merus length, narrow at junction with carpus; dactylus slender and acute, as long as propodus. Male first two pairs of pleopods (gonopods) slender and slightly arched, sclerotized (Figure 3.6E-F); female pleopods small, slender, similar in shape and size (Figure 3.6C-D).

Etymology.—The trivial name derives from the Greek ‘makros’ (large) and from the Latin ‘ophthalmos’ (eyes). Gender feminine.

Material examined.—The series of 42 type specimens: Holotype IGM p881215; Paratypes IGM p881184 to IGM p881214, and IGM p881216 to IGM p881221, are deposited in the

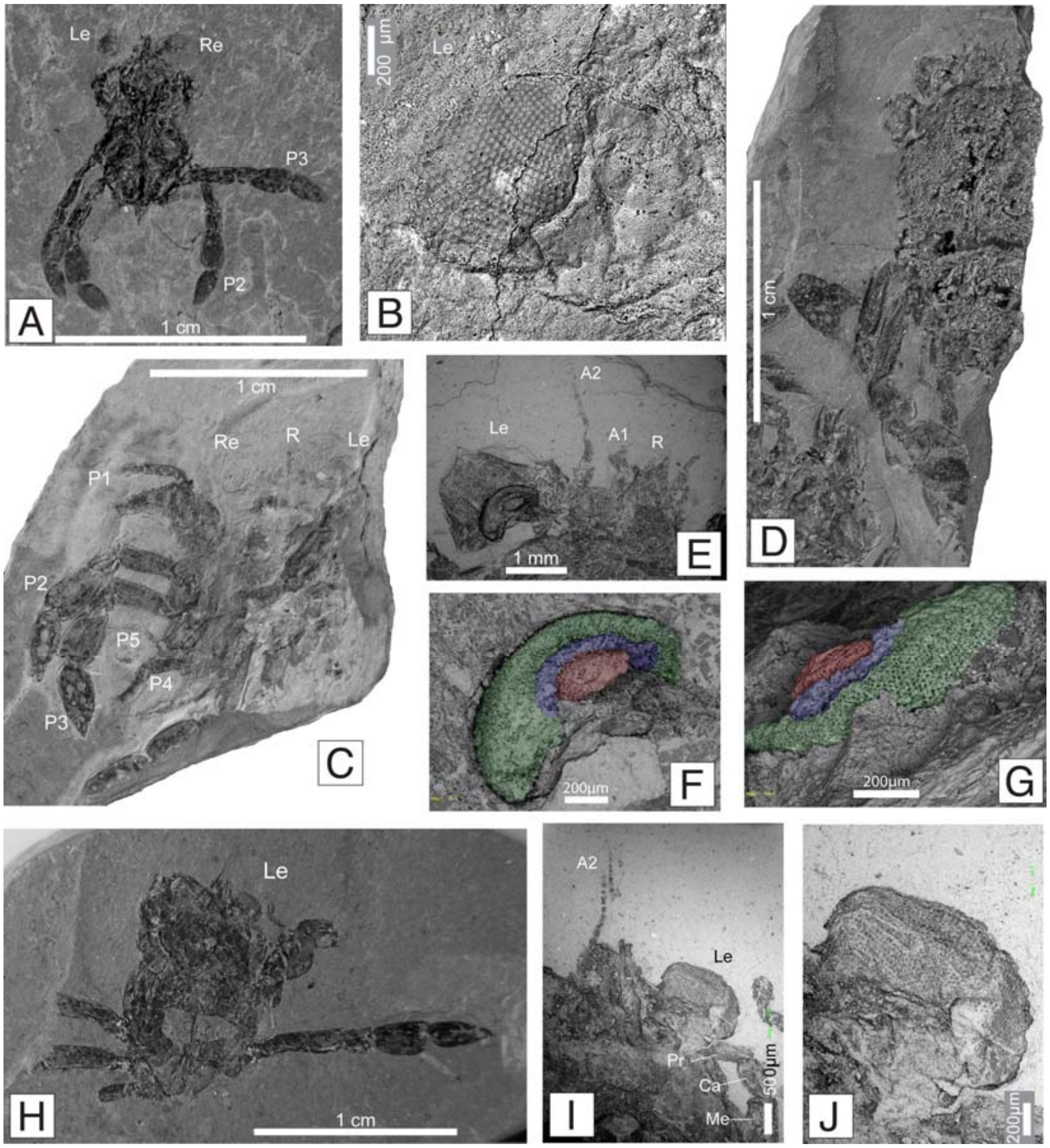

Figure 3.7. *Archaeochimaera macrophthalma* n. gen. n. sp. Specimens coated with ammonium chloride, except for SEM images. A-B, paratype IGM p881220, ventral view: A, specimen showing eyes and limbs. B, SEM image of left eye showing hexagonal facets in hexagonal arrangement at medial-posterior portion, and squarish facets in squarish arrangement at anterior portion. C, paratype IGM p881219, ventral view showing appendages, eyes and rostrum. D-G, paratype IGM p881209a, dorsal view: D, specimen lacking dorsal carapace, preserving internal remains, antennae and compound eye. E, close-up of anterior portion, showing the antennula, antenna, left eye, and rostrum. F, dorsal view of left eye showing three well-preserved retinal layers. G, oblique view of retinal layers, the external layer preserving ommatidial insertion spots arranged hexagonally. H-J, paratype IGM p881210, ventral view: H, specimen showing the limbs, mouthparts, antennae and compound eye. I, SEM image of anterior portion, showing the mxp3' merus, carpus and propodus, the antennae and left compound eye. J, SEM image showing left compound eye bearing facets. A1: antennula; A2: antenna; Ca: carpus; Le-Re: left and right eyes; Me, merus; P1: cheliped or claw; P2-P5: pereiopods 2 to 5; Pr: propodus; R: rostrum. In figures F-G, green, blue and red regions represents external, medial and internal retinal layers, respectively.

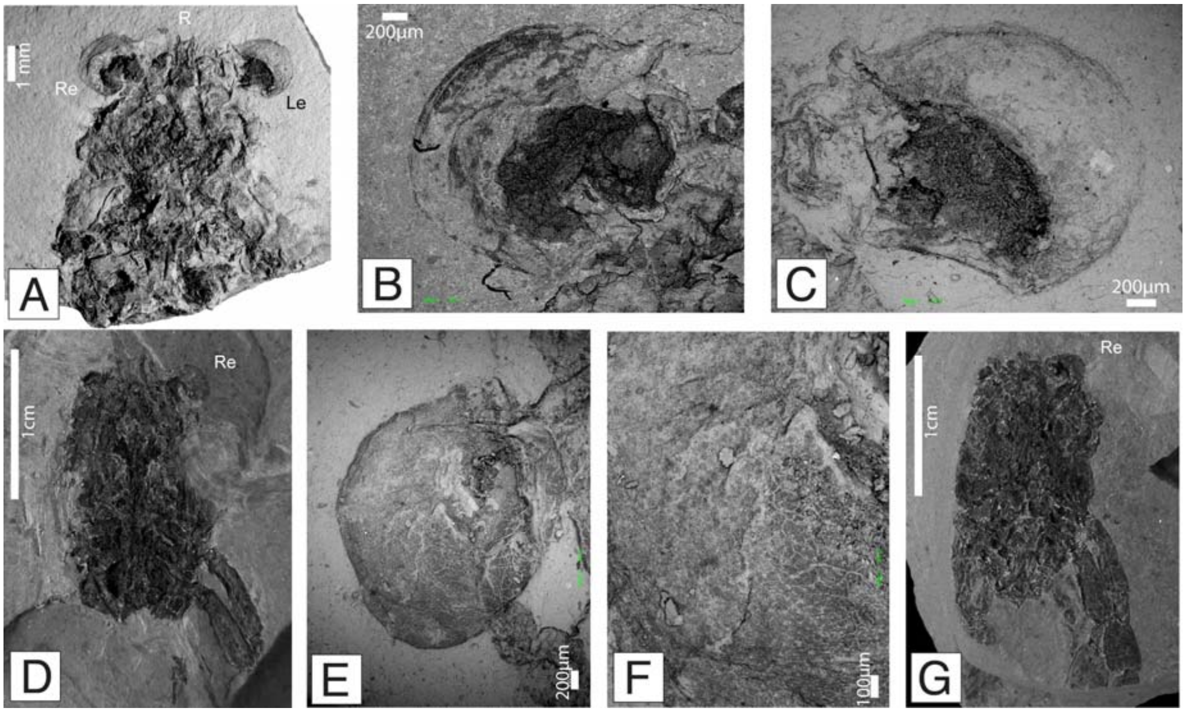

Figure 3.8. *Archaeochimaera macrophthalma* n. gen. n. sp. Specimens coated with ammonium chloride, except for SEM images. A-C, paratype IGM p881208, ventral view : A, specimen showing the large eyes and the rostrum bifid. B, close-up of left eye. C, close-up of right eye. D-F, paratype IGM p881207. D, specimen showing the limbs and right eye. E, SEM image of right eye. F, SEM close-up of the same eye, showing the facets. G, paratype IGM p881211, showing the right eye. Le : left eye; R : rostrum; Re : right eye.

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Measurements.—Measurements (in millimeters) taken on *Archaeochimaera macrophthalma* holotype IGM p881215, and paratypes IGM p881196, IMG p881206, IGM p881215, IGM p881219, and IMG p881220, are given in Table II (Appendix).

Occurrence.—Segment A, Nocuatá Section, Upper part of Churuvita Group (upper Cenomanian), Cordillera Oriental, Department of Boyacá, Colombia. Latitude 5.58102, Longitude -73.05266.

Remarks.—The Section Raninoida and its sole Superfamily Raninoidea, as currently defined, comprises six families of extinct and extant crabs that fit within two principal body plans: the ‘raninid-type’, grouping the families Palaeocorystidae Lőrenthey (in Lőrenthey and Beurlen, 1929), Raninidae De Haan, 1839, and Symethidae Goeke, 1981, sharing a fusiform carapace and absence of pleonal locking mechanisms; and the ‘necrocarcinid-type’, comprising the families Camarocarcinidae Feldmann, Li, and Schweitzer, 2007, Cenomanocarcinidae Guinot, Vega, and Van Bakel, 2008, and Necrocarcinidae Förster, 1968, sharing a broader, non-fusiform carapace, with wider thoracic sterna, and the possession of pleon locking mechanisms (Karasawa et al., 2011; Luque et al., in press). The possession of posterolateral spines is only known for Camarocarcinidae and Cenomanocarcinidae + Necrocarcinidae, whereas bifid rostra, well-developed cervical and/or branchiocardiac furrows, and longitudinal ridges or nodes in the dorsal carapace, are diagnostic for necrocarcinid-type and Palaeocorystidae ‘pro-parte’, the latter being the most basal and ancient of the fusiform families (Luque et al., in press, fig. 8). Despite these shared synapomorphies with the necrocarcinoids, Palaeocorystidae appears phylogenetically closer to the clade Raninidae + Symethidae (Karasawa et al., 2011) (Figures 3.9-3.10), united by the elongated carapace, and the lack of pleon locking mechanisms. Palaeocorystidae, or part of it, is deemed as the rootstock of the Raninidae + Symethidae. In the case of *Archaeochimaera*, a similar situation occurs. The fusiform carapace and the absence of pleonal locking devices unite *Archaeochimaera* with Palaeocorystidae + (Raninidae + Symethidae), while the reduced posterior sternites and the telson lying behind the coxa of P3 places it in between Palaeocorystidae and the clade Raninidae + Symethidae (Figure 3.10A). Conversely, the cervical and branchiocardiac grooves, the longitudinal axial and branchial ridges, bifid rostrum, and posterolateral spines, would support kinship with the most basal necrocarcinid-type and Palaeocorystidae. Furthermore, the pediform mouthparts with crista dentata, the markedly different P2-P3 from P4-P5, the unusual pattern of sternal sutures, the shape and size of the sternites, and the orbital and optical configuration, are discrepant with the diagnostic characters for the

Superfamily Raninoidea. For the Raninoidea to be monophyletic, the clade must contain all the descendants derived from the same last common ancestor.

Discussion

Phylogenetic Analysis

In order to assess the phylogenetic relationships of the new taxon, I have followed the methodology, selected taxa, and character state scoring from Karasawa et al. (2011), plus inclusion of Archaeochimaeridae n. fam. (Figure 3.9), and re-evaluation of some raninoid character states (Appendix Table III, IV). Herein, as in Karasawa et al. (2011), the clade Raninoidea stands as sister to the Dakoticancroida and Cyclodorippoida (Karasawa et al., 2011: p. 533). However, the internal topology of Raninoida differs in the collapsed clade Cenomanocarcinidae + Necrocarcinidae into a soft polytomy, given that the character that united them; i.e. longitudinal ridge or tubercles on branchial region (Appendix Table III, Character 19: (1)) (Karasawa et al., 2011: fig. 3), is present in Archaeochimaeridae, and polymorphic in Palaeocorystidae.

Camarocarcinidae still appears basal to the superfamily, although the possession of spines on the posterolateral margin (Ch. 6: (1), four steps) is shared with several cenomanocarcinids, necrocarcinids, and Archaeochimaeridae (Figure 3.10A). The clade Cenomanocarcinidae + (Necrocarcinidae + (Palaeocorystidae +(Archaeochimaeridae + (Raninidae + Symethidae)))) is united by the possession of a complete suture 6/7 (Ch. 33: (1), three steps). This trait appears to have evolved independently in the sections Homoloida and Cyclodorippoida. The raninoid families Palaeocorystidae + (Archaeochimaeridae + (Raninidae + Symethidae), sharing a fusiform body plan, typically lack any pleonal locking mechanism (Character 50: (2), six steps) clade (Figure 3.10A).

However, as discussed by Luque et al. (in press), this character is polymorphic within Raninidae, since sternal projections in the fifth sternite, engaged in locking the pleon, are well-developed in two genera within the subfamily Lyreidinae Guinot, 1993: *Lyreidus* De Haan, 1841, and *Lysirude* Goeke, 1985 (Guinot, 1993; Guinot and Bouchard, 1998; Luque et al., in press). Furthermore, pleonal locking mechanisms are still unconfirmed for the basal necrocarcinid-like Camarocarcinidae, casting doubts on whether the presence of sternal holding devices is the ancestral condition for Raninoida, lost in Palaeocorystidae + (Archaeochimaeridae + (Raninidae + Symethidae)), and reversed in the Lyreidinae, or rather absent in the last raninoidid common ancestor, and gained twice in the Cenomanocarcinidae + Necrocarcinidae and the Lyreidinae. The elongated dorsal carapace (Ch. 1: (0), 5 steps), is the ancestral condition for Brachyura, changing once in the Glaessneropsoidea Patrulius, 1959, once in the Dromioidea, and once in the branch that unites the clade Torynommoida with the remaining podotremes + Eubrachyura (Figure 3.9). In Raninoidea, the innovation of a fusiform carapace is assumed to have occurred once in the Palaeocorystidae + (Archaeochimaeridae + (Raninidae + Symethidae)), therefore a reversal to the ancestral state derived from a necrocarcinoid-like ancestor. Also, a carapace longer than wide is scored for several dromiaceans and Homoloida. The clade Archaeochimaeridae + (Raninidae + Symethidae) is united by the synapomorphies of posterior sternites reduced (Ch. 27: (1), two steps), and a telson lying behind the coxae of P3 (Ch. 54: (3), 3 steps). Outside the raninoidid clade, the trait is convergent with the clade Cyclodorippidae Ortmann, 1892 + Cymonomidae Bouvier, 1897.

One autapomorphy, the united spermatheca (Ch. 42: (1), one step), supports the Raninidae + Symethidae (Figure 3.10A), also suggested by four synapomorphies: a straight posterior margin (Ch. 7: (1), five steps), indistinct cervical (Ch. 16: (1), six steps) and branchiocardiac grooves (Ch. 18: (1), eleven steps), and the palp of mxp3 lying in a mesial-inner position (Ch. 64: (1), two steps) (Figure 3.10A). The straight posterior margin is polymorphic in Cenomanocarcinidae (Guinot et al., 2008: fig. 1B; Collins, 2010: fig. 1.4), and has been recently documented for the necrocarcinid *Planocarcinus olssoni* (Rathbun, 1937), from the Aptian of Colombia, and a putative planocarcinid specimen from the Albian of US (Rathbun, 1937; Vega et al., 2010, fig. 8.22; Luque et al., in press).

Interpreted as a derived brachyuran condition, straight posterior margins appear independently at least twice, in Dakoticancroida and eubrachyurans. Distinct cervical and branchiocardiac grooves are the ancestral conditions for podotremes, becoming indistinctive in Dromioidea 'pro parte' and Raninoida. In all necrocarcinoid-like families, this character is polymorphic. In the raninoid-like families, it is only polymorphic in Palaeocorystidae, reversing in Archaeochimaeridae to the ancestral states, and gained again in Raninidae + Symethidae.

The family Archaeochimaeridae is separated from the Raninidae + Symethidae by eleven traits (Figure 3.10A). In the superfamily Raninoidea, the possession of spines in the posterolateral margin (Ch. 6: (1), four steps) is restricted to the families with a necrocarcinid-type body plan plus Archaeochimaera. The absence of spines appears as the ancestral state, being gained once in the last common ancestor for Camarocarcinidae, Cenomanocarcinidae, and Necrocarcinidae, reversed in Palaeocorystidae, re-gained in Archaeochimaeridae, and reversed a second time in Raninidae + Symethidae. The remaining ten characters are autapomorphies for Archaeochimaeridae within the Clade Raninoida, but outside the clade they are homoplasic among most podotreme groups, and even with some eubrachyurans. Undefined orbits (Ch. 9: (0), four steps) are the primitive condition for Brachyura, becoming defined in the clade Konidromitioidea + (Glaessneropsoidea + Dromioidea), and at the clade C + (D + (E + (F + (G + H)))) (Figure 3.9). This character is not present in the cyclodorippoid Cymonomidae, nor in Archaeochimaeridae, therefore it is interpreted as a reversal. An undefined internal orbital angle (Ch. 12: (0), seven steps) is the ancestral condition for Brachyura, and becomes defined in Etyoida, Raninoida, and polymorphic in Cyclodorippoida and Eubrachyura. In Archaeochimaeridae, the character is not defined, so the primitive condition is considered a reversal. The lack of upper orbital fissures (Ch. 13: (0), six steps) is the primitive state,

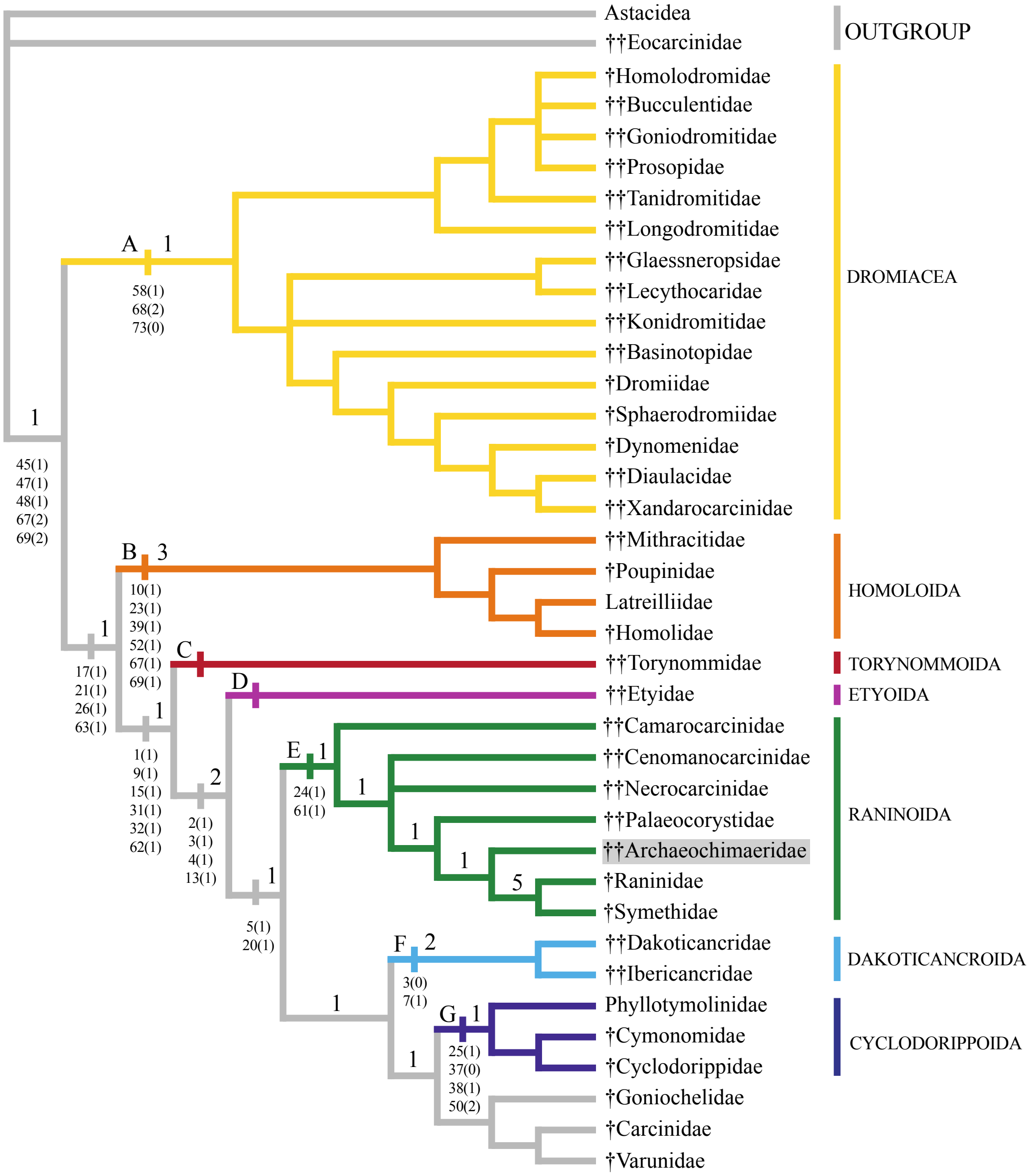

Figure 3.9. Strict consensus tree showing the character states that unite the different podotreme sections, with Archaeochimaeridae n. fam. as sister taxon of Raninidae + Symethidae. Treelength (TL)=240 steps; consistency index (CI)=0.57; retention index (RI)=0.78; rescaled CI (RC)=0.45. Diagnostic character states (in brackets) indicated vertically below branches. Clades constituting podotreme sections indicated by capital letters at the left of the branch. Bremer support for major branches indicated at the right. Taxa indicated by † known as both extant and fossil species, and †† only known as fossil. A tree for Clade E Raninoida with characters mapped is provided in Figure 3.10A. Base tree resulting from the phylogenetic analysis herein presented, following the work of Karasawa et al. (2011) with a modified character matrix (see Appendix).

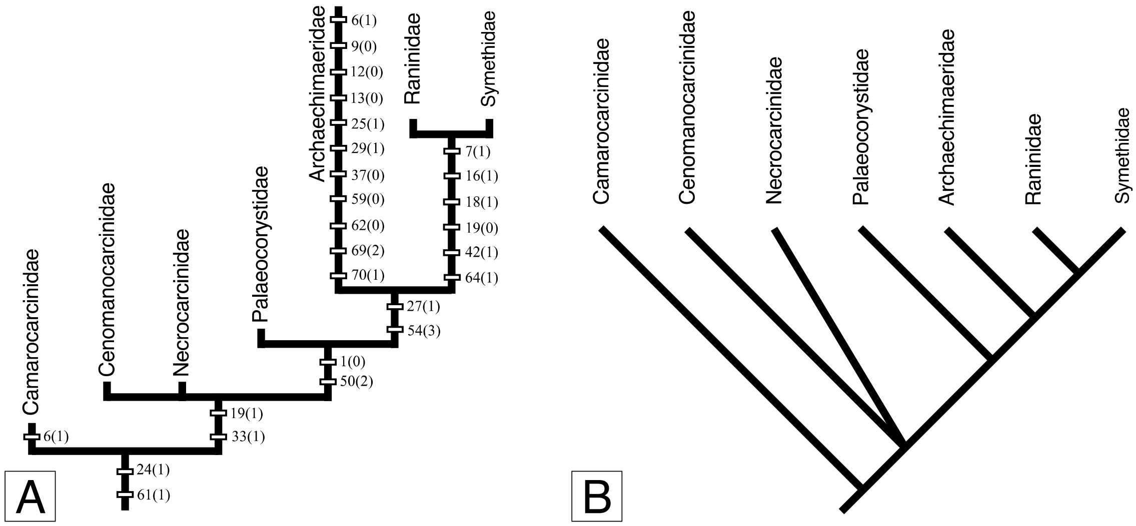

Figure 3.10. Trees for the clade Raninoida resulting form the phylogenetic analysis. A, tree with branches length proportional to changes. B, cladistic tree for the clade Raninoida showing Archaeochimaeridae standing as sister taxon for Raninidae + Symethidae. The clade Cenomanocarcinidae + Necrocarcinidae collapsed into a soft polytomy. Base tree resulting from the phylogenetic analysis herein presented, following the work and a modified character matrix after Karasawa et al. (2011).

evolving from absent to present in Glaessneropsoidea, and the clade D + (E + (F + (G + Eubrachyura)))). Within the latter, this trait appears to reverse four times, in Archaeochimaeridae, Dakoticancridae, Cymonomidae, and the eubrachyurans. Wide thoracic sternites (Ch. 25: (1), four steps) is a derived condition from a brachyuran ancestor with narrow sternites, appearing three times in Poupinidae + (Latreilliidae + Homolidae), Archaeochimaeridae, and Cyclodorippoida + Eubrachyura. The character is polymorphic in Dakoticancridae. It must be noted that, although the posterior sternites in Archaeochimaeridae are reduced, uniting the taxon with Raninidae + Symethidae, the broad and keeled sternite 5 is not seen in any raninoid nor in closely related podotreme sections (Figure 3.11). The episternites clearly defined by grooves (Ch. 29: (1), two steps), is not present in any podotreme section but Archaeochimaeridae, and is convergent with Eubrachyura. The absence of the sterno-abdominal depression (Ch. 37: (0), five steps) is the ancestral outgroup condition, appearing in Brachyura, and reversing/convergent in Archaeochimaeridae and Cyclodorippoida + Eubrachyura, and polymorphic in Raninidae

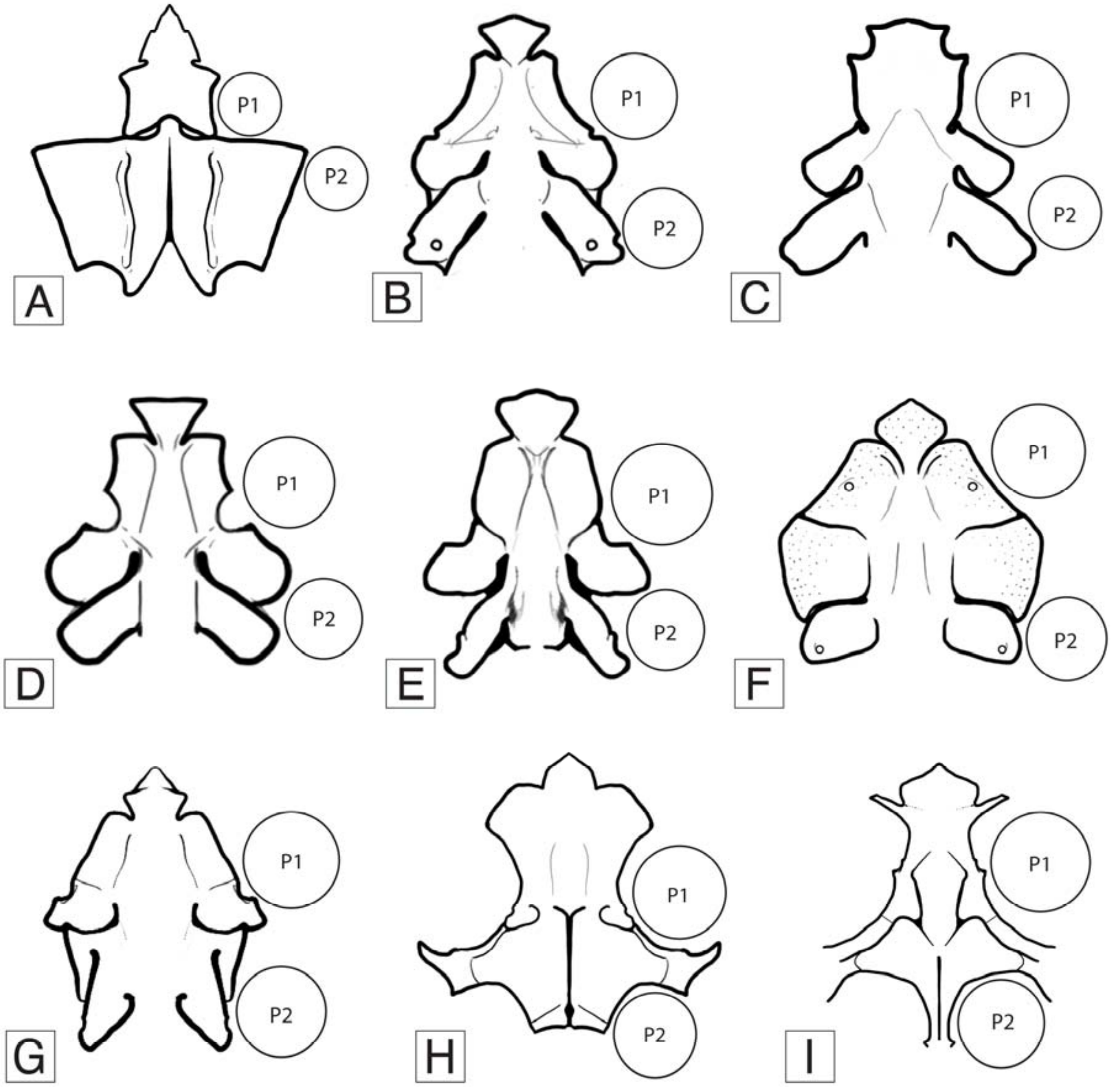

Figure 3.11. Sternal configuration of sternites 1-5 in Archaeochimaeridae n. fam., and representatives of the six known families comprising the Superfamily Raninoida. A, Archaeochimaeridae, *Archaeochimaera macrophthalma* n. gen. n. sp., B, Camarocarcinidae, *Camarocarcinus arnesoni* Holland and Cvancara, 1958. C, ?Camarocarcinidae, *Araripecarcinus ferreira*i Martins-Neto, 1987 (Luque et al., in progress). D, Necrocarcinidae, *Necrocarcinus labeschei* (Eudes-Deslongchamps, 1835). E, *N. labeschei* (Eudes-Deslongchamps, 1835). F, Cenomanocarcinidae, *Cenomanocarcinus vanstraeleni* Stenzel, 1945. G. Palaeocorystidae, *Eucorystes broderipi* (Mantell, 1844). H. Raninidae, *Raninoides benedicti* Rathbun, 1935b. I, Symethidae, *Symethis* sp. P1: cheliped; P2: pereiopod 2. Circles indicating the approximate location of coxae of P1 and P2. Line drawings D-E, G, after specimens illustrated in Karasawa et al., 2011.

and Dakoticancridae.

The pediform mxp3 (Ch. 59: (0), five steps), is only seen in the outgroup, the most primitive dromiaceans (Homolodromioidea), the clade Poupinidae + (Latreilliidae + Homolidae), and Archaeochimaeridae, whereas in the most derived Dromioidea, and the clade D + (E + (F + (G + Eubrachyura))) is operculiform. Pediform maxilliped 3 is polymorphic in Homolidae. The presence of crista dentata on maxilliped 3 (Ch. 62: (0), four steps), is the ancestral condition for the outgroup and Brachyura, disappearing once in Latreilliidae, polymorphic in Homolidae, and lost again in C + (D + (E + (F + (G + Eubrachyura)))). The presence of crista dentata in Archaeochimaeridae might represent a reversal to the ancestral state. The reduced P4-P5 (Ch. 69 (2), eleven steps), is the ancestral condition for Brachyura, not shared with the outgroup, deriving to P4 of normal size and P5 reduced in Longodromitidae, Dynomenidae, Diaulacidae, the clades Homoloida and Raninoida, and in Dakoticancroidea, and deriving once again to P4 and P5 of normal size in Xandarocarcinidae, some Raninidae, and most Eubrachyura. The reduced size of P4-P5 in Archaeochimaeridae would represent a reversal to the ancestral state. The last character, short coxa of pereiopods (Ch. 70: (1), 2 steps), is a derived condition from a brachyuran ancestor, and evolved twice in Archaeochimaeridae and the clade F + (G + Eubrachyura).

Phylogenetic Remarks

The general discrepancy of morphological traits between Archaeochimaeridae n. fam. and the Superfamily Raninoidea reflects the poorly resolved internal phylogeny for the clade Raninoida, casting doubts on its monophyletic status. Given this marked disparity, three phylogenetic scenarios including Archaeochimaeridae within Raninoida are depicted:

1) Section Raninoida monophyletic, Superfamily Raninoidea monophyletic: all of the taxa grouped within Raninoida and Raninoidea are descendent from a single common

ancestor, and both clades include all of its descendants. Then, Archaeochimaeridae stands as a true raninid-type crab, constituting the clade Palaeocorystidae + (Archaeochimaeridae + (Raninidae + Symethidae)), and sister taxon to the Raninidae + Symethidae. Archaeochimaeridae characters represent multiple reversals, either to an ancestral necrocarcinid-type condition (Ch. 6), or a non-raninoidid primitive condition (Ch. 9, 12, 13, 59, 62, 69). Further, many traits were independently gained in this group and are convergent with other higher podotremes, or even Eubrachyura (Ch. 25, 29, 37, 70). Thus, the fusiform carapace, narrow posterior sternites, and telson lying back to coxa of P3, would represent synapomorphies that warrant affiliation of *Archaeochimaera* n. gen. with the fusiform clade.

2) Section Raninoida monophyletic, Superfamily Raninoidea polyphyletic: all of the taxa grouped within Raninoida are descendent from a single last common ancestor, and the clade includes all of its descendants, but those within Raninoidea do not include the most recent common ancestor for all of its members. A polyphyletic Raninoidea containing Archaeochimaeridae is grouped based on homoplasic traits such as the position of the anterior end of the telson, also seen in Cyclodorippidae + Cymonomidae, and the fusiform carapace, a highly homoplasic trait that has evolved independently multiple times (Bourne, 1922; Števčić, 1973) in at least five superfamilies and ten families of Anomura and Brachyura (Figure 3.12, Table V). Hence, abandonment of a typical crab-like body form may have occurred twice within a monophyletic Section Raninoida, once in the primitive archaeochimaeroid lineage, and independently in the clade Palaeocorystidae + (Raninidae + Symethidae), the latter deemed as originating from a necrocarcinid-like ancestor. In addition, the shared archaeochimaeroid and necrocarcinoid traits (i.e. Ch. 6, 16, 18, 19) may have been already present in the last common ancestor for the Section Raninoida. Under this scenario, the diagnostic non-raninoid characters seen in Archaeochimaeridae (e.g. Ch. 9, 12, 13, 59, 62, 69) would represent its ancestral condition, basal for raninoidids, and more related with most dromiaceans and homolids, instead of indicating multiple

reversals in a single taxon within the non-necrocarcinoid Raninoidea clade. The remaining non-raninoid traits (e.g. Ch. 25, 37, 70) appear convergent with Cyclodorippoida.

3) Section Raninoida polyphyletic, Superfamily Raninoidea polyphyletic: the most recent ancestor for at least one taxon within Raninoidea, therefore for Raninoida, is not a member of the clade. The affiliation of Archaeochimaeridae to the Section Raninoida is uncertain since the two synapomorphies that unite the clade; i.e. the triangular buccal cavity and the mxp3 with two planes, are unknown or inconclusively preserved in the new family. Therefore, grouping Archaeochimaeridae with Raninidae + Symethidae based on homoplasies such as the elongated carapace, and anterior end of telson lying behind coxa of P3, makes Raninoida a polyphyletic section. Furthermore, the cervical grooves, branchiocardiac grooves, and the dorsal longitudinal ridges, although scored as ‘present’ as in most necrocarcinoid and some palaeocorystid crab, are unlike any other brachyuran crab, particularly the very long, thin and non-tuberculate branchiocardiac ridges, and the short longitudinal ridges of the postfrontal region that end at the anterior cervical groove (Figure 3.5A-B, D). The primitive characters shared with other podotreme clades (e.g. Ch. 9, 12, 13, 59, 62, 69) reflect its origins rooted in a different node within the clade Brachyura. Herein, *Archaeochimaera* has been scored as having narrow posterior sternites (Ch. 27: (1)). However, the character as originally envisioned by Karasawa et al. (2011), is scored for sternites 6 to 8, and in *Archaeochimaera*, S7 is somewhat reduced, whereas S6 is broad. The female abdomen is narrower than S6, leaving the lateral parts of the sternite visible. This is even more evident in males, where pleonite 6 and the telson are one-fourth the width of S6. Thus, the character for Archaeochimaera must be scored as 0 & 1. Further and detailed cladistic analyses examining the internal relationships among raninoids would shed lights on the matter.

By re-running the phylogenetic analysis by Karasawa et al. (2011: fig.2) including Archaeochimaeridae as sister taxon for Raninidae + Symethidae, and by re-scoring two

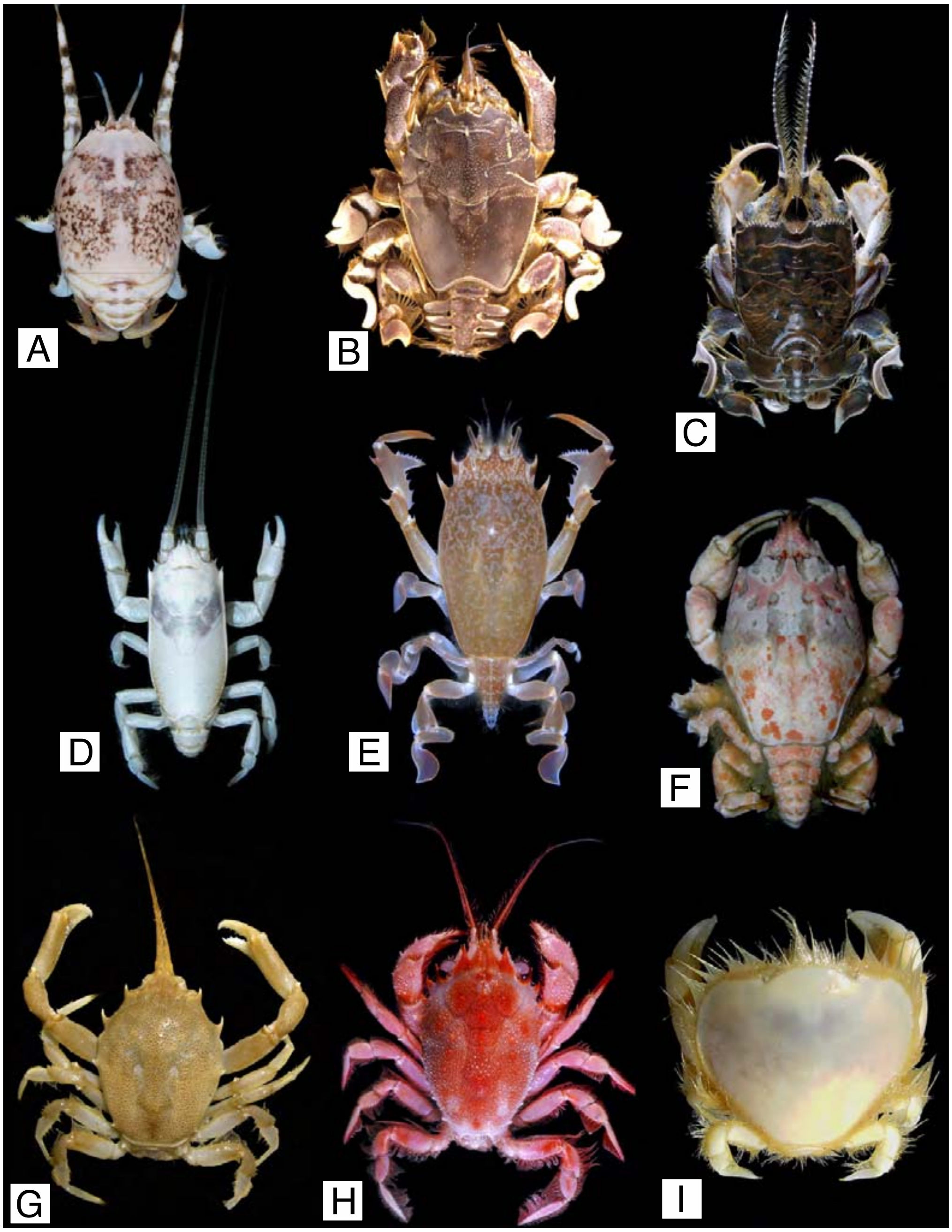

Figure 3.12. Convergent morphologies of some superfamilies and families of anomuran and brachyuran crabs. A-C, Anomura. Hippoidea. A, Hippidae, *Hippa marmorata* (Hombron and Jacquinot, 1846) Taiwan (Photo by Tin Yam Chan). B, Blepharipodidae, *Blepharipoda occidentalis* Randall, 1840, (photo by Christopher Boyko). C, Albuneidae, *Albunea occulta* Boyko, 2002, Taiwan (Photo by Tin Yam Chan). D, Galatheoidea, Porcellanidae, *Euceramus panatelus* Glassell, 1938, Panama (photo by Arthur Anker). E, Brachyura, Raninoidea, Raninidae, *Raninoides benedicti* (Rathbun, 1935), Panama (photo by Arthur Anker). F, Symethidae, *Symethis* sp., Panama (photo by Arthur Anker). G, Corystoidea, Corystidae, *Corystes cassivelaunus* (Pennant, 1777), Belgium (photo by Hans Hillewaert). H, *Jonas distinctus* (De Haan, 1835), Taiwan (Photo by Tin Yam Chan). I, Portunoidea, Thiidae, *Thia scutelata* (Fabricius, 1793), Belgium (photo by Hans Hillewaert). All photos used with permission of the photographers.

raninoid characters (Ch: 7, 50), the treelength (TL) increased from 224 steps to 240 steps. This is interpreted as related with the multiple reversals necessary to evolve the ancestral, homoplasic and convergent traits that distinguish Archaeochimaeridae from any other raninoidid crab. Furthermore, given the broad sternites 5 and 6 and the relatively reduced sternite 7 (8 is unknown) seen in *Archaeochimaera*, the character 27 as originally scored by Karasawa et al. (2011, 527) should be re-scored in the new taxon as 0 (i.e. posterior sternite 6 wide, S7 narrow-reduced, and S8 unknown, respectively). By re-scoring this character, TL increases to 241, CI=0.57, RI=0.78, and RC=0.45, supporting Archaeochimaeridae with the same number of steps as sister taxon for clades as Raninidae + Symethidae, G (Cyclodorippoida), Eubrachyura, or G + Eubrachyura, and only one step shorter from being sister for clade B (Homoloida), or even clade C (Torynommoida) + rest of ingroup. However, the strict consensus tree would set Archaeochimaeridae laying in a polytomy with Clade F (Dakoticancroida), Raninidae + Symethidae, Camarocarcinidae, Cenomanocarcinidae, Necrocarcinidae, Palaeocorystidae, Cyclodorippidae + Cymonomidae, Phyllotymolinidae, and Eubrachyura. Consequently, ascription of Archaeochimaeridae to any known Brachyura superfamily or section deemed as monophyletic is unwarranted.

Systematic Issues

Third maxillipeds equipped with serrated or spinose ischium (*crista dentata*) are known from adult and juvenile forms among many brachyuran and non-brachyuran decapods, including, but not exclusive to, some astacideans (e.g., Harlioglu, 2003, 2008), achelates (e.g., Suthers and Anderson, 1981; Guerao et al., 2006), anomurans (e.g., Martin and Felgenhauer, 1986; Ahyong and Baba, 2004; Hoyoux et al., 2009; McLaughlin and Lemaitre, 2009), dromiaceans (e.g. McLay, 2001; Guinot and Tavares, 2003; McLay and Ng, 2007), and eubrachyurans (e.g., Caine, 1974; Williams, 1978; Scholtz and Richter, 1995; Skilleter and Anderson, 1986; Marquez et al., 2003). Nonetheless, whether the spiniform structures found in some eubrachyurans, and the ‘crista dentata’ sensu stricto are homologous is still unclear (Ng et al., 2008). Scholtz and McLay (2009: 425) stated that: “the *crista dentata* (…) is a plesiomorphic reptant character that is present in the homolodromioids, dromiids, dynomenids, and homolids (except latreilliids)”, but lost once in the most recent common ancestor for the clade that unites Raninoida, Cyclodorippoida, and Eubrachyura. The crista dentata-like structure present in *Archaeochimaera* is constituted by four to five acute spines, positioned in the inner border of the mxp3 ischium (Figure 3.13A-B). Crista dentata and mxp3 bearing a long palp are traits absent in any fossil or extant adult raninoid, male or female, of any family (Figure 3.13C-F), a feature that obscures a presumed affinity with the known Raninoidea. In *Archaeochimaera*, the length of mxp3 ischium + merus (Is + Me) accounts for slightly more that half the endognath maximum length, and the palp (carpus + propodus + dactylus) the remaining (Figure 3.13A-B), whereas in extant raninoids the palp is considerably shorter than the Is + Me length. In the extant Raninoidea families, the mxp3’s Is + Me account for a large portion of the ventral carapace length, with the merus practically reaching the anterior portion and the base of the antennae (Figure 3.13E-F), whereas in *A. macrophthalma* the merus lies far from the anterior portion of the ventral carapace, and the Is + Me length barely accounts for one-fifth, of the carapace maximum length.

The presence of large eyes has been previously recognized in fossil brachyurans, e.g., the dromiacean *Ekalakia exophthalmops* Feldmann, Schweitzer and Wahl, 2008, and the eubrachyuran *Macrocheira yabei* (Imaizumi, 1957) (Imaizumi, 1965; Glaessner, 1969). Some species of the extant corystid genus *Jonas* Hombron and Jacquinot, 1846 [in Hombron and Jacquiton, 1842-1854], exhibit relatively large eyes as seen in *Archaeochimaera* (e.g., Ng et al., 2000; Ng et al., 2008) (Fig.12H). Members of the Raninoidae typically possess small eyes, particularly in Symethidae (Figure 3.13E-F).

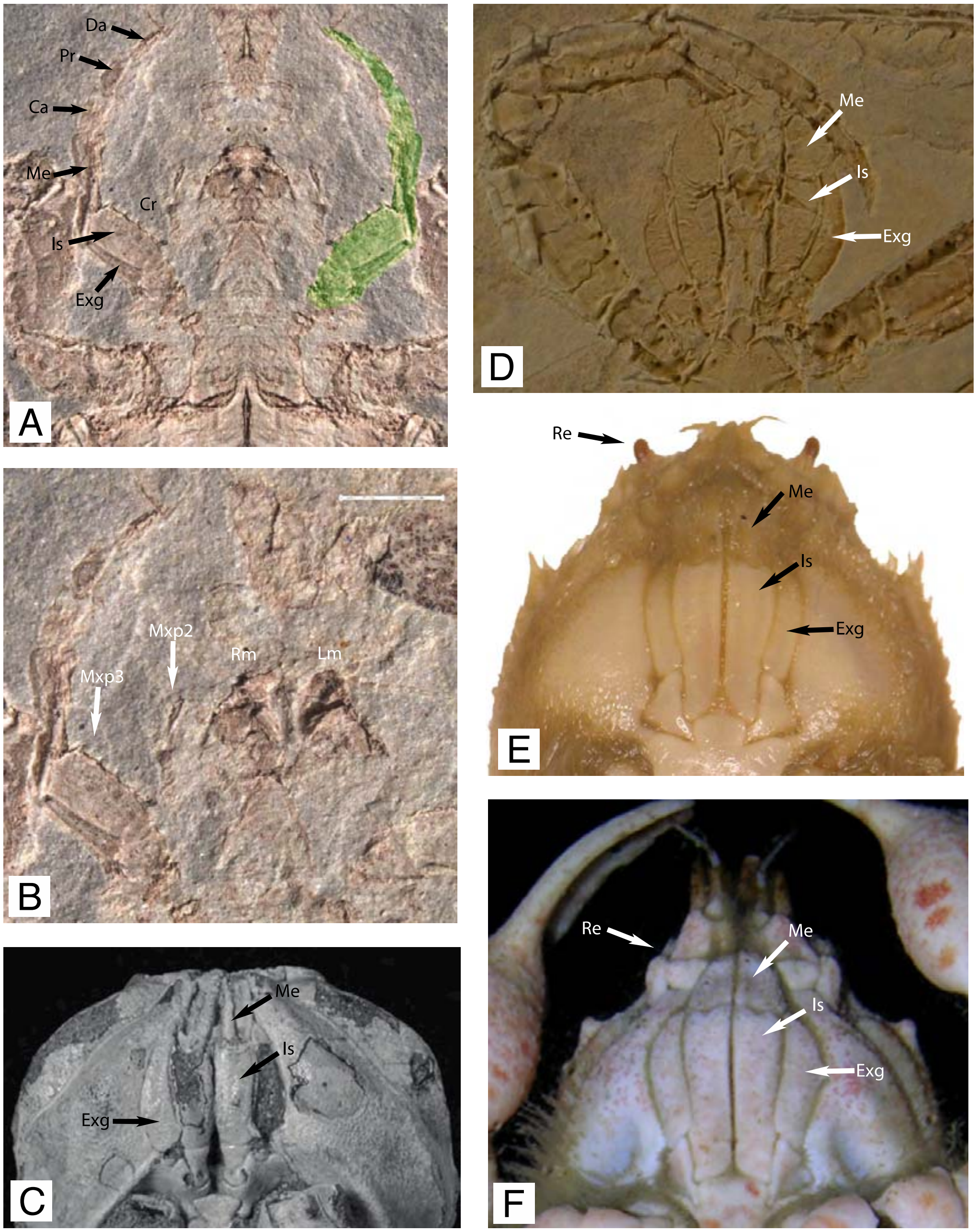

Figure 3.13. Comparison among Mxp3 of Archaeochimaeridae n. fam., and representatives of different raninoidid families. A-B, Archaeochimaeridae, *Archaeochimaera macrophthalma* n gen. n. sp., holotype IGM p881215, upper Cenomanian, Colombia. A, mirror image of the pediform right mxp3. B, close-up to the buccal appendages, showing Mxp2-Mxp3 and mandibulae. C, Camarocarcinidae, *Camarocarcinus arnesoni* Holland and Cvancara, 1958, hypotype USNM 103624, upper Cretaceous, US. D, Cenomanocarcinidae, *Cenomanocarcinus* sp., specimen 320032_014, lower Turonian, Colombia (photo by Rod Feldmann) (Luque et al., in progress). E, Raninidae, *Notosceles ecuadorensis* (Rathbun, 1935), recent, Panama. F, Symethidae, *Symethis* sp., recent, Panama (photo by Arthur Anker). Ca: carpus; cr: crista dentata; Da: dactylus; Exg: exognath; Is: ischium; Lm: left mandibula; Me: merus; Mxp2-Mxp3: maxillipeds 2-3; Pr: propodus; Re: right eye; Rm: right mandibula.

Taphonomy

Three taphofacies in Segment A of the Nocuatá Section were recognized, with crustaceans overwhelmingly dominating the fossil assemblage: crustacean-rich surfaces (Tf-I), appendage-rich surfaces (Tf-II), and scattered debris surfaces (Tf-III) (Feldmann et al., 1999) (Figure 3.2, Figure 3.3). The crustacean-rich surfaces (Tf-I) contain abundant cumaceans, some penaeid? shrimps, and juvenile and adult articulated *Archaeochimaera macrophthalma*. n. gen. n. sp. In this taphofacies, low post-mortem reorientation, low disarticulation of skeletal elements, and low fragmentation predominate. Among the samples collected, cumaceans (~0.2 to 0.3 cm in length) are the most abundant element, being found in high density on crustacean-rich surfaces (Figure 3.3A-B). Shrimp corpses (~1 cm), on the other hand, are uncommon (Figure 3.3E-F). Both cumaceans and shrimps are preserved with pereiopods, pleopods, and pleon attached to the body. *Archaeochimaera macrophthalma* is the largest macrofaunal element (~0.7 to 1.8 cm in length) with specimens occurring throughout the first 15 m (Figure 3.2), where remains are often found close to one another, preserving fine and delicate ornamentation of the carapace and limbs, and often laterally relaxed locomotory appendages (Feldmann et al*.,* 1999). In this taphofacies, no exuviae in Salter's, or molting position, nor corpses preserved in traumatic or escape positions were recognized (Schäfer, 1951; Bishop, 1986). On the contrary, *Archaeochimaera* corpses are often preserved in relaxed normal or non-traumatic postures, with chelae closed and held along the anterior portion of the carapace and with walking legs along the sides (Figures 3.5E, 3.6A, E). The burrowing behavior and fine-grained sediment preference displayed by cumaceans, and probably *A. macrophthalma*, are expected to increase the likelihood of complete organism preservation, under low scavenging, minimal bacterial decay, and low energetic settings. It has been suggested that the combination of upwelling, high primary productivity, potentially resulting in anoxic conditions in bottom-waters, and mass mortality events in the Colombian epicontinental seas, led to an unusual abundance of crustacean corpses in the upper Churuvita Group, increasing the possibility of preservation (Feldmann et al., 1999).

In the appendage-rich surfaces (Tf-II) (Figure 3.3D), *Archaeochimaera* carapaces are often dislocated, but it remains uncertain whether they belong to exuviae and/or re-worked carcasses. Nevertheless, the process of molting in a sheltered location such as within the sediment is expected to increase the chance of preserving exuviae (Schäfer, 1972). The carapaces, when complete, are preserved in traumatic positions, with P1 turned outwards, pereiopods interlaced, and mouthparts open (Figure 3.4A, F). *Archaeochimaera* remains dominate the assemblage, occasionally associated with fish remains (scales, vertebrae, spines), with no preferential orientation, but carapaces are mainly parallel to the lamination layers. Largest limbs are most common (Ch, P2, P3). Occasional low hydrodynamic periods of bottom currents would facilitate accumulation of fragmented appendages, segments, and carapaces, following decay and disarticulation, with fragmentation near the site of deposition. In both Tf-I and Tf-II, the thoracic sternum, Ch, P2-P3 and mouthparts of *A. macrophthalma*, are highly sclerotized and well preserved, strongly contrasting with the poorly sclerotized and badly preserved anteriormost portion of the ventral carapace (e.g. pterygostomian region, buccal cavity).

Scattered debris surfaces (Tf-III) are the most common along Segment A (Figure 3.2), and are characterized by the presence of scarce, single detached limbs and/or limb-segments of *Archaeochimaera*, mainly appendicular elements of the Ch, P2 and P3. In this taphofacies, the disarticulation/fragmentation of remains is high, suggesting high-energy conditions. The preservation of fine delicate remains such as eyes, antennae, mouthparts and pleopods, appears not to be taphofacies-related. The only evident difference among taphofacies is the density and completeness of the accumulated remains.

The Churuvita Formation, at its type locality, has been calculated to be 405 m thick, and to be deposited approximately between 100-93.5 M.y (Etayo, 1979). Assuming constant sedimentation rates, the unit would be deposited at a rate of 61.54 m/M.y. If we assume a similar rate for the Churuvita Formation at the Nocuatá section, the approximate time-interval represented in the 15.5 m of shales bearing *Archaeochimaera* would be near

252,000 years; or one centimeter every 162.5 years, suggesting that the crustacean-rich surfaces (Tf-I) might represent sporadic mass mortality surfaces and condensed sections that preserved the crustaceans.

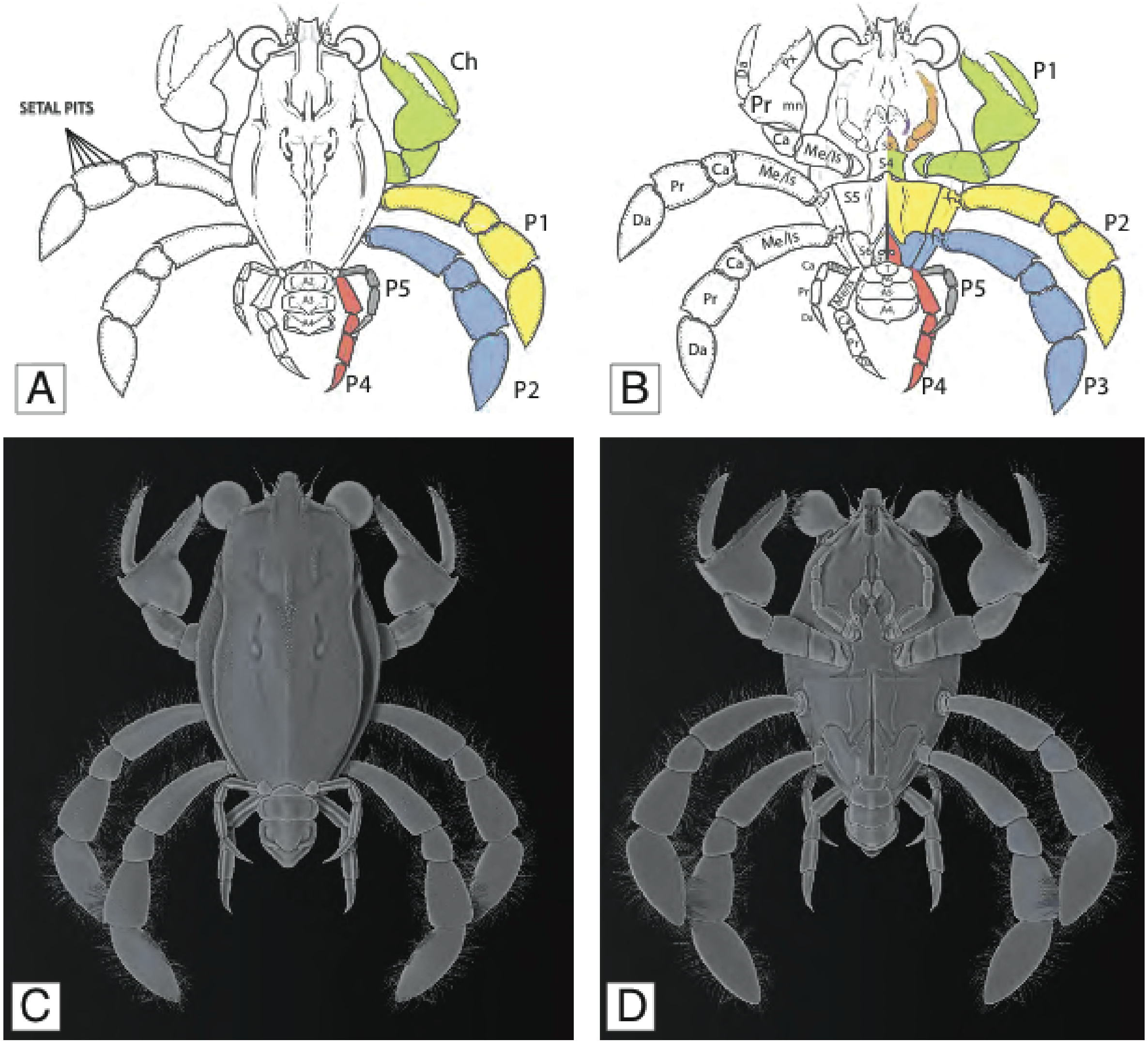

Figure 3.14. Reconstruction of *Archaeochimaera macrophthalma* n. gen. n. sp. A-B, composite line drawings in camera lucida, showing the appendages, carapace, pleon and sternum. A, dorsal view. B, ventral view. C-D, preliminary digital reconstructions. C, dorsal view. D, ventral view. Two preliminary three-dimensional reconstructions of *Archaeochimaera* are presented in Videos 1-2 (see Appendix) (digital reconstructions and animations by Alex Duque).

Paleobiology and Paleoecology

Raninoida is an extant clade containing tropical and temperate, marine-restricted crabs principally adapted to burying in sand or soft sediments (Borradaile, 1903; Bourne, 1922; Gordon, 1966; Abele and Felgenhauer, 1982; Števčić, 2005). Extant raninoids are abundant and widespread around the world but due to their cryptic lifestyle and subtidal range (from ~5 to 1000 m depth) (Tucker, 1995), little is known about their behavior and ecology. Frog crabs remain buried in the substratum during the day, emerging at night to search for food (Skinner and Hill, 1986). Skinner and Hill (1987) noted that *Ranina ranina* display a rapid emerging response towards food. The flattened paddle-like pereiopods possessed by most Raninids allow them to dig rapidly backward into the sediment (Bellwood, 2002), and occasionally swim. Some inherent advantages of burying are to avoid visual detection by predators, as well as from prey allowing ambush predation. Gaten (1998) suggested that in *Ranina* Lamarck, 1801*,* the relatively small size of the eyes reflects an adaptation to its burrowing habit. Raninoids have orbits that are usually ornamented with spines, protecting the eyes when they are retracted. The lack of true orbits and protective structures associated with the large *Archaeochimaera* eyes, would have prevented the animal from retracting them even under times of stress.

During Cenomanian times, approximately 94 million years ago, *Archaeochimaera* inhabited shallow, micaceous clayish bottoms at the eastern margin of Colombia's epicontinental sea, at paleolatitudes between 5 to 10 degrees North (Feldmann et al., 1999), and depths close to 50 m (Villamil, 1998). A NNE-SSW facing epicontinental sea, limited on the west by a volcanic arc-trench-system (part of what is today the Central Cordillera), and on the east by the Guayana Craton (Mann et al. 1994), covered most of what is today the emerged Andean Eastern Cordillera (Villamil, 1998; Villamil and Arango, 1998; Cáceres et al., 2005) (Figure 3.1A). Large swarms of small cumaceans inhabited the surface of the seabed and buried below the sediment-water interface (Figure 3.3A-B). Extant shallow water cumaceans remain buried during the day, and are active at night (Schram, 1986). Due to their small size, they usually prefer soft bottoms at depths where wave action does not affect them. In addition to the cumaceans and *Archaeochimaera*, small shrimps also dwelled in this benthic habitat, where small fish remains (vertebrae, scales, and spines) sporadically enriched the fine-grained sediment.

Although *Archaeochimaera* would be expected to display burrowing behavior, its enlarged paddle-like pereiopods 2 and 3 (Figures 3.4A, D-E; 3.5C, E, G), associated with broad sternites 5 and 6 (Figure 3.4A-B, D-G; 3.5E), and dorsally and ventrally keeled body (Figures 3.4; 3.5, 3.14), indicates both an agile burrower and active swimmer, while its strong P1, spinose mouthparts and specialized eyes appear well suited for predatory purposes. The last pereiopods 4-5, reduced, narrow and keeled (Figure 3.5C, E, H), would be of low utility for digging, being more useful for steering when swimming by mean of the large and flattened first pairs of pereiopods. It is possible that *Archaeochimaera* would have remained burrowed in the sediment waiting for prey to ambush, and/or that it swam or crawled over the sediment by mean of its paddle-like pereiopods. Whatever its lifestyle was, *Archaeochimaera* is expected to have used its large compound eyes actively out of the sediment. Given that *Archaeochimaera* is the largest macrofaunal element found in the crustacean-rich layers, the new taxon might have preyed on the abundant small cumaceans. Shrimps also may have been included in its diet, but their relatively large size and low population density would make them a less frequent prey item, although a larger meal.

Conclusions

The relatively high abundance of well-preserved cumaceans and archaeochimaerid crabs might be related to the availability of food, sporadic mass mortality events, low scavenging and minimal bacterial decay of corpses, and/or with their benthic burrowing lifestyle, increasing the chance of preservation of carcasses and exuviae. It is possible that a limited supply of clastic sediments to the basin may have enhanced the accumulation of organic remains over short stratigraphic intervals.

The functional morphology of *Archaeochimaera macrophthalma* n. gen. n. sp., particularly the dorsally and ventrally keeled carapace, the broad sternites 5-6, and their associated enlarged paddle-like pereiopods 2-3, indicate a lifestyle of agile burrower and swimmer that inhabited soft bottoms in relatively shallow, low energy subtidal settings. The large and unprotected eyes of *Archaeochimaera macrophthalma* likely remained above the sediment while the animal was buried, and/or were used when swimming to locate food items, predators, and conspecifics. The robust and strongly bent chelipeds, and the spinose ischium of the pediform Mxp3, are characters well suited for predatory purposes. Both the large eyes and pediform Mxp3 might represent neotenic traits retained in the adulthood, as specializations for certain dietary habits and/or local ecological pressures. The longitudinal keels on sternite 5 are unique among fossil or extant brachyuran crabs, leaving the question of their functionality open but they may have assisted in holding the abdomen against the chest, or enhanced the hydrodynamics of the animal.

The early burst of morphological diversification experienced by brachyurans during late Jurassic and the Cretaceous times, led to a broader niche occupation than previously expected (Schweitzer and Feldmann, 2010b, 2011a; Karasawa et al., 2011). Episodes of high global sea levels during the Mesozoic may have promoted the evolution and diversification of different burying clades. It is conceivable that within the podotreme crabs, the innovation of a fusiform carapace may have evolved more than once (e.g. in

Raninoidea and Archaeochimaeridae), just as it has within Anomura and Brachyura (Figure 3.11, Table V). This is likely related to their infaunal burrowing lifestyles, with similar selective forces acting on the phenotypes and selecting for similar adaptative traits. Other examples of trait convergence associated with a burrowing lifestyle may include paddle-like limbs, reduced posterior sternites and pereiopods, closer coxae of posterior pereiopods axially, and an abdomen forced backwards. Given this scenario and the phylogenetic remarks discussed, hypothesis 3 is supported, with Archaeochimaeridae representing an independent brachyuran lineage, envisioned as more related to the branch that includes clades E, F, and G than to the most primitive podotremes. However, given the many diagnostic traits shared with the basal raninoidids, hypothesis 2 is supported to some extent, with Archaeochimaeridae interpreted as an early offshoot within the Section Raninoida, and standing as sister to the monophyletic superfamily Raninoidea. The fusiform carapace may have evolved parallel in distantly related raninoidid taxa sharing similar underlying genetic toolkit that permitted to evolve similar traits, probably triggered by similar niche occupancy. Therefore, despite the morphological completeness of the new chimaeric taxon, its phylogenetic affinity remains uncertain, and further paleontological material and cladistic analyses are expected to enhance the phylogenetical resolution.

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4. CONCLUSIONS

The relatively abundant fossil record of frog crabs displaying strong phenotypic disparity permits the examination of general trends in their evolution and diversity throughout time. The stratigraphic and paleontological information herein presented provides additional evidence that supports the hypothesis of a raninoid-type architecture derived from a necrocarcinoid-type ancestor. The former is thus a highly specialized clade of advanced podotreme crabs well adapted for a fossorial lifestyle, with an early fossil record extending back into the Aptian of the Neotropics, falsifying the hypothesis that modern frog crabs represent a primitive brachyuran group reminiscent of an anomuran ancestor.

The occurrence of *Notopocorystes kerri* n. sp. in Aptian rocks (Chapter 1) suggest that the evolutionary innovation of elongated carapaces in frog crabs might be rooted in the early Cretaceous, or even the late Jurassic. Furthermore, the discovery of the new enigmatic family Archaeochimaeridae (Chapter 2), presumably related to the fusiform clade within Raninoida, might actually represent an independent evolution of a fusiform body plan within early podotreme crabs, convergent with many other anomurans and brachyuran clades adapted to similar burrowing habits. It is also plausible that the new taxon represents an early raninoidid lineage in which the general morphology evolved in a parallel way to the advanced and fusiform raninoid-type clade.

The early Neotropical presence of frog crabs during Cretaceous times is represented by the Aptian *Planocarcinus olssoni* n. comb., (Necrocarcinidae), and *Notopocorystes kerri* n. sp. (Palaeocorystidae) from Colombia. *Planocarcinus* is one of the oldest known necrocarcinids, and *N. kerri* the oldest known palaeocorystid. In addition, the Albian *Cenomanocarcinus vanstraeleni* Stenzel, 1945, (Cenomanocarcinidae) from Colombia (Vega et al., 2010), and *Araripecarcinus ferreirai* Martins-Neto, 1987 (?Necrocarcinidae) from Brazil (Luque et al., in progress), account for some of the oldest, or the oldest, occurrences of their families. The aforementioned taxa, plus the new monotypic family

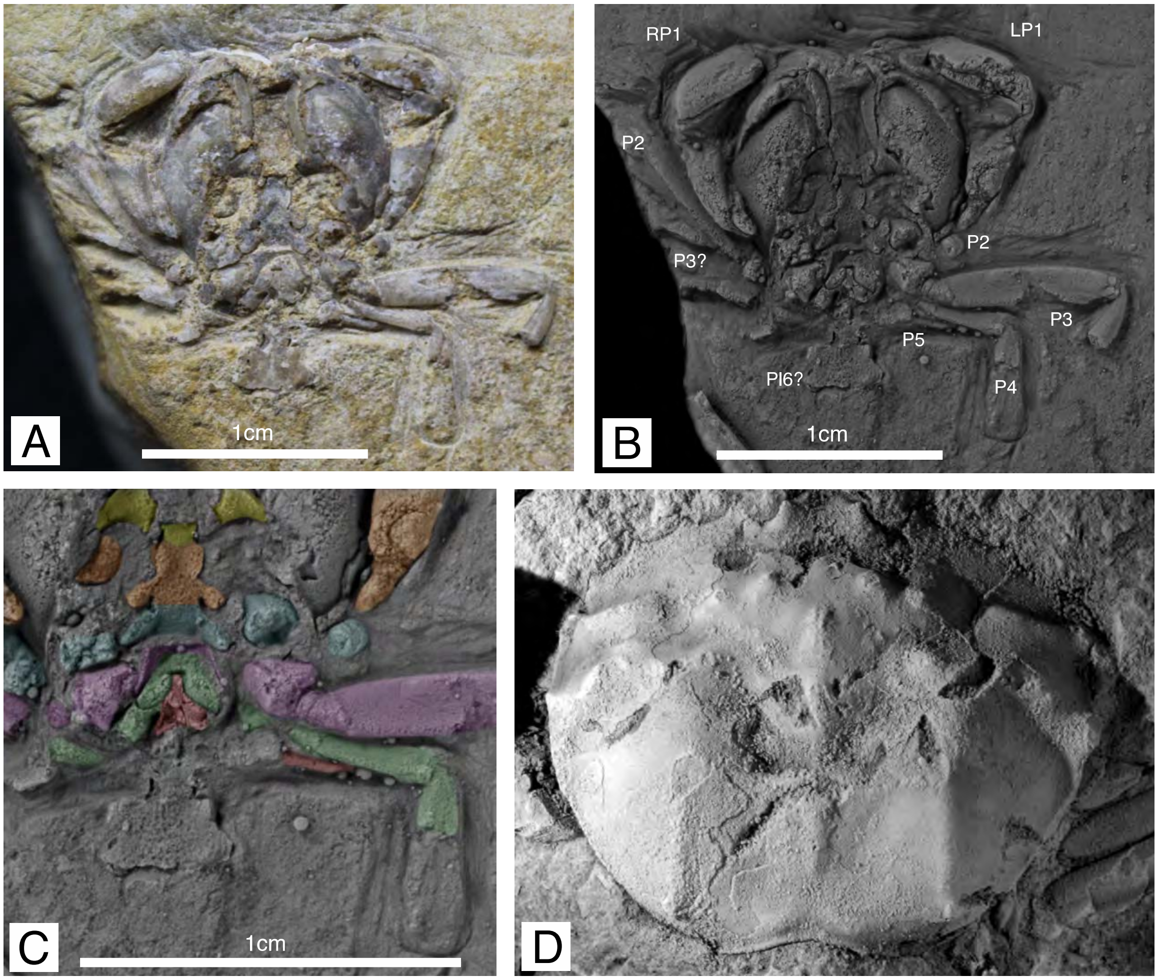

Figure 4.1. Albian raninoids from Northern South America. A-C, ?Camarocarcinidae, *Araripecarcinus ferreirai* Martins-Neto, 1987, ventral view, lower Albian, Brazil. A, holotype GP-1T 1477 (photo by Paula Sucerquia). B-C, cast of holotype. B, specimen showing the roundish carapace outline, the limbs and the thoracic sternum (photo by Rodney Feldmann). C, close-up to the thoracic sternum and the pereiopods. D, Cenomanocarcinidae, *Cenomanocrcinus vanstraeleni* Stenzel, 1945, hypotype INGEOMINAS-JCR-1, upper Albian, Colombia (photo by Francisco Vega). Body parts in C as follow: yellow: Mxp3 coxae associated to S3; orange: P1 associated to S4; blue: P2 associated to S5; purple: P3 associated to S6; green: P4 associated to S7; red: P5 associated to S8. LP1: left cheliped; P2-P5: pereiopods 2 to 5; Pl6?: pleonite ?six; RP1: right cheliped.

Archaeochimaeridae, from the Cenomanian of Colombia, indicate that many lineages of frog crabs and frog-like podotremes were well established, and possibly originated, in Cretaceous equatorial Neotropics.

As a whole, the morphological diversity held by frog crabs during Early Cretaceous times is considerably broader than previously envisioned, and their pre-Albian paleogeographic distribution was already extensive. The evolution and diversification of Raninoida appears to be coincident with some of the major environmental disturbances in the last ~130 My., including high sea levels, Oceanic Anoxic Events, and warmer temperatures worldwide. However, correlation does not necessarily proves causation, and still little is known about the phenotypic response of most brachyuran crabs to ecological pressures associated with particular environmental disturbances during Cretaceous times. The problem of understanding the evolution of the group will be accessible with continued investigations into their stratigraphic record, phylogenetic affiliations and paleobiogeographic patterns.

Appendix

Table I. Updated list of Early Cretaceous families, genera and species within the Section Raninoida 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 Guinot, Vega and Van Bakel, 2008	*Cenomanocarcinus* Van Straelen, 1936	*C. armatus* (Rathbun, 1935)	Texas, USA						**X**
		C. oklahomensis (Rathbun, 1935)	Oklahoma, USA						**X**
		C. renfroae (Stenzel, 1945)	Texas, USA; Colombia						**X**
		C. vanstraeleni Stenzel, 1945	Texas and New Mexico, USA; Mexico; Colombia						**X**
Necrocarcinidae Förster, 1968	*Araripecarcinus* Martins-Neto, 1987	*A. ferreirai* Marrins-Neto, 1987	Brazil						**X**
	Necrocarcinus Bell, 1863	*N. bedrakensis* Levitski, 1974	Crimea						**X**
		N. labeschei (Eudes-Deslongchamps, 1835)	Great Britain; France						**X**
		N. tauricus Ilyin and Alekseev, 1998	Crimea						**X**
		N. texensis Rathbun, 1935	Texas, USA						**X**
		N. undecimtuberculatus Takeda and Fujiyama, 1983	Japan					**X**	
		N. woodwardi Bell, 1863	Great Britain						**X**
	Paranecrocarcinus Van Straelen, 1936a	*P. graysonensis* (Rathbun, 1935)	Texas, USA						**X**

		P. hexagonalis Van Straelen, 1936	France	**X?**	**X?**	**X?**			
		P. kennedyi Wright, 1997	South Africa				**X**		
		P. moseleyi (Stenzel, 1945)	Texas, USA						**X**
	Planocarcinus n. gen.	*P. olssoni* (Rathbun, 1937)	Colombia					**X**	
	Pseudonecrocarcinus Förster, 1968	*P. scotti* (Stenzel, 1945)	Texas, USA						**X**
		P. stenzeli Bishop, 1983	Texas, USA						**X**
Palaeocorystidae Lőrenthey, in Lőrenthey and Beurlen, 1929	*Cretacoranina* Mertin, 1941	*C. punctata* (Rathbun, 1935a)	Texas, USA						**X**
	Eucorystes Bell, 1863	*E. broderipii* (Mantell, 1844)	England; France; Swiss Jura						**X**
		E. carteri (M'Coy, 1854)	Egland						**X**
		E. mangyshlakensis Ilyin and Pistshikova in Ilyin, 2005	Kazakhstan						**X**
		E. oxtedensis Wright and Collins, 1972	England						**X**
		E. platys Schweitzer and Feldmann, 2001	Oregon, USA; British Columbia, Canada						**X**
	Notopocorystes M'Coy, 1849	*N. bituberculatus* Secretan, 1964	Madagascar						**X**
		N. kerri n. sp.	Colombia					**X**	
		N. parvus Rathbun, 1935a	Texas, USA						**X**
		N. stokesii (Mantell, 1844)	England						**X**
		N. xizangensis Wang, 1981	Lhasa, China; Iran						**X**
Raninidae De Haan, 1839 [in De Haan, 1833-1850]	*Hemioon* Bell, 1863	*H. cunningtonni* Bell, 1863	England						**X**
		H. elongatum (A. Milne Edwards), 1862	England, France, Czech, Germany, UK						**X**

	H. novozelandicum Glaessner, 1980	New Zealand	**X**
	H. yanini Ilyin and Alekseev, 1997	Crimea	**X**
Raninella A. Milne Edwards, 1862	*R. armata* Rathbun, 1935	Texas, USA	**X**
	R. atava Carter, 1898	England	**X**
	R. mucronata Rathbun, 1935	Texas, USA	**X**

Table II. Measurements (mm) of specimens of *Archaeochimaera macrophthalma* n. gen. n. sp. Maximum lengths (L), and maximum widths (W) of chelipeds (P1), pereiopods 2 to 5 (P2-P5), sternal crown (S1-4), sternite 5 (S5), sternite 6 (S6), and left and right eyes (Le, Re).

SPECIMEN	**P1**	**P2**	**P3**	**P4**	**P5**	**S1-4**		**S5**		**S6**		**Le**		**Re**	
	(L)	(L)	(L)	(L)	(L)	(L)	(W)	(L)	(W)	(L)	(W)	(L)	(W)	(L)	(W)
Holotype IGM p881215	9.8	11.1	10.8			2.8	1.8	2.5	2.4	1.6	1.8				
Paratype IGM p881196	7.2	9.5		4.4		2.1	1.4	2.0	2.3	1.2	1.5				
Paratype IGM p881206	10.8	13.4	12.7	6.7	4.7					2.1	2.1				
Paratype IGM p881214	10.6	16.8	15.1	8.6	7.6	3.3	1.9	3.4	4.4	2.7	2.9				
Paratype IGM p881219		10.2	9.9	5.5	4.0							1.9	2.0	2.0	2.1
Paratype IGM p8812202		7.3	7.3			1.2	10.9					1.3	1.1	1.3	1.1

Table III. Characters list for 74 morphological characters scored for 2 taxa in outgroup and 36 taxa in ingroup, including Archaeochimaeridae n. fam.. (see Appendix Table IV). Character scores: undetermined or not preserved (?), inapplicable characters states (-). Base character list provided by Hiroaki Karasawa, and modified after Karasawa et al. (2011).

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1. Carapace proportions: elongate (0); as long as wide or wider (1)
2. Anterolateral margins: indistinct (0); distinct (1)
3. Spines or teeth on anterolateral margins: absent (0); present (1)
4. Carapace with well differentiated anterolateral and posterolateral margins: absent (0); present (1)
5. Posterolateral margins: rounded, not defined (0); defined (1)
6. Spines on posterolateral margin: absent (0); present (1)
7. Posterior margin: concave (0); straight (1)
8. Re-entrants on posterior margin: absent (0); present (1)
9. Orbit: not defined (0); defined (1)
10. Augenrest: absent (0); present (1)
11. Augenrest, if present: shallow (0); deep (1)
12. Inner orbital angle: not defined (0); defined (1)
13. Upper orbital fissures: absent (0); present (1)
14. Subhepatic swelling: present (0); absent (1)
15. Antennal groove: present (0); absent (1)
16. Cervical groove: distinct (0); indistinct (1)
17. Postcervical groove: present (0); absent (1)
18. Branchio-cardiac groove: distinct (0); indistinct (1)
19. Longitudinal ridge or tubercles on branchial region: absent (0); present (1)
20. Cervical or branchio-cardiac groove: reaching ventral carapace (0); ending anterolateral margin (1)
21. Intestinal region: very narrow, limited by branchio-cardiac grooves (0); wide (1)
22. Lateral lineae: absent (0); present (1)
23. Epistominal spine: absent (0); present (1)
24. Buccal cavern: wide (0); elongated, triangular (1)
25. Thoracic sternum: narrow (0); wide (1)
26. Sternites 1-3: indistinct ventrally (0); distinct ventrally (1)
27. Posterior sternites: wide (0); narrow, reduced (1)
28. Lateral position of posterior sternites: not visible (0); visible (1)
29. Episternites: not clearly defined (0); clearly defined by grooves (1)
30. Episternites 4-5: process-like (0); wide (1)
31. Suture 4-5: only lateral position (0); well developed (1)
32. Suture 5-6: only lateral position (0); well developed (1)
33. Suture 6-7: incomplete (0); complete (1)
34. Sternite 4 with anteriorly protruded plate: absent (0), present (1)
35. Median line on sternite 8: absent (0); present (1)
36. Sterno-coxal depression: present (0); absent (1)
37. Sterno-abdominal depression: absent (0); present (1)
38. Sterno-abdominal cavity in male: absent (0); present (1)
39. Homolid press-button: absent (0); present (1)
40. Sella turcica: absent (0); present (1)
41. Spermatheca: absent (0); present (1)
42. Spermatheca: if present, paired (0); united (1)
43. Spermatheca position: if present, back or P3 coxa (0); anterior to P3 coxa (1)
44. Aperture of spermatheca: if present, margins not raised (0); raised (1)
45. Abdomen: not folding (0); folding (1)
46. Abdominal somites: visible dorsally (0); not visible (1)
47. Abdominal pleura: well developed (0); reduced (1)
48. Articulating rings of abdomen: present (0); absent (1)
49. Fusion of abdominal somites and telson in male: absent (0); present (1)
50. Abdominal locking: coxal spine (0); sternal lobe (1); absent (2)
51. Abdominal somite 6 with triangular lateral lobes: present (0); absent (1)
52. Socket on sternite 6: absent (0); present (1)
53. Telson of male: elongate, much longer than wide (0); about as long as wide or wider than long (1)
54. Anterior end of telson, if folding present: between Mxp 3 (0); anterior sternite 4 (1); posterior sternite 4 (2); behind coxa pereiopods (3)
55. Uropodal plate: absent (0); present (1)

56. Male gonopore position: coxal (0); sternal (1)
57. Female gonopore position: coxal (0); sternal (1)
58. Renal opening of 2nd antennal coxa with beak-like structure: absent (0); present (1)
59. Maxilliped 3: pediform (0); operculiform (1)
60. Maxilliped 3 much longer than wide: present (0); absent (1)
61. Maxilliped 3 with two plains: absent (0); present (1)
62. Maxilliped 3 with crista dentata: present (0); absent (1)
63. Maxilliped 3 coxa: large, touched (0); small, not touched (1)
64. Palp of maxilliped 3 merus: distal position (0); inner-mesial position (1)
65. Palp of maxilliped 3 merus: different plane (0); same level to merus (1)
66. Pereiopods 2-4 form: normal (0); wide, flattened (1)
67. Pereiopods 4-5 condition: normal (0); P5 dorsal (1); P4-5 dorsal (2)
68. Pereiopods 4-5 condition: normal (0); P5 chelate (1); P4-5 chelate (2)
69. Pereiopods 4-5 size: normal (0); P5 reduced (1); P4-5 reduced (2)
70. Coxae of pereiopods: elongate, large (0); short (1)
71. Male coxa P5: not modified (0); modified (1)
72. Male coxa P5: penial tube absent (0); penial tube present (1)
73. Pleopods on segments 3-5 in male: present (0); absent (1)
74. Male second pleopod with exopod: present (0); absent (1)

Table IV. Character data matrix of brachyuran clades included in the phylogenetic analysis. Taxa indicated by † known as both extant and fossil species, and †† only known as fossil. The remaining taxa are only known from extant species. Base character data matrix provided by Hiroaki Karasawa, and modified after Karasawa et al. (2011).

	Character States							
Family	**0-10**	**11-20**	**21-30**	**31-40**	**41-50**	**51-60**	**61-70**	**71-74**
Astacidea	0000000000	-000000000	0000001-0-	---0-10000	0---000002	000-000000	0000000000	0010
††Eocarcinidae	0000000000	-000000000	000????-??	??????????	????00000?	1??-??????	?????0000?	????
††Archaeochimaeridae	0???110000	-001?01011	?0??11101(01)	1110?1000?	100?101102	1?030???00	?010?(01)1021	????
†Homolodromiidae	0000000101	1000000000	0000000000	0000001000	1001100100	0011000100	0000002220	1001
††Bucculentidae	0000000101	1000000000	000???????	??????????	??????????	??????????	??????????	????
††Goniodromitidae	(01)(01)(01)(01)000101	1000000000	000?0???00	00???010??	?????0????	??????????	??????????	????
††Prosopidae	0000000101	1000000000	000???????	??????????	????1?110?	001?0?????	??????????	????
††Tanidromitidae	0000000101	0000000000	000???????	???0??????	??????????	??????????	??????????	????
††Glaessneropsidae	0000000010	-010000000	000???????	??????????	??????????	??????????	??????????	????
††Konidromitidae	0000000010	-000000000	000???????	??????????	??????????	??????????	??????????	????
††Lecythocaridae	1000000010	-010000000	000???????	??????????	??????????	??????????	??????????	????
††Longodromitidae	0000000001	0000000000	0000000000	0000?0100?	???101100	10110?0?00	0?0??01?10	????
†Dromiidae	1111(01)00010	-000(01)00000	1000000000	0001001000	1011101100	10(01)1(01)00111	0000002220	01(01)1
†Dynomenidae	1111100010	-001100(01)00	10000(01)0000	0000001000	100110110(01)	0001100111	00(01)0001110	1000
†Sphaerodromiidae	1111(01)00010	-0011(01)(01)(01)00	1000000000	0001001000	1001101100	0011100111	0000002220	1000
††Diaulacidae	1111000010	-001101(01)00	1000010000	000000100?	100?10110?	100?0?????	????01?10	????
††Xandarocarcinus	1111100010	-001101100	10000100??	???0??100?	????111100	1?11000?11	0?0??00000	????
††Basinotopidae	0111000010	-000000000	1000000000	000100100?	1001100100	000?1?0?10	000??02?20	????
†Homolidae	0000000101	0000001000	(01)110110001	0010101010	1000101100	11(01)00000	(01)00(01)10001110	0011
Latreilliidae	0000000000	-000001000	1010110001	0010101010	1000101100	1100000000	0110001110	0011
†Poupiniidae	0000000001	0000001000	1010110001	0010101010	1000101100	1100000000	0010001000	0011

Mithracitidae	0100000001	0000001000	10100100??	???0?0101?	????101100	11000???11	001??01?10	????
††Etyidae	1111000010	-111101000	1000010001	110001100?	1000101101	1002000?11	0110102?20	0???
††Dakoticancridae	1101101010	-001101(01)01	1000(01)10101	110001(01)(01)0?	1000101101	1002000?11	0110101?11	0???
††Ibericancridae	1101101010	-011101001	1000010101	110001100?	1000101101	1002000?11	0110102?21	0???
†Raninidae	01(01)0101010	-111111101	1001011(01)01	111011(01)000	110010110(12)	1(01)03000010	11111110(01)0	0011
Symethidae	0100101010	-111111101	1001011101	1110111000	1100101102	1003000010	1111111010	0011
††Camarocarcinidae	1111110010	-1111(01)1(01)0(01)	1001010?01	110001100?	?????0????	?0???0??10	111???????	????
††Cenomanocarcinidae	11111(01)(01)010	-1111(01)1(01)11	1001010001	111001100?	1000101101	1002000?10	11101(01)1010	????
††Necrocarcinidae	11111(01)(01)010	-111101(01)1(01)	1001010001	111001100?	????101101	1002000?10	111???1??0	????
††Palaeocorystidae	0111100010	-1111(01)1(01)(01)(01)	1001010001	111001100?	1000101102	1002000?10	1110111010	0???
†Cyclodorippidae	11(01)(01)000010	-(01)11101001	1001110101	1110010100	1000101112	1003000010	1111102221	0011
†Cymonomidae	10(01)(01)000000	-001101001	1001110101	1110010100	1000101112	1003000010	1111102221	0011
Phyllotymolinidae	1111(01)00010	-(01)11101001	1000110101	1110010100	1000101102	1002000010	1111102221	0011
††Torynommidae	1000000010	-000101000	1000010001	110001100?	????10110	?10020?0??	??11???2?20	????
††Goniochelidae	1111100010	-111101011	1000110?11	11?0?101??	0--?101102	1?0?0?1?1?	011??02?2?	????
†Carcinidae	1111101010	-111111101	1000110111	1100110101	0---111102	1102001011	0110100001	0011
†Varunidae	1111101010	-001111101	1000110111	1100110101	0---111102	1101011011	0110100001	0011

Table V. Convergent superfamilies and families of extant anomurans and brachyurans. Systematic arrangement following the works of De Grave et al., 2009, and Schweitzer et al., 2010. Taxa indicated by † are known as both extant and fossil species.

- Infraorder Anomura MacLeay, 1838.
  - **SUPERFAMILY GALATHEOIDEA** † Samouelle, 1819
    - **Family Porcellanidae** † Haworth, 1825

  - **SUPERFAMILY HIPPOIDEA** † Latreille, 1825a
    - **Family Albuneidae** † Stimpson, 1858d
    - **Family Blepharipodidae** † Boyko, 2002
    - **Family Hippidae** Latreille, 1825a

- Infraorder Brachyura Linnaeus, 1758
  - **SUPERFAMILY RANINOIDEA** † De Haan, 1839 [in De Haan, 1833-1850]
    - **Family Raninidae** † De Haan, 1839 [in De Haan, 1833-1850]
    - **Family Symethidae** Goeke, 1981

  - **SUPERFAMILY CORYSTOIDEA** † Samouelle, 1819
    - **Family Corystidae** † Samouelle, 1819

  - **SUPERFAMILY PORTUNOIDEA** † Rafinesque, 1815
    - **Family Thiidae** † Dana, 1852c