



THE OLDEST HIGHER TRUE CRABS (CRUSTACEA: DECAPODA: BRACHYURA): INSIGHTS FROM THE EARLY CRETACEOUS OF THE AMERICAS

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Abstract: Despite the extensive fossil record of higher crabs (Eubrachyura) from Late Cretaceous and Cenozoic rocks worldwide, their Early Cretaceous occurrences are scarce and fragmentary, obscuring our understanding of their early evolution. Until now, representatives of only two families of eubrachyuran-like crabs were known from the Early Cretaceous: Componocantridae and Tepexicarcinidae fam. nov., both monospecific lineages from the Albian (~110–100 Ma) of North and Central America, respectively. The discovery of *Telamonocarcinus antiquus* sp. nov. (Telamonocarcinidae) from the early Albian of Colombia, South America (~110 Ma), increases to three the number

of known Early Cretaceous eubrachyuran-like families. The ages and geographical distributions of the oldest eubrachyuran-like taxa (i.e. Componocantridae, Telamonocarcinidae and Tepexicarcinidae fam. nov.) suggest that the oldest higher true crabs might have originated in the Americas; that they were already morphologically diverse by the late Early Cretaceous; and that their most recent common ancestor must be rooted in the Early Cretaceous, or even the Late Jurassic.

Key words: Americas, crab, Early Cretaceous, Eubrachyura, evolution, neotropics.

TRUE crabs (Brachyura) are the most derived clade of decapod crustaceans and exhibit an astonishing diversity of body plans not seen among other decapods. The most debatable trait for grouping brachyurans is the position of the female's sexual openings, either at the base of the legs (= podotremes) or at the thoracic sternum (= eubrachyurans; Guinot 1977; Saint Laurent 1980; Guinot and Quenette 2005; Guinot *et al.* 2013). Although the monophyly of podotremes is still debated, there is a general consensus that Eubrachyura, or 'higher' true crabs, is a monophyletic clade (Spears *et al.* 1992; Ah Yong *et al.* 2007; Brösing *et al.* 2007; Ng *et al.* 2008; Scholtz and McLay 2009; Karasawa *et al.* 2011; Tsang *et al.* 2014; among others). However, while fossil eubrachyurans are relatively well known from Late Cretaceous and Cenozoic deposits worldwide, little is known about their Early Cretaceous history, obscuring our understanding of their early disparity. Documenting the fossil record of Brachyura is crucial to our comprehension of the relationships among the main extant crab lineages. This is because all the diversity seen today is the result of millions of years of evolution; thus, modern body plans are derived lineages descending from early branches in the brachyuran evolutionary tree. In addition, many distinctive body plans are restricted to the Cretaceous, a time when

Brachyura flourished and diversified. These groups provide unique information about the relatedness by common ancestry of extant clades and the polarity of changes in diagnostic traits that unite today's main body plans. Representatives of only two Early Cretaceous eubrachyuran families have previously been described: Componocantridae Feldmann, Schweitzer and Green, 2008, and Tepexicarcinidae fam. nov., both from the Albian of North and Central America (~110–100 Ma). Herein, I report a new species of early eubrachyuran, *Telamonocarcinus antiquus* sp. nov., from the early Albian of Colombia, South America (~115 Ma), and discuss its spatial and temporal implications for the origins of higher true crabs.

GEOLOGICAL SETTING

Telamonocarcinus antiquus sp. nov. was discovered in black-greyish, terrigenous, gypsum-rich, micaceous shales of the lowermost Tablazo Formation, cropping out near the contact with the underlying Paja Formation in a small quarry, approximately 30 m from El Salitre Creek, countryside of El Batán, Montegrande, near the town of La Fuente, Department of Santander, Colombian Eastern Cordillera; latitude N 06°43'30", longitude W 73°15'32"

(Fig. 1A). The Tablazo Formation was described by Wheeler (in Morales *et al.* 1958) as a succession consisting principally of thick fossiliferous limestone in the upper portion and calcareous mudstones with arenitic intervals in the lower portion, cropping out in the area known as El Tablazo, where the main road from Bucaramanga to San Vicente de Chucurí intersects the Sogamoso River, approximately 36 km north–north-west from where *Telamonocarcinus antiquus* sp. nov. was discovered. Here, the unit overlies the grey fossiliferous shales and limestones with concretionary levels of the Paja Formation (Barremian – upper Aptian) and underlies the predominant light to dark mudstones interspersed with sporadic sandstones of the Simití Formation (middle–upper Albian; Morales *et al.* 1958; Julivert 1968; Pulido 1985; Moreno and Sarmiento 2002; Fig. 1B). Morales *et al.* (1958) reported from the Tablazo Formation the ammonite genera *Uhligella* Jacob, 1907, *Chelonicerias* Hyatt, 1903, *Parahoplites* Anthula, 1899, and stratigraphically above, the genus *Douvilleicerias* Gros-souvre, 1894, indicating a late Aptian – early Albian age (Julivert 1968; Moreno and Sarmiento 2002). The area of study is structurally complex, with several faults dislocating blocks associated with the trace of the Suarez fault

(Pulido 1979, 1985; Fig. 1B). In addition, the region is densely vegetated, resulting in poor exposure of outcrops that are mainly restricted to some road cuts. Despite this, recent field explorations resulted in the discovery of several decapod crustacean remains at the base of the Tablazo Formation near the contact with the Paja Formation, associated to ammonite fragments of *Neodeshayesites* sp. indet. which correspond to the *Douvilleicerias solitae* – *Neodeshayesites columbianus* zone (Etayo-Serna 1979, p. 14), thus indicating an early Albian age for the rocks containing *Telamonocarcinus antiquus* sp. nov. (F. Etayo-Serna, R. Terraza and D. Montoya pers. comm. September 2014).

The Paja Formation is one of the most prolific and most extensively studied fossiliferous units in Colombia, and has yielded an impressive array of plants (Huertas 1967, 1970, 1976; van Waveren *et al.* 2002); marine vertebrates including fishes and reptiles (Acosta *et al.* 1979; Hampe 1992, 2005; Schultze and Stöhr 1996; Páramo 1997); invertebrates such as ammonites and bivalves (Etayo-Serna 1968a, b, 1979; Villamil 1998; Patarroyo 2000; Hoedemaeker 2004; among many others); and most recently decapod crustaceans such as the homoloid crab

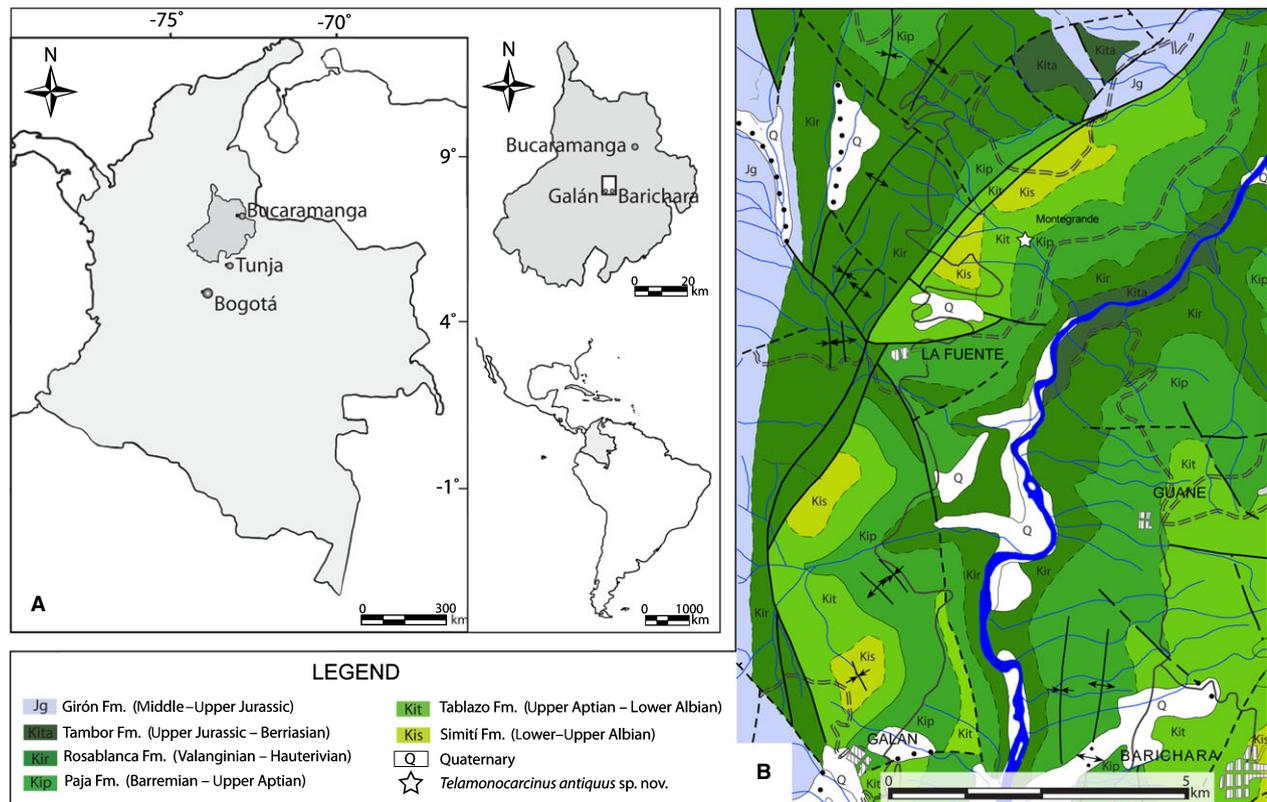


FIG. 1. A, locality map showing the approximate geographical provenance of *Telamonocarcinus antiquus* sp. nov., holotype IGM p881012, near the town of La Fuente, Department of Santander, Colombia, South America. B, geological map of the area where the holotype of *Telamonocarcinus antiquus* sp. nov. was recovered (white star). Abbreviations: J, Jurassic; Ki, Lower Cretaceous; Q, Quaternary. Base map modified from INGEOMINAS Plancha 135 San Gil (after Pulido 1985).

Mithracites takedai Van Bakel, Guinot *et al.*, 2012b, the raninoidans *Planocarcinus olssoni* (Rathbun, 1937), *Joerana kerri* (Luque, Feldmann *et al.*, 2012), *Colombicarcinus laevis* Karasawa, Schweitzer *et al.*, 2014, a new genus and species of necrocarcinoid crab (Luque In press), and other podotreme crabs (D. Cortés and J. Luque, unpub. data). However, little is known about the palaeontological content of the Tablazo Formation, and no fossil crustaceans from this unit have been reported to date. The discovery of *Telamonocarcinus antiquus* sp. nov. (Fig. 2A), in association with callianassid shrimps, mecochirid lobsters and palaeocorystid crabs (Fig. 3), represents the first record of marine arthropods known from the Tablazo Formation and provides valuable information for more detailed palaeoecological reconstructions of these shallow marine settings during Late Cretaceous times.

MATERIAL AND METHODS

The holotype and sole specimen of *Telamonocarcinus antiquus* sp. nov. under acronym and catalogue number IGM p881012 was collected in May 2012 and is deposited in the palaeontological collections of the Colombian Geological Survey, Bogotá, Colombia. The specimen was coated with sublimated ammonium chloride before photography to enhance relief of dorsal grooves, regions and fine tubercles and photographed under a Leica Macroscope with Spotflex digital camera. The resulting multilayered stack of photos was merged into a single high-definition image using the stacking software Helicon Focus Pro 6.2.2.

Institutional abbreviations. IGM, Colombian Geological Survey, Bogotá, Colombia; MFM, Mizunami Fossil Museum, Japan; MSNMi, Museo Civico di Storia Naturale di Milano; NZGS, New Zealand Geological Survey.

SYSTEMATIC PALAEOLOGY

This published work and the nomenclatural acts it contains have been registered in Zoobank: <http://zoobank.org/References/996C0842-8077-4F4A-AD55-A71FC0171A0C>.

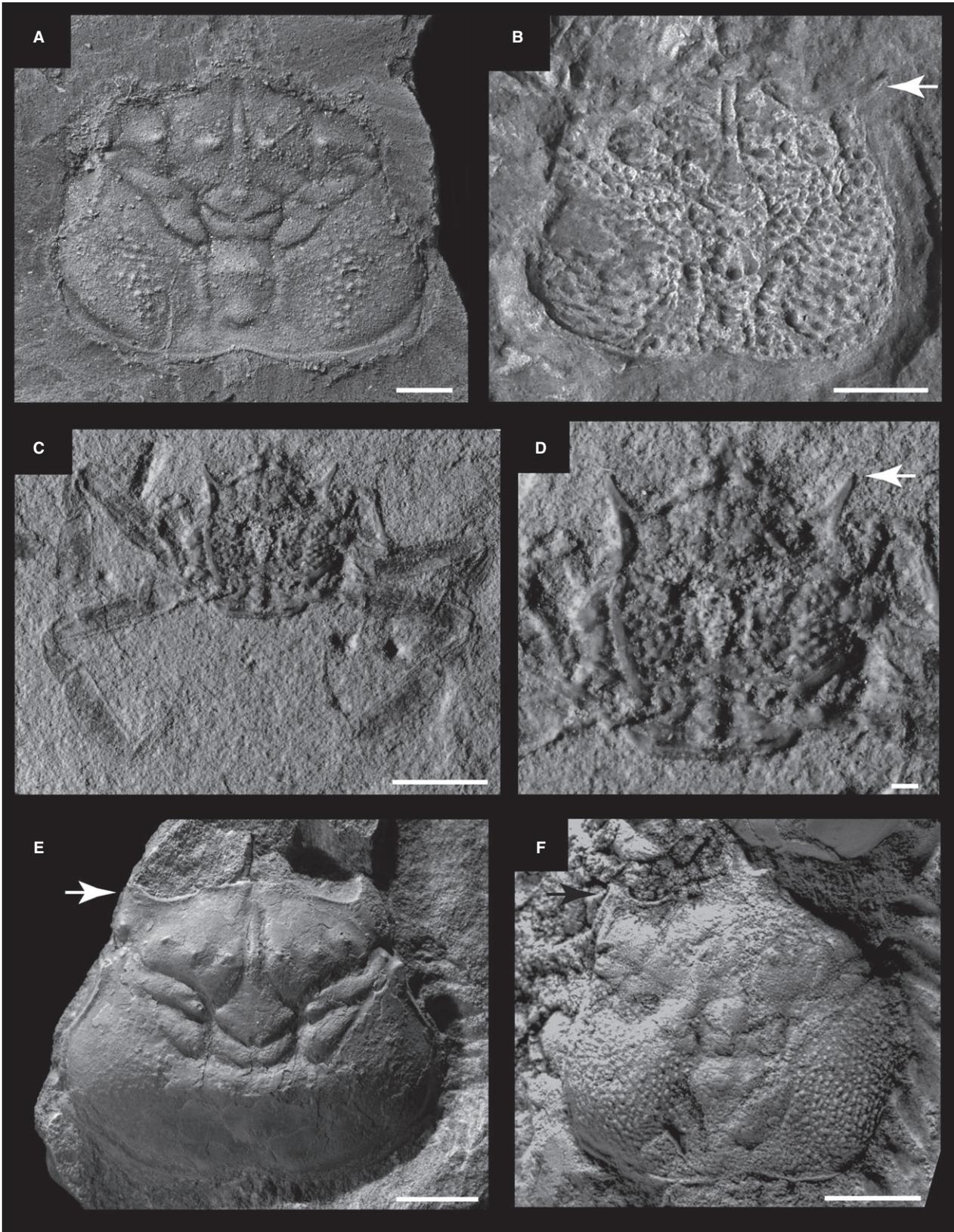
Infraorder BRACHYURA Latreille, 1802
Section EUBRACHYURA de Saint Laurent, 1980
Superfamily DORIPPOIDEA MacLeay, 1838
Family TELAMONOCARCINIDAE Larghi, 2004

Figure 2

Included genera. *Eodorippe* Glaessner, 1980; *Telamonocarcinus* Larghi, 2004 (type genus).

Emended diagnosis. Dorsal carapace nearly as wide as long (*Eodorippe*) or wider (*Telamonocarcinus*), broadly pyriform in outline; carapace maximum width at about posterior third of carapace, at level of branchial regions. Fronto-orbital margin broad, slightly more than half carapace width; rostrum long, narrow, subtriangular, broader at the base; orbits wide, lacking orbital fissures and spines; eyes large, with long eyestalks in *Telamonocarcinus*, unknown for *Eodorippe*; outer-orbital spine produced and diverging anterolaterally (*Telamonocarcinus*) or less produced and converging anteromesially (*Eodorippe*). Anterolateral margin short, lacking spines posterior to outer-orbital spine; posterolateral margin poorly defined, longer than anterolateral margin, broad, rounded; posterior margin shorter than fronto-orbital margin, about one-third carapace width, slightly concave, rimmed. Cervical and branchial grooves distinct, reaching anterolateral margin, subparallel, close to one other, delimiting a narrow epi-branchial region. Dorsal carapace moderately to coarsely granulate; carapace regions well delimited by grooves. Chelipeds nearly isochelous (*Telamonocarcinus*, unknown for *Eodorippe*). Pereiopods 2 to 3 the longest, very similar in shape, with P3 slightly longer than P2; pereiopods 4 to 5 reduced, without a subchelate dactyl (*Telamonocarcinus*, unknown for *Eodorippe*). Thoracic sternum subpentagonal, with large sternites 5 and 6; sternal sutures 4/5 to 6/7 incomplete, only known for *Telamonocarcinus*. Male pleon with six somites and telson; first 3 pleonites dorsally exposed (*Telamonocarcinus*, unknown for *Eodorippe*). Absence of female gonopores on coxa of third pereiopod (*Telamonocarcinus*; after Larghi 2004, p. 535; Guinot *et al.* 2013, p. 306).

Taxonomic remarks. The fossil record of Telamonocarcinidae is sparse and fragmentary, with three of the four known species represented only by the dorsal carapace of their holotypes. The lack of preserved thoracic sternum, pleon or appendages in both species of *Eodorippe* and in *Telamonocarcinus antiquus* sp. nov. precludes detailed discussion of their phylogenetic affinities with other brachyurans. Based on the carapace outline, Glaessner (1980) and Collins *et al.* (1993) included *Eodorippe* within the podotreme Torynommidae Glaessner, 1980, and highlighted their resemblance to Dorippidae, a family purported as one of the most basal eubranchyuran clades. *Telamonocarcinus gambalatus* Larghi, 2004, is the only telamonocarcinid species known from dorsal and ventral specimens, and its distinctive carapace outline, dorsal regions, groove patterns, orbital configuration and the females apparently lacking gonopores in the coxa of P3 led Larghi (2004) to conclude that the subfamily Telamonocarcininae might be closer to the eubranchyuran Dorippidae than to the podotreme Torynommoidea or Cyclodorippoidea. This subfamily was



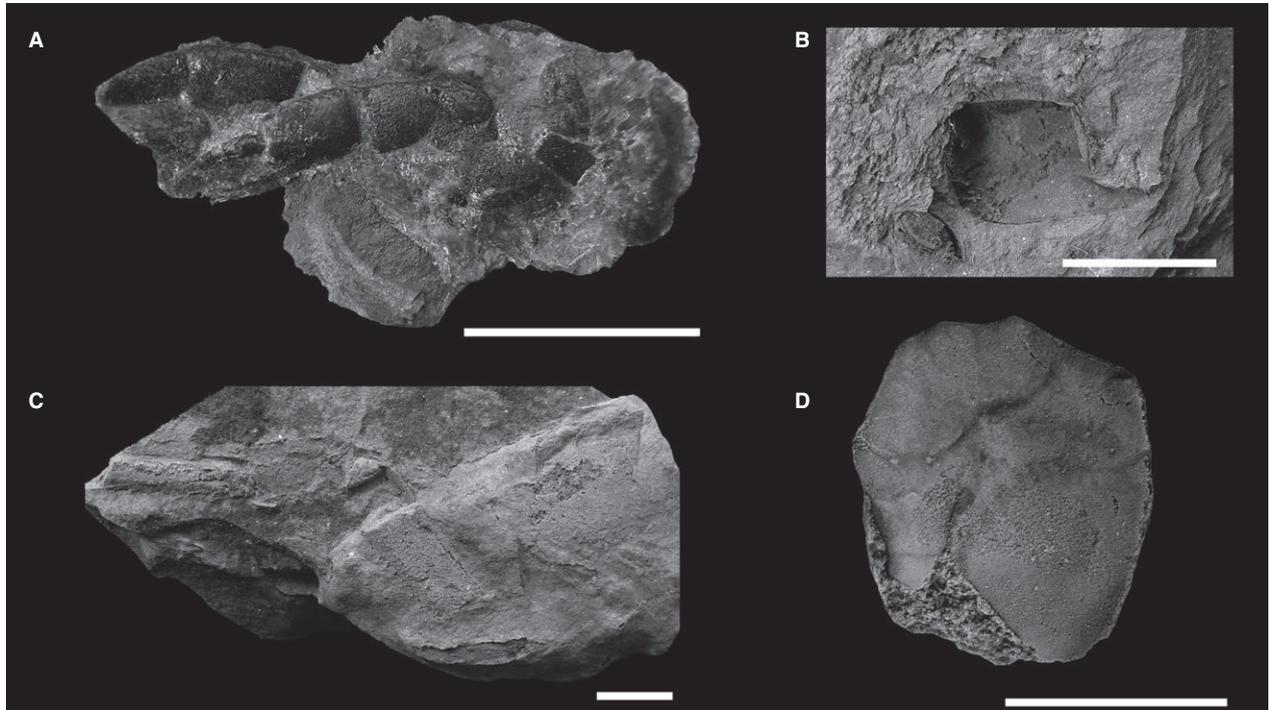


FIG. 3. Decapod crustaceans from the lowermost Tablazo Formation associated with the holotype of *Telamonocarcinus antiquus* sp. nov. A–B, callianassid shrimps indet. preserved in gypsum-rich layers; A, specimen IGM p881021, left side of specimen preserving both chelipeds; B, specimen IGM p881018, negative mould of cheliped. C, mecochirid-like lobster, specimen IGM p881014, preserving an elongate and slender first pereiopod. D, Palaeocorystoidea, Palaeocorystidae, *Joeranina* cf. *J. kerri* (Luque, Feldmann *et al.*, 2012), specimen IGM p881013, internal negative mould of anterior right dorsal carapace. All scale bars represent 10 mm.

recently elevated to full family status by Guinot *et al.* (2013), and with Dorippidae, Ethusidae and Goniochelidae Schweitzer and Feldmann, 2011b, constitutes the superfamily Dorippoidea (Glaessner 1969; Castro 2005; Guinot *et al.* 2008; Ng *et al.* 2008; Schweitzer and Feldmann 2011b). A detailed discussion of the dorippoid affinities of Telamonocarcinidae was provided by Guinot *et al.* (2013), who stated that its mixture of dorippid and ethusid traits might indicate that the family is not monophyletic. I concur. *Telamonocarcinus* and *Eodorippe* have a combination of dorsal traits that can be seen in either Dorippidae or Ethusidae. Larghi (2004) and Guinot *et al.* (2013) commented on the similarities and differences between the two telamonocarcinid genera. Among the most conspicuous differences is the configuration of the fronto-orbital margin. In *Telamonocarci-*

nus, the outer-orbital spine is produced and directed anterolaterally, whereas in *Eodorippe*, it is reduced and converges anteromesially. Similar variation in shape, size and orientation of the outer-orbital spines can also be seen among dorippids and ethusids. Although the rostrum is poorly known in *Telamonocarcinus*, in *Eodorippe*, it seems to be subtriangular, long and narrow. Unfortunately, based solely on the illustrated ventral females of *T. gambalatus* in Larghi (2004), I cannot conclude whether the position of the gonopores is sternal or coxal, warranting placement of *Telamonocarcinus* and *Eodorippe* within Eubranchyura, and particularly with Dorippidae or Ethusidae. On the other hand, based on the morphology of *Telamonocarcinus* and *Eodorippe* dorsal carapaces, they appear to be closer to the dorippoid body plan than to any other brachyuran.

FIG. 2. Telamonocarcinidae. A–D, *Telamonocarcinus* Larghi, 2004; A, *Telamonocarcinus antiquus* sp. nov., holotype, IGM p881012, dorsal carapace, early Albian of Colombia; B, *T. gambalatus* Larghi, 2004, holotype, MSNMi26033, dorsal carapace, Cenomanian of Lebanon; C–D, *Telamonocarcinus* sp. specimen P1010408, Cenomanian of Japan. E–F, *Eodorippe* Glaessner, 1980; E, *E. spedeni* Glaessner, 1980, holotype, NZGS., AR 675, dorsal carapace, Campanian–Maastrichtian of New Zealand; F, *E. binodosus* Collins, Kane and Karasawa, 1993, holotype, MFM247,003, dorsal carapace, Cenomanian of Japan. Arrows indicate the position of large, divergent (*Telamonocarcinus*) and short, convergent (*Eodorippe*) outer-orbital spines. Scale bars in A, B and D represent 1 mm, and in C, E, and F represent 5 mm. Images courtesy of Hiroaki Karasawa (C–D, F), Alessandro Garassino (B) and John E. Simes (E).

Members of the Telamonocarcinidae share superficial similarities in carapace shape and dorsal features with some taxa within Retroplumoidea Gill, 1894, but differ considerably on the narrower, nonbilobate rostrum, the fronto-orbital configuration, and having both P4 to P5 reduced, while in retroplumoids only P5 is reduced. Telamonocarcinidae shares with Torynommoidea the reduced P4 to P5, but the latter differs in exhibiting wider orbits with a short intraorbital spine, the rostral configuration, the less inflated branchial regions, the subquadrate carapace with nearly parallel lateral margins, and the subparallel cervical and branchiocardiac grooves (Schweitzer and Feldmann 2011a; Karasawa *et al.* 2014). Due to the nature of the information available on telamonocarcinid taxa, affiliation with Dorippoidea seems to be the most supported hypothesis.

A taxon that has been previously included within Telamonocarcinidae is *Tepexicarcinus tlayuaensis* Feldmann, Vega, Applegate, and Bishop, 1998 (Larghi 2004; Guinot *et al.* 2008). However, based on the work of Guinot *et al.* (2013), and following the original descriptions and illustrations by Feldmann *et al.* (1998) and Vega *et al.* (2005), *Tepexicarcinus* appears to be distinctive dorsally and ventrally enough from Telamonocarcinidae, Ethusidae or Dorippidae, that it may represent its own evolutionary lineage of early eubranchyuran or stem-eubranchyuran crabs. Therefore, *Tepexicarcinus* warrants independent suprageneric placement, as discussed below.

Stratigraphical range. Lower Cretaceous (lower Albian) to Upper Cretaceous (Campanian–Maastrichtian) (Table 1).

Genus EODORIPPE Glaessner, 1980

Figure 2E–F

Type species. *Eodorippe spedeni* Glaessner, 1980, by original designation.

Other species. *Eodorippe binodosus* Collins, Kanie and Karasawa, 1993.

Emended diagnosis. Dorsal carapace nearly as wide as long or slightly wider; with maximum width at posterior third of carapace. Fronto-orbital margin broad, with orbits lacking spines or fissures; rostrum subtriangular, short (*E. binodosus*) or long (*E. spedeni*), broader at its base. Cervical and branchiocardiac grooves distinct, as are carapace regions; cardiac region not flanked laterally by two subparallel narrow lobes. Dorsal carapace moderately to faintly granulated.

Taxonomic remarks. *Eodorippe spedeni* differs from *Telamonocarcinus gambalatus* and *T. antiquus* sp. nov. in the degree of development of the outer-orbital spine that is more produced and diverging anterolaterally in *Telamonocarcinus*, but less produced and converging anteromesially in *E. spedeni* (Fig. 2, arrows). *Eodorippe binodosus* was considered to be congeneric with *Telamonocarcinus* by Larghi (2004) and Guinot *et al.* (2013). In my view, the presence of short and converging outer-orbital spines in *E. binodosus* and the lack of the narrow and subparallel lobes flanking the cardiac region differ from *Telamonocarcinus* spp., suggesting affinity with *Eodorippe*, as originally

TABLE 1. List of known taxa within Telamonocarcinidae and Tepexicarcinidae fam. nov.

Taxon	Age (Ma)	Unit	Locality
<i>Telamonocarcinus antiquus</i> sp. nov.	Early Albian (~110)	Lower Tablazo Formation	La Fuente, Santander
<i>Telamonocarcinus gambalatus</i> Larghi, 2004	Cenomanian–Turonian (~97–90)	‘Fish Beds’ of western Lebanon	Hgula and Haqil, Lebanon
<i>Telamonocarcinus</i> sp.	Cenomanian (~97)	Mikasa Formation, Middle Yezo Group	Hokkaido, Katsurazawa, Ikushunbetsu, Mikasa City, Japan
<i>Eodorippe binodosus</i> (Collins, Kanie and Karasawa, 1993)	Cenomanian (~97)	Mikasa Formation, Middle Yezo Group	Hokkaido, Katsurazawa, Ikushunbetsu, Mikasa City, Japan
<i>Eodorippe spedeni</i> Glaessner, 1980	Campanian–Maastrichtian (~72)	Not specified by author	Stream boulders from bed of Mangahouanga Stream, a tributary of the Te Hoc River, New Zealand
<i>Tepexicarcinus tlayuaensis</i> Feldmann, Vega <i>et al.</i> , 1998	Albian (~110)	Middle member of the lithographic limestones of the Tlayúa Formation	Tepexi, Mexico
Tepexicarcinidae? genus and species indet. (<i>in</i> Schweitzer <i>et al.</i> 2003b)	Cenomanian (~96)	Bahariya Formation	Near Gebel el Dist, Egypt

envisioned by Collins *et al.* (1993). Discovery of ventral material will allow testing its generic placement.

Stratigraphical range. Upper Cretaceous (Cenomanian–?Maastriichtian) (Table 1).

Genus TELAMONOCARCINUS Larghi, 2004

Figure 2A–D

Type species. *Telamonocarcinus gambalatus* Larghi, 2004, by original designation.

Other species. *Telamonocarcinus antiquus* sp. nov.

Emended diagnosis. Crabs with carapace wider than long, broadly pyriform in outline, with maximum width at posterior third of carapace; anterolateral margin poorly defined, short, lacking teeth; posterolateral margin poorly defined, longer than anterolateral margin, broad, rounded; posterior margin short, about one-third carapace width, weakly concave, rimmed; fronto-orbital margin broad, with orbits lacking spines or fissures; rostrum long and narrow, subtriangular, broader at its base. Cervical and branchiocardiac grooves distinct, as are carapace regions; cardiac region flanked laterally by two subparallel narrow lobes. Dorsal carapace moderately to coarsely granulated. Male pleon with six somites and telson.

Taxonomic remarks. In addition to the more produced and anterolaterally diverging outer-orbital spine, *Telamonocarcinus* also differs from *Eodorippe spedeni* and *E. binodosus* in the possession of subparallel narrow lobes laterally flanking the cardiac region (Fig. 2). Given the low species richness of Telamonocarcinidae, it is hard to tell whether these traits represent the plesiomorphic or apomorphic conditions for the clade.

Schweitzer *et al.* (2003b) described an indeterminate genus and species of brachyuran crab from the Cenomanian of Egypt, which was considered by Garassino *et al.* (2008, p. 61) to be conspecific with *Telamonocarcinus gambalatus*. Unfortunately, the material is poorly preserved, and not much can be concluded regarding its systematic affinities. Nevertheless, it must be noted that a specimen illustrated by Schweitzer *et al.* (2003b, fig. 1.1) lacks the diagnostic wider than long pyriform carapace, indicating that the taxon is not conspecific with *T. gambalatus*, nor it is congeneric with *Telamonocarcinus*. In fact, its apparently longer-than-wide carapace with long and nearly straight posterolateral margins aligns it more closely to Tepexicarcinidae fam. nov., to which the enigmatic taxon is herein assigned until better material becomes available for study.

Stratigraphical range. Lower Cretaceous (lower Albian) to Upper Cretaceous (Cenomanian) (Table 1).

Telamonocarcinus antiquus sp. nov.

Figure 2A

LSID. urn:lsid:zoobank.org:act:BDC32DC8-3327-4E1D-B94B-6D620D255310

Derivation of name. From the Latin word for ‘ancient, old’, alluding to its age with respect to the oldest records of telamonocarcinid, dorippoidean and eubrachiuran crabs.

Diagnosis. Carapace wider than long, broadly pyriform in outline, with maximum width at posterior third of carapace; anterolateral margin poorly defined, short, lacking teeth; posterolateral margin poorly defined, broad, rounded; posterior margin short, slightly concave, rimmed; fronto-orbital margin poorly preserved, apparently wide, with orbits lacking spines or fissures. Cervical and branchiocardiac grooves distinct, as are carapace regions; cardiac region flanked laterally by two subparallel narrow lobes. Dorsal carapace moderately granulated.

Description. Carapace pyriform in outline, wider than long, maximum width at posterior third; fronto-orbital margin poorly preserved in the holotype, apparently wide, about 60% as wide as carapace maximum width; anterolateral margin distinct, short, weakly convex, lacking spines; posterolateral margin distinct, about twice as long as anterolateral margin, strongly convex, lacking spines; posterior margin sinuous, rimmed dorsally, concave at mid portion and convex towards posterolateral margin. Cervical groove distinct, well developed, slightly interrupted axially, reaching anterolateral margin of carapace; branchial groove distinct, well developed, deep, flanking the metagastric region; branchiocardiac groove distinct, well developed, reaching anterolateral margin of carapace, subparallel to cervical groove, bounding a very narrow epibranchial region. Epigastric region distinct, narrow, wider than long, extending from base of rostrum to mesogastric region, axially ridged and delimited by two parallel ridges; protogastric region distinct, wide, separated mesially by mesogastric region, bearing one tubercle; hepatic region distinct, small, subtriangular, bearing a central tubercle; mesogastric region distinct, wider than long, bearing a small medial tubercle; metagastric region small, wider than long, subtrapezoidal, lying posterior to mesogastric region and separated by axial portion of cervical groove, flanked laterally by branchial groove and posteriorly depressed at boundary with urogastric region; urogastric region small, subrectangular; cardiac region about as long as wide, wider anteriorly at contact with urogastric region, narrowing posteriorly, flanked laterally by two subparallel narrow lobes, separating the cardiac region from the branchial regions; intestinal region wide, narrower axially near contact with cardiac region. Epibranchial region distinct, well developed, narrow, extending anterodistally from branchial region, delimited anteriorly by cervical groove

and posteriorly by branchiocardiac groove; branchial regions well developed.

Anterior carapace regions well defined; epigastric region ridged axially, delimited by lateral, nearly parallel grooves; proto-gastric and hepatic regions bearing one tubercle; mesogastric region subpentagonal in outline, narrower anteriorly, rapidly broadening posteriorly, bearing one tubercle anterior to axial portion of cervical groove; metagastric region distinct, subtrapezoidal, wider anteriorly, about as wide as mesogastric region, narrower posteriorly, bounded laterally by branchial grooves; cardiac region well defined, narrow anteriorly, separated from metagastric region by a shallow groove, wider posteriorly, separated from cardiac region by a short, transverse ridge; cardiac region subtriangular, wider anteriorly, narrowing posteriorly, bearing one posterior swollen node, laterally delimited by short, deep longitudinal furrows, flanking two lateral, subparallel narrow lobes; intestinal region wide.

Measurements. Carapace maximum length: ~4.7 mm, measured from posterior margin to the base of rostrum; carapace maximum width: ~6.5 mm; fronto-orbital margin estimated width: ~3.6 mm.

Remarks. *Telamonocarcinus antiquus* sp. nov. is assigned to *Telamonocarcinus* based on its carapace outline, the dorsal groove patterns, the well developed epigastric and mesogastric regions, and the small subparallel swellings flanking the cardiac region. This taxon markedly differs from *T. gambalatus*, the only other described species in the genus, in the size and density of the dorsal granules, being coarser in the latter. Unfortunately, the holotype and sole specimen of *T. antiquus* sp. nov. has a poorly preserved fronto-orbital margin, and no thoracic sternum, appendages or pleon was recovered, precluding a more detailed comparison with *T. gambalatus* or other taxa within Telamonocarcinidae at this time.

Stratigraphical range. Lower Cretaceous (lower Albian; Table 1).

Superfamily uncertain
TEPEXICARCINIDAE fam. nov.

LSID. urn:lsid:zoobank.org:act:AC082EBE-3C94-4F7E-B511-C10626ED40F4

Included genera. *Tepexicarcinus* Feldmann, Vega *et al.*, 1998, by original designation; tentatively genus and species indeterminate in Schweitzer *et al.* 2003b, p. 890, figs 1–2.

Diagnosis. Carapace longer than wide, with subrectangular outline; carapace maximum width positioned at anterior third of carapace. Fronto-orbital margin wide, about 70% carapace width; rostrum square, conspicuously bifid, broader at the tip, sulcate axially; orbits semi-circular, short, bearing two orbital fissures; outer-orbital spine

short, directed forward; anterolateral margin short, slightly convex, bearing three spines. Lateral margins long, straight, nearly parallel; posterior margin about 75% carapace width, almost straight, slightly convex axially, nearly as wide as fronto-orbital margin. Dorsal carapace finely punctate. Cervical and branchiocardiac grooves distinct, reaching lateral margins, nearly parallel but distant from each other, bounding a broad epibranchial region. Epibranchial region wide, comprising about the 33% of dorsal carapace, bounded by cervical and branchiocardiac grooves. Chelipeds subequal. Pereiopods 2 to 3 the longest, similar in shape, with P3 larger than P2; pereiopods 4 to 5 shorter; P5 shortest, and carried subdorsally. Thoracic sternum subpentagonal, with large sternites 5 and 6. Pleon with four free somites and two fused, plus telson (after Feldmann *et al.* 1998, pp. 86–87, fig. 7; and Vega *et al.* 2005, pp. 28–29, fig. 4, pl. 2; and following Larghi 2004, and Guinot *et al.* 2013).

Taxonomic remarks. The distinctive set of diagnostic traits of *Tepexicarcinus* is unique among Telamonocarcinidae, Dorippidae and even Ethusidae, meriting its elevation to family rank. In fact, Tepexicarcinidae fam. nov. might actually represent an independent evolutionary lineage of early eubranchyurans and probably should be better placed in its own superfamily Tepexicarcinoidea, as no other brachyuran superfamily matches its body plan. *Tepexicarcinus* shares with some dorippoids the long pereiopods 2 to 3 with large dactyli (Schweitzer and Feldmann 2011b), and particularly with extant Ethusidae males, the possession of a pleon constituted by free and fused somites, unlike *Telamonocarcinus* and extant Dorippidae that have six free somites (Larghi 2004; Guinot *et al.* 2013), but these traits do not warrant affiliation with Dorippoidea. Future specimens preserving additional dorsal and ventral features will allow detailed comparisons with other ‘basal’ fossil and extant eubranchyurans.

Genus TEPEXICARCINUS Feldmann, Vega *et al.*, 1998

Included species. *Tepexicarcinus tlayuaensis* Feldmann, Vega *et al.*, 1998, by original designation.

Taxonomic remarks. *Tepexicarcinus tlayuaensis*, the sole genus and species within Tepexicarcinidae, was described and illustrated in detail by Feldmann *et al.* (1998) and Vega *et al.* (2005). The specimen-designated genus and species indeterminate of Schweitzer *et al.* (2003b) shares with *Tepexicarcinus* the longer-than-wide carapace with long and nearly straight posterolateral margins, but differs from the latter in its noticeably shorter P2 with respect to P3; its P3 merus is slightly curved backwards and is wider

at the junction with the carpus; and its P3 dactyl is longer than the propodus and the merus. The two taxa seem not to be congeneric, and provisional placement of the genus and species indeterminate of Schweitzer *et al.* (2003b)

within Tepexicarcinidae should be reconsidered in the light of new material, when it becomes available.

Stratigraphical range. Lower Cretaceous (Albian; Table 1).

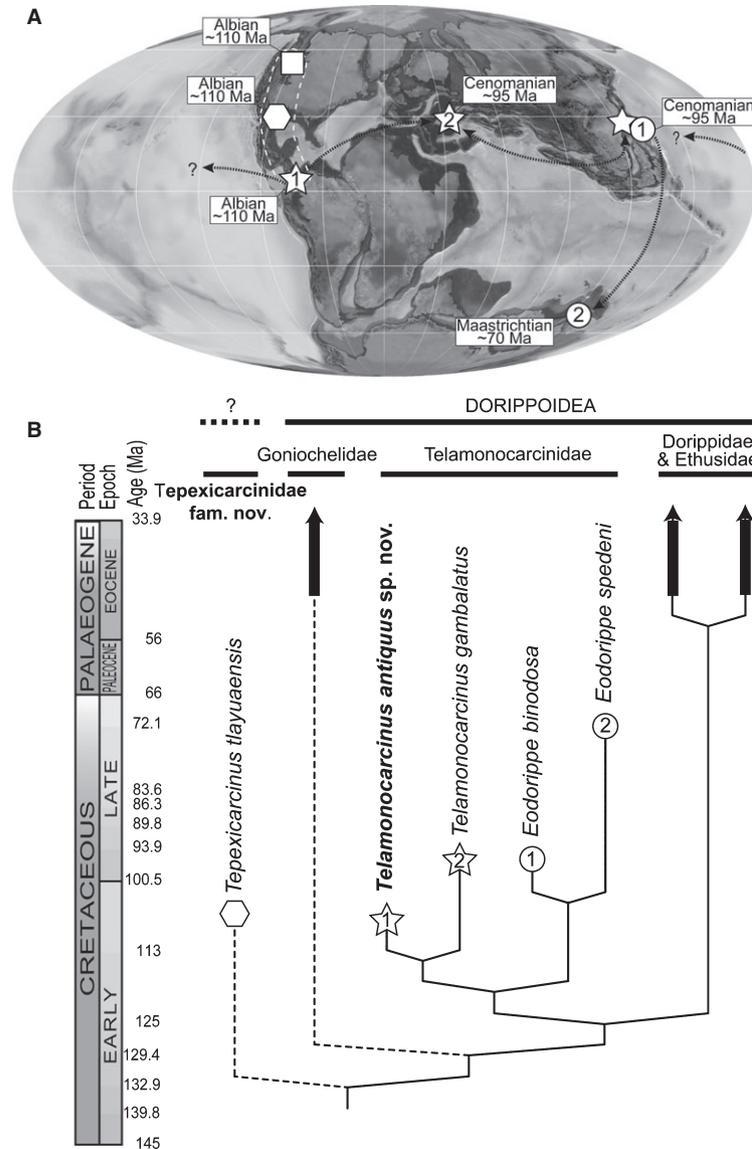


FIG. 4. Spatial and temporal ranges of the taxa currently included in Telamonocarcinidae and Tepexicarcinidae fam. nov. A, palaeobiogeographical distribution of *Tepexicarcinus* Feldmann, Vega *et al.*, 1998 (hexagon); *Telamonocarcinus* Larghi, 2004 (stars); and *Eodorippe* Glaessner, 1980 (circles). Black dotted lines and arrows indicate plausible dispersal routes. White square represents the occurrence of *Componocancer roberti* Feldmann, Schweitzer and Green, 2008, which is the oldest confirmed sternitreme eubrachyuran. White dotted line indicates the geographical distribution of the oldest known eubrachyuran and eubrachyuran-like crabs, all from the Early Cretaceous (Albian) of the Americas. Base map for the Early Cretaceous (Aptian, ~120 Ma) modified after Blakey (2006). B, chronostratigraphical distribution of the taxa within Telamonocarcinidae and Tepexicarcinidae fam. nov. Telamonocarcinidae is the only known family of Dorippoidea that lived in the Cretaceous. All other dorippoid families have their oldest representatives in the Eocene, as indicated by *Ethusa evae* Müller and Collins, 1991 (Ethusidae Guinot, 1977); *Bartethusa hepatica* Quayle and Collins, 1981 (Dorippidae MacLeay, 1838); *Goniochele angulata* Bell, 1858; and *G. madseni* Collins and Jakobsen, 2003 (Goniochelidae Schweitzer and Feldmann, 2011b). Dotted lines indicate the uncertain phylogenetic position of Goniochelidae among dorippoideans and the doubtful phylogenetic affinity of Tepexicarcinidae fam. nov. with Dorippoidea.

DISCUSSION

Besides *Telamonocarcinus antiquus* from the early Albian Tablazo Formation of Colombia, and *Tepexicarcinus tlayuaensis* from the Albian Tlayúa Formation of Mexico (Table 1), the only other Early Cretaceous eubranchyuran-like crab known is *Componocancer roberti* Feldmann, Schweitzer and Green, 2008, from the Albian Shell Creek Shale of Montana, USA. *Componocancer roberti*, the sole species in the superfamily Componocaneroidea, displays a combination of brachyuran plesiomorphies (e.g. laterally unfused thoracic sternites, posterior thoracic sternites and their associated legs reduced and directed posterodorsally) and eubranchyuran synapomorphies (i.e. a large vulva on female's sixth thoracic sternites) that set it apart from other early-branching eubranchyuran clades. The Albian crab *Hillius youngi* Bishop, 1983, was once considered as a possible eubranchyuran with dorippoid affinities (Bishop 1983; De Grave *et al.* 2009; Schweitzer *et al.* 2010), but recent works documented *Hillius* as a podotreme, either related to cyclodorippoidans, particularly with Cyclodorippidae Ortmann, 1892 (Karasawa *et al.* 2011; Schweitzer and Feldmann 2011b), or raninoidans, particularly with Orithopsidae Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg, and Ross, 2003a (Van Bakel *et al.* 2012a; Guinot *et al.* 2013).

Telamonocarcinus ranged from the south-western margin of the Caribbean Tethys to the Eurasian margins of the Mediterranean Tethys and Japan, whereas *Eodorippe* appears to have been restricted to the western Pacific realm (Fig. 4A, Table 1). *Tepexicarcinus* is known only from the Gulf of Mexico (Fig. 4A). Abundant callianasid chelipedial remains, a mecochirid-like lobster and a fragmented dorsal carapace of a palaeocorystid crab putatively assigned to *Joeranina kerri* (Fig. 3) were found associated with *Telamonocarcinus antiquus* sp. nov. All three taxa are known to have been infaunal benthos dwellers. Feldmann *et al.* (1998) and Vega *et al.* (2005) suggested that the morphology of the pereopods seen in *Telamonocarcinus gambalatus* and *Tepexicarcinus tlayuaensis* might indicate that the taxa inhabited shallow marine waters, more likely in coral reefs. *Telamonocarcinus antiquus* sp. nov. might also have inhabited shallow marine waters, but its occurrence in dark grey, terrigenous, micaceous clay-shales with gypsum indicate that it must have been deposited in low hydrodynamic, poorly oxygenated settings. Although the specimen of *T. antiquus* sp. nov. might be allochthonous for the faunule, coral reefs from the Tablazo Formation are unknown, suggesting that the specimen rather inhabited settings proximal to the area of burial.

CONCLUSIONS

Following recent work, and given the nature of the information available, Telamonocarcinidae is considered to be closer to Dorippidae and Ethusidae than to other brachyuran clades and reinforces the hypothesis that Dorippoidea is among the most basal groups of eubranchyuran crabs. If this dorippoidean affinity proves to be correct, it would mean that *Telamonocarcinus antiquus* sp. nov. is, together with *Componocancer roberti* and putatively *Tepexicarcinus tlayuaensis*, the oldest eubranchyuran-like crab known to date. The broad range of body plans seen among Albian brachyurans indicates that the Early Cretaceous was a time of rapid evolution for crabs, where most of the higher clades (e.g. Raninoidea, Cyclodorippoida, Etyoidea, Torynommoidea, Eubranchyura) originated and/or rapidly diversified. Given our current knowledge of the geographical and geological ranges of early eubranchyurans, it can be stated that: (1) the oldest eubranchyurans are known from the Americas; (2) eubranchyurans were already morphologically diverse in Albian times; and (3) that their most recent common ancestor most likely is pre-Albian in age and probably rooted in the earliest Cretaceous or Late Jurassic.

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