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Eogeryon elegius n. gen. and n. sp. (Decapoda: Eubrachyura: Portunoidea), one of the oldest modern crabs from late Cenomanian of the Iberian Peninsula

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Abstract

A new Heterotremata (Eubrachyura) decapod from the late Cenomanian of Condemios de Arriba (Guadalajara, Spain) is described. The new taxon has affinities with the basal portunoids and their features suggest placement within the Portunoidea. Comparisons with all the currently known Cretaceous Eubrachyura taxa demonstrates how *Eogeryon elegius* is an advanced crab in spite of its Cenomanian origins, suggesting that it evolved from ancestors previously unknown according to the current fossil record. As a result of those comparisons, a new family, Eogeryonidae, within Portunoidea, is proposed to accommodate the new genus and species. In addition, *Eogeryon elegius* is also compared with early Eocene and extant related taxa, with emphasis on the non-swimming portunoid family Geryonidae. *Eogeryon elegius* appears to be an ancestor of most derived forms of Portunoidea, suggesting that the evolution of Eubrachyura must have occurred at least during the Early Cretaceous.

Keywords: Crustacea, Brachyura, Heterotremata, Geryonidae, Cretaceous, Spain.

Resumen

Se describe un nuevo decápodo Heterotremata (Eubrachyura) procedente del Cenomaniano tardío de Condemios de Arriba (Guadalajara, España). Las afinidades con portunoideos basales que presenta el nuevo taxón, sugieren que su ubicación en Portunoidea es apropiada. Las comparaciones con todos los Eubrachyura del Cretácico actualmente conocidos, muestran que Eogeryon elegius es un cangrejo avanzado, a pesar de sus orígenes cenomanianos, lo que sugiere que evolucionó de ancestros mucho antes de lo que se podía prever a la vista del actual registro fósil. Como resultado de esas comparaciones, se propone una nueva familia, Eogeryonidae, incluida en Portunoidea, para acomodar el nuevo género y especie. Eogeryon elegius se compara, además, con taxones del Eoceno temprano y también actuales, con especial énfasis con la familia de portunoideos no nadadores Geryonidae. Eogeryon elegius podría ser un ancestro de formas más derivadas de Portunoidea, sugiriendo así, que la evolución de los Eubrachyura ocurrió, al menos durante el Cretácico temprano

Palabras clave: Crustacea, Brachyura, Heterotremata, Geryonidae, Cretácico, España.

1. Introduction

The discovery of *Eogeryon elegius* n. gen., n. sp. in the late Cenomanian strata is paramount. The well-preserved ventral features leave no doubt about their belonging to Heterotremata (Eubrachyura). The general aspect, flattened body plan, sternum, abdomen and heterodontic right chela are attributes that correspond to a decapod with an advanced degree of carcinisation, notwithstanding its old age. This report indicates clearly that the Eubrachyura evolved earlier than we could foresee in view of the fossil record. Even though the fossil record shows that Eubrachyura are already present in the Early Cretaceous (Luque, 2015), for instance Telamonocarcinidae Larghi, 2004 (Dorippoidea) and Tepexicarcinidae Luque, 2015 (uncertain superfamily) (see Luque, 2015), they are considered primitive (Guinot *et al.*, 2013). Therefore, it seems that *Eogeryon elegius* n. gen., n. sp. evolved from more advanced Early Cretaceous forms than the aforementioned families. Comparisons with all the known eubrachyuran Cretaceous taxa show how *Eogeryon elegius* n. gen., n. sp. differs from many of those taxa, as is explained below. However, some affinities are found with its coeval *Marocarcinus pasinii* Guinot, De Angeli and Garassino, 2008, and also with other younger taxa such as genera and species belonging to the portunoid families Carcineretidae Beurlen, 1930 and Longusorbiidae Karasawa, Schweitzer and Feldmann, 2008, and with the portunoid-like *Styracocarcinus meridionalis* (Secrétan, 1961). Affinity of *Eogeryon elegius* n. gen., n. sp. with Portunoidea Rafinesque, 1815, appears to be evident, and their dorsal characters and chela fit well with the diagnosis provided for this superfamily by Karasawa *et al.* (2008) and Spiridonov *et al.* (2014). Regarding their portunoid affinities, it is noteworthy that the fullness of the typical ventral features of the most derived portunoids, for instance the Portunidae Rafinesque, 1815, were not completely acquired, according to the fossil record, until the middle-late Eocene. Therefore, in principle, it cannot be expected to find entirely portunid ventral structures in Cretaceous and Paleocene portunoid specimens. Particularly, the general features, both dorsal and ventral of *Eogeryon elegius* n. gen., n. sp. recall those of the non-swimming portunoids Geryonidae Colosi, 1923, considered the most basal family of Portunoidea (Karasawa *et al*., 2008; Schubart and Reuschel, 2009; Spiridonov *et al.*, 2014). In this sense, some early Eocene species of *Litoricola* Woodward, 1873, formerly referred to *Coeloma* A. Milne-Edwards, 1865, and probably related with Geryonidae, show affinities with *Eogeryon elegius* n. gen., n. sp. and they may be considered as intermediate forms between *Eogeryon elegius* n. gen., n. sp. and the extant Geryonidae. However the differences found amongst *Eogeryon elegius* n. gen., n. sp. and the above-mentioned taxa, and the time difference between them, warrants the proposal of a new family, within Portunoidea, to accommodate the new taxon. *Eogeryon elegius* n. gen., n. sp. appears to be an ancestor of the most derived forms of Portunoidea. Portunoidea are the most represented Eubrachyura group during the Middle and Late Cretaceous. They successfully surpassed the K/P event, being at the present time one of the most diverse and species-rich groups of known eubrachyuran.

2. Locality and geological setting

Specimens of *Eogeryon elegius* n. gen., n. sp. were recovered from outcrops near the village of Condemios de Arriba (Northern Guadalajara Province, Spain) (Figure 1). The Condemios area is located in the Central Sector of the Inner Castilian Platform of the Iberian Trough, which connected from north to southeast the open waters of Proto-Atlantic Ocean and the Tethys Sea, through the Basque Basin and Levantine Basin (Barroso-Barcenilla *et al.*, 2009, p. 139) (Figure 2). During the late Cenomanian-Turonian interval, increased subsidence and sea-level rise caused a broad and rapid transgression from the Proto-Atlantic that flooded the entire Iberian Trough, which was partially closed towards the Western Tethys in the south (Caus *et al.*, 2009, p. 173-174, fig. 2). The Iberian Trough, bordered by the Hesperian Massif on the west and the Ebro Massif on the east, was temporally or permanently flooded by the Proto-Atlantic Ocean. According to Barroso-Barcenilla *et al.* (2009, p. 139, figure 1), during intervals of relatively high sea level the Iberian Trough extended from the Inner Castilian Platform to the southeast along the Levantine Platform, from which it directly received Tethyan influence. In the vicinity of Condemios de Arriba, a stratigraphic series of late Cenomanian-Turonian is well exposed. In the section, four lithostratigraphic units are recognised: the upper part of the Arenas de Utrillas Formation (Aguilar *et al.*, 1971), Dolomías tableadas de Villa de Vés Formation (Vilas *et al.*, 1982), Margas de Picofrentes Formation (Floquet *et al.*, 1982) and Dolomías de la Ciudad Encantada Formation (Meléndez, 1971) (see Peyrot *et al.*, 2012). The level bearing crab corresponds to the Villa de Vés Formation. This unit is frequently attributed to either the Utrillas Formation or as a mere member of the overlying Picofrentes Formation (Peyrot *et al.*, 2012, p. 27; F. Barroso-Barcenilla, pers. com., 2014). The Villa de Vés Unit is characterized in this outcrop by a thin bed of sandy limestone that overlies the uppermost marine levels of the Utrillas Formation. It contains marine fauna of bivalves, gastropods, echinoids, and the ammonite *Vascoceras gamai* Choffat, 1898, whose Zone represents the upper part of the late Cenomanian, just below the *Spathites* (*Jeanrogericeras*) *subconciliatus* Zone which marks the end of Cenomanian. The Villa de Vés Unit is interpreted as a shallow marine platform of Tethyan affinity (Peyrot *et al.*, 2012, p. 27) (Figure 3).

Figure 1. General map with location of type locality (star).

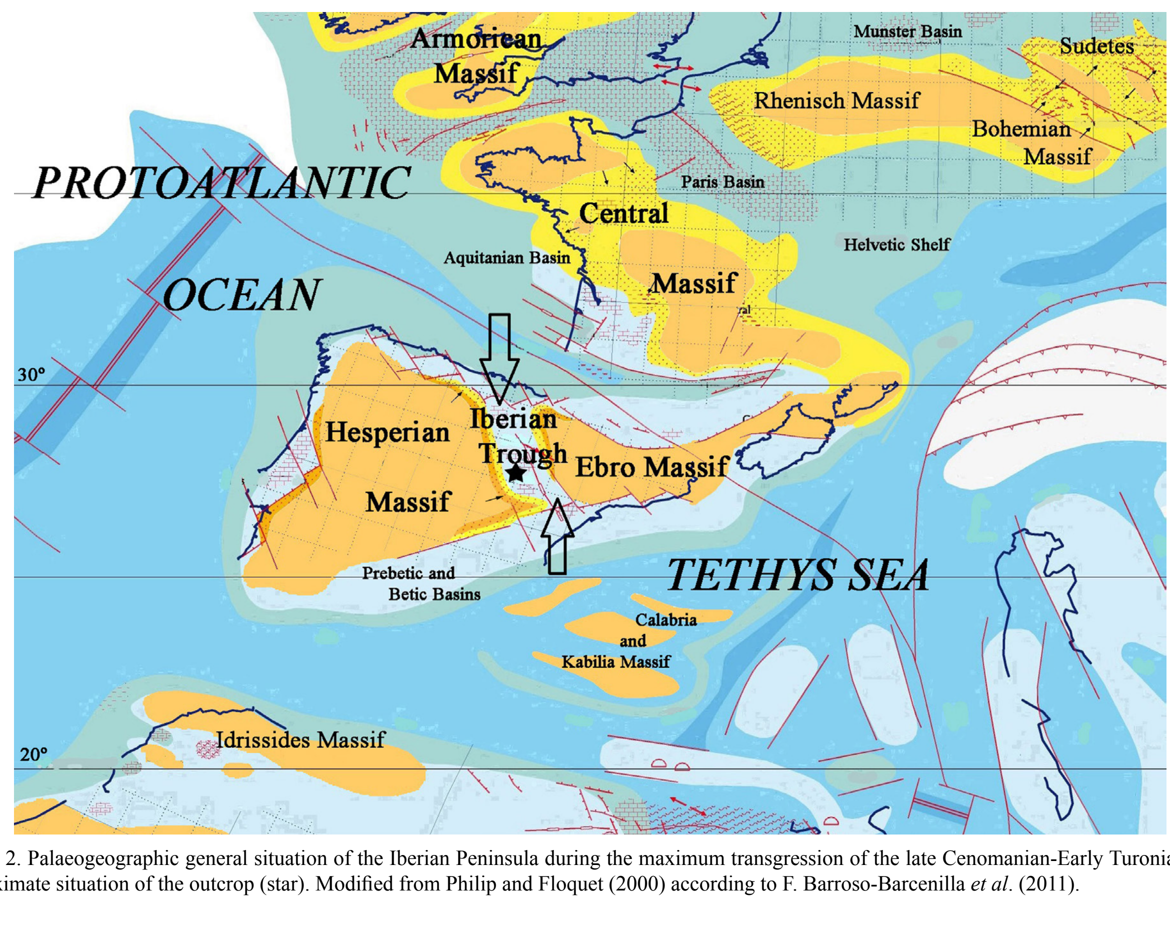

Figure 2. Palaeogeographic general situation of the Iberian Peninsula during the maximum transgression of the late Cenomanian-Early Turonian, with approximate situation of the outcrop (star). Modified from Philip and Floquet (2000) according to F. Barroso-Barcenilla *et al*. (2011).

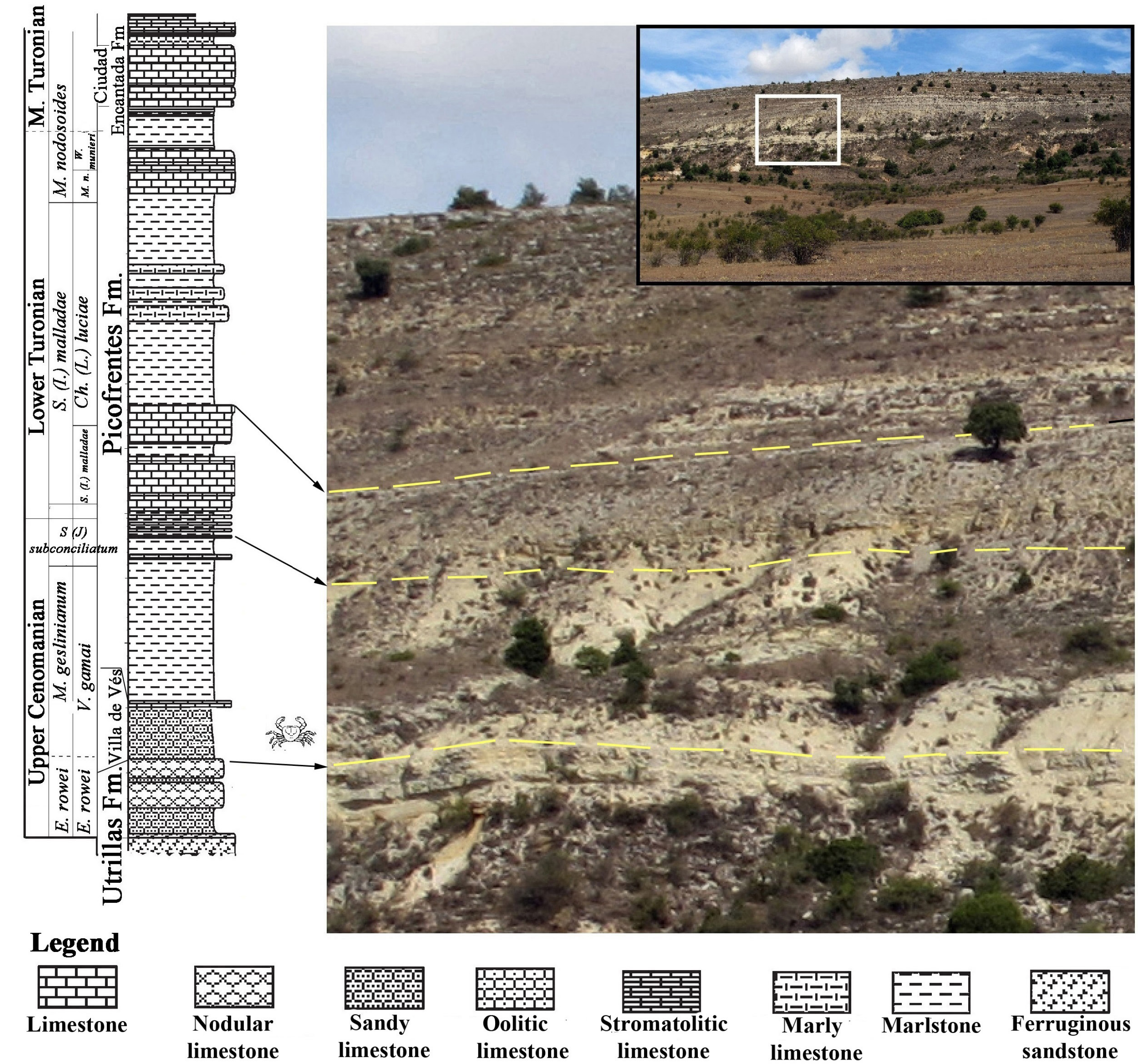

Figure 3. Stratigraphic column and schematic distribution of lithostratigraphic units with position of the crustacean-bearing level. Modified from Barroso-Barcenilla *et al.* (2009) [www.schweizerbart.de] and Barroso-Barcenilla (pers. comm., 2014). (Drawing by Fernando Ari Ferratges Kwekel).

3. Material

Holotype MGB 69151, male, with decorticated carapace and front absent, with nearly complete sterno-abdominal structures, and complete right chela. Reconstruction of carapace is based on pictures of a second specimen from the same outcrop, with complete dorsal carapace and front preserved, in private collection, not available for study (a cast of this specimen is deposited at MGB under registration MGB 69152).

4. Systematic Paleontology

Order Decapoda Latreille, 1802
Infraorder Brachyura Latreille, 1802
Section Eubrachyura de Saint Laurent, 1980
Subsection Heterotremata Guinot, 1977
Superfamily Portunoidea Rafinesque, 1815
Family Eogeryonidae n. fam.

Type genus. *Eogeryon* n. gen

Diagnosis. Carapace sub-hexagonal, medium sized, flattened, slightly wider than long, gently convex longitudinally at anterior third. Maximum width at anterior third, at level of third anterolateral tooth. Regions fairly defined. Gastric process poorly defined; mesogastric region not defined; protogastric lobes slightly swollen with transverse ridges; epigastric region medially depressed; epibranchial lobe sigmoidal, inflated, ridged; mesobranchial lobe inflated; metabranchial area depressed; urogastric region depressed; cardiac region slightly swollen. Cervical groove V shaped; branchiocardiac grooves deep. Front bilobed, lobes bifid. Orbits large, two supra-orbital fissures, eyestalks well calcified. Lateral margins strongly stepped. Anterolateral margins with four teeth (including exorbital tooth); first and second teeth strong, subtriangular; third tooth conical; fourth tooth (epibranchial) small blunt node. Posterolateral margins slightly convex. Posterior margin straight, rimmed laterally. Sternum relatively narrow; sternite 3 subrectangular; sternite 4 subtrapezoidal elongate, both slightly depressed medially; sternites 3-4 fused; suture 3/4 well distinct by a deep groove; sternites 5-6 subtrapezoidal, laterally downward directed. Episternites 4-5-6 downward directed. Male abdomen narrow, with 6 somites free and telson covering sterno-abdominal cavity; telson subtriangular reaching 2/3 of sternite 4, somite 4 the broader; somites 1 and 3 subtrapezoidal, transversally narrow, somite 2 not preserved; somites 4-5-6, subrectangular becoming progressively narrower, somite 6 twice as high as 4 and 5. Right cheliped strong, smooth; merus massive, smooth; carpus massive, strong inner spine; propodus strong, smooth; dactyli with strong proximal molariform tooth followed by conical teeth. Ambulatory legs P2- P4 proportionally long, smooth, equal, sub-oval in section; P5 not preserved, appears to be smaller, probably subdorsal.

Genus *Eogeryon* n. gen.

Type species. *Eogeryon elegius* n. gen., n. sp.

Etymology. From the Greek *Eo*-, primeval, early, and *Geryon*, from Greek mythology, usual in carcinology.

Diagnosis. As for the family

Discussion. Although the most distinctive character for the Heterotremata (Eubrachyura) is the presence of vulvae in thoracic sternites of females (Guinot, 1977), and the holotype of *Eogeryon elegius* n. gen., n. sp. is clearly a male, there is no doubt on the heterotreme condition of the new genus. The dorsal carapace morphology of the new genus is typical of the Eubrachyura. The general body plan indicates that *Eogeryon elegius* n. gen., n. sp., is an advanced brachyuran: carapace flattened without transverse grooves, even though its postero-lateral margins are stepped and the branchiostegite are not completely folded under the carapace (Schram, 1980, 1983; Feldmann *et al.*, 2008); front bilobed and relatively large, shape of orbits, straight posterior margin (Dixon *et al.*, 2003, p. 966; Guinot *et al.*, 2013, p. 203); more or less equal ambulatory pereiopods (Schram, 1980, 1983; Feldmann *et al.*, 2008) and massive specialized right chela (Spiridonov *et al.*, 2014). Beyond its eubrachyuran dorsal appearance, the ventral structures are very informative and confirms its heterotreme condition: the thoracic sternum is relatively wide, having a true sterno-abdominal cavity, where a relatively narrow abdomen, folded between abdominal sternites 2-3, is inserted leaving exposed the rest of the sternum (Guinot *et al.*, 2013). According to Guinot and Tavares (2001) all the Eubrachyura (Heterotremata + Thoracotremata) males have the sternum visible in both sides of the abdomen. On the contrary, in Podotremata the male sternum is usually completely covered by the abdomen.

After establishing the heterotreme condition of the new taxon, all the currently known Heterotremata Cretaceous taxa are compared with *Eogeryon* n. gen., namely: *Archaeopus* Rathbun, 1908 (?Retroplumidae Gill, 1894); members of Carcineretidae Beurlen, 1930 (Portunoidea Rafinesque, 1815); *Componocancer* Feldmann, Schweitzer and Green, 2008 (Componocancridae Feldmann, Schweitzer and Green, 2008); *Costacopluma* Collins and Morris, 1975 (Retroplumidae Gill, 1894); members of Icriocarcinidae Števčić, 2005 (Portunoidea Rafinesque, 1815); *Lithophylax* A. Milne-Edwards and Brocchi, 1879 (Lithophylacidae Van Straelen, 1936); members of Longusorbiidae Karasawa, Schweitzer and Feldmann, 2008 (Portunoidea Rafinesque, 1815); *Marocarcinus* Guinot, De Angeli and Garassino, 2008 (Marocarcinidae Guinot, De Angeli and Garassino, 2008); *Megaxantho* Vega, Feldmann, García-Barrera, Filkorn, Pimentel and Avendaño, 2001 (?Eriphioidea MacLeay, 1838); *Ophthalmoplax* Rathbun, 1935 (Portunoidea Rafinesque, 1815); *Palaeoxanthopsis* Beurlen, 1958 (Palaeoxanthopsidae Schweitzer, 2003); *Parapirimela* Van Straelen, 1937 (?Portunoidea Rafinesque, 1815); *Titanocarcinus* A. Milne-Edwards, 1864 (Tumidocarcinidae Schweitzer, 2005); and *Styracocarcinus* Schweitzer and Feldmann, 2012 (?Portunoidea Rafinesque, 1815). Also other admitted Eubrachyura taxa (Luque, 2015, p. 5 and 10) such as: Telamonocarcinidae Larghi, 2004 (?Dorippoidea MacLeay, 1838) and Tepexicarcinidae Luque, 2015 (uncertain Superfamily), are compared with *Eogeryon* n. gen. as well.

Cretaceous members of the family Retroplumidae such as *Costacopluma* from Late Cretaceous of Mexico, western Africa, and India, or those who are considered as such, as *Archaeopus* (see Guinot *et al.*, 2013, pp. 140-141), from Late Cretaceous of the West Coast of the United States and Canada, clearly differ from *Eogeryon* n. gen. in having a more squarish or transversely ovate and ridged carapace, with a narrow rostrum usually bifid or spatulated, whereas in *Eogeryon* n. gen. the carapace is subhexagonal, smooth, and the front is larger. Also, they have much broader orbits than the new genus. Differences in sterno-abdominal pattern are very evident, whereas in *Costacopluma* and *Archaeopus* the sternum is large and the thoracic sternites are transversely ridged, in *Eogeryon* n. gen. the sternum is narrower and the thoracic sternites are flattened. Also, members of Retroplumidae possesses a thin and reduced fifth pereiopod whereas in the new taxon it appears to be only slightly reduced (see also de Saint Laurent, 1989; McLay, 2006). Members of Carcineretidae such as *Carcineretes* Beurlen, 1930 from Maastrichtian of Jamaica, Belize and Mexico and *Woodbinax* Stenzel, 1952 from the Cenomanian of Texas (US) have affinities with *Eogeryon* n. gen. such as: a bilobed and downturned front; large orbits with two well-marked fissures; similar outline of carapace; transverse ridges in protograstric lobes; conspicuous swollen epibranchial ridge and mesobranchial lobes; well-marked branchiocardiac groove bounding urogastric and cardiac regions; and a relatively narrow sternum. But they differ from *Eogeryon* n. gen. in having: a squarish carapace; an axial inflation in the front; not well-defined antero- and posterolateral margins; and broader orbits than *Eogeryon* n. gen. In addition, they lack the anterolateral teeth that *Eogeryon* n. gen. possesses. The sterno-abdominal cavity is much deeper in *Carcineretes*, reaching the sternite 3. Moreover, Vega *et al.* (2001) mentioned the sternite 8 was visible; however, Schweitzer *et al.* (2007b) and Karasawa *et al.* (2008) indicated the sternite 8 was not visible. In any case, in *Eogeryon* n. gen. sternite 8 is not visible. In addition, the chelae of *Carcineretes* are keeled in their outer surface whereas in *Eogeryon* n. gen. they are smooth and much more massive. The P2-4 are equal in size and P5 paddle-like in *Carcineretes*, whereas in *Eogeryon* n. gen. the P5 appears to be slightly reduced. Relationships between those taxa could not be discarded but differences appear to be clear (see Withers, 1922; Beurlen, 1930; Guinot and Bréton, 2006; Schweitzer *et al.*, 2007b). *Componocancer*, the sole member of Componocancroidea from the Albian of Montana (US), has in dorsal view some affinities with *Eogeryon* n. gen. Even though the holotype and paratypes of *Componocancer* are poorly preserved dorsally (Feldmann *et al.*, 2008, f. 2 A, B, C, E), the supraorbital margin has two fissures as in *Eogeryon* n. gen.; *Componocancer* shows a similar anterolateral margin, mainly regarding the outer orbital tooth, formed by three broad projections (possibly broken triangular teeth) and small last anterolateral tooth (epibranchial) as in *Eogeryon* n. gen., and the maximum width is also placed at the level of third anterolateral tooth. The regions are fairly marked in both genera, sharing a short V-shaped cervical groove with gastric pits at the same level, a well-marked branchiocardiac groove bounding urogastric and cardiac regions, slightly inflated branchial regions and the pterygostome is similar in shape (see Feldmann *et al.*, 2008, f. 2). However, differences are evident, for instance dorsally *Eogeryon* n. gen. is more flattened than *Componocancer* and the general outline is hexagonal, slightly elongate whereas in *Componocancer* the general outline is rectangular and wider than long. In ventral view, the male sternum of *Eogeryon* n. gen. is broader than in *Componocancer*, and sternites 3-4 are less depressed axially, in addition *Componocancer* has somites 4 and 5 free laterally, while in *Eogeryon* n. gen. they are fused; in *Componocancer* sternites 7-8 are reduced in size indicating that P4 and P5 are carried dorsally, in *Eogeryon* n. gen. sternites 7-8 are not preserved but the coxae of P2-P4 are equal in size, and the remains of arthrodial cavity of P5, even appearing possibly smaller than the rest of periopods, indicates that P5 was not clearly dorsally carried (see also Guinot *et al.*, 2008; Guinot *et al.*, 2013). Members of Icriocarcinidae such as *Icriocarcinus* Bishop, 1988 and *Branchiocarcinus* Vega, Feldmann and Sour-Tovar, 1995, from Campanian-Maastrichtian of West and East Coast of the US and Mexico in the Americas (see Phillips *et al.*, 2014), and *Cancrixantho* Van Straelen, 1934 from Southern France and Catalonia (NE Iberian Peninsula) in Europe, are clearly distinguishable from *Eogeryon* n. gen. in having: inverted subtrapezoidal carapace, twice as wide as long; very broad orbits without fissures occupying completely anterior margin; long and narrow pseudorostrum; dorsal carapace regions marked by strong transverse ridges and deep cervical groove; wide thoracic sternum and deep sterno-abdominal cavity and keeled spiny chelae. None of these features can be seen in *Eogeryon* n. gen., beyond the obvious transverse ridges in protogastric lobes, thus ruling out a close relationship with *Eogeryon* n. gen. (see Téodori *et al.*, 2013; Nyborg *et al.*, 2014). *Lithophylax*, the sole member of Lithophylacidae Guinot and Bréton, 2006, tentatively placed within Portunoidea (see Karasawa *et al.*, 2008) differs clearly from *Eogeryon* n. gen. in having an inverted subtrapezoidal carapace with regions well differentiated by grooves; front large, straight, with narrow rostrum; orbits extremely broad with a unique fissure; wide thoracic sternum and broad sterno-abdominal cavity; chelae weakly homodont; P5 subdorsal and markedly reduced. All of these features preclude, at least, a closer relationship with *Eogeryon* n. gen. (see Guinot and Bréton, 2006). Members of Longusorbiidae such as *Longusorbis* Richards, 1975 from the Coniacian to Campanian of the Pacific Coast of Northern and Central America, and *Binkhorstia* Noetling, 1881 from the Maastrichtian of Europe, differs from *Eogeryon* n. gen. in having: inverted subtrapezoidal to squarish carapace with well-marked regions; front straight with narrow and downturned spatulated rostrum; large orbits and spiny upper margin of chelae (*Longusorbis*). However, posterolateral margins are similarly stepped and eyestalks are well calcified in Longusorbiidae as in *Eogeryon* n. gen. Ventrally, similarities are evident, they share with *Eogeryon* n. gen.: a similar thoracic sternal structure, more or less elongate, widest at level of sternite 5, sternites 3-4 fused, sternite 4 long, sternites 5-6 subtrapezoidal; suture2/3 complete; suture 3/4 distinct, well-marked by a groove; sutures 4/5 and 5/6 not parallel, and abdominal somites free, somite 6 being the longest. Even though sternite 3 is shorter in Longusorbiidae and the telson seems to be more acute than in *Eogeryon* n. gen. and in *Binkhorstia*, the thoracic sternum is broader than in *Eogeryon* n. gen. The differences notwithstanding, similarities between Longusorbiidae and the new genus cannot be precluded, mainly regarding sterno-abdominal characters (see Richards, 1975; Schweitzer *et al.*, 2003; Fraaije *et al.*, 2006; Schweitzer and Feldmann, 2011). *Marocarcinus*, the sole member of Marocarcinidae from the Cenomanian of Morocco, has many affinities with *Eogeryon* n. gen. but also differences. Careful observations of the figures and descriptions in Guinot *et al.* (2008), and on new material available (author, personal observation), *Marocarcinus* possesses antero- and posterolateral margins defined, with anterolateral margin armed with four teeth, the first and second ones being subtriangular, as *Eogeryon* n. gen. possesses. *Marocarcinus* also has: a similar carapace outline, flattened with regions faintly defined; similar frontal pattern, straight but faintly bilobed, but not four tipped like as in *Eogeryon* n. gen.; similar orbits with two fissures and well-calcified eyestalks, as in *Eogeryon* n. gen. Regarding sterno-abdominal characters, a new available male specimen of *Marocarcinus* (A. Garassino pers. comm., 2014), presents an elongate and ovoid thoracic sternum with maximum width at the level of sternite 5, similar to the *Eogeryon* n. gen. sternum. However, the suture 2/3 appears to be incomplete in this new male material, although the diagnosis of Guinot *et al.* (2008) indicates suture 2/3 complete (for female), as in *Eogeryon* n. gen.; the suture 3/4 is almost complete, only interrupted medially in the male *Marocarcinus*, whereas it is distinct, only discernible by a well-marked groove in *Eogeryon* n. gen.; sternite 4 possesses two marked protrusions in both sides of sterno-abdominal cavity in *Marocarcinus* whereas in *Eogeryon* n. gen., sternite 4 is smooth; also, abdominal somite 5 is as long as somite 6, whereas in *Eogeryon* n. gen., somite 5 is half the length of somite 6 (A. Garassino pers. comm., 2014). Chelae seems to be strong and massive with marked heterochely as in *Eogeryon* n. gen., and probably homodonty (see Guinot *et al.*, 2008, f. 2, 3A), but in *Eogeryon* n. gen. right chela is even stronger and dactily are clearly heterodontic. According to the above-mentioned similarities between both genera, a possible relationship could exist. *Megaxantho* Vega, Feldmann, García-Barrera, Filkorn, Pimentel and Avendaño, 2001, tentatively placed in Xanthoidea, could be placed into Menippidae Ortmann, 1893 (Eriphioidea: F. Vega pers. comm., 2015). *Megaxantho* differs from *Eogeryon* n. gen. in having: a more flattened and slightly broader carapace; larger front and smaller orbits; rectangular anterolateral teeth whereas in *Eogeryon* n. gen. they are pointed subtriangular; dactylus of right chela has a strong eccentric basal tooth, whereas in *Eogeryon* n. sp. it is flattened. Ventrally, differences are not so evident, but *Megaxantho* has more elongate sternites 3-4, broader somite 6 and telson is more acute subtriangular than in *Eogeryon* n. gen. (see Vega *et al.*, 2001). *Ophthalmoplax* (?Macropipinae Stephenson and Campbell, 1960) from the late Campanian of Morocco and Maastrichtian of Atlantic and Gulf coasts of the Americas, differs from *Eogeryon* n. gen. (as in the case of Carcineretidae) in having: a subquadrate carapace with not well-defined lateral margins; regions well defined, many of them ridged, while in *Eogeryon* n. sp. regions are poorly defined and ridges are present only in protogastric lobes; posterolateral margins are rimmed, spiny or nodose; fronto-orbital margin is broader in *Ophthalmoplax* than in *Eogeryon* n. gen.; supra-orbital margin presents stronger spines than in *Eogeryon* n. gen.; front is bilobed and strongly downturned, but not with four- tipped appearance as in *Eogeryon* n. gen.; sternite 4 is broader; sterno-abdominal cavity is deeper than in *Eogeryon* n. sp., and it reaches sternite 3; sternite 8 is visible ventrally in *Ophthalmoplax* in contrary to *Eogeryon* n. gen. in which it is not visible. In addition, in *Ophthalmoplax* chelae are keeled and spiny whereas in *Eogeryon* n. gen. they are stronger and smooth, and *Ophthalmoplax* has a lanceolate propodus of P5, not present in *Eogeryon* n. gen. Possible relationships, if existing, are remote (see Rathbun, 1935; Karasawa *et al.*, 2008; Ossó-Morales *et al.*, 2010; Vega *et al.*, 2013). Parapirimela Van Straelen, 1937 (?Portunoidea), erected to accommodate the portunoid-like Parapirimela Van Straelen, 1937 from Angola, was first assigned to Miocene, but subsequently assigned with reservations to Albian by da Veiga-Ferreira (1957), has a similar anterolateral margin with well-developed subtriangular teeth, and massive right chela, but differs clearly from *Eogeryon* n. gen. in having an uneven number of frontal spines, well-marked regions and grooves, and having right chela with knobstick molariform tooth in polex instead of dactylus as is usually the case (Van Straelen, 1937; Veiga-Ferreira, 1957). *Palaeoxanthopsis* Beurlen, 1958, the Cretaceous member of Palaeoxanthopsidae Schweitzer, 2003, from the Maastrichtian of Brazil and Mexico, clearly differs from *Eogeryon* n. gen. in having: a strongly vaulted longitudinally carapace, wider than long, maximum width about two-thirds posteriorly at level of last anterolateral spine (epibranchial), which is long and posterolaterally directed; and regions well defined by deep grooves, inflated, with spherical swellings. Only the four tipped aspect of its bilobed front is similar to the new genus (see Beurlen, 1958; Schweitzer, 2003, p. 21, fig. 5, 4-5). Cretaceous species of *Titanocarcinus* A. Milne-Edwards, 1864 (Tumidocarcinidae) such as *T. mamillatus* Secrétan, 1964 from the Late Cretaceous of Madagascar, differs clearly from *Eogeryon* n. gen. in having: a subquadrate carapace, moderately vaulted; regions well marked by deep grooves, granular, instead of smooth and fairly marked regions in *Eogeryon* n. gen., and by absence of triangular teeth in its anterolateral margins as in *Eogeryon* n. sp. (see Schweitzer *et al.*, 2007a; Charbonnier *et al.*, 2012). *Styracocarcinus*, genus erected to accommodate *Titanocarcinus meridionalis* Secrétan, 1961 from the Late Cretaceous of Morocco, questionably placed within Tumidocarcinidae on the basis of its Y-shaped sternum (see Schweitzer and Feldmann, 2012) but that shows clear portunoid affinities, shows similarities with *Eogeryon* n. gen. Thorough observation of the images presented in Sécretan, 1961, a cast of the holotype in Schweitzer and Feldmann (2012), and of new material available (Figure 6 A-B), from the Late Cretaceous (probably Campanian) of the Moyenne Moulouya (Morocco), which presents well-preserved fronto-orbital features, shows that both genera share: similar flattened subhexagonal carapace, maximum width at level of third anterolateral tooth; regions faintly marked, transverse ridges on protogastric lobes, conspicuous sigmoidal epibranchial ridge, hepatic swellings; deep branchiocardiac grooves; stepped posterolateral margins; front bilobed, four-tipped appearance; orbits relatively large with two supraorbital fissures; anterolateral margin with four teeth, first (exo-orbital) and second ones subtriangular, serrated or slightly nodose outer margin; similar elongate and ovoid thoracic sternum; and a strong and massive right chela of adult specimens (slightly spiny in juvenile specimens of *Styracocarcinus*). Differences, however, are present. *Styracocarcinus* possesses: regions of carapace more rounded and slightly inflated; not so clearly marked protogastric ridges; developed epigastric swellings; subtriangular third and fourth anterolateral teeth as the first and second; lobes or teeth in posterolateral margins (spiny in juvenile specimens); slightly narrower thoracic sternum; suture 3/4 laterally visible, suture 4/5 laterally directed whereas in *Eogeryon* n. gen. it is downward directed; telson more acute, and somite 6 higher than the somite 6 of *Eogeryon* n. gen. In addition, in *Styracocarcinus*, the propodus of P4-P5 are flattened, which are not preserved in *Eogeryon* n. gen. Despite these differences, relationships between both genera are possible (Secrétan, 1961; Schweitzer and Feldmann, 2012, p. 23-25, fig.1, 1-3).

Members of Telamonocarcinidae, Larghi, 2004, such as *Telamonocarcinus* Larghi, 2004 and *Eodorippe* Glaessner, 1980, from the Cretaceous of Colombia, Lebanon, Japan and New Zealand, differ from *Eogeryon* n. gen. by its general appearance, in having: a broadly pyriform carapace, granulate; broader front and narrow rostrum; anterolateral margin without spines; and P4 and P5 reduced (see Larghi, 2004; Guinot *et al.*, 2013; Luque, 2015). *Tepexicarcinus* Feldmann, Vega, Applegate and Bishop, 1998 (Tepexicarcinidae, Luque, 2015) from the Cretaceous of Mexico and Egypt differs clearly from *Eogeryon* n. gen. in having: a subrectangular carapace; broader fronto-orbital margin; square rostrum; nearly parallel posterolateral margins, among other evident differences. (See Feldmann *et al.*, 1998; Vega *et al.*, 2005; Larghi, 2004; Guinot *et al.*, 2013; Luque, 2015).

As is indicated above, *Eogeryon* n. gen. is an advanced crab, but its systematic placement is unclear. As it is seen in the precedent comparisons, it seems to be only related with some of the Late Cretaceous heterotrematous taxa, mainly with the coeval *Marocarcinus* and/or other younger taxa such as members of Carcineretidae or Longusorbiidae, both Portunoidea, and *Styracocarcinus* (probably Portunoidea). In many aspects, general dorsal appearance of *Eogeryon* n. gen. recalls that of some portunoids, regarding its anterolateral margin with acute teeth, and transverse ridges in several regions (see Karasawa *et al.*, 2008). Also, dactylus of its massive right chela present well- differentiated and specialized teeth (see Spiridonov *et al.*, 2014). Based upon the diagnosis of Portunoidea, the *Eogeryon* n. gen. features fit with several of the mentioned characters: "carapace subhexagonal… generally wider than long but occasionally equant… front typically with median notch… anterolateral margins almost always spinose or dentate, ranging from 3-9 spines or lobes… regions poorly or moderately defined, carapace with arcuate epibranchial ridge…" (Karasawa *et al.*, 2008, p. 94), "fronto-orbital margin broader than posterior margin… chelipeds usually robust, heterolochelic and/or heterodontic…" (Spiridonov *et al.*, 2014, p. 418). Nevertheless, regarding sterno-abdominal characters, even taking account that the holotype is ventrally incomplete, *Eogeryon* n. gen. does not present the typically portunid appearance as is evident in many of the portunoid families, for instance: usually large and flattened sternum, sternite 8 visible, inverted T-shaped male abdomen, somites 3-5 fused, somite 3 keeled, and neither the paddle-like 5th pereiopod, which is very usual in this superfamily. However, *Eogeryon* n. gen. has apparent affinities with some fossil portunoid-like taxa and also with the non-swimming portunoid family Geryonidae Colosi, 1923, which belonging to the Portunoidea, as already suggested by Manning and Holthuis (1981, p. 110) and admitted by Bowman and Abele (1982, p. 24). The portunoid status of Geryonidae is well supported by cladograms based on external morphology of Portunoidea from Karasawa *et al.* (2008, figs. 3-6) and cladograms based on molecular methods using two independent sources of DNA sequences as nuclear and mitochondrial genes by Schubart and Reuschel (2009, fig. 1) and Spiridonov *et al.* (2014, figs. 4-7), which place the clade Geryonidae, without exception, as the most basal Portunoidea.

Affinities among *Eogeryon* n. gen. and Geryonidae are observed, for instance: "carapace hexagonal, wider than long, smooth to granular, regions weakly or moderately defined, often with arcuate ridge on epibranchial area; front with even number of spines and axial notch; orbits only moderately wide, fissured, inner orbital angle defined by a node or spine, lower orbital spine long, visible dorsally; anterolateral margin convex with 3-5 spines suture 3/4 well marked, sternite 8 not visible" (Karasawa *et al.*, 2008, p. 96), among other affinities regarding chelipeds and thoracic and abdominal features (see also Manning and Holthuis, 1989). Previously, some authors have suggested the possible Cretaceous origins of Geryonidae. For instance, Karasawa *et al.* (2008, p. 115) indicate: "The positions of Carcineretidae and *Ophthalmoplax* in the cladogram suggest that Geryonidae, Mathildellidae, Catoptridae, and Carcinidae must have had Cretaceous origins, but as yet there are no fossils to support this hypothesis… Thus, it appears that Portunoidea in general, and especially the more derived groups, are a geologically young group. Indeed, they have geologically older relatives, extending into the Eocene and even the Cretaceous". Also, regarding the evolution of swimming capacities in portunoids, Spiridonov *et al.* (2014, p. 418) suggested: "Furthermore Geryonidae which have many plesiomorphies may be similar to the hypothetical common ancestor and are generally non-swimming or non-regularly swimming forms."

Therefore, *Eogeryon* n. gen. shares with members of Geryonidae: a smooth sub-hexagonal carapace that is slightly wider than long; regions fairly marked; conspicuous epibranquial ridge; similar cardiac region, swollen; mesobranchial region swollen; gastric pits at level of cervical groove; well-marked branchio-cardiac grooves bounding urogastric region; front bilobed, bifid lobes with four-tipped appearance; similar fronto-orbital ratio; orbits moderately large; supraorbital margin with two fissures or notches; anterolateral margins armed with four spines or teeth (including exo-orbital spine); posterolateral margins convex, stepped; posterior margin straight, re-entrant not well marked; possibly supradorsal position of P5; chelipeds robust, not keeled; merus of cheliped with dorsal subdistal spine; carpus with strong inner spine; propodus massive with dactylus and fixed finger with flattened molariform teeth, followed by serial conical teeth; thoracic sternites 3 and 4 fused, forming an elongate plastron; and suture 3/4 distinct, well-marked by a transversal groove. Nevertheless, differences between *Eogeryon* n. gen. and members of Geryonidae are also present such as: the epibranchial spine delimiting antero- and posterolateral margins is placed more anteriorly in Geryonidae than in *Eogeryon* n. gen.; smaller rounded orbits in Geryonidae (rectangular in *Zariquieyon* Manning and Holthuis, 1989); absence of transverse ridges in protogastric lobes in Geryonidae; outer surface of propodus sometimes ridged in Geryonidae, being smooth in *Eogeryon* n. gen.; suture 4/5 laterally upward directed whereas they are downward directed in *Eogeryon* n. gen. as in many primitive Eubrachyura (see Larghi, 2004; Feldmann *et al.*, 2008); male abdomen markedly triangular in Geryonidae, whereas it is subrectangular, narrowing progressively in *Eogeryon* n. gen.; male somites 3-5 separated by sutures but immovable, whereas they appear completely free in Eogeryon n. gen. (see Karasawa *et al.*, 2008; Spiridonov *et al.*, 2014).

Similarities among *Eogeryon* n. gen. with other portunoid-like fossil taxa are also observed. In this sense, as it is explained above, the Campanian *Styracocarcinus* (Figure 6 A-B) presents an array of characters shared with *Eogeryon* n. gen., as general carapace shape, construction of front, orbits and anterolateral margins, strong heterochelic and heterodontic chelae, and similar ventral pattern with elongate thoracic sternum and abdomen with all somites free, showing clearly their portunoid affinities (*sensu* Spiridonov *et al.*, 2014). Therefore, *Styracocarcinus* is herein tentatively transferred to Portunoidea (uncertain Family). As well, some species referred to *Coeloma* A. Milne-Edwards, 1865 from the Early and Middle Eocene, share with *Eogeryon* n. gen. a: similar carapace with weakly defined regions; similar orbito-frontal features with four-tipped front and relatively large orbits with fissured or bi-fissured supraorbital margin; chelae with strongly heterochely and clearly heterodonty, carpus with strong inner spine, merus with dorsal sub-distal spine; elongate thoracic sternum with suture 3/4 distinct, discernible by a well-marked groove; male sternite 7 without posterior prolongation; sternite 8 not visible and abdomen with all somites free. The *Coeloma* species: *C. dentata* (Woodward, 1873), *C. glabra* (Woodward, 1873) (types species) *C. martinezensis* Rathbun, 1926 and *C. vareoloata* Lőrenthey, 1898, are considered primitive and grouped in a first group by Jagt *et al.* (2010, p. 247), following Beurlen in Lőrenthey and Beurlen (1929, p. 241- 243), and were transferred to the genus *Litoricola* Woodward, 1873 by these authors (p. 247), who considered the name *Litoricola* valid for these four species. In addition, the same authors (p. 249) pointed out that Pedro Artal (pers. comm., May 2010) had informed them that based upon a suite of crabs, referred to as *Litoricola* by Woodward (1873), in the collections of the Sedgwick Museum, Cambridge, placement of the Ypresian (early Eocene) subspecies *Xanthilites macrodactylus pyrenaicus* Artal and Via, 1989 in that genus could be confirmed. However, they do not mention the Thanetian (late Paleocene) *Xanthilites macrodactylus* Van Straelen, 1924 (=*Coeloma*, see Schweitzer *et al.,* 2010), which is herein provisionally referred to the genus *Litoricola* as well. *Litoricola macrodactylus* (Van Straelen, 1924), presents all the characters above described, showing furthermore an extraordinary variability of chelae, being documented specimens with the upper margin of chelae either spiny or smooth, either massive and short or extremely long portunoid-like major chela, (see also Van Straelen, 1924; Schweitzer *et al.,* 2010, Pl. 1, figs. 1A-B, 2A; Goret *et al.*, 2013, figs. 26, Pl. E4, 7, 8, 9; Figure 6 C-E). Affinities of *Litoricola* with Portunoidea (*sensu* Spiridonov *et al.*, 2104) appear to be evident, and although there are differences, many of these characters are shared with the most basal non-swimming portunoids Geryonidae (Geryoninae Colosi, 1923 and Benthochasconinae Spiridonov, Neretina and Schepetov, 2014). Thus, until a review of this group is made, as it was suggested by Jagt *et al.* (2010, p. 246), a provisional placement of *Litoricola* within Geryonidae, seems to be more appropriate, as it was previously placed (Beurlen, 1930; Balss, 1957; Glaessner, 1969; Karasawa and Schweitzer, 2006), than their current placement as *Coeloma*, within Mathildellidae Karasawa and Kato, 2003 (Goneplacoidea MacLeay, 1838). It is noteworthy that in the above-mentioned genera and species, a progressive displacement of the epibranchial spine or corner marking the separation between the antero- and posterolateral margins is observed, from approximately half of carapace in *Eogeryon* n. gen., toward the anterior third of carapace in *Litoricola martinezensis* (see Rathbun, 1926, Pl. 2fig.1-3), *L. dentata* (Figure 6 F-I) and members of Geryonidae, with intermediate positions in *Styracocarcinus meridionalis* and *L. macrodactylus* (Figure 6 A-E). Other progressive variations are observed: the angle of sternal suture 4/5, whereas it is downward directed in *Eogeryon* n. gen., it is laterally directed in *S. meridionalis*, and progressively upward directed in *L. macrodactylus*, *L. macrodactylus pyrenaicus*, *L. martinezensis* and in Geryonidae; and in the same order, a progressive widening of the male abdomen is observed, becoming subtriangular in Geryonidae instead of subrectangular in *Eogeryon* n. gen. (see Rathbun, 1926; Artal and Via, 1989; Karasawa *et al.*, 2008; Jagt *et al.*, 2010; Schweitzer and Feldmann, 2012; Goret *et al.*, 2013; Spiridonov *et al.*, 2014; Figure 6).

However, the presence of well-marked transverse ridges in the protogastric lobes in *Eogeryon* n. gen. is not seen in any of the above-mentioned fossil taxa, nor in Geryonidae, thus blurring a potential direct phylogenetic relationship among *Eogeryon* n. gen. and the extant Geryonidae through some intermediate fossil taxa. Therefore, if the placement of *Eogeryon* n. gen. within Portunoidea seems to be appropriate, its familial placement is still obscure, despite the array of affinities with Geryonidae and related above-mentioned taxa. Therefore, none of Portunoidea known families can accommodate the new taxon, although some early Eocene portunoid fossil taxa, for instance *Pleolobites* Rémy, 1960 and *Portunites* Bell, 1858, currently included in the Macropipinae within Polybiidae (*sensu* Schubart and Reuschel, 2009), share with *Eogeryon* n. gen. a similar fronto-orbital pattern as front bilobed and four-tipped like and relatively broad orbits with supraorbital margin bi-fissured, as possible plesiomorphies. In addition, they share a relatively broad thoracic sternum, suture 3/4 well defined by a groove, sternite 8 not visible, and male somites completely free. However, they differs from *Eogeryon* n. gen. in having a broader carapace with well-marked regions, absence of ridges, and regarding *Pleolobites* in having keeled and spiny chelae (see Rémy, 1960, p. 59, Figure. 4, T1, 10-11; Bell, 1858, p. 20-22, T. 3, Figure 1-5).

Although it may be very suggestive establishing a direct phylogenetic relationship with *Eogeryon* n. gen. and the extant Geryonidae through intermediate forms such as the aforementioned, taking account the basal portunoid condition of Geryonidae, it seems more prudent to erect a different family to accommodate *Eogeryon* n. gen. within Portunoidea until new findings may enlighten our current knowledge. Thus, *Eogeryon* n. gen. is placed tentatively in its own family Eogeryonidae n. fam.

Eogeryon elegius n. sp.
Figures 4, 5

Diagnosis. As for the family.

Etymology. From the Latin *Elegius*, the chosen, dedicated to my son Eloi.

Measurements (in mm.). Holotype MGB 69151, carapace length = 30, width = 33, orbito-frontal width = 24, frontal width = 7. Cast of second specimen MGB 69152, carapace length = 37, width = 45, orbito-frontal width = 32, frontal width = 12.

Description. Carapace sub-hexagonal, medium sized, flattened, slightly wider than long, gently convex longitudinally at anterior third, epicuticle smooth. Maximum width at anterior third, at level of third anterolateral tooth. Regions fairly defined. Hepatic region with swollen semi-circular lobe, half-moon ridged. Gastric process poorly defined. Epigastric region medially depressed; protogastric lobes slightly swollen with well-marked transverse ridges; mesogastric region not defined; metagastric lobes slightly swollen separated from mesogastric region by deep V-shaped cervical groove; urogastric region fairly marked, depressed; gastric pits present. Cardiac region slightly swollen. Intestinal region depressed. Space between both, urogastric and cardiac regions, bounded by deep cardio-branchial grooves. Epibranchial lobe sigmoidal, inflated, partially ridged; mesobranchial lobe inflated; metabranchial area depressed. Front bilobed, bimarginate, slightly downturned, lobes bifid, four-tipped appearance. Orbits moderately large; supra-orbital margin slightly rimmed, two supra-orbital fissures; eyestalks relatively long, well calcified. Lateral margins strongly stepped, mainly posterolateral margin. Anterolateral margins with four teeth; first anterolateral tooth (exo-orbital), subtriangular, large, inward directed; second anterolateral tooth subtriangular, forward directed, outer margin ornate with very small nodes; third tooth conical, upward directed; fourth anterolateral tooth (epibranchial) small, blunt node. Posterolateral margins convex, stepped. Posterior margin straight, rimmed laterally. Sternum relatively narrow, longitudinally medially concave at level of sternites 3-4; sternites 1-2 not present; sternite 3 subrectangular; sternite 4 subtrapezoidal elongate; sternites 3, 4 fused; suture 3/4 well discernible by a deep transverse groove; sternites 5-6 subtrapezoidal, downward directed laterally, sternal sutures 4/5 and 5/6 not parallel. Episternites 4-5-6 downward directed. Male abdomen narrow, with 6 somites free, and telson covering sterno-abdominal cavity; telson subtriangular reaching 2/3 of sternite 4, somite 4 the broader; somites 1 and 3 subtrapezoidal, transversally narrow; somite 2 not preserved; somites 4-5-6, subrectangular becoming progressively narrower, somite

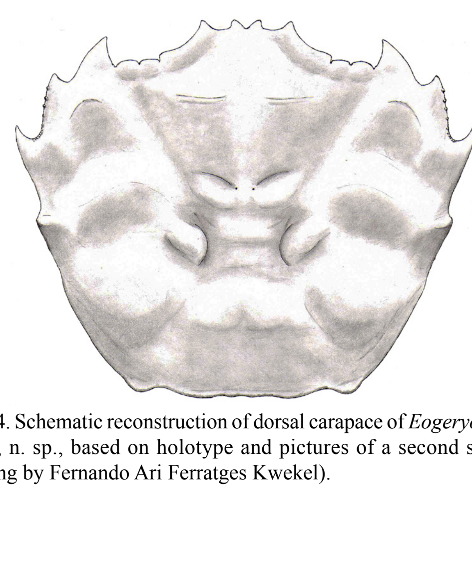

Figure 4. Schematic reconstruction of dorsal carapace of *Eogeryon elegius* n. gen., n. sp., based on holotype and pictures of a second specimen. (Drawing by Fernando Ari Ferratges Kwekel).

6 twice as high as 4 and 5. Right cheliped strong, smooth, suggesting marked heterochely; merus with subdistal dorsal spine, carpus massive, with inner strong spine; propodus strong, smooth; dactylus length equal as propodus; both, dactylus and fixed finger with proximal strong, flattened, molariform tooth, followed by five serial conical teeth. Ambulatory legs P2-4 proportionally long, smooth, equal, sub-oval in section; coxae of P2-4 subquadrate, equal; P5 not preserved, appears to be slightly smaller, probably subdorsal

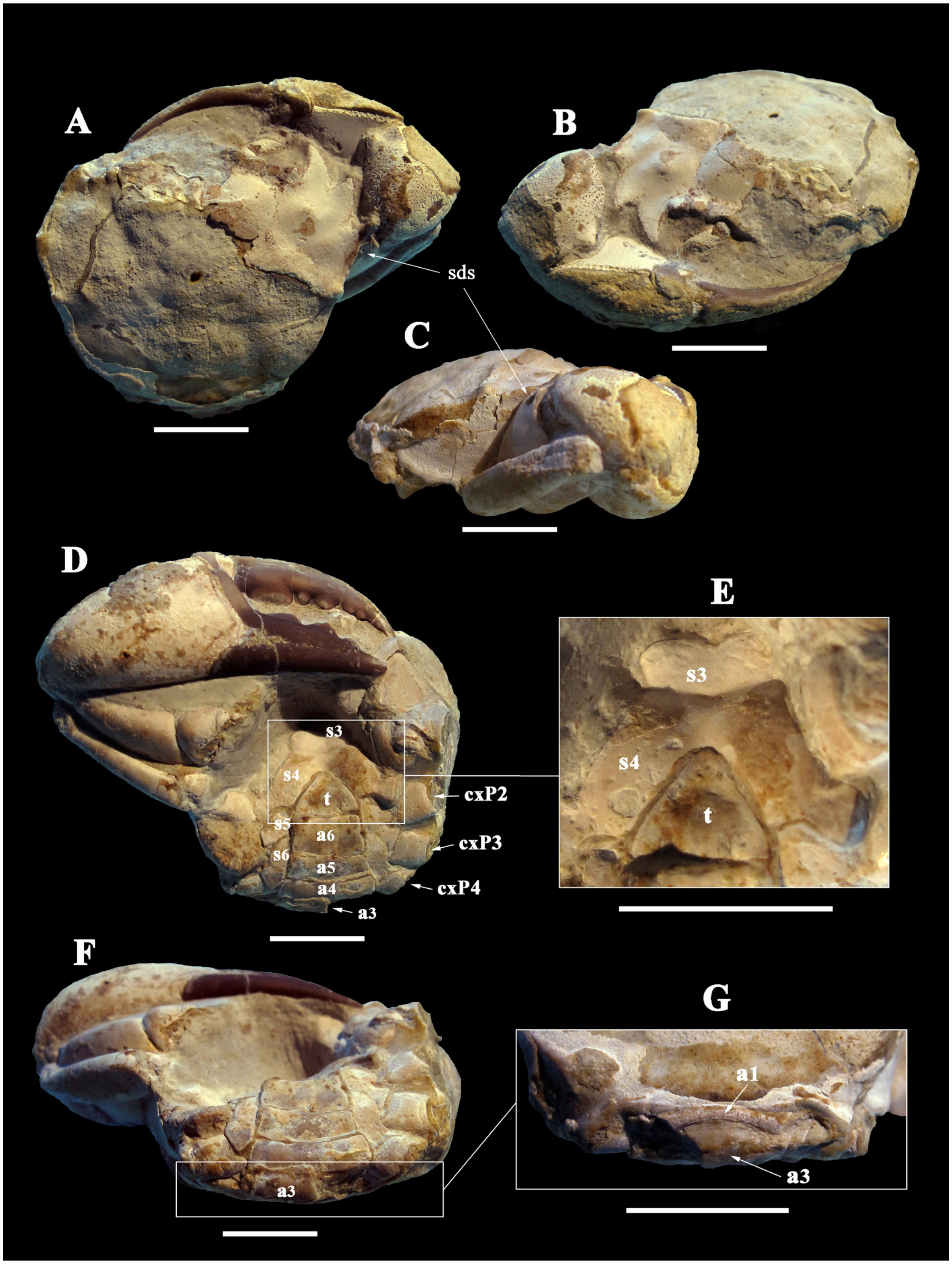

Figure 5. *Eogeryon elegius* n. gen, n. sp. Holotype MGB 69151, late Cenomanian, Condemios de Arriba (Guadalajara, Spain). A: dorsal view; B: frontal view; C: lateral view; D: ventral view; E: close-up of sternum; F: postero-ventral view; G: close-up of posterior-dorsal view. Abbreviations: a = abdominal somite; cxP = coxa of pereiopod; s = thoracic sternite; sds = dorsal subdistal spine; t = telson.

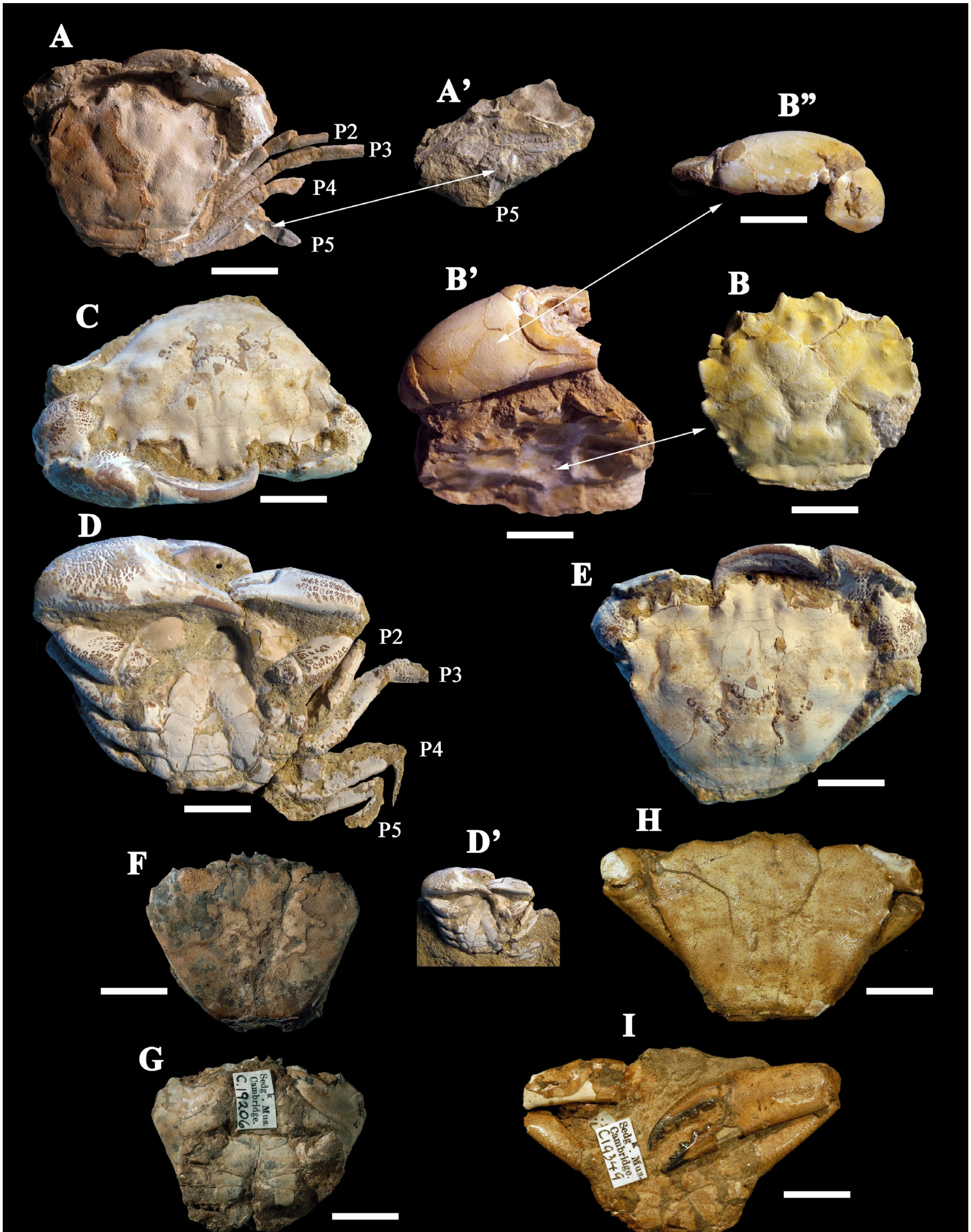

Figure 6. A, B: *Styracocarcinus meridionalis* (Sécretan, 1961) from probably Campanian, Moyenne Moulouya, Morocco; A, MGB 69153: dorsal view; A’: remain of propodus of P5, digitally transferred from matrix to the specimen; B, MGB 69154: dorsal view; B’: counterpart with right chela attached to the matrix; B”: dorsal view of right chela. C, D, E: *Litoricola macrodactylus* (Van Straelen, 1924) MGB 69155 from the lower Thanetian (Paleocene), Boussens, Haute-Garonne, France; C: frontal view; D: ventral view; D’: same specimen attached to the matrix; E: dorsal view. F, G, H, I: *Litoricola* Woodward, 1873 from the Ypresian of Portsmouth, Hampshire, United Kingdom; F, G: *L.* cfr. *dentata* Woodward, 1873 SGC C19206; F: dorsal view; G: ventral view; H, I: *L. dentata* Woodward, 1873 SGC C19349; H: dorsal view; I: ventral view.

5. Final remarks

The surprising discovery of *Eogeryon elegius* n. gen., n. sp. in late Cenomanian rocks allows a new insight on the eubrachyuran decapod evolution. Compared with other coeval or older eubrachyuran taxa, *Eogeryon elegius* n. gen., n. sp. appears to be an advanced Eubrachyura, much more so than might be expected by its old age. If compared with Albian taxa such as Dorippoidea, admitted as the oldest known eubrachyurans (see Luque, 2015), whether with the Albian *Componocancer roberti* Feldmann, Schweitzer and Green, 2008 or its coeval *Marocarcinus pasinii* Guinot, De Angeli and Garassino, 2008, *Eogeryon elegius* n. gen., n. sp. presents a higher degree of carcinisation, suggesting that it evolved from ancestral forms during the earliest Cretaceous. Moreover, the African portunoid-like *Parapirimela angolensis* Van Straelen, 1937, if its Albian age is confirmed, would represent the oldest known advanced eubrachyuran. The Portunoidea, despite their old origins, confirmed herein, are shown as more advanced eubrachyuran, in contrary to the primitive Dorippoidea, which are considered one of the most basal eubrachyuran groups. Portunoidea appears to be the most diverse and well-represented Eubrachyura group in the Cretaceous as demonstrated by the occurrence of *Eogeryon elegius* n. gen., n. sp., the portunoid-like *Parapirimela*, the possible portunoid *Lithophylax* during the Middle Cretaceous, and by the numerous taxa and families during the Late Cretaceous, such as members of Carcineretidae, Icriocarcinidae and Longusorbiidae or *Ophthalmoplax* and *Styracocarcinus*. It is noteworthy that these Late Cretaceous portunoid taxa present a random combination of typical characters seen in the most derived portunoids such as: a carapace broader than long often with epibranchial ridge; sternite 8 visible; inverted T-shape abdomen; transverse keel in somite 3; keeled and/or spiny chelae; modified paddle-like P5. However, none of these characteristics are present as a whole. It is not until the middle-late Eocene that, according to the fossil record, representatives of Portunidae *sensu stricto* appear, adding to the array of characters previously cited, the fusion of somites 3, 4 and 5, which is typical for this family and many other portunoid families. Therefore, apparently, the typical portunid ventral features cannot be expected in most of Cretaceous and Paleocene portunoid genera. The fossil record shows how Portunoidea were well recovered after the K/P event and the Early Eocene, a time of diversification for this group. For example, the Ypresian genus *Archaeoportunus* Artal, Ossó and Domínguez, 2013 (Archaeoportunidae) shows clearly how under a completely portunid-like carapace and with paddle-like P5 (author pers. obs.), its thoracic sternum and abdomen do not correspond to the typical portunid-like ventral features (see Artal et al., 2013). Therefore, *Eogeryon elegius* n. gen., n. sp. appears as one of the ancestors of portunoid forms that, through intermediate forms, originated one of the most diverse and species-rich groups of Eubrachyura. Further discoveries in other Late Cretaceous strata, such as Coniacian and Santonian, which have the poorest eubrachyuran fossil record, should enlighten our current knowledge.

6. Acronyms

MGB: Museu de Geologia de Barcelona; SGC: Sedgwick Museum of Earth Sciences, Cambridge.

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