

New Albian-Cenomanian crabs (Crustacea, Decapoda, Podotremata) from Monte Orobe, Navarra, northern Spain

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ABSTRACT

Collections made by Máximo Ruiz de Gaona and Luis Via Boada between 1940 and 1982, from the Albian-Cenomanian reefal limestones at Monte Orobe (Navarra, northern Spain), now housed at the Museo Geológico del Seminario de Barcelona together with newly recovered material, have enabled the recognition of two new primitive crabs. A new genus, *Viaia* n. gen. (type: *Viaia robusta* n. sp.), is compared to the closely related *Heeia* from northern France and southern England; both genera are referred to *Viaiidae* n. fam., which is characterised by clearly distinguishable features, notably a peculiar cavity at the lateral sides of the carapace. A new genus and species of homolid, *Navarrahomola hispanica* n. gen., n. sp., is also described and discussed. The two new genera are closely related to podotreme crabs from Albian-Cenomanian levels in southern England and northern France, which confirms the close biogeographic links between these areas.

Key words: Crustacea, Decapoda, Brachyura, Podotremata, Albian-Cenomanian, Spain, new taxa.

RESUMEN

La recuperación de material para estudio, recolectado por Máximo Ruiz de Gaona y Luis Via Boada entre 1940 y 1982 en las calizas arrecifales del Albiano-Cenomaniano del Monte Orobe (Navarra, norte de España), depositado en la actualidad en el Museo Geológico del Seminario de Barcelona, junto a nuevos materiales disponibles, permite confirmar la presencia de dos interesantes braquiuros primitivos. Un nuevo género, *Viaia* n. gen. (tipo: *Viaia robusta* n. sp.), cercano al género *Heeia*, permite la comparación con material francés e inglés y el registro de una nueva familia, *Viaiidae* n. fam., basándose en caracteres claramente diferenciadores, en particular una peculiar cavidad en las porciones laterales del caparazón. Se describe y justifica también un nuevo género y especie asignado a la familia Homolidae, *Navarrahomola hispanica* n. gen. n. sp. Los dos nuevos géneros están estrechamente relacionados con decápodos registrados en capas del Albiano-Cenomaniano del sur Inglaterra y norte de Francia, lo que contribuye a confirmar importantes implicaciones biogeográficas en las áreas mencionadas en ese tiempo.

Palabras clave: Crustacea, Decapoda, Brachyura, Podotremata, Albiano-Cenomaniano, España, nuevos taxones.

INTRODUCTION

During the decades of 1930 to 1950, Máximo Ruiz de Gaona collected an extraordinary assemblage of Cretaceous decapod crustaceans at the quarry of Monte Orobe (Olazagutía, Navarra, northern Spain), close to the village of Alsasua (see Klompmaker *et al.*, 2011a, Figure 1). The fauna turned out to be very rich both in diversity and number of specimens. A substantial portion of the collection was sent to Victor Van Straelen, then director of the Institut Royal des Sciences Naturelles de Belgique, Brussels (Ruiz de Gaona 1943, 1952). Unfortunately, it has not yet been possible to trace this material to date, with the exception of merely three specimens, two anomurans and a brachyuran (Fraaije *et al.*, 2008). Additional collections from the same beds were made by Máximo Ruiz de Gaona and Luis Via Boada, who were in contact during the decades of 1950 and 1960. Subsequent lots have been recovered by ourselves and by local collectors. Together with specimens at the MGSB, these now permit to propose two new genera and species.

Decapod crustaceans collected at Monte Orobe (municipality of Olazagutía) have previously been considered to be of Cenomanian age, following some controversial and diverse assignments (Ruiz de Gaona 1943, 1952, 1954). Ruiz de Gaona came to the conclusion that different highs in the area corresponded to a large number of patch reefs aligned from Alsasua into the province of Vitoria. In addition to Monte Orobe, Ruiz de Gaona (1952) mentioned other localities, such as Olazagutía, Peña Eguino, Peña Aldorair and Arlabán where decapod crustaceans and similar associated faunas were found, confirming that the old quarry of Cementos de Olazagutía had yielded some crabs then referred to as *Distefania centrosa* (Van Straelen, 1940). López-Horgue *et al.* (1996) suggested an Albian-Cenomanian date for the patch reefs in the area, describing them and their palaeoecology in detail, with special reference to crabs, illustrating a few of them. Some of the decapod crustaceans recovered in the mid-Twentieth Century from the now abandoned quarry at Monte Orobe, were described and discussed by Van Straelen (1940, 1944), Ruiz de Gaona (1943) and Via Boada (1982). The last named researcher focused principally on anomurans. More recently (Fraaije *et al.*, 2008), studies on crabs from the same locality have received a new impetus. José Ramón Bataller, the director of the MGSB at the time when Ruiz de Gaona carried out his studies, summarised and illustrated the species then known in a synopsis of Cretaceous species of Spain (see Bataller, 1950). Gómez-Alba (1989) listed and illustrated all the decapod species from Monte Orobe housed at the MGB, but these do not include any holotypes. Via Boada (1981) listed only nineteen decapod crustaceans, as mentioned by Fraaije *et al.* (2008), and had plans for a future study, but did not illustrate nor describe any of them. Although the now abandoned Koskobilo quarry was active during Ruiz de Gaona's days, other working quarries in the area were the main suppliers of crustaceans in the area (see López-Horgue

et al., 1996). The first papers on decapod crustaceans from the Koskobilo quarry have appeared only recently (Fraaije *et al.*, 2009; Klompmaker *et al.*, 2011a, b, c, d). Of *Viaia* n. gen. we here use portions of the ventral surface collected recently from the Koskobilo quarry (see Klompmaker *et al.*, 2011a, Figure 1), where the epistome and ventral aspects of the front are perfectly preserved.

The assemblage of the decapod fauna preserved in Cretaceous deposits from Navarra (Spain) shows a particular similarity with the Albian-Cenomanian decapod fauna from southern England and northern France (see Wright and Collins, 1972; Breton and Collins, 2011). The main difference corresponds to the provenance, a perfectly preserved reefal environment in the layers of northern Spain, which could explain the more diversified fauna, with numerous, abundant anomurans, common primitive reef dwelling crabs, and the absence of raninoids, which are indicators of soft, sandy or muddy substrate.

Abbreviations: MGSB, Museo Geológico del Seminario de Barcelona, Spain; MAB, Oertijdmuseum De Groene Poort, Boxtel, the Netherlands; MGB, Museo Geológico de Barcelona, Spain; IRScNB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium.

SYSTEMATIC PALAEOLOGY

Order Decapoda Latreille, 1802
 Infraorder Brachyura Latreille, 1802
 Section Podotremata Guinot, 1977
 Superfamily Glaessneropsoidea Patruilius, 1959
 Family Viaiidae n. fam.

Type genus. *Viaia* n. gen.

Included genera. *Heeia* Wright and Collins, 1972 and *Viaia* n. gen.

Diagnosis. Carapace small (*Heeia*) to medium (*Viaia* n. gen.) in size, subtriangular in outline, much longer than wide; maximum width in the posterior half of carapace; front triangular, moderately (*Viaia* n. gen.) to widely projected (*Heeia*); ventral side of the front inclined (*Viaia* n. gen.); orbits relatively large, deep, oblique, directed forwards and outwards; anterolateral margins of carapace short, posterolateral margins longer and convex; posterior margin short, nearly straight, bounded laterally by small concavities; dorsal regions in anterior portion of carapace weakly differentiated, small mesogastric region, defined only by short basal grooves; urogastric region crescent shaped; epibranchial regions arched, inclined; posterior branchial regions large, swollen; cardiac region narrow; intestinal region small, subtriangular; cervical groove well marked, complete from side to side; branchiocardiac grooves sinuous, long, reaching the anterior portions of the cardiac region; posterior branchial grooves well marked, arched from the lateral margins of carapace towards the axis, bounding the posterior lateral portions of the cardiac region; lateral sides of the carapace

with deep cavity at the level of the cervical groove, bounded by strong spines or nodes; epistome triangular, smooth, with strong spine ventral of front (*Viaia* n. gen.); dorsal surface of carapace densely granulated.

Discussion. The deep and complete orbits, the blunt lateral sides of the carapace, the well-defined posterior regions of carapace, the front projecting well beyond the orbits, and the deep, well-marked dorsal grooves (mainly the arched branchial grooves), permit inclusion of the *Viaidae* n. fam. in the superfamily Glaessneropsoidea (sensu Schweitzer and Feldmann, 2009). However, the general outline of carapace, the triangular front, the construction of the orbits, and, in particular, the peculiar cavity in the lateral sides of the carapace at the position of the cervical groove, clearly distinguish this family from other glaessneropsoids. This deep lateral cavity, with the complex nodes surrounding it, has not been previously noted. However, in our opinion, a similar lateral cavity appears to be a common feature in different genera within the superfamily Glaessneropsoidea, as mentioned in detail in the general discussion (see Feldmann et al., 2008a, Figure 1; Schweitzer and Feldmann, 2009, figure 6, figure 10).

Genus *Viaia* n. gen.

Type species. *Viaia robusta* n. sp.

Diagnosis. Carapace medium sized, subtriangular in outline, elongate, much longer than wide, maximum width situated about three-quarters of the total length from tip of front, at the level of the posterior branchial region; front triangular, fairly advanced, stout, massive, with rounded sides, small lateral concavities and angular nodes at base; ventral portion of front strongly downturned from the tip of the rostrum; orbits large, deep, oblique, directed forwards and outwards, protected by three long and robust teeth, between them two deep incisions, orbital cavity deep; anterolateral margins very short, slightly concave; a complex lateral cavity, surrounded by strong nodes at the level of the cervical groove, divides the lateral margins; posterolateral margins longer, fairly convex, narrowing when reaching the posterior margin; posterior margin narrow, nearly straight, only slightly concave at axis; dorsal regions and grooves of carapace well defined, mainly in the posterior half; epigastric, protogastric and hepatic regions barely differentiated; mesogastric region small, bounded only by short basal grooves; urogastric region large, crescent shaped, with small indentations in the posterior margin; epibranchial region arched, directed obliquely, narrow and long; postbranchial regions large, swollen; cardiac region relatively narrow, subpentagonal in shape; intestinal region small, triangular; cervical groove deep, arched, complete;

branchiocardiac grooves sinuous, long; posterior branchial grooves well marked, long, arched, converging to the axis towards the intestinal region; epistome triangular, smooth, axially advanced; dorsal surface of carapace densely granulated.

Etymology. Named after the late Luis Via (Boada), prolific Spanish author, who studied the Monte Orobe decapod crustacean fauna.

Viaia robusta n. sp.

Figures 1, 2

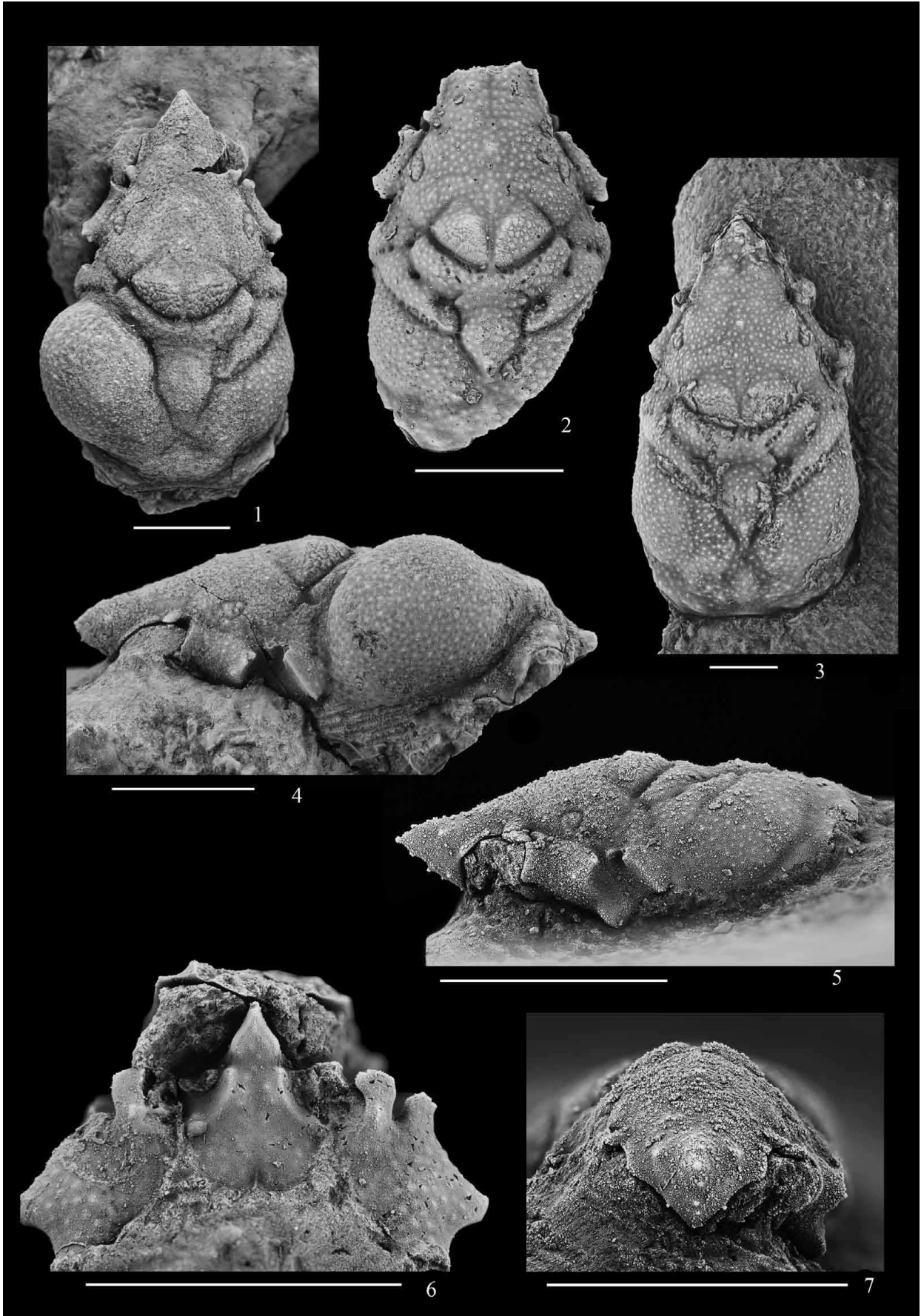
Diagnosis. As for genus.

Etymology. From Latin *robustus* (-a, -um), in allusion to a crab of strong build.

Material. The holotype is MGSB75298, paratypes are MGSB28146a-b, from the old quarry of Monte Orobe (Olazagutía, Navarra, Spain). Additional paratypes are MAB k.3200, k.3201, k.3202, from the Albian-Cenomanian reefal limestones of the Koskobilo quarry.

Measurements (in mm). See Table 1.

Description. Carapace medium sized (see Table 1), subtriangular in outline, much longer than wide, W/L ratio approximately 0.57, maximum width situated about three-quarters from front, at the level of the posterior branchial regions; dorsal surface convex in longitudinal and transverse sections. Front fairly advanced, triangular in shape, stout, with rounded lateral sides; salient lateral nodes and marked angular nodes at base (Figure 2.3). In frontal and lateral views, the ventral sides of the front are strongly downturned towards the epistomial area (Figure 1.5 and 1.7). Orbits large, oblique, deep, directed forwards and outwards, orbital margin with three notable teeth, separated by two open and deep fissures; the inner tooth is relatively small and laterally oriented, the outer orbital tooth longer, directed forwards, rounding towards the ventral side, forming a lateral wall; the suborbital tooth is pronounced and stout. Below the orbit is an enigmatic small, elliptical area. Lateral margins of carapace diverge backwards. Anterolateral margin short, somewhat concave, followed by a complex, large and deep cavity at the level of the cervical groove. The lateral cavity dividing the margins is hooded by three dorsal teeth, two of them large and stout, the intermediate small and spine like; in the ventral side of the cavity there is a large additional node (Figure 1.4-1.5). Posterolateral margins longer, fairly convex, narrowing towards the posterior margin. Posterior margin short, nearly straight, only slightly concave and rimmed axially. The lateral angles of the posterior margin are bounded by notable concavities (Figure 1.1 and 1.3). Dorsal regions relatively well marked by swellings and grooves. Epigastric and protogastric regions weakly differentiated.



The hepatic region, defined by the position of orbits and the cervical groove, is relatively small and only slightly swollen. Mesogastric region small, only defined by short oblique basal grooves, bearing two small inflations with scabrous ornament. Urogastric region large, stout, crescent shaped, with short indentations in the lower portion. Cardiac region relatively narrow, elongated, subpentagonal in shape. Intestinal region subtriangular. Epibranchial region arched, swollen, obliquely oriented. Posterior branchial regions large, notably swollen; mesobranchial and metabranchial areas weakly differentiated. Cervical groove deep, complete, reaching lateral margins, with defined gastric pits axially. Branchiocardiac groove sinuous, reaching anterior portion of cardiac region and intersecting posterior branchial groove and cervical groove. Posterior branchial grooves deep and long, broadly arched, bounding the rear of the epibranchial region and posterior lateral margins of cardiac region, and reaching axially the intestinal region. Dorsal surface of carapace densely covered by clear granules, all of similar size. Epistome large, stout, anterior portion elongate, subtriangular, with a relatively robust and spiny area anterior of small notches. Space for the antennule, antenna and eyestalk situated in the same room. Pterygostomial region relatively small, oblique, covered by granules. Sternum, abdomen and pereopods unknown.

Discussion. In his study of galatheoids from Monte Orobe, Via Boada (1981) listed, but did not describe nor illustrate, specimen MGSB28146 as *Heeia* cf. *villersensis* (Hée, 1924); this is also what the accompanying label says. In a study of a similar form from Cenomanian sands at Wilmington (Devon, southern England), Wright and Collins (1972) erected the genus *Heeia* to accommodate *Prosopon villersensis* Hée, 1924. Judging from the description and illustration in Hée (1924, pp. 142-147; pl. 5, figures 1a-1b) and from data supplied in 2006 by J. S. H. Collins (London), *Viaia* n. gen. is closely related, but does present notable differences. The detailed text by Hée (1924) clearly indicates a narrower, thus more elongate carapace, with noticeably complete and transverse depressions in the medial dorsal regions, posterior to the mesogastric region, mainly between the urogastric and cardiac regions. The cervical groove is fairly anteriorly placed, and the posterior branchial regions are strongly elongate. The front of *Heeia*, incompletely preserved, was assumed to have exhibited a downturned rostrum (Hée, 1924, p. 143), while the lateral spines shown in the drawing are only a supposition as indicated in the text. The preserved ventral portions of the carapace also show some differences with *Viaia* n. gen., according to the description (Hée, 1924, p. 143); the epistome presents a large and long plate, divided into two lobes by a longitudinal axial depression. In *Viaia* n. gen. the epistome is smooth, without axial depression. According to Wright and Collins (1972, pp. 31-32), the form from Wilmington is extremely elongate and slender; however, the cavity in the lateral margin is not mentioned in the text, suggesting that this feature was less evident than in *Viaia* n. gen. However, it is seen in the

illustrations (Wright and Collins, 1972, pl. 22, figure 3a). The front is particularly elongate and narrow, (see Figure 2.1, a cast donated by J. S. H. Collins). The drawing with an extremely long and bifurcated front (Wright and Collins, 1972, p. 32, text-figure 5) is a misinterpretation of a natural imprint (J. S. H. Collins, pers. comm., 2006). *Viaia* n. gen. is characterised by a robust appearance of the carapace, being broadly triangular, with fairly divergent margins from the front to the rear, the dorsal regions being broader than in the british specimens. The cervical and branchial grooves are much more posteriorly placed in *Viaia* n. gen., which is in accordance with the more posteriorly placed gastric, cardiac and epibranchial regions. In addition, the posterior branchial regions are less elongate. In frontal and lateral views, *Viaia* n. gen. presents a more regular and convex dorsal surface. In lateral view, the dorsal surface presents a rather regular convexity, with the highest point of the carapace in the mesogastric region, with a subtle depression posterior to the urogastric region.

The illustration in Hée (1924, pl. 5, figures 1a-1b) appears to be more or less precise; unfortunately, the type material is lost (G. Breton, pers. comm., 2009). A specimen from the same beds and locality (kindly loaned to us by G. Breton, see Figures 2.2 and 2.4) does show similarities to the genus *Heeia* Wright and Collins, 1972. Despite these differences, *Viaia* n. gen. appears to be closely related to *Heeia*. Therefore, we include both genera here in *Viaiidae* n. fam., a family which displays several unusual features. The characters described above preclude assignment to a more carcinized superfamily, being typical of primitive crabs: the dorsal regions are fairly swollen and divided by numerous grooves, mainly in the posterior half of the carapace such as the cervical and branchiocardiac grooves. Of special interest is the well-defined branchial groove, bounding the posterior lateral margins of the cardiac region and reaching the intestinal area. The complex cavity dividing the lateral margins of the carapace is so large and elaborate that we may safely assume that it was functional, probably acting as a locking mechanism for the chelae. The epistome is very long and stout, triangular in shape, with an acute terminal spine behind slight notches; no integrated urinal plate is present. All the characters mentioned above are unlike those of any eubranchyuran family.

The new family is tentatively assigned here to the superfamily Glaessneropsoidea (sensu Schweitzer and Feldmann, 2009). Despite the superfamily lacks clear apomorphies, the broadly triangular shape of the carapace, the division of main dorsal grooves, the primitive shape of regions, mainly the urogastric, cardiac, and branchial regions, favour placement in the Glaessneropsoidea. As mentioned by Wright and Collins (1972, p. 31), *Heeia* displays primitive characters that are reminiscent of elongate, pyriform “prosopids”. *Viaia* n. gen. exhibits the same primitive features, such as the shape of urogastric, epibranchial and cardiac regions and the division of dorsal grooves. Nevertheless, no primitive form has such

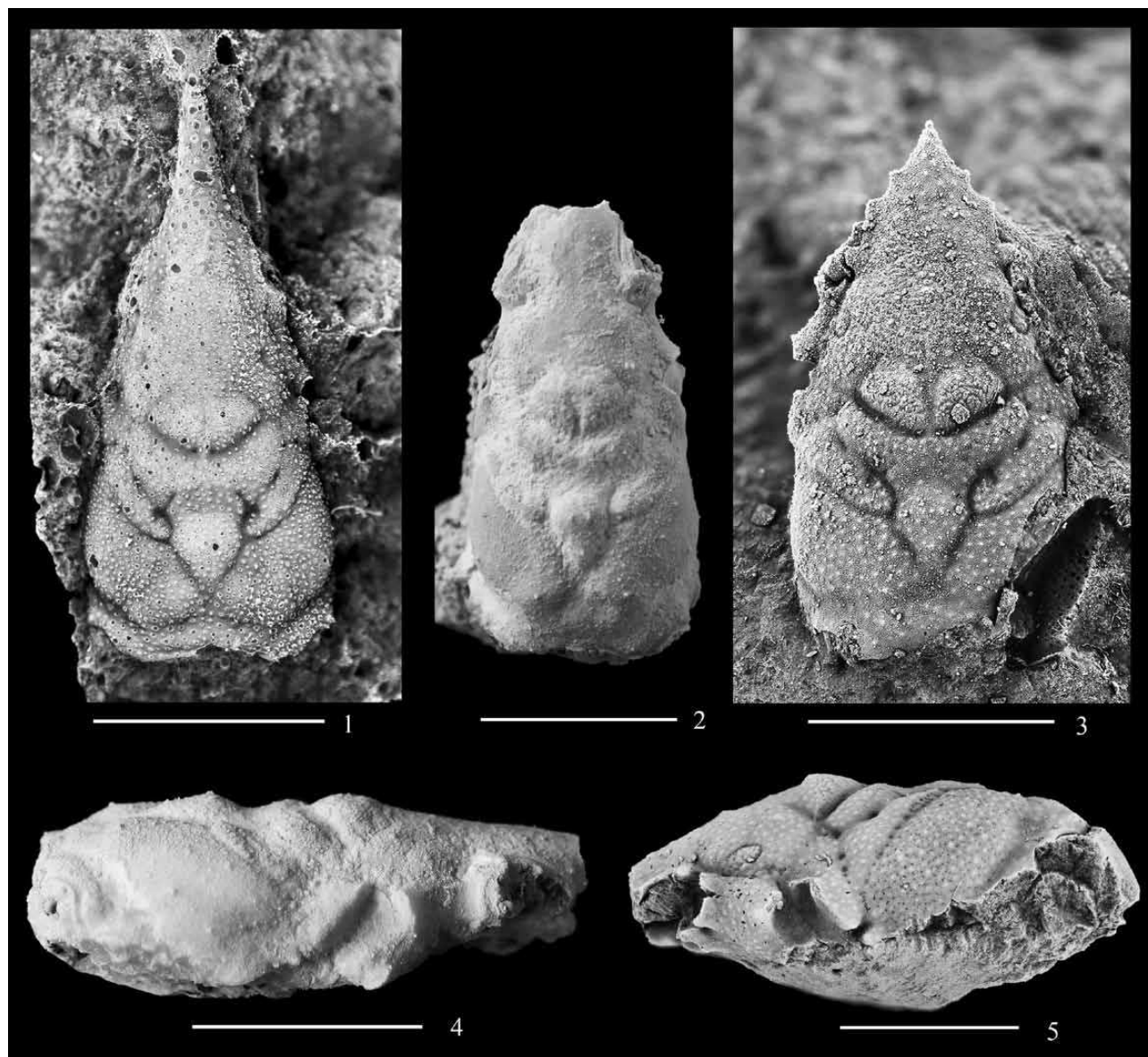


Figure 2. 1, *Heeia villersensis*, dorsal view, cast of JSHC 2035 (London, UK). 2 and 4, *Heeia villersensis*, from France, dorsal and lateral views. 3, *Viaia robusta* new genus, new species, dorsal view of paratype MABk 3200. 5, *Viaia robusta*, lateral view of paratype MABk 3201. All scale bars represent 5 mm.

a characteristic front and these distinct lateral cavities surrounded by large nodes. *Nodoprosopon ornatum* (von Meyer, 1842), as noted by Wright and Collins (1972, p. 31), shows a rather similar posterior half of the carapace, with comparable dorsal regions and grooves. However, the anterior half is easily distinguished. The front of *Nodoprosopon* is clearly trifid, with long lateral spines, and the gastric and hepatic regions are swollen and ornamented with large tubercles. The diagnosis for the Nodoprosopidae (see Schweitzer and Feldmann, 2009, pp. 116-117) mentions the lateral margins to be spinose, while the illustrations (see their figure 10) show salient nodes at the lateral margins of the carapace, similar to the lateral complex in *Viaia* n. gen., but preservation-induced issues make it difficult

to determine if this structure is similar or not. The genus *Verrucarcinus* Schweitzer and Feldmann, 2009, assigned to the Glaessneropsidae (see Schweitzer and Feldmann, 2009) is characterised by a similar outline and superficially similar dorsal regions in the posterior half of the carapace, except for the urogastric and epibranchial regions. Nevertheless, the clear frontal convexities, not present in *Viaia* n. gen., and the swollen and differentiated anterior regions, preclude placement in that genus. The front in *Verrucarcinus* is dorsally bilobed, with two advanced and semicircular lobes bounding an axial elevation (Schweitzer and Feldmann, 2009, Figure 5). The anterior regions of the carapace are fairly swollen and relatively well defined in *Verrucarcinus*, while they are much smoother in *Viaia* n. gen. The hepatic

Table 1. *Viaia robusta* new genus, new species (Spain) and *Heia villersensis* (France, UK); measurements in mm. L1: carapace length, including tip of rostrum. L2: length between posterior carapace margin and outer orbital corner. W1: carapace width. W2: width between outer orbital corners.

Specimen	Figure	L1	L2	W1	W2
MGSB28146	2.1	22	17.6	13.8	7.6
MABk3201	2.2	--	10.1	7.1	4.7
MGSB75298	2.3	28.8	23.3	15.8	9.3
UK (cast)	3.1	14.2	9.0	6.2	3.4
France	3.2	--	9.7	5.7	3.8
MABk3200	3.3	10.4	8.5	5.8	3.2

regions invariably are swollen and individualised, and the urogastric region is always axially depressed. The family Glaessneropsidae is diagnosed by a characteristic front: “rostrum projected well in advance of orbits, spatulate, downturned, with longitudinal swellings” (see Karasawa *et al.*, 2011, pp. 537-538), thus *Viaia* n. gen. cannot be placed in this family. Assignment of *Viaia* n. gen. to the family Lecythocaridae Schweitzer and Feldmann, 2009 is impossible either due to the broadly triangular shape of carapaces, the highly protuberant regions and the spatulate rostrum, main characters in members of the family (see Karasawa *et al.*, 2011).

The lateral cavity is an important characteristic of the new genus. Hereunder, we discuss other decapods that show this cavity and discuss its function and the reason that explains why *Viaia* n. gen. cannot be assigned to these families. With regard to the characteristic lateral cavities in *Viaia* n. gen., some genera assigned to the Glaessneropsoidea appear to have a comparable structure. The genus *Lecythocaris* von Meyer, 1860 has salient lateral nodes in the hepatic and epibranchial regions; a complex cavity surrounded by large blunt nodes is also seen (see Schweitzer and Feldmann, 2009, figure 6). However, other characters are absolutely distinct, in particular the outline of the carapace, broadly triangular, and the peculiar shape of the dorsal regions, which are strongly protuberant and bounded by deep grooves. The genus *Ekalakia* Bishop, 1976 presents similar lateral cavities (see Feldmann *et al.*, 2008a, figure 1-10), with lateral salient nodes in the epibranchial region and below the orbit. The characteristic orbits, with prominent rim, the outline of the carapace, from pentagonal to ovoid, and the shape of the dorsal grooves, the cervical and branchiocardiac subparallel, distinguishes *Ekalakia* from *Viaia* n. gen. The genera *Konidromites* Schweitzer and Feldmann, 2010 and *Concavolateris* Frantescu, 2011 both have lateral margins with salient nodes, and present ventral corrugated concavities along the carapace flanks, which were interpreted to have possibly functioned as accommodation for the pereopods. Both genera present an ovate shape of carapace, and weakly differentiated regions, which are characters clearly differentiated from *Viaia* n. gen.

Some carcinized crabs, such as xanthids, also exhibit

a cavity in the subhepatic area. For example, the genus *Hepatoporus* Serène, 1984 shows a deep and well-defined cavity in the ventral portion of the carapace (Mendoza and Ng, 2008). This cavity affects the anterolateral margins as well, but the placement and shape are clearly differentiated. It probably serves as a respiratory purpose (D. Guinot, pers. comm., 2011).

Members of the family Latreilliidae Stimpson, 1858 (superfamily Homoloidea sensu De Haan, 1839) are characterised by small-sized, delicate, strongly elongated carapaces with a salient lateral node below the long “neck”, which is defined as a lateral hepatic swelling (see Castro *et al.*, 2003, p. 603). However, latreilliids differ from viaiids in having an extremely short rostrum, which is bounded by two long supraorbital spines, by the absence of true orbits (the eyestalks are protected between the two supraorbital spines), and by the posterior carapace margin, which is fairly concave, with room for the dorsal fifth pereopods. The epistome in latreilliids is characterised by peculiar moulting lines in the lateral margins, and for the placement of antennae and antennules (D. Guinot and J.-F. Dejouannet, pers. comm., 2011). Thus, *Viaia* n. gen. cannot be assigned to the Latreilliidae.

Some majoid crabs may be considered very primitive, probably the most primitive within the Eubrachyura, but not as primitive as dromioidian crabs (D. Guinot, pers. comm., 2011). In all majoids the basal article of the antenna is fused to the epistome, which is why the epistome appears trifid, instead of triangular. The urinal article of the antenna opens posteriorly, whereas the antennal flagellum is anteriorly placed. The antennules are situated between the fused basal articles of the antenna in a separate fossa. Thus, in majoids the antennules are in sockets, the antennae anteriorly placed and the orbits laterally placed. In *Viaia* n. gen. the antennule, the antenna and the eyestalk are situated in the same location, which is common in primitive crabs.

Extant members of the family Inachoididae Dana, 1851 are typified by pyriform, relatively robust and broad carapaces of small size and exhibit a subtriangular front, the eyestalk projected laterally, and without orbits (Coelho, 2006, p. 679). Salient nodes below the eyestalks, referred to as “post-ocular lobes” by Coelho (2006, p. 679), are present, as in *Anisonotus* A. Milne-Edwards, 1879 or in *Coryrhynchus riisei* (Stimpson, 1860). In lateral view (see Coelho, 2006, figure 1-10; Santana and Tavares, 2008, figure 1), the salient and swollen lateral nodes exhibit some superficial resemblance to those seen in *Viaia* n. gen. However, the complex cavity is absent. Additionally, the main characters for inachoidids are the small spinose anterior axial process of the epistome, which at the same time presents long, arched lateral projections; the eyestalks project laterally, without true orbits; all these characters are absent in *Viaia* n. gen. Thus, *Viaia* n. gen. cannot be assigned to the Inachoididae either.

The genus *Priscinachus* Breton, 2009, assigned to the Majoidea Samouelle, 1819 (Breton, 2009), shows an

elongate, pyriform carapace. The dorsal regions are superficially similar to those in *Viaia* n. gen.; however, the front in *Priscinachus* is bifid, with two long spines, the orbits are close to the base of frontal spines, with the orbital margin laterally salient, bearing only a single supramarginal fissure; the anterior process of the epistome is broadly triangular, with the anterior projection distinctly advanced, bearing two divergent small ridges.

Paratype MGSB28146a exhibits a strong inflation in the left branchial regions (see Figure 1.1 and 1.4), to the point of absolute deformation of the branchial lobe. This confirms the former presence of a parasitic bopyrid isopod (see Rasmussen *et al.*, 2008).

Superfamily Homoloidea De Haan, 1839

Family Homolidae De Haan, 1839

Genus *Navarrahomola* n. gen.

Diagnosis. Carapace medium sized (see Table 2), suboval in outline, somewhat longer than wide, strongly convex in both longitudinally and transversely, maximum width of the intralineal carapace is in anterior portion, about one third of length of carapace from front. Dorsal surface fairly areolated, with swollen regions and numerous grooves. Front relatively broad, strongly downturned, medially depressed, broadly triangular with a slight notch at apex; lateral angles of front well defined by small, subtriangular raised nodes. Orbits not well defined, supraorbital margin large, inclined, directed forwards and outwards. Margins completely preserved along split of *lineae homolicae*, all specimens collected present the same intralineal shape. Anterolateral margins short, arched. Posterolateral margins longer, converging backwards. Posterior margin only partially preserved. Epigastric and protogastric regions fairly swollen, crossed by oblique, complete grooves. Mesogastric region large, medially ridged, partially divided at base; anterior process very short, ridged. Hepatic region fused with protogastric region. Urogastric region arched, thin, wide. Cardiac region subpentagonal, bearing three small tubercles, posteriorly fairly salient and directed backwards. Epibranchial region divided into three differentiated portions, the lateral subtriangular, the two axial ones transversely sulcate. Posterior branchial regions large, swollen, mesogastric and metagastric areas undifferentiated. Cervical groove arched, complete, reaching lateral margins; branchiocardiac groove short, bounding anterior portion of

cardiac region; branchial grooves arched, long, bounding posterior portion of cardiac region. Dorsal regions of carapace covered by small irregular tubercles, posterior portion of dorsal regions bearing dense small granules.

Etymology. Named after the region of provenance, Navarra.

Navarrahomola hispanica n. sp.

Figure 3

Diagnosis. As for genus.

Etymology. From the Latin name for the Iberian Peninsula, Hispania.

Description. Carapace medium to large sized (see Table 2), longitudinally suboval in outline, somewhat longer than wide, W/L ratio about 0.87; strongly convex in longitudinal and transverse sections; maximum width in anterior third of length of carapace, at level of hepatic region. Front relatively broad, strongly downturned, nearly 90° from dorsal surface, medially depressed, with raised lateral angles which are defined by small subtriangular nodes; from frontal view broadly triangular, with weak but noticeable notch at tip; in dorsal view the small raised corners at the base of front are visible. Orbits not well defined, supraorbital margin large, inclined, directed forwards and outwards; broadly convex when seen in frontal view. Lateral margins of visible carapace only defined by *lineae homolicae* (see comment above). Anterolateral margins very short, arched. Posterolateral margins longer than anterolateral, convergent posteriorly. Posterior margin only partially preserved. Dorsal regions well defined by swellings and grooves. Mesogastric region notably large, triangular in shape with arched sides and rounded angles, divided into posterior portion by a relatively deep and short groove; exhibits two clear bosses at base with dense scabrous ornament, axial portion marked by a thin longitudinal crest; anterior extension of mesogastric region broad and short, only reaching posterior portion of epigastric region. Epigastric regions defined by transverse inflations, bounded by inclined and continuous, yet shallow grooves; anterior inflation marks width of front in dorsal view. Protogastric lobes strongly inflated, forming two bosses that are divided by inclined shallow grooves. Hepatic region large, swollen; protogastric and hepatic scarcely differentiated, fused. Urogastric region crescent shaped, ridged, thin and wide. Epibranchial region divided into three portions, the lateral triangular, the inner margin bounded by an oblique groove, the two axial elongated, inclined, divided by a transverse shallow groove; anteriormost portion fused with urogastric region. Posterior branchial regions large, swollen, mesobranchial and metabranchial areas weakly differentiated. Cardiac region subpentagonal, apex posteriorly directed; bearing three clear tubercles, of which the posteriormost one is somewhat salient, posteriorly projecting. Intestinal region narrow and elongate, somewhat ridged at axis. Cervical groove deep, arched, well defined and continuous, reaching lateral margins. Branchiocardiac grooves short, bounding

Table 2. *Navarrahomola hispanica* new genus, new species; measurements in mm. L1: total carapace length. W1: intralineal carapace width.

Specimen	Figure	L1	W1
MGSB28147	4.1	36.8	28.9
MGSB28141	4.2	18.0	14.3
MABk3203	4.3	24.9	19.6

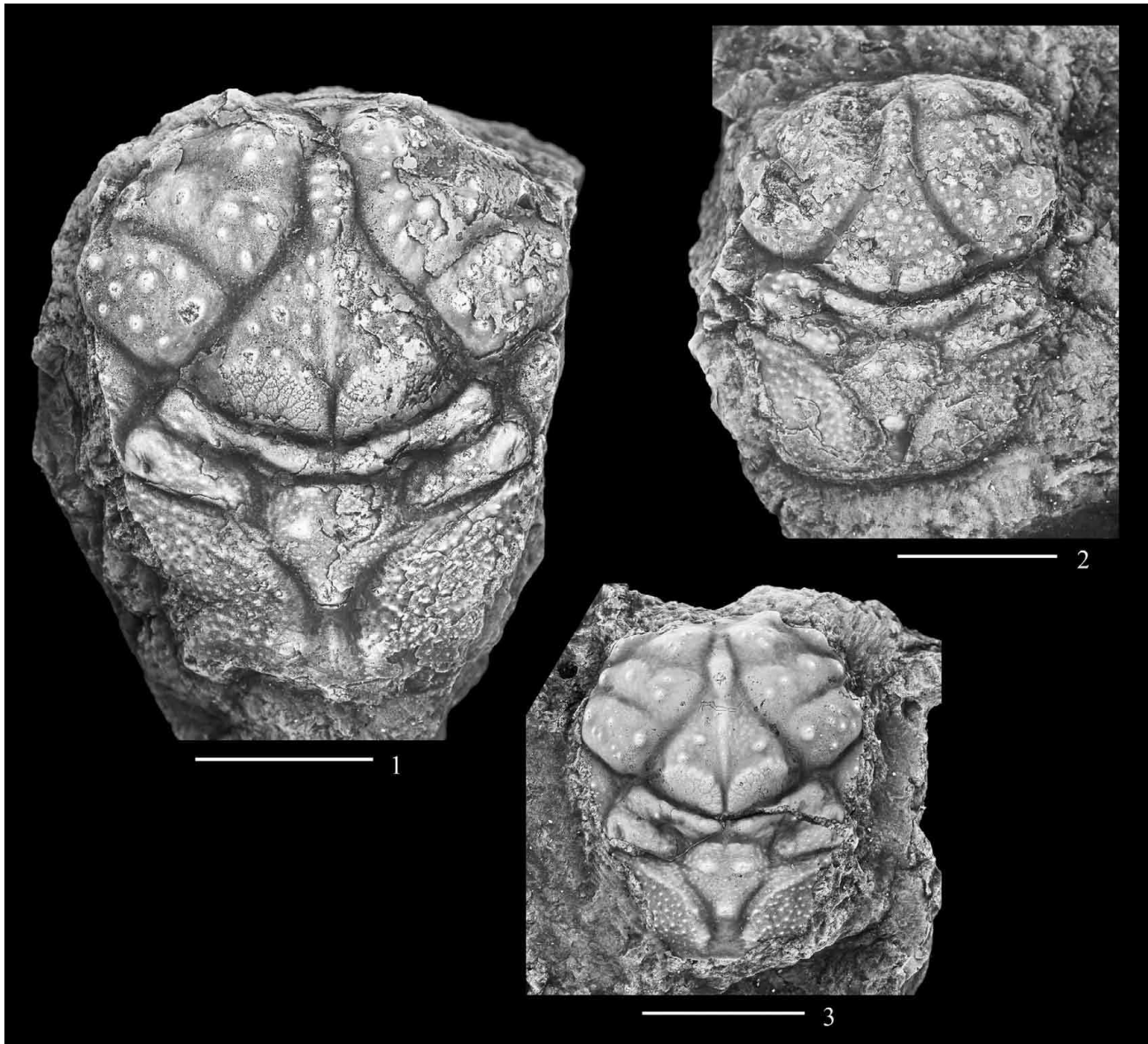


Figure 3. *Navarrahomola hispanica* new genus, new species. 1, dorsal view of holotype MGSB28147. 2, dorsal view of paratype MGSB28141. 3, dorsal view of paratype MABk 3203. All scale bars represent 10 mm.

anterior portion of cardiac region. Branchial grooves long, arched, bounding posterior lateral margins of cardiac region, intersecting at axis in a small depression. Anterior portion of carapace covered by numerous, irregular tubercles of small size, posterior portion densely covered by granules; base of mesogastric region with scabrous dense ornament. Cuticle only partially preserved; ventral sides of carapace and appendages unknown.

Material. The holotype is MGSB28147, paratype is MGSB28141. The type locality is Olazagutia (Navarra, Spain), the material having been collected during the decades of 1940 and 1950 from Albian-Cenomanian reefal limestones at the Monte Orobe quarry. Paratypes, MGSB78332, MABk 3203, from the Koskobilo quarry.

Measurements (in mm). See Table 2.

Discussion. The distribution and shape of dorsal regions and grooves, the frontal construction, the absence of a true orbit, and the presence of a *linea homolica* favour assignment to the family Homolidae (see Guinot and Richer de Forges, 1995). All specimens examined present lateral margins without rounded or ridged portions towards the ventral side, thus all lack complete lateral margins. This confirms that the carapace has split over a dorsal line; the split being in the same position on both lateral sides, meaning that a genuine *linea homolica* is present.

Concerning the orbitofrontal construction, which is diagnostic of extinct genera within the Homolidae (Schweitzer *et al.*, 2004), *Navarrahomola* n. gen. shares the downturned front and inclined supraorbital margins with *Zygastrocarcinus* Bishop, 1983, *Homolopsis* Bell, 1863 and

Latheticocarcinus Bishop, 1988. However, *Navarrahomola* n. gen. exhibits unique, fairly differentiated dorsal regions and a frontal construction as defined below. The genus *Zygastrocarcinus* presents a much flatter dorsal carapace, described as “level” (Bishop, 1986, p. 1097; Collins, 1997, p. 62); the maximum width between the *lineae homolicae* is at the position of the epibranchial region, whereas in *Navarrahomola* n. gen. this is at the level of the hepatic region; the dorsal ornament consists of much larger tubercles within the regions and coarser and denser, general dorsal granulation; the dorsal surface invariably presents a smaller mesogastric region, with more elongated anterior extension; less developed urogastric region, which is usually bilobed and not fused with the epibranchial; the well-defined triangular epibranchial portion in *Navarrahomola* n. gen. is not seen in *Zygastrocarcinus*. Additional differences are confirmed by *Z. waagei* Feldmann, Schweitzer and Green, 2008 which was diagnosed (Feldmann *et al.*, 2008b, p. 503) as having the maximum width in the posterior third of the carapace and being only moderately vaulted transversely and longitudinally, with the anterior portion of the mesogastric region with a long process; these characters do not correspond with *Navarrahomola* n. gen. In addition, in the illustrations (Feldmann *et al.*, 2008b, figures 1B-C), the front is clearly advanced, beyond the epigastric lobes, and partially visible in dorsal view, whereas in *Navarrahomola* n. gen. the front turns down at the level of the upper margins of the epigastric lobes. *Homolopsis edwardsi* Bell, 1863, the type species of the genus, exhibits a flatter carapace, with the maximum width at the level of the epibranchial region, which is extremely salient; a narrower front, which is axially advanced, fairly projecting beyond the epigastric lobes; a more complex set of dorsal grooves, which are deeper; the epigastric lobes are more discrete; the epibranchial region stouter, not divided into portions and more laterally salient (see Collins, 1997, p. 57). All species currently assigned to the genus *Homolopsis* (see Collins, 1997; Schweitzer *et al.*, 2004) show similar characters which clearly differentiate them from *Navarrahomola* n. gen. The carapace of *Latheticocarcinus shapiro* Bishop, 1988, the type species of the genus, a very small form, is widest at the epibranchial region, posterior to the cervical groove, and the dorsal surface is weakly convex in longitudinal section. The front is broad, subtriangular and downturned, as in *Navarrahomola*, n. gen., but clearly advanced and fairly well visible in dorsal view (see Crawford *et al.*, 2006, figure 4). The dorsal regions and grooves in *Latheticocarcinus* are easily distinguished from *Navarrahomola* n. gen. by its peculiar cervical groove, which is oblique, nearly straight at the lateral margins, medially intersecting the well-marked branchiocardiac groove (while in *Navarrahomola* n. gen. is arched); the mesogastric region is relatively narrow in *Latheticocarcinus*, fairly inflated and divided at the base, weakly differentiated from the urogastric lobe, which is extremely short, with two differentiated swellings and a slight depression at the axis (while in *Navarrahomola* n. gen. is fused to the anterior

portion of the epibranchial region). In *Navarrahomola* n. gen., the configuration of grooves is significantly characteristic, the lateral grooves of the mesogastric regions are divergent, extending obliquely towards the lateral margins, in the same direction as the oblique groove that divides the lateral portion of the epibranchial region, which is unique in the genera assigned to the family.

Concerning the dorsal regions and grooves, *Navarrahomola* n. gen. is clearly differentiated from any other homolid genera in having a large subtriangular mesogastric region, which is slightly ridged medially and with a very short anterior extension; the urogastric region, fused with a portion of the epibranchial region, is extremely elongate, surpassing the base of the mesogastric region. The epibranchial region is divided into three distinct portions. The genus *Hoplitocarcinus* Beurlen, 1928 (Collins *et al.*, 2000) is distinguished by strong tubercles in the dorsal regions, a long anterior extension of the mesogastric region and a peculiar urogastric region which is depressed axially and bounded by two large tubercles, characters clearly different from *Navarrahomola* n. gen. The genus *Homoliformis* Collins, Schulz and Jakobsen, 2005 is characterised by a smoother carapace, fewer, yet deep grooves, and the absence of posterior branchial grooves bounding the posterior portion of the cardiac region.

Other fossil genera assigned to the Homolidae share the general distribution pattern of dorsal regions and grooves, but the frontal construction strongly diverges from that of *Navarrahomola* n. gen. In most of the genera the front is fairly advanced and directed forwards, with more or less long rostral and pseudorostral spines, well visible in dorsal view, as in *Homola vancouverensis* Schweitzer, 2001, with notable frontal spines directed forwards, *Paramola* Wood-Mason, 1891, with three long frontal spines, *Doerflesia* Feldmann and Schweitzer, 2009 with two strong and relatively long pseudorostral spines, and most of the species currently assigned to *Latheticocarcinus* (sensu Schweitzer *et al.*, 2004) in which the front is narrow and fairly well visible in dorsal view, bearing clear pseudorostral spines that may be long (see Schweitzer *et al.*, 2004, figure 2); the supraorbital margin usually is armed with small spines and it bears a strong lateral supraorbital spine. The genera *Lignihomola* Collins, 1997 and *Prohomola* Karasawa, 1992 are characterised by a projected front, fairly advanced forwards. The genus *Dagnaudus* Guinot and Richer de Forges, 1995 has a single rostrum visible in dorsal view and strongly projected pseudorostral spines. The genus *Londinomola* Collins and Saward, 2006 is diagnosed by a front with a narrow triangular rostrum bounded by pseudorostral spines. *Paramolopsis piersoni* Schweitzer, Nyborg, Feldmann and Ross, 2004, the only fossil species assigned to the genera to date, is characterised by a narrow, triangular, strongly projected front, well visible in dorsal view. In addition to it, the intralineal portion of the carapace is fairly ovoid, which clearly distinguishes this genus from *Navarrahomola* n. gen. (see Schweitzer *et al.*, 2004, p. 140, figure 5).

The genus *Laeviprosopon* Glaessner, 1933, originally included in the Homolidae (Collins, 1997, p. 55; Schweitzer *et al.*, 2004, p. 134), later transferred to the Prosopidae von Meyer, 1860 (Schweitzer and Feldmann, 2008), presents a dorsal carapace aspect which is similar to that of *Navarrahomola* n. gen. However, the front in the former genus is advanced, visible in dorsal view, projecting beyond well-defined epibranchial lobes, with three frontal spines in a narrow front, or broadly convex in dorsal view (see Schweitzer and Feldmann, 2008, figure 1). The carapace sides of *Laeviprosopon* appear to be complete, convex, rounded towards the ventral side of the carapace. In *Laeviprosopon* the epigastric and protogastric grooves are transverse, usually with well-marked and complete grooves bounding the epibranchial lobes and with absent or only laterally marked short transverse grooves in the large protogastric lobes. The dorsal surface is generally smooth with occasionally scattered sometimes some granules in *Laeviprosopon* in contrast to the fairly tuberculate carapace of *Navarrahomola* n. gen. *Laeviprosopon lazarae* Franțescu, 2011 shows the main characters mentioned above, in having the front extremely advanced, well beyond the epigastric lobes; this species exhibits the most differentiated frontal construction in comparison with the weakly advanced front in *Navarrahomola* n. gen. In *Navarrahomola* n. gen., as mentioned above, we define the branchiocardiac groove as the groove that curves at the upper lateral angles of the cardiac region, and the posterior branchial groove as the well-marked, arched and deep groove behind the epibranchial lobe, running towards the posterior lateral margins of the cardiac region.

Extant homolids may have a closely similar distribution and shape of carapace regions to *Navarrahomola* n. gen.; for example, *Homola ikedai* Sakai, 1979 (see Richer de Forges and Ng, 2007) exhibits comparable dorsal regions and grooves, but the swellings of the regions and the depth of the grooves are less marked. In this species, the groove behind the epibranchial region is barely marked to nearly absent. Extant homolids appear to have evolved a less areolate carapace, shallower dorsal grooves and a modified, attenuated *linea homolica*. Guinot and Richer de Forges (1995), in their revision of extant homolids, presented schematic representations of the carapace with the posterior branchial groove absent. The deep groove bounding the lower margin of the epibranchial region and the lateral sides of the cardiac region present in *Navarrahomola* n. gen. are not as complete or well defined in Guinot and Richer de Forges (1995) due to the evolutionary pathway towards a smoother dorsal carapace. Cretaceous homolids, such as *Navarrahomola* n. gen., *Homolopsis*, *Latheticocarcinus* or *Hoplitocarcinus*, appear to be more primitive; usually the *linea homolica* is more clearly marked, the dorsal grooves are deeper and better defined; the posterior branchial grooves very well marked, intersecting at the level of the intestinal region, and the dorsal regions more swollen.

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