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New data on *Eogeryon elegius* Ossó, 2021 (Decapoda: Eubrachyura: Portunoidea), one of the oldest modern-looking crabs, from the mid-Cretaceous of Iberia

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Abstract

A new specimen of the mid-Cretaceous portunoid *Eogeryon elegius*, preserving complete fronto-orbital features, confirms the preliminary interpretations that were made based on the holotype and complemented with pictures and a cast of a second specimen unavailable for study. The particular fronto-orbital pattern of *Eogeryon elegius*, can be considered of taxonomic value, and it turns out to be very similar to that of other portunoids from the Late Cretaceous, as well as those of other Cenozoic portunoids, in particular some geryonid genera. These similarities, among others, could suggest a certain degree of phylogenetic relationship, which deserves a more in-depth study to explore this hypothesis.

Key words: Eubrachyura, heterotreme, phylogeny, Portunoidea, Geryonidae, Eogeryonidae

1. Introduction

The discovery of *Eogeryon elegius* Ossó, 2021 in the upper Cenomanian (mid-Cretaceous) Villa de Vés Formation of Condemios de Arriba (Guadalajara, Spain), was paramount, considering the scarcity of eubrachyurans crabs of that age known at that time. Indeed, *Eogeryon elegius* is a heterotreme eubrachyuran that shows advanced features for a mid-Cretaceous crab. The well-preserved ventral features leave no doubt about their belonging to the heterotreme Eubrachyura. The general aspect, flattened body, relatively broad sternum, pleon, and heterodontic right chela are features that correspond to a more derived decapod notwithstanding its old age (Ossó, 2016, 2021).

Originally described in 2016, and subsequently redescribed in 2021 in order to validate the nomenclatural acts according to the rules of International Code of Zoological Nomenclature (ICZN, 2012), *Eogeryon elegius* was erected based on a sole almost complete specimen, but with the dorsal carapace decorticated, and the front not preserved (Ossó, 2016, figs. 5A, B; 2021, figs. 1A, B; Luque et al., 2021, fig. 5H). However, the reconstruction of the carapace was based on pictures of a second specimen from the same outcrop, with complete dorsal carapace and front preserved (Ossó, 2016, fig. 4; 2021, fig. 2), from a private collection, and not formally available for study (a cast of that specimen was deposited at MGB under registration MGB 69152). Since then, only isolated chelae have been found in these late Cenomanian outcrops

(e.g., Méndez et al., 2022, p. 72, fig. 1L, P), that will serve as a basis for a future study on brachyurans crabs evolution.

The discovery of a third specimen, available for study, which preserves important and diagnostic fronto–orbital features not clearly defined in the type material, confirms the preliminary reconstruction and diagnosis, and sheds light on the complete morphology of this ancient, modern-looking crab, and in particular on the true nature of its fronto-orbital margin.

Repository: Museu de Geologia de Barcelona (Barcelona, Catalonia), under acronym MGB.

2. Geological setting

See Ossó (2016, p. 232, figs. 1–3) and references therein.

3. Systematics palaeontology

Order Decapoda Latreille, 1802
Infraorder Brachyura Latreille, 1802
Section Eubrachyura de Saint Laurent, 1980
Subsection Heterotremata Guinot, 1977
Superfamily Portunoidea Rafinesque, 1815
Family Eogeryonidae Ossó, 2021

Genus *Eogeryon* Ossó, 2021

Type species: *Eogeryon elegius* Ossó, 2021, by O.D.

Diagnosis (emended): Carapace sub-hexagonal, medium-sized, flattened dorso-ventrally, slightly wider than long, gently convex longitudinally at anterior third. Maximum width at anterior third, at level of third anterolateral tooth. Regions moderately defined. Front bilobed, lobes bifid (with prominent inner orbital teeth, giving tetra-lobed appearance), with median notch, slightly downturned, protruding beyond the orbits. Orbits broad, three supra-orbital fissures separating three lobes; eyestalks well calcified. Fronto-orbital width about 0.63. 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, acute edge, lateral walls subvertical. Posterior margin straight, rimmed laterally. 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. Sternum relatively broad; 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, postero–laterally directed. Episternites 4–5–6 posteriorly directed. Male pleon narrow, with 6 somites free and telson covering sternopleonal 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 male cheliped strong, smooth; merus massive, smooth bearing a inner subdistal spine; 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, could be smaller, probably subdorsal.

Eogeryon elegius Ossó, 2021

(Figs. 1, 2)

Eogeryon elegius Ossó, 2016, pp. 21 –246, figs. 4 – 5. [unavailable]

Eogeryon elegius Ossó, 2016 [*sic*]. Schweitzer et al., 2018, p. 12, figs. 4–5; Prado et al., 2018, p. 11; Vega et al., 2018, p. 4; Guinot et al., 2019, pp. 308–309; Robin et al., 2019, p. 4; Spiridonov, 2020, pp. 149, 157–158; Luque et al., 2021, pp. 2, 8, fig. 5H; Wolfe et al., 2022, t. S1.

Eogeryon elegius Ossó, 2021, pp. 144–158, figs. 1, 2.

Eogeryon elegius Ossó, 2021. Méndez et al., 2022, pp. 72, 73, figs. 1L, 1P; Luque et al., 2023, pp. 42, 43, figs 1, 4D.

Material and measurements: One specimen, embedded in soft limestone, with cuticle preserved, lacking the anterior left third of the dorsal carapace and the posterolateral right corner, but with well–

preserved front and right orbital margin, and right cheliped. MGB 94627, carapace length = 36 mm; carapace width = 39 mm.

Locality: Condemios de Arriba (Guadalajara, Spain).

Stratigraphic horizon: Villa de Vés Formation, upper Cenomanian, mid-Cretaceous (*Vascoceras gamai* Biozone) (see Ossó, 2016).

Description: Carapace sub-hexagonal, medium sized, flattened, slightly wider than long, gently convex longitudinally mainly at anterior third. Dorsal regions moderately defined. Front bilobed, lobes bifid (with prominent inner orbital teeth giving tetra-lobed appearance), with median notch, slightly downturned, protruding beyond orbits; each lobe is strongly rimmed so that the medial teeth are placed at a much lower level. Orbits broad; upper margin with three supra-orbital fissures separating three lobes placed in the outer half of the supraorbital margin; the inner half of the margin gently concave, entire, ending in the intraorbital tooth (front). Anterolateral margins with first (exorbital tooth) and second teeth strong, subtriangular; third tooth not preserved; fourth tooth (epibranchial) small blunt node. Posterolateral margins slightly convex, acute edge, lateral walls subvertical. Gastric process poorly defined; mesogastric region not well 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; hepatic region with swollen semicircular lobe, half-moon ridged. Cervical groove V-shaped; branchiocardiac grooves deep. Posterior margin straight, rimmed laterally. Right male cheliped extremely strong, smooth; merus massive, smooth; carpus massive, strong inner spine; propodus strong, slightly longer than high; palm about 70 percent of carapace length, outer surface smooth, gently convex; dactyli broken, not preserved. Sterno-pleonal elements and ambulatory legs not preserved.

4. Discussion

The new specimen of *Eogeryon elegius* offers new perspectives on its possible relationship with several Late Cretaceous eubrachyuran decapods, portunoids in particular. The construction of the fronto-orbital margin of *E. elegius*, reveals a pattern that, besides of taxonomic value, can be of phylogenetically value (e.g., Luque et al., 2021, 2023).

The features of the supraorbital margins of *Eogeryon elegius*, formed by a strong exorbital tooth (first anterolateral tooth), followed by a closed fissure at the inner side of its base, and three lobes separated by more or less separated fissures at the distal half of the margin, are identical to those of the coeval *Marocarcinus pasinii* Guinot, De Angeli and Garassino, 2008 (http://www.mbfossilcrabs.com/Others.html; accessed October, 07, 2023), and those of the Maastrichtian *Carcineretes woolacotti* Withers, 1922, although the latter presents an accessory small lobe at the inner side of the exorbital tooth (see Withers, 1922, figs. 1, 3; Vega et al., 2001, fig. 3.1 [as *C. planetarius*]; Jagt et al., 2015, fig. 71-15.2C). The same features can be observed in the supraorbital margin of some species of *Ophthalmoplax* Rathbun, 1935, such as the late Campanian *O. minimus* Ossó-Morales, Artal and Vega, 2010, with the only difference of the absence of the fissure at the base of the inner side of the exorbital tooth or perhaps the complete fusion of that fissure (see Ossó-Morales et al., 2010, figs. 6.1, 2, 4, 6), and also in the late Campanian *Longusorbis cuniculosus* Richards, 1975, where the first and second fissures appear to be widely opened (e.g. Schweitzer et al., 2003, figs. 15.1, 2).

In this sense it is worth point out that a similar pattern of broad orbits, but having only two supraorbital fissures and two more or less marked lobes, instead of three, is seen in different portunoids, such as the late Campanian *Styracocarcinus meridionalis* (Secrétan, 1961) (see Secrétan, 1961, figs. 2, 5, pls. 1–3; Schweitzer and Feldmann, 2012, figs. 7.1, 2; Ossó, 2016, figs. 6A, B), and also in some of Cenozoic non-swimming portunoids, such as in species of geryonids, such as *Litoricola* Woodward, 1873 (cf. Woodward, 1873, pl. 2, figs. 1–3; Ossó, 2016, figs. 6F, H), particularly in "*L.*" *macrodactyla* (Van Straelen, 1924) (cf. Goret et al., 2013, pl. E, fig. 8; Ossó, 2016, figs. 6C, E), and in species of *Coeloma* A. Milne–Edwards, 1865 (e.g., Bittner, 1875, pl. 5, figs. 3a, 4a; Rathbun, 1926, pl. 2, fig. 2; Bachmayer and Mundlos, 1968, pl. 14).

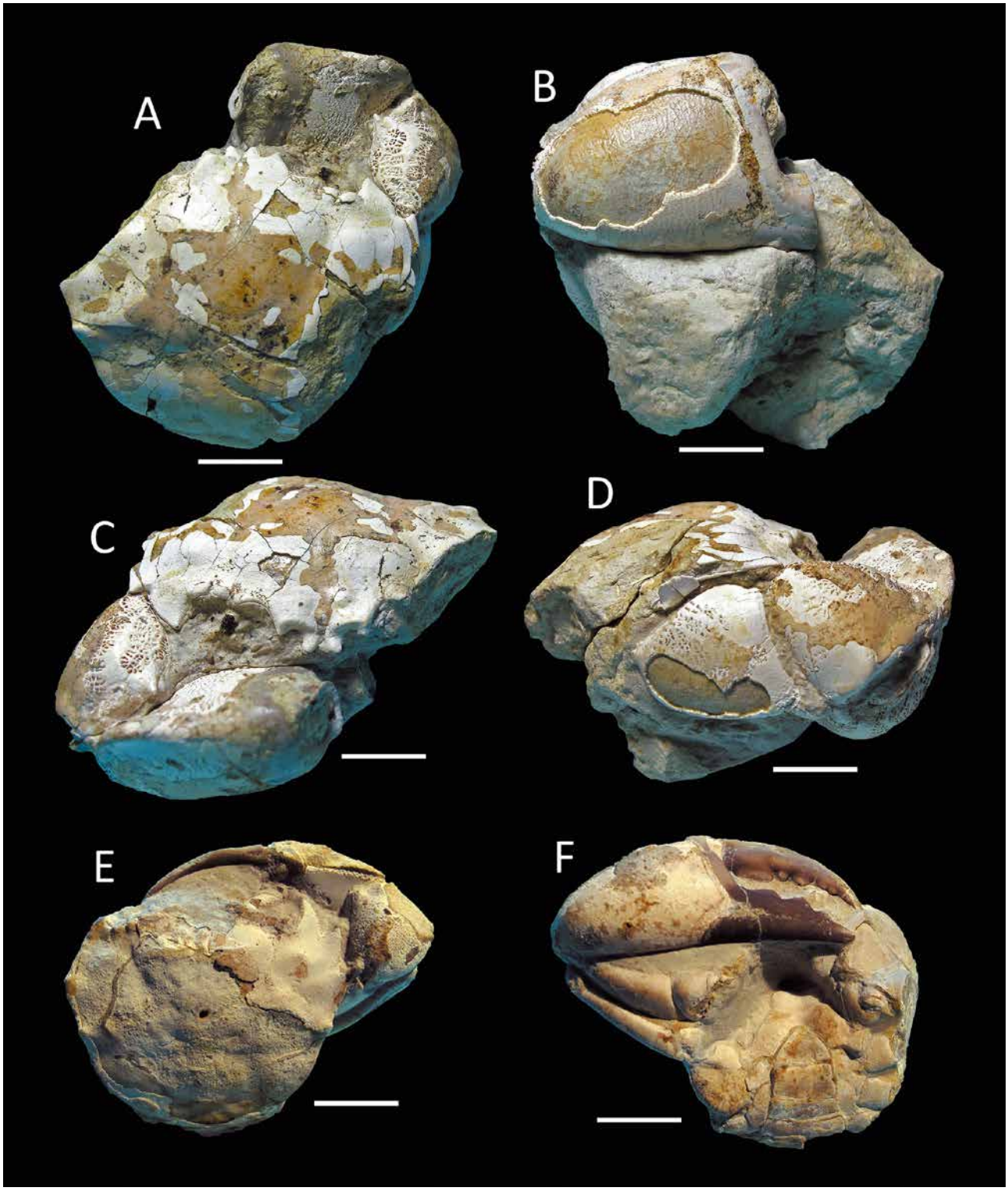

Fig. 1. A–F, *Eogeryon elegius* Ossó, 2021, from the Villa de Vés Formation, upper Cenomanian, Condemios de Arriba (Guadalajara, Spain). A–D, MGB 94627, *A*, dorsal view; *B*, ventral view; *C*, frontal view; *D*, right lateral view. E, F, Holotype MGB 69151, *E*, dorsal view; *F*, ventral view. Scale bar equal to 10 mm.

Such features are also seen in other portunoid genera e.g., *Portunites* Bell, 1858 (cf. Quayle, 1984, pl. 1, figs. 4, 5; http://www.mbfossilcrabs.com/Portunoidea.html; accessed October, 07, 2023), and *Pleolobites* Rémy, 1960 (see Rémy, 1960, pl. 1, fig. 11; Ossó et al., 2022, figs. 2, 3), among others (cf. http://www.mbfossilcrabs.com/Portunoidea.html; accessed October, 07, 2023).

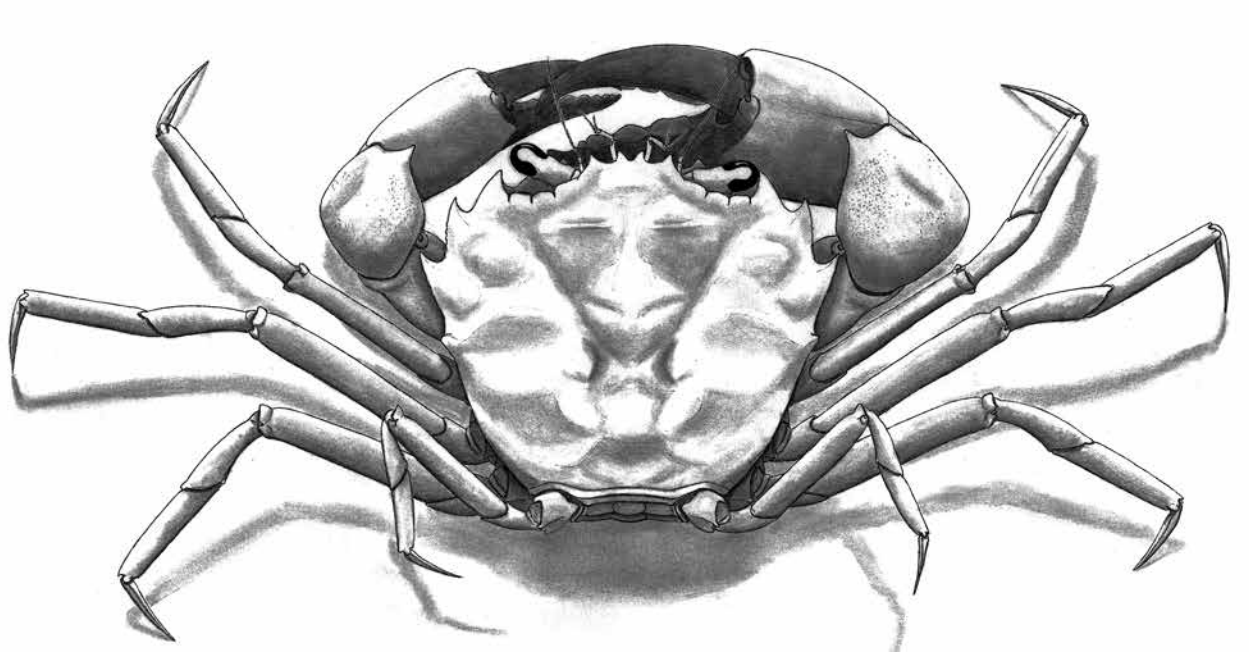

Fig. 2. Reconstruction of dorsal carapace and appendages of *Eogeryon elegius* Ossó, 2021 (from Ossó, 2021; drawing by Fernando Ari Ferratges).

Interestingly, all the aforementioned genera and species share with *Eogeryon elegius*, in more or less extent, a similar orbito-frontal construction: a bilobed rostrum, protruding beyond the orbits, and with bifid lobes bearing prominent inner orbital teeth which gives it a tetra-lobed appearance. This fronto-orbital pattern is also seen in members of non-portunoid families such as *Paraverrucoides alabamensis* (Rathbun, 1935) (see Rathbun, 1935, pl. 20, figs. 3, 5; Schweitzer, 2003, fig. 6.1, 3; Armstrong et al., 2009, Fig. 6.5, 6). Some extant species of non-swimming portunoids such as the geryonids *Geryon* Krøyer, 1837, and *Chaceon* Manning and Holthuis, 1989, also exhibit a similar fronto orbital pattern as aforementioned (e.g., Manning and Holthuis, 1989; Spiridinov, 2020, figs. 3A, 5A).

Although it is not the purpose of the present note, it is worth noting that, as indicated in Ossó (2021, p. 155), the potential portunoid condition of *Eogeryon elegius* proposed by Ossó (2016) does not have been rejected by most subsequent works, for example Vega et al. (2018), Guinot et al. (2019), Van Bakel et al. *in* Robin et al. (2019), Spiridonov (2020), or Wolfe (2022). Furthermore, phylogenetic analyses have recovered *Eogeryon* as sister to crown Portunoidea (Luque et al., 2021, fig 5H; 2023, pp. 5, 31, 33, figs. 1, 4D). Therefore, the assimilation of *Eogeryon elegius* to Tumidocarcinidae (Carpilioidea) made by Schweitzer et al. (2018, pp. 10, 12, figs. 8.5a–5b) is not accepted herein.

Detailed phylogenetic works on this group of fossil portunoids, would help to disentangle the current systematic placement of many of them (see Spiridonov, 2020, p. 158; Ossó et al., 2022, p. 2; Luque et al., 2021, fig. 5H; 2023, fig. 1), particularly those currently placed within Polybiinae Paulson, 1875 (see Schweitzer et al., 2021).

5. Conclusions

The discovery of the new specimen of *Eogeryon elegius* increases our knowledge of its almost complete external morphology. The fronto-orbital features of *Eogeryon elegius*, seem to be shared by a number of coeval and younger taxa, mainly by basal portunoids, and in particular by non-swimming geryonids, and are reminiscent of extant geryonids. Whether those characters are conservative through time should be investigated. It would be interesting to explore if that fronto-orbital pattern composed by broad orbits and supraorbital margins fissures and a bilobed rostrum, with tetra-lobed aspect and protruding beyond the

orbits, are phylogenetically informative, in addition to their taxonomic value. Further detailed analyses should determine if there is a phylogenetic relationship between those 'modern-like' mid-Cretaceous crabs and the apparently related younger taxa, and at the same time to find a proper systematic placement for some of them.

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