



Systematics and distribution of decapod crustaceans associated with late Eocene coral buildups from the southern Pyrenees (Spain)

Fernando A. Ferratges, Samuel Zamora, and Marcos Aurell

With 9 figures and 3 tables

Abstract: A new decapod crustacean assemblage associated with late Eocene coral reef deposits in northeast Spain (southern Pyrenees) is recorded; it includes *Gemellarocarcinus riglosensis* sp. nov., *Daira corallina* sp. nov., *Lobogalenopsis joi* sp. nov., *Liopsalis* cf. *anodon* (Bittner, 1875) and *Galenopsis crassifrons* A. Milne-Edwards, 1865. The genera *Gemellarocarcinus*, *Daira* and *Lobogalenopsis* are here recorded for the first time from Eocene strata of the Iberian Peninsula, extending their palaeobiogeographical distribution. Detailed sampling from three different coral reef facies within the La Peña buildup, here referred to as branching, tabular and massive, suggest that the core of the reef, which was dominated by branching corals, hosted the highest diversity and abundance of decapod crustaceans. *Daira corallina* sp. nov. predominated in the branching corals facies, while *G. crassifrons* was the most abundant taxon within the tabular coral facies and carapiliids showed preferences for environments with massive corals. Thus, this constitutes a good example of primary ecological zonation among decapod crustaceans within a discrete reef.

This paper is part of the special volume: Jagt, J.W.M., Fraaije, R.H.B., Van Bakel, B.W.M., Donovan, S.K., Mellish, C. & Schweigert, G. (eds.): A lifetime amongst fossil crustaceans: a tribute to Joseph S.H. Collins (1927–2019).

Key words: Crustacea, Brachyura, coral-associated crabs, taxonomy, Paleogene, cryptofauna.

1. Introduction

The Eocene Epoch was crucial in the development of many present-day features of the Earth. In particular, new palaeogeographical configurations and ocean circulation patterns forced by tectonic plate rearrangement, led to the initial development of Antarctic ice sheets during the late Eocene and a progressive switch from greenhouse to icehouse climatic conditions (e.g., HALLOCK *et al.* 1991; HALLOCK & POMAR 2008; STICKLEY *et al.* 2009). These climatic changes had an impact on the evolution of reefs and associated metazoan communities (POMAR *et al.* 2017). Coral reefs were fully established in this period (POMAR *et al.*

2017), hosting decapod crustacean communities with taxa that are similar to those that inhabit modern reefs (MÜLLER & COLLINS 1991; DE ANGELI & GARASSINO 2002; BUSULINI *et al.* 2006; BESCHIN *et al.* 2007; TESSIER *et al.* 2011; BESCHIN *et al.* 2012, DE ANGELI & CECCON 2012; DE ANGELI & CECCON 2013a, DE ANGELI & CECCON 2013b; DE ANGELI & CECCON 2014; DE ANGELI & GARASSINO 2014; BESCHIN *et al.* 2015; DE ANGELI & CECCON 2015; BESCHIN *et al.* 2016; DE ANGELI & CECCON 2016; BESCHIN *et al.* 2017). The Eocene is also considered an important period in the evolution of brachyurans (e.g., FRAAIJE 2003; BRÖSING 2008; TSANG *et al.* 2014; SCHWEITZER & FELDMANN 2015). Despite a good understanding of the taxonomic

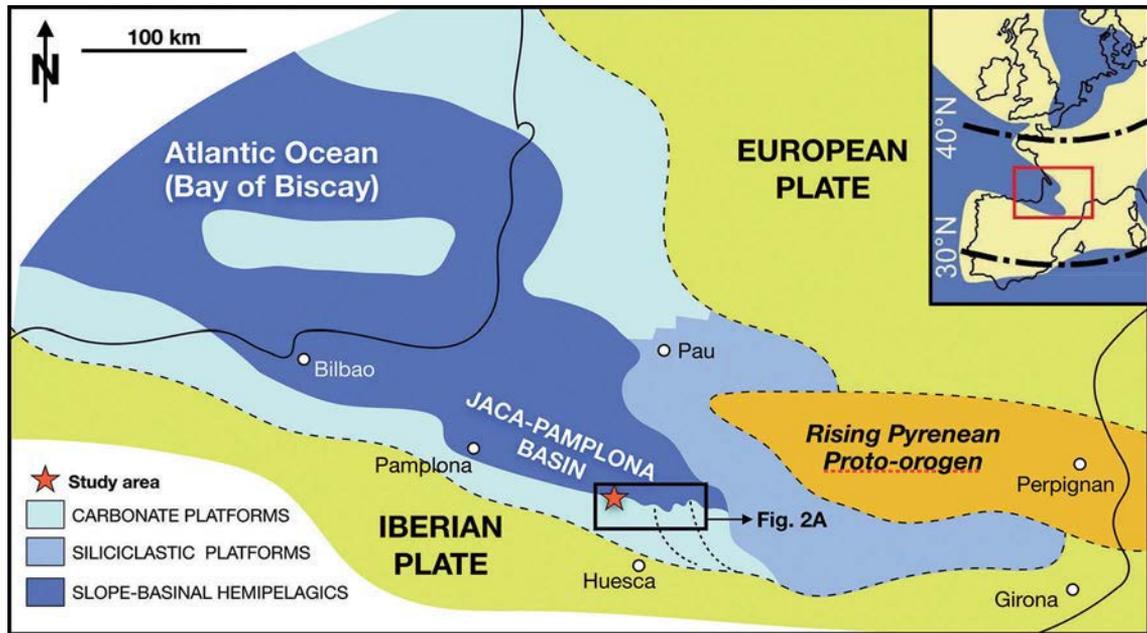


Fig. 1. Mid-Eocene palaeogeographical map of the Pyrenean area, showing the location of the Jaca-Pamplona Basin (modified from SILVA-CASAL *et al.* 2017). The squared area in the southern part is enlarged in Fig. 2.

composition of decapod assemblages associated with reef environments during the Eocene, little is known about how these faunal assemblages are distributed at outcrop level. In contrast, other periods have been further investigated in this respect and some palaeoecological studies have been published for the Cretaceous (KLOMPMAKER *et al.* 2013), Paleocene (KLOMPMAKER *et al.* 2016) and the modern day (ABELE 1979).

Outcrops located in the central part of the southern Pyrenees include an extraordinary record of middle–upper Eocene rocks with coral buildups and associated benthic faunas at several time intervals (PUIGDEFABREGAS 1975; MILLÁN *et al.* 1994; POMAR *et al.* 2017). Upper Eocene reefs are well represented in the upper portion of the Arguis-Pamplona Marls Formation, along the southern margin of the Jaca-Pamplona Basin (Fig. 1). The upper part of the prodeltaic, clay-dominated succession represented by the Arguis Formation includes levels with early Priabonian (latest Eocene) mesophotic coral buildups. These buildups, between the localities of Rasal and La Peña (province of Huesca, northern Spain), were characterised by MORSILLI *et al.* (2012). In order to understand decapod crustacean composition and their distribution in these lower Priabonian reefs, detailed sampling in the La Peña reef was carried out. Specimens were collected in association with specific microfacies (see ‘Ma-

terials and methods’ below). The aim of the present study is to describe all material collected and discuss the presence of certain taxa in different parts of the reef.

2. Geological setting

The southern Pyrenean basins record one of the most complete Eocene marine sedimentary successions in Europe, with decapod crustaceans previously described from several outcrops (see e.g., VÍA 1969; VÍA-BOADA 1973; ARTAL & VÍA 1988; ARTAL & CASTILLO 2005; ARTAL *et al.* 2013; OSSÓ *et al.* 2014; DOMÍNGUEZ & OSSÓ 2016; LÓPEZ-HORGUE & BODEGO 2017; OSSÓ & DOMÍNGUEZ 2017; ARTAL & VAN BAKEL 2018a; ARTAL & VAN BAKEL 2018b; FERRATGES *et al.* 2019). Palaeogeographically, the southern Pyrenean basin was located at approximately 35°N palaeolatitude during the Eocene (e.g., HAY *et al.* 1999; SILVA-CASAL *et al.* 2017) and corresponded to an elongated gulf connected towards the west by the Bay of Biscay, located on the southern limit of the axial zone of the Pyrenees. The gulf was flanked by shallow-water carbonate platforms, with accumulations of hemipelagic sediments at the bottom of the basin (Fig. 1).

The Jaca-Pamplona Basin corresponds to an elongated basin from east to west in the south-central Pyrenean Zone (Fig. 1). This basin was formed as a result of the southward propagation of the tectonic structures during the Paleogene (MILLÁN *et al.* 1994; MUÑOZ *et al.* 1994; CASTELLTORT *et al.* 2003; HUYGHE *et al.* 2009). The propagation of the southern Pyrenean fold and thrust belt resulted in the formation of a coeval relief, acting as a sediment source area for deltaic complexes (e.g., DREYER *et al.* 1999). These deltaic complexes prograded westwards in the southern part of the Jaca-Pamplona Basin, progressively covering the turbiditic systems of the lower and middle Eocene of the Hecho Group (MUTTI *et al.* 1985; REMACHA *et al.* 2003; REMACHA *et al.* 2005).

The Sierras Exteriores includes outcrops located along the southern margin of the Jaca-Pamplona Basin (Fig. 2A). The middle and upper Eocene (Lutetian–Priabonian) units form a c. 2-km-thick succession, including shallow-marine limestones of the Guara Formation, the prodelta/outer ramp marls/clays of the Arguis Formation, the deltaic Belsue-Atares Formation and its lateral counterpart (i.e., coastal siliciclastics of the Yeste-Arres Formation) and the fluvial Campodarbe Formation (PUIGDEFABREGAS 1975; SILVA-CASAL *et al.* 2019). These units are diachronous and record the late-stage infilling of the foreland basin (MILLÁN *et al.* 1994; MILLÁN *et al.* 2000). Coeval to basin infill, a series of thrust ramps and oblique folds with a north-south axis started to develop during the Lutetian and progressively propagated westwards until the Bartonian to early Priabonian with variable shortening rates (MILLÁN *et al.* 1994; CASTELLTORT *et al.* 2003; HUYGHE *et al.* 2009). The uppermost Lutetian–lower Priabonian sedimentary units coevally deposited with these growth structures are arranged in four Depositional Sequences I–IV (Fig. 2A). Their boundaries correspond to flooding surfaces, which grade basinwards into correlative conformities. These boundaries are related to tectonic pulses, as indicated by the presence of both angular unconformities and onlap geometries (MILLÁN *et al.* 1994). These sequences were correlated across a nearly dip-section which displays the transition from the inner areas located to the east to the outer areas towards the west. Their age is constrained by magnetostratigraphical and palaeontological data (CANUDO *et al.* 1988; CANUDO *et al.* 1991; HOGAN 1993; PUEYO *et al.* 2002; SILVA-CASAL *et al.* 2019). As a whole, each depositional sequence consists of a lower, poorly fossiliferous to barren clayey-marly unit and an upper shallow-marine siliciclastic or carbonate unit

that yields abundant benthic fossils. The lateral extent of the shallow-marine units overlying the relatively deep marly facies is progressively larger in younger sequences, with progradation advancing from east to west. Siliciclastic components also increase according to the same pattern and they become clearly dominant in the uppermost depositional sequence (Fig. 2A). Specifically, the decapod crustaceans studied for the present paper come from lower Priabonian coral buildups developed in the middle part of Sequence IV. These buildups form discontinuous outcrops between the localities of Rasal and La Peña (Fig. 2B). These coral buildups provided a good opportunity for other invertebrates to colonise such a specific environment (e.g., echinoderms, molluscs, decapod crustaceans etc). Although several outcrops have been sampled for decapod crustaceans, only the one located east of La Peña provided fresh rock and enough material to be analysed in detail.

3. The early Priabonian coral reefs of La Peña

An integrative analysis of rock textures, skeletal components, buildup anatomy and facies architecture has revealed that the early Priabonian coral buildups exposed between the localities of La Peña and Rasal (Fig. 2B) developed in a prodelta setting (MORSILLI *et al.* 2012). There, shifting of delta lobes episodically resulted in periods of water transparency that allowed zooxanthellate coral growth. A bathymetric position of the buildups around 15–25 m was constrained by MORSILLI *et al.* (2012) from the analysis of light-dependent communities and lithofacies distribution within the buildups. Most of the zooxanthellate corals grew under mesophotic conditions, around storm wave base action (MORSILLI *et al.* 2012). Coral buildups occur as low-relief bioherms and are up to 20 to 30 metres thick and a few hundred metres wide. The buildups grade basinwards to skeletal-rich beds of bryozoan floatstone with a wackestone to packstone matrix. Basal coral biostromes found in many buildups consist of platy-coral colonies ‘floating’ in a fine-grained matrix rich in branches of red algae. Corals with a domal or massive shape, locally mixed with branching corals and phaceloid coral colonies, predominate in the buildup cores (MORSILLI *et al.* 2012). The coral boundstone facies present in the core of the buildups consists of scleractinian coral colonies (platy, massive, thick branched), mostly in growth position.

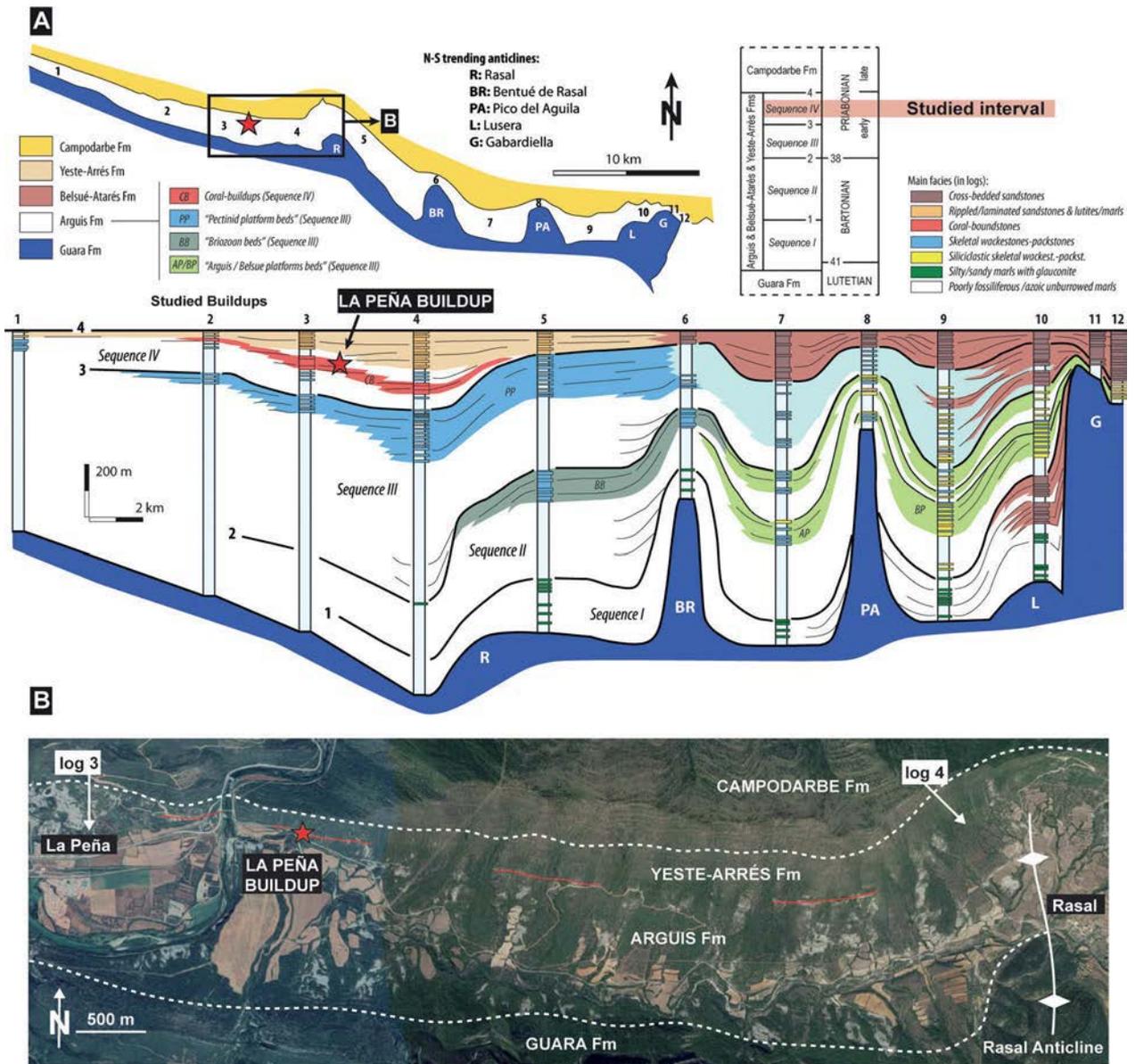


Fig. 2. **A** – Location of logs 1–12 studied by MILLÁN *et al.* (1994) in the Sierras Exteriores area (for location, see Figure 1). These logs are used as a reference for correlation of Sequences I–IV within the Arguis, Belsué-Atares and Yeste-Arres formations that are shown in the central part of the figure. The inset in the upper right-hand side shows the age of these sequences [modified from MILLÁN *et al.* (1994) and SILVA-CASAL *et al.* (2017)]. **B** – Distribution of uppermost Lutetian–Priaetian lithostratigraphical units between the villages of Rasal and La Peña (see A for location). The red lines indicate the distribution of coral buildups in outcrops.

The skeletal matrix commonly consists of floatstone/ rudstone with fine-grained, poorly sorted packstone to mud-dominated wackestone. Red algae are conspicuous as both laminar and branching forms, and coral and echinoid fragments are abundant. Bryozoans, bivalves (oysters, pectinids and *Spondylus*), serpulids,

ostracods and, locally, chaetetid sponges are common. In addition, regular and irregular echinoids, gastropods and brachiopods have been found. Planktonic and smaller to large benthic foraminifera are present (genera *Nummulites*, *Heterostegina*, *Asterocyclina* and *Operculina*). Polygenic laminar red algae and encrust-

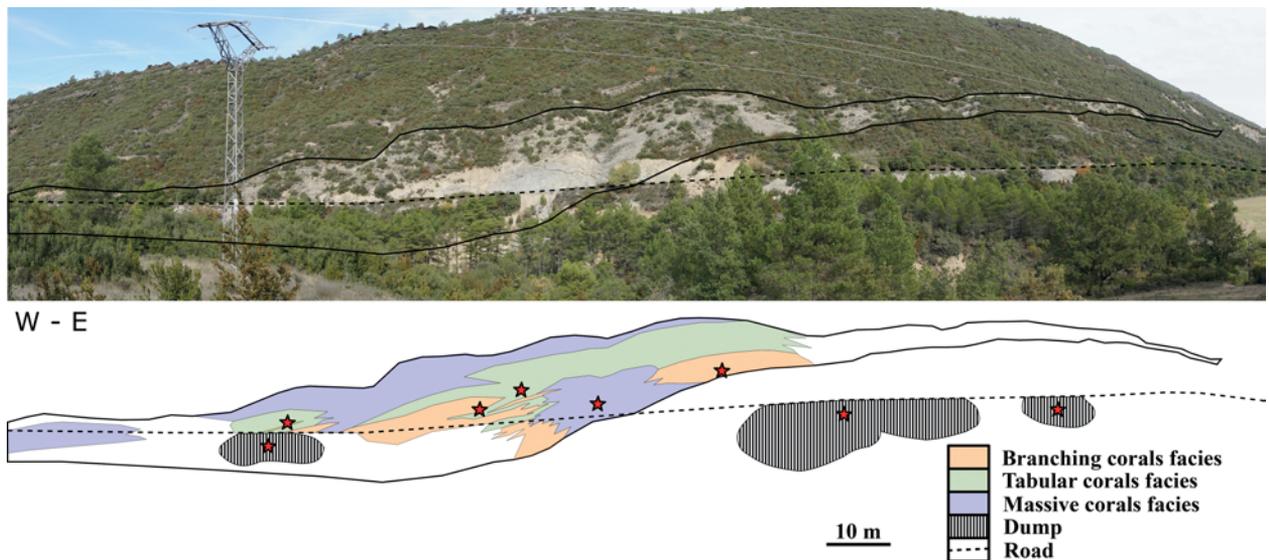


Fig. 3. General view of the outcrop studied (La Peña reef) in a west-east (or distal-proximal) panoramic view. The sketch shows the distribution of the three facies identified on the basis of predominant coral morphologies. Red stars correspond to sample points (for location, see Fig. 2B). Dumped material correspond to an admixture of the different facies from the outcrop, accumulated during road works.

ing foraminifera (*Miniacina*, *Haddonina*, *Carpenteria*, *Victoriella*, *Fabiania*, *Gyroidinellamagna*, *Acervulina linearis*, and *Gypsina*) are also common (for details, see MORSILLI *et al.* 2012).

Episodic high-hydrodynamic pulses provided the energy needed to rework skeletal sediments and to produce the coral rudstone and skeletal packstone wedges around the buildups. Clay/marl lithofacies also occur around the coral buildups, representing the background sedimentation of the overall deltaic setting. Sandstone beds occur locally interbedded as very thin beds, with parallel lamination, normal grading and, locally, wave ripples, suggesting that sedimentation occurred as episodic events related to storm-induced density flows or triggered by floods, via hyperpycnal flows. However, these events did not suffocate the coral bioherms when they were still active.

4. Materials and methods

The specimens studied were collected directly from outcrop in the section along the road between the villages of Rasal and La Peña (Fig. 3). This locality corresponds to the coral buildup developed in the middle part of the lower Priabonian Sequence IV, which

is referred here as the La Peña buildup (Fig. 2). The La Peña buildup includes a diverse invertebrate fauna associated with corals, including a diverse assemblage of decapod crustaceans associated with several lithofacies.

Wherever possible, specimens were collected directly from the reef exposures with special indication of the lithofacies in which they were preserved. Some specimens were collected from blocks derived from road construction and lithofacies were interpreted from the surrounding matrix.

In the La Peña buildup fifteen different genera of corals have been recognised. Three different reef facies have been differentiated based on the predominance of the different morphologies of coral taxa. These include branching, tabular and massive corals facies (Fig. 3). It is important to point out that some coral taxa can generate different morphologies (for example *Actinacis*, *Astreopora* and *Goniopora*) so they can be included into different facies depending on their form. Thus, the genera included into the “branching coral facies” are the following: *Actinacis*, *Caulastrea*, *Stylophora*, *Acropora*, *Pocillopora*, *Astreopora*, *Alveopora*, *Astrocoenia* and *Bacarella*; in the “tabular coral facies”: *Cyathoseris*, *Actinacis*, *Goniopora* and *Astreopora*; and finally, in the “massive coral facies”: *Actinacis*, *Goniopora*, *Astreopora*, *Siderastrea*, *Colpophyllia*,

Table 1. Abundance and distribution of decapod crustacean taxa recognised at the outcrop studied (for location of sample points, see Fig. 3).

Taxon	Branching corals		Tabular corals		Massive corals		Total	%of total
	Specimens	%	Specimens	%	Specimens	%		
Carpiliid indet.	4	5.2	2	3.5	15	55.6	21	13
<i>Daira corallina</i> sp. nov.	26	33.8	5	8.8	1	3.7	32	19.9
<i>Enoploclytia?</i> sp.	1	1.3	1	1.8	2	7.4	4	2.5
<i>Galenopsis crassifrons</i>	15	19.5	47	82.5	4	14.8	66	41
<i>Gemellarocarcinus riglosensis</i> sp. nov.	1	1.3	–	0	–	0	1	0.6
<i>Liopsalis</i> cf. <i>anodon</i>	–	0	–	0	1	3.7	1	0.6
<i>Lobogalenopsis joei</i> sp. nov.	1	1.3	–	0	–	0	1	0.6
<i>Ocalina?</i> sp.	–	0	–	0	1	3.7	1	0.6
<i>Petrochirus?</i> sp.	2	2.6	–	0	–	0	2	1.2
Trapeziidae?	6	7.8	–	0	–	0	6	3.7
Taxon indet. 1	11	14.3	–	0	–	0	11	6.8
Taxon indet. 2	1	1.3	–	0	–	0	1	0.6
Taxon indet. 3	1	1.3	–	0	–	0	1	0.6
Indeterminate fragments	8	10.4	2	3.5	3	11.1	13	8.1
TOTAL	77		57		27		161	

Leptoria, and *Agathiphyllia*. In order to differentiate the various facies, the relative proportion of each coral type has been measured per square metre. A facies is assigned to one or another coral-type when there is more than 50 per cent of predominance of a particular coral type relative to the others.

To carry out the sampling, a similar period of time was dedicated to sample each type of facies visiting the outcrop regularly during the year 2019. A similar volume of material was processed from the different facies either from surface collecting or splitting rock cobbles and boulders. Specimens from the La Peña buildup preserve the cuticle in all cases and preservation is different from other reef facies (e.g., [KLOMPMAKER et al. 2013](#)).

A total of 161 specimens of decapod crustaceans have been collected from different coral reef facies (Table 1). The specimens have been prepared mechanically using a Micro Jack 2 air scribe (Paleotools; Brigham, Utah, USA) and chemically, using potassium hydroxide (KOH). The specimens were then photographed dry and coated with an ammonium chloride sublimate. Detailed photography of the carapace surfaces and appendages was done using a Nikon d7100 camera with a macro 60-mm-lens.

Only specimens preserving complete carapaces have been treated systematically. Other material, including partial chelipeds and limbs have been treated

only in the discussion (see below) and formal description awaits the discovery of more complete material.

To check if there is a distinctive species distribution associated with each facies, statistical calculations have been performed applying the Fisher's-exact test. This test has been selected because we use contingency tables constructed with categorical variables. After finding significant differences in the Fisher's-exact test, we applied a pairwise comparison of the same test to determine exactly the distributions of the species that are significantly linked to a specific facies.

Specimens were legally sampled under permit EXP: 032/2018 from the Servicio de Prevención, Protección e Investigación del Patrimonio Cultural (Gobierno de Aragón) and are deposited in the palaeontological collections of the Museo de Ciencias Naturales de la Universidad de Zaragoza under the acronym MPZ (see [CANUDO 2018](#)).

5. Decapod crustacean composition

The decapod assemblage collected from the La Peña buildup corresponds to taxa associated with reef environments. Moreover, these taxa show significant variation with respect to their relative abundance

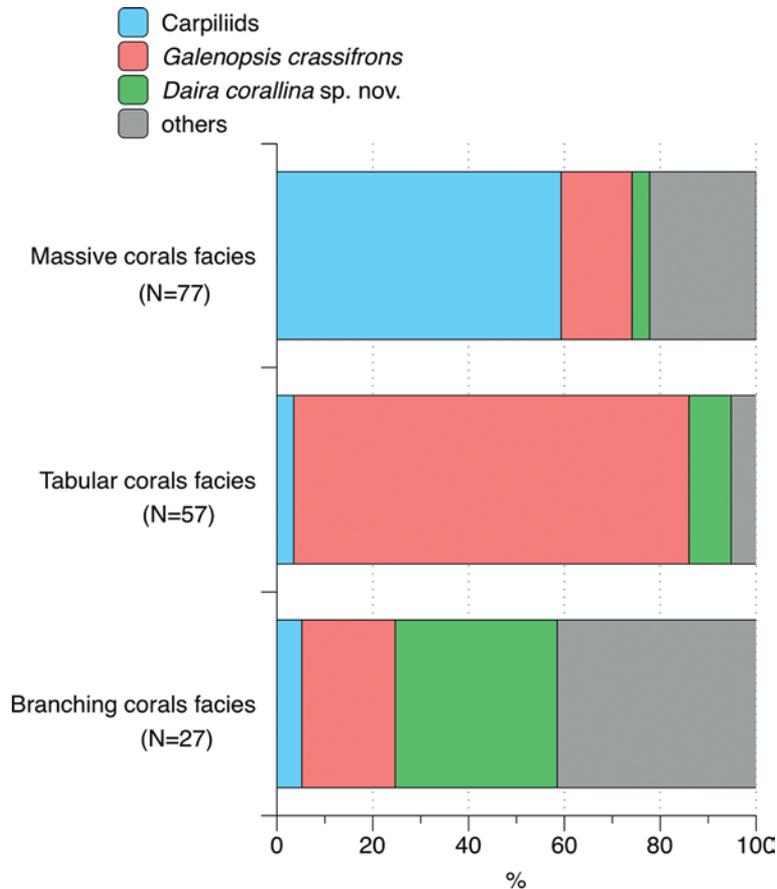


Fig. 4. Relative abundance of the main decapod crustacean taxa in the three different facies within the La Peña reef.

in the different facies identified within the La Peña reef (Fig. 4). These taxa include representatives of the genera *Enoplocyrtia*? MCCOY, 1849 (Fig. 5I), *Petrochirus*? STIMPSON, 1858 (Fig. 5J), *Gemmelarocarcinus* CHECCHIA-RISPOLI, 1905 (Fig. 5A–C), *Liopsalis* VON MEYER, 1862 (Fig. 6C, D), *Ocalina*? RATHBUN, 1929 (Fig. 5E), *Galenopsis* A. MILNE-EDWARDS, 1865 (Figs. 6E–G, 7), *Lobogalenopsis* MÜLLER & COLLINS, 1991 (Fig. 6H–J), and *Daira* DE HAAN, 1833 (Figs. 8B–K, 9). In addition, representatives of the family Trapeziidae? MIERS, 1886 (Fig. 5H), carpiliids (Figs. 5D, 6A, B) and remains of four other indeterminate taxa have been found (Table 1; Fig. 5F, G).

This decapod assemblage has similarities to material collected at some localities with Eocene strata in Italy where they appear associated with reef facies (see e.g., BESCHIN et al. 2007; TESSIER et al. 2011; BESCHIN et al. 2015). However, the exceptional state of preser-

vation of the outcrop described herein and its optimal exposure, have allowed a detailed sampling of different lithofacies in order to quantify the occurrence of each taxon.

In general, the most abundant species is *Galenopsis crassifrons*, which accounts for 41 per cent of the total assemblage, followed by *Daira corallina* sp. nov. (19.9 per cent) and carpiliids (13.6 per cent). Minor components include *Enoplocyrtia*? sp. (2.5 per cent), *Petrochirus*? sp. (1.2 per cent), *Gemmelarocarcinus riglosensis* sp. nov. (0.6 per cent), *Ocalina*? (0.6 per cent), *Lobogalenopsis joei* sp. nov. (0.6 per cent), Trapeziidae? (3.7 per cent) and 26 remains of indeterminate taxa that correspond to 16.1 per cent of the total sample (see Table 1). The branching corals facies hosts the greatest diversity and abundance of decapod crustaceans. The most abundant taxon is *Daira corallina* sp. nov., representing 34 per cent of the sample, followed by *Galenopsis crassifrons* (19.5 per cent) and

Trapeziidae indet. (7.8 per cent). The last-named is represented only by fragments of chelipeds. There are also abundant remains of several indeterminate taxa, which represent 27.3 per cent of the total assemblage (Fig. 4A).

The tabular corals facies shows the lowest diversity and intermediate abundance. In this lithofacies, the most abundant taxon is *Galenopsis crassifrons* (82.5 per cent), followed by *Daira corallina* sp. nov. (9 per cent), carpiliids (3.5 per cent) and indeterminate taxa (4 per cent) (Fig. 4B).

The massive coral facies has an intermediate diversity and the lowest abundance. In this lithofacies, the dominant group are carpiliids (59.3 per cent), followed by *Galenopsis crassifrons* (15 per cent) and very rare *Daira corallina* sp. nov. (3.7 per cent) (Fig. 4C).

Faunal distribution within the La Peña buildup is not random and shows important differences in both abundance and diversity. In order to test if there was a relationship between species distribution and facies, we performed a non-parametric Fisher's-exact test (because the number for some species is lower than five), using only the three groups with highest representation in our record: carpiliids, *Galenopsis crassifrons* and *Daira corallina* (Table 2). The statistical analysis was computed with R, with a package called "RVAideMemoire" and the function "fisher.test".

Our null hypothesis (H_0) was that there was no relationship between species distribution and facies (Table 3). The alternative hypothesis (H_1) was that there was a relationship between facies and species distribution. The p -value of the Fisher's-exact test was $p=2.64e^{-14}$, which means that there is a significant link between species and the different facies (acceptance of H_1).

In order to analyse which distribution of the species are significantly linked to a specific facies we applied the command "fisher.multcom" from the same R-package (see above) to apply a pairwise comparison of the Fisher's-exact test. We detected significant differences in the distribution of carpiliids and *Galenopsis crassifrons* in branching corals facies and massive corals facies ($p=2.04e^{-03}$), and carpiliids and *Daira corallina* sp. nov. in the same facies ($p=3.20e^{-07}$). There were significant differences in the distribution of *Galenopsis crassifrons* and *Daira corallina* sp. nov. in the branching corals facies and massive corals facies ($p=1.87e^{-07}$). Finally, we also found significant differences in the distribution of carpiliids and *Galenopsis crassifrons* in the massive corals facies and tabular corals facies ($p=9.22e^{-09}$) and carpiliids and *Daira*

Table 2. P-values obtained from pairwise comparison of the Fisher's-exact test. P-values above 0.05 are considered not significant; bold numbers indicate significant values (P-values < 0.05).

	Branching corals facies/ Massive coral facies	Branching corals facies/ Tabular corals facies	Massive coral facies/ Tabular corals facies
Carpiliid/ <i>Galenopsis</i>	2.04E-03	7.07E-02	9.22E-09
Carpiliid/ <i>Daira</i>	3.20E-07	3.55E-01	6.12E-03
<i>Galenopsis</i> / <i>Daira</i>	1.85E-01	1.87E-07	4.39E-01

corallina sp. nov. in the same facies ($p=6.12e^{-03}$). The rest of species distribution are not significantly linked to any specific facies.

The branching corals facies shows the highest diversity and abundance, and this may have been controlled by both biological and taphonomic factors. The branching corals of the genus *Acropora*, *Pocillopora* and *Stylophora* identified in the La Peña reef (MORSILLI et al. 2012) are also common in the modern Indo-Pacific and host a diverse community of decapod crustaceans (PATTON 1994). Branches between corals provide a large number of places for refuge to decapod crustaceans, especially to small forms like *Daira* and this can be the reason why the branching corals facies shows the highest diversity. This is also the area with the lowest energy within the reef, favouring preservation of the smallest taxa within the sediment accumulating in the spaces between the coral branches. Small-sized specimens of *Goniodromites laevis* were also found particularly in between coral branches in the Albian of northern Spain (KLOMPMAKER et al. 2013) supporting the idea that branching corals are favourable places for small decapods. Coral species with tabular growth forms are particularly important ecosystem engineers on wave-exposed Indo-Pacific reefs (MADIN et al. 2012). The La Peña reef tabular facies was dominated by *G. crassifrons*, which is the largest form collected; it probably lived in the spaces under and between tabular corals. The massive coral facies shows the lowest abundance and this was probably a consequence of both taphonomic and biological reasons. Massive corals provide little space for sediment accumulation between the colonies and also fewer opportunities

for refuge than other type of colonies. Despite the fact that there are still many uncertainties in our understanding of zonation patterns of different species within the reef, carefully collected material associated with sedimentological information could provide important data for future palaeoecological studies. The La Peña reef decapod community is a small, yet interesting example.

6. Systematic palaeontology

The classification used here follows [GUINOT et al. \(2013\)](#) and [JAGT et al. \(2015\)](#).

Infraorder Brachyura LINNAEUS, 1758

Section Podotremata GUINOT, 1977

Superfamily Dromioidea DE HAAN, 1833

Family incertae sedis

Genus *Gemellarocarcinus* CHECCHIA-RISPOLI, 1905

Type species: *Gemellarocarcinus loerentheyi* CHECCHIA-RISPOLI, 1905, by monotypy.

Other species included: *Gemellarocarcinus disalvoi* BESCHIN, BUSULINI & TESSIER, in BESCHIN, BUSULINI, FORNACIARI, PAPAZZONI & TESSIER, 2018 and *G. riglosensis* sp. nov.

Gemellarocarcinus riglosensis sp. nov.

Fig. 5A–C

Etymology: The specific name comes from “Los Mallos de Riglos”, a natural monument consisting of rock faces rising to heights of 300 metres and located a few kilometres south of where the material was collected.

Material: The sample studied includes only the holotype, a partial carapace (MPZ 2019/1722) with a maximum preserved length and width of 25.7 and 23.8 mm, respectively. Cuticle is well preserved.

Diagnosis: Carapace slightly wider than long (L/W ratio about 1.41), slightly swollen, descending rapidly in the anterior part; orbits small, suboval and deep, with a blunt sub-orbital tooth. Anterolateral margins depressed, strongly convex. Dorsal regions well defined. Cervical groove wide and deep, especially in the median portion. Cardiac region with transverse swelling continuing onto metabranchial lobes; intestinal region wide and smooth. Lateral regions with four transverse swellings. Surface smooth.

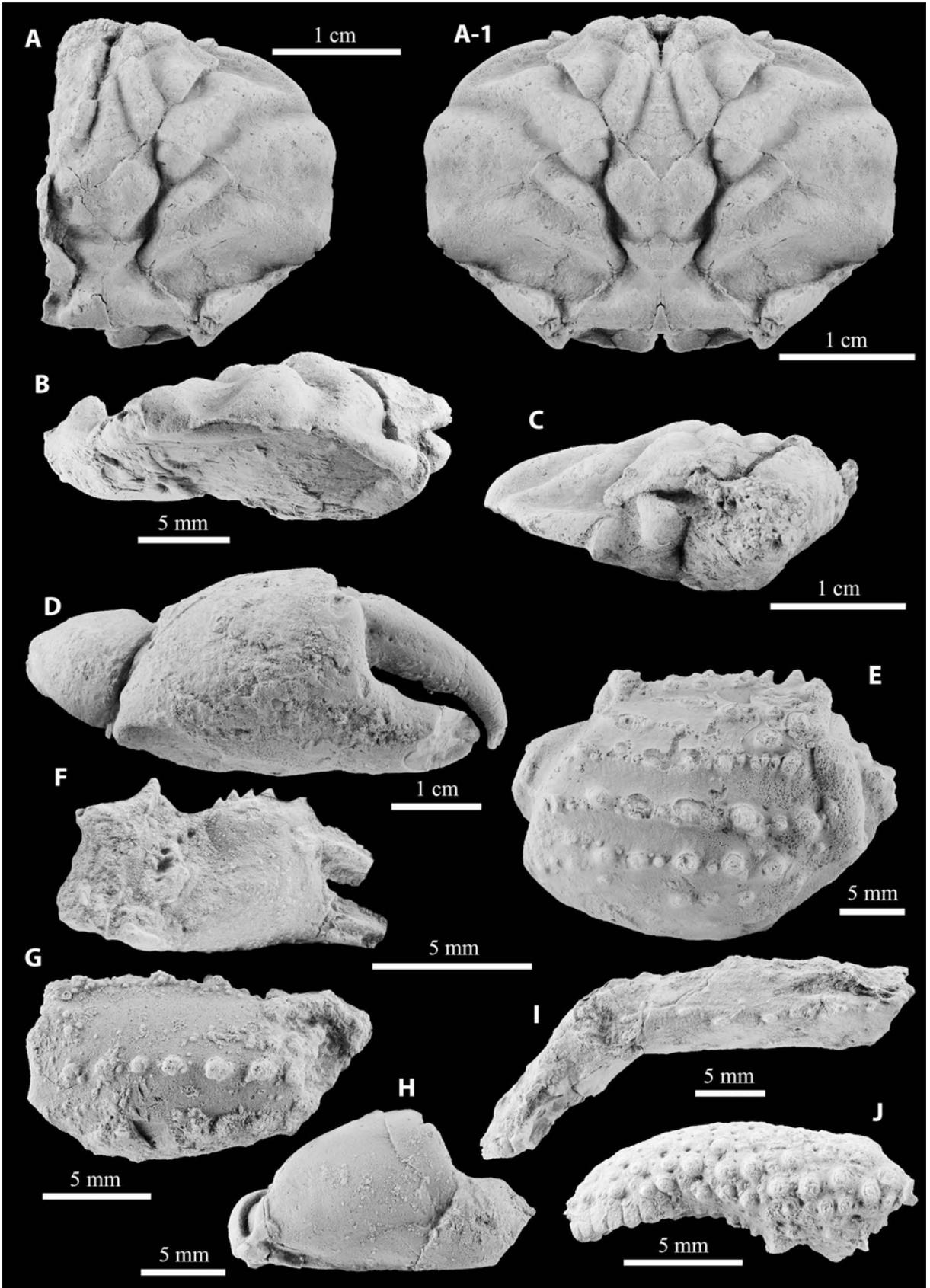
Description: Carapace longitudinally subovate; maximum width at level of mesobranchial region, about midlength of

carapace. Carapace strongly convex longitudinally in anterior third, less in posterior two-thirds (Fig. 5B); transversely slightly convex. Front narrow, not well preserved; small and deep orbits, directed frontally, margins markedly raised; infraorbital tooth robust, with blunt tip, directed forwards, clearly visible dorsally. Fronto-orbital width about 33 per cent of maximum carapace width. Anterolateral margin broadly arched, with prominent hepatic lobe; portion behind orbit short and depressed. Posterolateral margins shorter and less arched than anterolateral margin. Lateral carapace margins with three notable depressions, corresponding to cervical, postcervical and branchial grooves. Posterior margin not well preserved.

Dorsal surface with wavy appearance due to shallow grooves crossing carapace transversely. Cervical groove shallow, broadly U shaped, weakly marked from side to side of carapace, deeper medially, confluent with branchiocardiac and gastric grooves. Postcervical groove shallow, wide, broadly U shaped, weakly marked, interrupted by branchiocardiac groove. Branchial groove well defined, arched, shallow, bounded by smooth ridge, interrupted by cardiac area. Branchiocardiac grooves arched, deep. Epigastric region with semi-circular elevated area surrounded by groove. Mesogastric and metagastric regions undifferentiated, large, smooth. Urogastric region trapezoidal in shape, inflated. Cardiac region surrounded by arched branchiocardiac grooves. Hepatic region with elongated swelling. Subhepatic region large, without ornamentation. Epi-, meso- and metabranchial regions not well differentiated. Lateral regions with four transverse swellings, separated by cervical, postcervical and branchial grooves.

Discussion: The new taxon is similar to *G. loerentheyi* from the Lutetian of Hungary and Italy, as illustrated by various authors (e.g., [CHECCHIA-RISPOLI 1905](#): pl. 1, figs. 1, 2; [MÜLLER & COLLINS 1991](#): pl. 2, fig. 15; [BESCHIN et al. 2018](#): figs. 66–68) and to *G. disalvoi* from the Priabonian of Italy. However, the new species differs in several respects that include: branchiocardiac grooves are deeper in the new species in comparison with *G. loerentheyi* and *G. disalvoi*; the gastric regions are bordered by deeper grooves in *G. riglosensis* sp. nov. than in *G. loerentheyi* and *G. disalvoi*; the carapace in *G. riglosensis* sp. nov. is narrower than in *G. loerentheyi* and slightly narrower than in *G. disalvoi*, yielding a more rounded appearance (subcircular) in outline of the new species (Fig. 5A-1); a larger infraorbital spine in *G. riglosensis* sp. nov. than in the other two species; transversely oblique dorsal grooves are more or less distinct in shape and depth and are wider in the hepatic and branchial regions than in the other two species; the angle of the cervical groove is more oblique in the new species. With the description of *G. riglosensis* sp. nov., the range of the genus *Gemellarocarcinus* is extended to the upper Eocene of the Iberian Peninsula.

The placement of *Gemellarocarcinus* at family level is problematic ([KARASAWA et al. 2011](#)) because of the absence of sternal and pleonal elements. We consider *Gemellarocarcinus riglosensis* sp. nov. to be *incertae sedis* within the superfamily Dromioidea.



Section Eubrachyura DESAINTLAURENT, 1980
 Subsection Heterotremata GUINOT, 1977
 Superfamily Carpilioidea ORTMANN, 1893
 Family Carpilidae ORTMANN, 1893
 Genus *Liopsalis* VON MEYER, 1862

Type species: *Cancer klipsteini* VON MEYER, 1842, by monotypy.

Other species included: *L. anodon* (BITTNER, 1875) and *L. simplex* (STOLICZKA, 1871).

Liopsalis cf. *anodon* (BITTNER, 1875)
 Fig. 6C, D

Material: A single, partial carapace (MPZ 2019/1803), with a maximum preserved length and width of 23.1 and 34.3 mm, respectively. Cuticle is partially preserved.

Discussion: *Liopsalis anodon* was originally described by BITTNER (1875); a detailed description has subsequently been provided by FELDMANN et al. (2011) and SCHWEITZER et al. (2018). The present specimen is referred to as *Liopsalis* cf. *anodon* on the basis of the following features:

- carapace ovate, wider than long, strongly vaulted longitudinally, convex transversely;
- carapace smooth; regions and grooves not defined;
- rostrum triangular, extending well beyond orbits, 45 per cent of maximum width, strongly downturned, weakly sinuous;
- orbits small, subcircular, directed weakly antero-laterally, fronto-orbital width about 61 per cent of maximum carapace width;
- anterolateral margin convex, rounded, smooth for anterior half, then arching more strongly over posterior third;
- a single blunt projection marks the anterolateral angle; it extends into a rim along the posterolateral margin and onto the dorsal carapace;
- posterolateral margin initially concave (see BITTNER 1875: pl. 2, fig. 3a–c; BESCHIN et al. 2007: pl. 3, fig. 4a, b; BESCHIN et al. 2012: fig. 57, pl. 10, fig. 1a, b).

The type material of *Liopsalis anodon* comes from the middle Eocene of Italy. Two other species have been assigned to this genus, namely *L. klipsteini* from the middle Eocene of Germany and *L. simplex* from the middle Eocene (Lutetian) of India. Our present find extends the distribution of the genus to the upper Eocene of the Iberian Peninsula.

Superfamily Pilumnoidea SAMOUELLE, 1819
 Family Pilumnidae SAMOUELLE, 1819
 Genus *Galenopsis* A. MILNE-EDWARDS, 1865

Type species: *Galenopsis typica* A. MILNE-EDWARDS, 1865, by subsequent designation of GLAESSNER (1929).

Other species included: *Galenopsis crassifrons* A. MILNE-EDWARDS, 1865, *G. depressa* (A. MILNE-EDWARDS, 1872), *G. purchisoni* A. MILNE-EDWARDS, 1865, *G. pustulosa* (A. MILNE-EDWARDS, 1865), *G. ristorii* CHECCHIA-RISPOLI, 1905, *G. schopeni* CHECCHIA-RISPOLI, 1905, and *G. similis* BITTNER, 1875.

Galenopsis crassifrons A. MILNE-EDWARDS, 1865
 Figs. 6E–G, 7

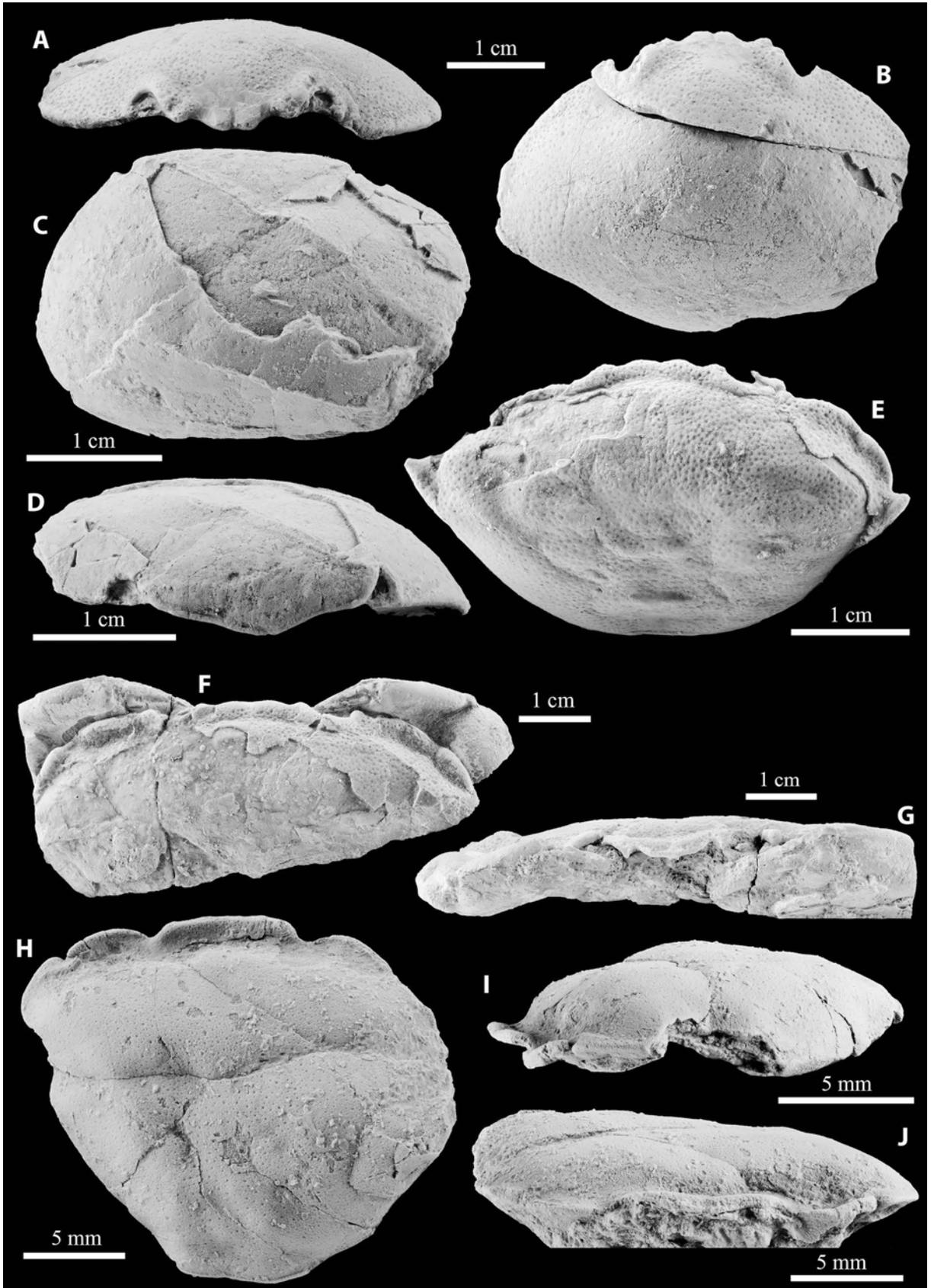
- 1865 *Galenopsis crassifrons* A. MILNE-EDWARDS, p. 319, pl. 7, fig. 2a–d.
 1901 *Galenopsis crassifrons*. – OPPENHEIM, p. 284.
 1908 *Galenopsis crassifrons*. – FABIANI, p. 211.
 1929 *Galenopsis crassifrons* – GLAESSNER, pp. 177, 178.
 1991 *Galenopsis crassifrons*. – VÍA-BOADA, p. 184, pl. 1, fig. 7a, b.

Material: Four partially articulated specimens (MPZ 2019/1737, MPZ 2019/1738, MPZ 2019/1743 and MPZ 2019/1788), 8 carapaces (MPZ 2019/1736, MPZ 2019/1739, MPZ 2019/1740, MPZ 2019/1745, MPZ 2019/1749, MPZ 2019/1787, MPZ 2019/1789 and MPZ 2019/1791) and 54 fragments of chelae and pereopods. Average carapace size: W – 47.8 mm; L – 30 mm. Cuticle preserved in all specimens studied.

Discussion: The newly collected material shows important dorsal features that allow placement in *G. crassifrons* including:

- carapace expanded laterally, wider than long;
- orbits small;
- anterior part bowed as in other species of *Galenopsis*, but the front edge rises so as to form a rather thick bead which continues to the anterolateral margins; antero-lateral margins slightly trilobate and shorter than posterolateral ones;
- latero-posterior margins almost straight;
- surface of carapace covered by small pits;
- dorsal regions poorly marked;
- elongated chelipeds;
- ambulatory legs long and slender (see Fig. 7; A. MILNE-EDWARDS 1875: pl. 7, fig. 2).

Fig. 5. A–C – *Gemmellarocarcinus riglosensis* sp. nov., holotype (MPZ 2019/1722), in dorsal, right lateral and frontal views, respectively (A–1: mirrored reconstruction). D – Cheliped of a carpilid (MPZ 2019/1805). E – Propodus of *Ocalina* ? sp. (MPZ 2019/1723). F, G – Indeterminate chelipeds (MPZ 2019/1852 and MPZ 2019/1837, respectively). H – Cheliped of a trapeziid? (MPZ 2019/1724). I – *Enoplocyrtia* ? sp. (MPZ 2019/1730). J – *Petrochirus* ? sp. (MPZ 2019/1734).



The type material of *G. crassifrons* was recovered from the upper Eocene of Vicenza (Italy) (A. MILNE-EDWARDS 1865); subsequently, it has also been recorded from the middle Eocene of Alicante (Spain; see VÍA-BOADA 1991: pl. 1, fig. 7). Its discovery in the La Peña buildup (Huesca) extends the range of the species to the upper Eocene of northern Spain.

Genus *Lobogalenopsis* MÜLLER & COLLINS, 1991

Type species: *Galenopsis quadrilobatus* LÖRENTHEY, 1898, by the subsequent designation of MÜLLER & COLLINS (1991).

Other species included: *Lobogalenopsis joei* sp. nov.

Lobogalenopsis joei sp. nov.

Fig. 6H–J

Etymology: Named after the late JOE S.H. COLLINS, in recognition of a lifetime dedicated to the study of fossil brachyurans.

Material: A single, incomplete carapace (holotype, MPZ 2019/1721), with a maximum preserved length and width of 18.3 and 21.6 mm, respectively. Cuticle is well preserved.

Diagnosis: Carapace wider than long, slightly convex longitudinally. Straight front, depressed below gastric regions. Orbits small; orbital edge undifferentiated. Three lobes on anterolateral margins; posterior margin slightly concave, with flange ornamented by row of small granules. Dorsal surface covered with very fine granulation.

Description: Carapace wider than long, slightly convex longitudinally, less convex transversely. Front straight, depressed below gastric regions. Orbits small and subcircular; continuous supraorbital margins; fronto-orbital width about 43 per cent of maximum carapace width. Anterolateral margin convex, with three lobes or blunt teeth, first of which immediately behind orbit; long and convergent posterolateral margins. Dorsal regions not well differentiated. Dorsal surface covered with small granules and pits; posterior margin slightly concave, shorter than frontal margin, two lateral corners inflated, ornated with row of small granules.

Discussion: The present specimen shows a combination of characteristics proposed by MÜLLER & COLLINS (1991) that allow it to be assigned to the genus *Lobogalenopsis*. These include:

- carapace convex, elliptical with a sharp keel along the anterolateral margin;

- straight front in top view, depressed below gastric regions;
- orbits small;
- anterolateral margin lobate.

Although only a single carapace is available to date, we consider it to be a new species on the basis of the following features:

- the carapace is less wide (estimated L/W ratio: 1.24) than that of the type species, *L. quadrilobata* (L/W ratio: 1.31);
- the groove behind the front is deep and extends parallel to the anterior margin down to the end of the first anterolateral lobe, unlike *L. quadrilobata*, which only reaches half the orbit;
- the anterolateral margin has three lobes, the two first rounded (the third is broken on both sides, but the gap occupied by it is seen), the first one expanding almost to the height of the front, unlike in *L. quadrilobata* where it is much more retracted;
- *L. joei* sp. nov. shows a slightly concave posterior margin, with a flange ornamented by a row of small granules; in contrast, *L. quadrilobata* has a straight and smooth margin;
- the dorsal surface of *L. joei* sp. nov. is covered by fine granulation, unlike *L. quadrilobata* where it is smooth;
- branchiocardiac grooves are more marked in *L. joei* sp. nov.

Until now, only the type species, *L. quadrilobata*, was assigned to this genus, with records from the lower Eocene of northern Italy (TESSIER *et al.* 2011; BESCHIN *et al.* 2015, BESCHIN *et al.* 2016; BESCHIN *et al.* 2018) and the upper Eocene of Hungary (MÜLLER & COLLINS 1991) and Sicily (Italy) (DI SALVO 1933). With *L. joei* sp. nov. from Huesca, the range of the genus is extended to the upper Eocene of the Iberian Peninsula.

Superfamily Dairoidea SERÈNE, 1965

Family Dairidae SERÈNE, 1965

Genus *Daira* DE HAAN, 1833

Type species: *Cancer perlatus* HERBST, 1790, by monotypy.

Other species included: *Daira americana* STIMPSON, 1860, *D. depressa* (A. MILNE-EDWARDS, 1865), *D. coccoi* BESCHIN, DE ANGELI, CHECCHI & ZARANTONELLO, 2012, *D. Coronata* BESCHIN, DE ANGELI, CHECCHI & ZARANTONELLO, 2005, *D. eocaenica* (LÖRENTHEY, 1898), *D. iugata* BESCHIN, BUSULINI & TESSIER, *in* BESCHIN, BUSULINI, FORNACIARI, PAPAZZONI & TESSIER, 2018, *D. pseudovulgaris* BESCHIN, BUSULINI & TESSIER, *in* BESCHIN, BUSULINI, FORNACIARI, PAPAZZONI & TESSIER, 2018, *D. Salebrosa*

Fig. 6. A–B – Indeterminate carpiliid, in frontal and dorsal views, respectively (MPZ 2019/1804). C, D – *Liopsalis cf. anodon* (BITTNER, 1875) (MPZ 2019/1803) in dorsal and frontal views, respectively. E – *Galenopsis crassifrons* A. MILNE-EDWARDS, 1865 (MPZ 2019/1736), in dorsal view. F, G – *Galenopsis crassifrons* (MPZ 2019/1738), in dorsal and frontal view, respectively. H–J – *Lobogalenopsis joei* sp. nov., holotype (MPZ 2019/1721), in dorsal, left lateral and frontal views, respectively.

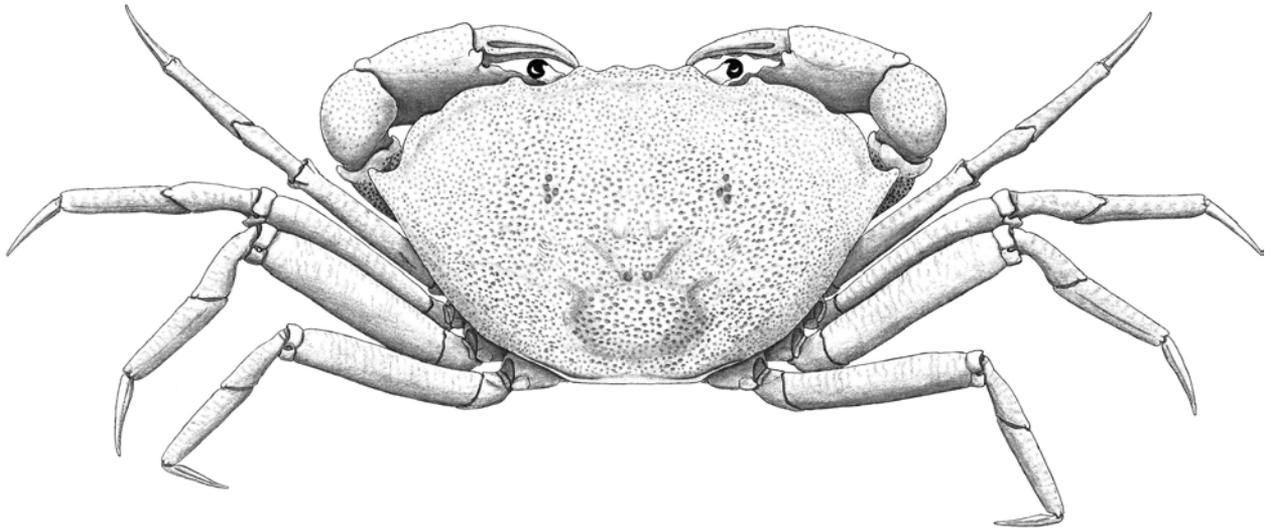


Fig. 7. Reconstruction of *Galenopsis crassifrons* A. MILNE-EDWARDS, 1865, on the basis of material recovered from the outcrop studied (see also Fig. 6E–G).

BESCHIN, BUSULINI, DE ANGELI & TESSIER, 2002, *D. sicula* (DI SALVO, 1933), *D. speciosa* (REUSS, 1871), *D. vestenano-venensis* BESCHIN, BUSULINI & TESSIER, 2015, and *D. vulgaris* PORTELL & COLLINS, 2004.

Daira corallina sp. nov.
Figs. 8B–K, 9

Etymology: Latin *corallium*, meaning coral, in reference to the preference of this taxon for coral reef environments.

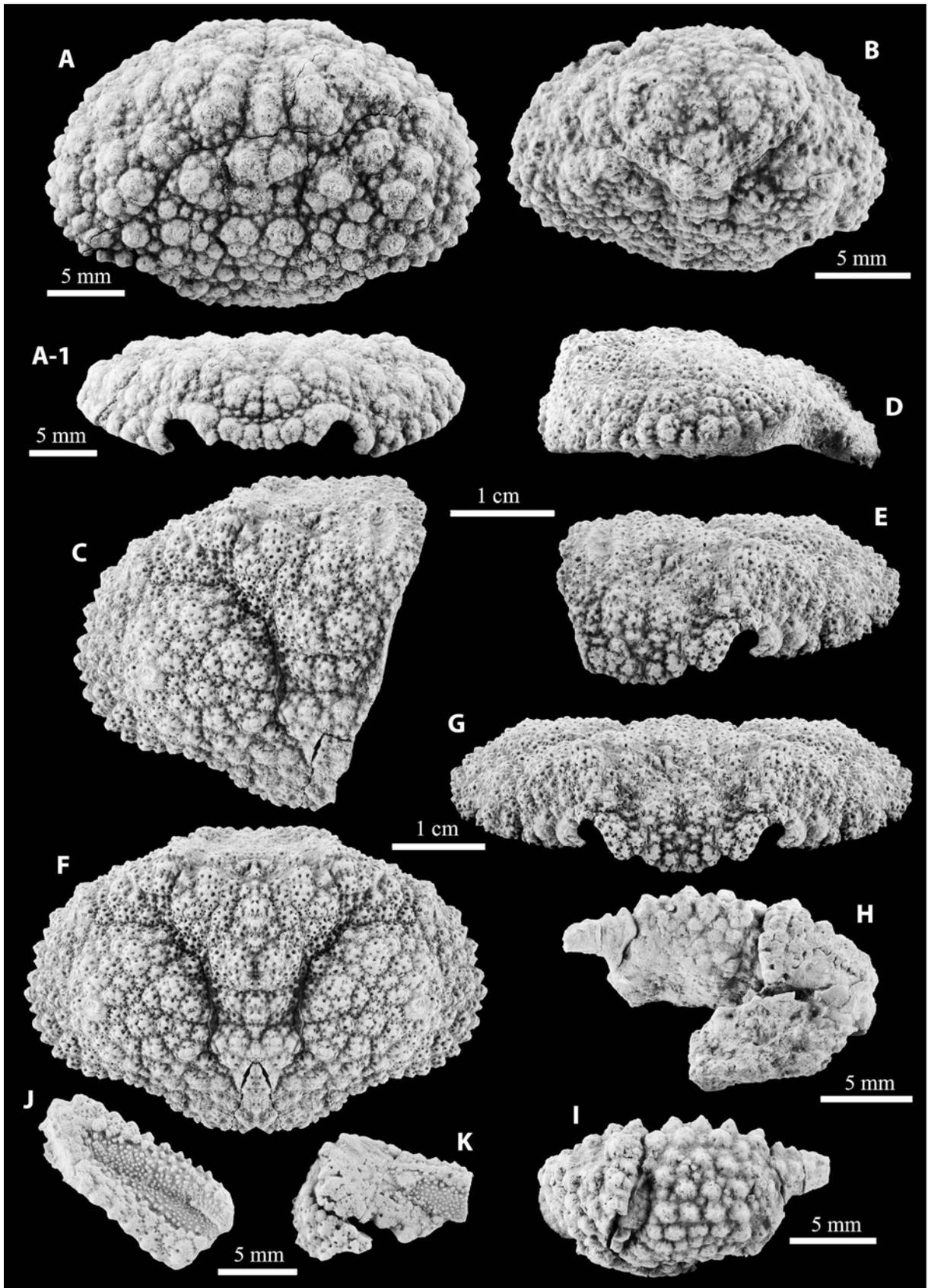
Material: The holotype (MPZ 2019/1691) is half a carapace with a maximum preserved length and width of 34 and 52 mm, respectively. In addition, we have 19 fragmentary carapaces (paratypes MPZ 2019/1692, MPZ 2019/1693, MPZ 2019/1694, MPZ 2019/1695 and MPZ 2019/1696), eight chelipeds (paratypes MPZ 2019/1701 and MPZ 2019/1702) and two isolated ambulatory legs (paratypes MPZ 2019/1703 and MPZ 2019/1704). Cuticle is well preserved in all specimens.

Diagnosis: Carapace suboval, wider than long, very convex longitudinally, transverse convexity less pronounced. Front sinuous. Orbits circular, with supraorbital margins covered

with coalescent tubercles with micropores. Anterolateral margins convex, with conical tubercles; posterolateral margins concave, ornamented with slightly smaller tubercles. Regions well differentiated by grooves. Dorsal surface covered with mushroom-shaped tubercles with micropores.

Description: Carapace transversely ovate, wider than long, L/W ratio about 1,5; convex longitudinally and transversely, domed. Orbits small and circular; upper orbital margins thickened and lined with tubercles; fronto-orbital width about 50 per cent of maximum carapace width; frontal margin tuberculate; frontal and anterolateral margins forming wide arch; antero- and posterolateral margins broadly rounded, not clearly distinct from one another; posterolateral margins shorter than anterolateral ones and concave. Gastric regions moderately well defined; narrow anterior mesogastric process; mesogastric region rhomboidal, relatively narrow. Dorsal surface covered with mushroom-shaped tubercles, more or less uniformly distributed and conical, with slightly hexagonal outline and perforated with pores (Fig. 8). Tops of these „mushrooms“ petaloid; edges of „petals“ forming pore, rendering image of conical elevation, surrounded by pores. Upper part of tubercles in contact with neighbouring tubercles and creating network of channels communicating with exterior through small pores. Grooves separating different regions well defined, but covered by hats of tubercles. Cuticle well preserved, thick.

Fig. 8. A, A-1 – *Daira salebrosa* BESCHIN, BUSULINI, DE ANGELI & TESSIER, 2002, Eocene of Arzignano (Main quarry, Vicenza, Italy; MPZ 2019/1690) in dorsal and frontal view, respectively. B–K – *Daira corallina* sp. nov. B. Paratype (MPZ 2019/1692). C–E. Holotype (MPZ 2019/1691) in dorsal, left lateral and frontal views, respectively. F, G. Mirrored reconstruction of holotype in dorsal and frontal views, respectively. H, I. Right chelipeds (paratypes MPZ 2019/1701 and MPZ 2019/1702). J, K. Ambulatory legs (paratypes MPZ 2019/1703 and MPZ 2019/1704).



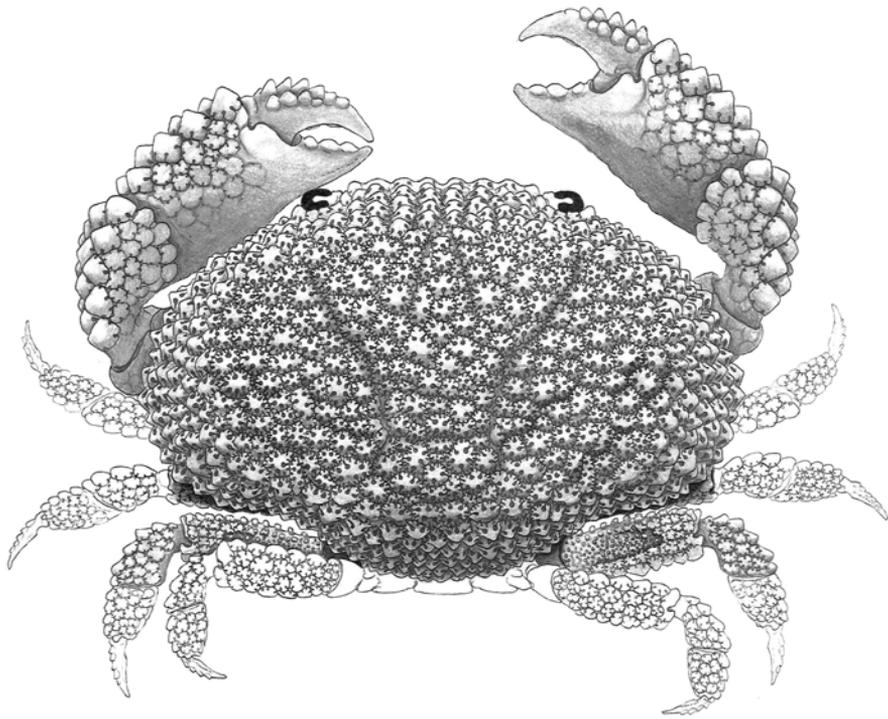


Fig. 9. Reconstruction of *Daira corallina* sp. nov., on the basis of material recovered from the outcrop studied. Parts without shading correspond to those that have been not found and have been reconstructed on the basis of a comparison from modern species.

Chelipeds include a carpus that is slightly longer than tall. The propodus is 1.5 times the length and height of carpus; upper margin curved with four conical tubercles (Fig. 8H, I). Fixed finger less than half length of manus, smooth. Upper margin of dactylus provided with pointed, forwardly facing tubercles, reducing in height distally. Tip rounded; occlusal margin concave, dentate.

Discussion: *Daira corallina* sp. nov. is characterised by a carapace that is convex longitudinally, with anterolateral margins not clearly distinct from posterolateral ones, with a relatively narrow mesogastric region, distinct dorsal regions that are ornamented with irregular mushroom-shaped tubercles, provided with micropores and protuberances. These features allow this species to be attributed to *Daira*.

The genus *Daira* comprises only two extant species, *D. perlata* from coralline settings in the Indo-Pacific (e.g., PEYROT-CLAUSADE 1989; MORGAN & BERRY 1993), and *D. americana*, which typically occurs in rocky or coral habitats along the Pacific coasts of central America, from southern California to Ecuador (RATHBUN 1930). As far as extinct species are concerned, the genus *Daira* appears to have preferred coral or reef environments. Frequently, its presence is indicative of a diverse reefal decapod crustacean assemblage (see BESCHIN et al. 2002; PORTELL & COLLINS 2004; BESCHIN et al. 2005; BESCHIN et al. 2017; DE ANGELI et al. 2010; GATT & DE ANGELI 2010; BESCHIN et al. 2012; BE-

SCHIN et al. 2015; BESCHIN et al. 2016; BESCHIN et al. 2018; TESSIER et al. 2011).

This genus is represented by eleven extinct species and two recent ones. The latter have carapaces that are completely covered by mushroom-shaped tubercles, the “petaloid hats” of which are in contact with each other and form a mosaic of polygons. *Daira corallina* sp. nov. shows similarities to its modern congeners *D. perlata* and *D. americana* where dorsal tubercles are concerned. However, in the new species, the tubercles are much smaller and more closely set.

A comparison of *Daira corallina* sp. nov. with other extinct congeners shows similarities particularly to *D. salebro-sa* (Fig. 8A) from the Eocene of northern Italy, in carapace shape, ornamentation (i.e., abundant mushroom-shaped tubercles) and in the lateral margins that are provided with

Table 3. Contingency table used for the Fisher’s-exact test.

	Branching corals facies	Massive corals facies	Tabular corals facies
Carpiliids	4	15	2
<i>Galenopsis</i>	15	4	47
<i>Daira</i>	26	1	5

pointed tubercles (see Fig. 8). However, *D. salebroza* differs from *D. corallina* sp. nov. in the following features:

- in *D. corallina*, the frontal margin is projected downwards more than in *D. salebroza* (see Fig. 8A-1 and E);
- in *D. salebroza*, the frontal region is clearly divided by a longitudinal groove (see Fig. 8A and A-1) which is absent in the new species (Fig. 8E);
- in *D. salebroza*, the orbits are slightly larger than those of *D. corallina* (see Fig. 8A-1 and E);
- in the new species, the tubercles of the anterolateral margins are less rounded than in *D. salebroza*;
- in *D. salebroza*, dorsal regions present themselves as bulges that are formed by groups of tubercles (Fig. 8A). In the new species, the dorsal surface lacks such elevations and has a more uniform appearance (Fig. 8B–F);
- in *D. salebroza*, the dorsal tubercles are more rounded and have smaller pores than in *D. corallina* sp. nov. (see BESCHIN et al. 2002: pl. 2, figs. 5, 6).

The other known Eocene congeners have a different dorsal ornamentation. *Daira coronata*, *D. coccoi* and *D. pseudovulgaris* are ornamented with more rounded and larger, pearl-like tubercles than in *D. corallina* sp. nov. *Daira sicula* and *D. vestenanovensis* both have distinct dorsal carapace regions that are covered with irregular tubercles. In addition, these two species differ from *D. corallina* sp. nov. in that they have a medially furrowed frontal margin, better-defined dorsal regions and broad and convex anterolateral margins, subdivided into four large teeth constituted by fusion of small groups of tubercles. In addition, *D. sicula* has a more prominent frontal region that projects forwards giving the carapace a more rhomboidal shape (see DI SALVO 1933: pl. 1, fig. 5a–d; BESCHIN et al. 2005: pl. 4, fig. 13; 2012: pl. 8, fig. 48; BESCHIN et al. 2015: pl. 3, fig. 6; BESCHIN et al. 2018: figs. 95–97). *Daira iugata* and *D. eoacena* from the upper Eocene of Italy are both based on internal moulds and specimens with rather poorly preserved cuticle. It is important to mention that the presence of cuticle is a key for the appearance of *Daira* spp. (KLOMPMAKER et al. 2015). In any case, these species show much denser and smaller tubercles and dorsal regions are better demarcated than in the new species (see LÖRENTHEY 1898: figs. 91, 92a, b; BESCHIN et al. 2018: figs. 93, 94).

Daira speciosa from the Miocene of Europe and *D. depressa* from the Oligocene of Italy differ from *D. corallina* sp. nov. in having well-defined regions bordered by grooves and an ornament of large, aligned tubercles, larger epi- and mesobranchial tubercles and a sharper delineation of these from the smaller metabranchial tubercles (see REUSS 1871: figs. 1–4; MILNE-EDWARDS 1865: pl. 33, fig. 2). *Daira vulgaris*, from the Miocene of Jamaica, shows a close similarity to *D. speciosa*. It differs from the new species because of the presence in *D. vulgaris* of deep grooves without tubercles that separate the different dorsal regions; in addition, tubercles are more flattened and the anterolateral margins have elongated spiny or tooth-like tubercles (see PORTELL & COLLINS 2004: pl. 1, figs. 7, 8).

Chelipeds and isolated legs have been assigned to the new species because they have the same characteristic ornamentation.

Some authors have suggested that the genus originated in the western part of the Tethys (BESCHIN et al. 2002), in view of the presence of several species in this region. Subsequently, representatives migrated and radiated both towards the Atlantic and Indo-Pacific areas (BESCHIN et al. 2016).

7. Conclusions

Modern reefs represent biodiversity hotspots. The data reported in the present work support the widely accepted assumption that past reefs had similar characteristics (e.g., MÜLLER et al. 2000; KROBICKI & ZATOŃ 2008; KLOMPMAKER 2013; KLOMPMAKER et al. 2013). Although past reefs show low fossilisation potential for decapod crustaceans because of low sedimentary rates and high-energy settings (SCHWEITZER & FELDMANN 2015), the sediment trapped within the framework of the La Peña reef has yielded a rich and diverse assemblage of decapod crustaceans that includes *Gemellarocarcinus riglosensis* sp. nov., *Liopsalis* cf. *anodon*, *Galenopsis crassifrons*, *Lobogalenopsis joi* sp. nov., *Daira corallina* sp. nov., and eight additional, indeterminate taxa.

The La Peña buildup provides good opportunities for quantifying decapod crustacean assemblages in three different coral facies that developed at intermediate depths of c. 15–25 metres (MORSILLI et al. 2012) and are dominated either by branching, tabular or massive corals. There is a strong statistical correlation between decapod taxa and specific coral facies. The branching corals facies documents the highest diversity and abundance of decapod crustaceans with a predominance of small taxa such as *Daira corallina* sp. nov. This is probably related to its location within the reef, under the lowest-energy conditions and also to abundant crevices that this environment provided for refuge, feeding and other interactions. The tabular corals facies has mainly *G. crassifrons*, and domal corals show the lowest abundance with carpiliids as the most abundant group. The latter is probably controlled by both taphonomic (amount of sediment between colonies) and biological (limited space for refuge) conditions. Although our present work discusses only a single reef of early Priabonian (late Eocene) age, similar studies in other areas could potentially provide important ecological data on the distribution of decapod crustaceans in ancient marine settings.

Acknowledgements

The present work has been supported by CGL2017-85038-P, subsidised by the Spanish Ministry of Science and Innovation, the European Regional Development Fund and Project E18 *Aragosaurus: Recursos Geológicos y Paleoambientes* of the government of Aragón-FEDER. We thank RICCARDO ALBERTI (Associazione Amici del Museo “G. Zannato”, Montecchio Maggiore, Vicenza) for donation of a specimen of *Daira salebrosa* from the type locality and for valuable information provided, ÀLEX OSSÓ (Tarragona) for help and advice and VANESSA VILLALBA (Max Planck Institute for the Science of Human History) for her suggestions and help with statistical analysis. Finally, we are grateful to the journal reviewers, ADIËL KLOMPMAKER (University of Alabama, Tuscaloosa, Alabama, USA) and JOHN W.M. JAGT (Natuurhistorisch Museum Maastricht, the Netherlands), for pertinent comments on an earlier version of the typescript.

References

- ABELE, L.G. (1979): The community structure of coral-associated decapod crustaceans in variable environments. – In: LIVINGSTON, R.J. (ed.): *Ecological processes in coastal and marine systems*: 165–187; New York (Plenum Press). doi: [10.1007/978-1-4615-9146-7_13](https://doi.org/10.1007/978-1-4615-9146-7_13)
- ARTAL, P. & CASTILLO, J. (2005): *Cyrtorhina ripacurtae* n.sp. (Crustacea, Decapoda, Raninidae), primera cita del género en el Eoceno inferior español. – *Batalleria*, **12**: 33–38.
- ARTAL, P. & VAN BAKEL, B.W.M. (2018a): Aethrids and panopeids (Crustacea, Decapoda) from the Ypresian of both slopes of the Pyrenees (France, Spain). – *Scripta Musei Geologici Seminarii Barcinonensis*, **22**: 3–19.
- ARTAL, P. & VAN BAKEL, B.W.M. (2018b): Carpiliids (Crustacea, Decapoda) from the Ypresian (Eocene) of the northeast of Spain. – *Scripta Musei Geologici Seminarii Barcinonensis*, **22**: 20–36.
- ARTAL, P., VAN BAKEL, B.W.M., FRAAIJE, R.H.B. & JAGT, J.W.M. (2013): New retroplumid crabs (Crustacea, Brachyura, Retroplumidae Gill, 1894) from the Eocene of Huesca (Aragon, Spain). – *Zootaxa*, **3652**: 343–352. doi: [10.11646/zootaxa.3652.3.3](https://doi.org/10.11646/zootaxa.3652.3.3) PMID: [26269837](https://pubmed.ncbi.nlm.nih.gov/26269837/)
- ARTAL, P. & VÍA, L. (1988): *Xanthilites macrodactylus pyrenaicus* (Crustacea, Decapoda) nueva subespecie del Ilerdiense medio del Pirineo de Huesca. – *Batalleria*, **2**: 57–61.
- BESCHIN, C., BUSULINI, A., CALVAGNO, M., TESSIER, G. & ZORZIN, R. (2017): Ypresian decapod crustacean faunas from the coral-algal environments in the eastern Lessini Mountains (Vicenza and Verona territory – NE Italy): a comparative analysis. – *Bulletin de la Société géologique de France*, **188** (3): 13–26. doi: [10.1051/bsgf/2017177](https://doi.org/10.1051/bsgf/2017177)
- BESCHIN, C., BUSULINI, A., DE ANGELI, A. & TESSIER, G. (2002): Aggiornamento ai crostacei eocenici di Cava “Main” di Arzignano (Vicenza - Italia settentrionale) (Crustacea, Decapoda). – *Studi e Ricerche, Associazione Amici del Museo Museo Civico “G. Zannato”* (Montecchio Maggiore, Vicenza), **9**: 7–28.
- BESCHIN, C., BUSULINI, A., DE ANGELI, A. & TESSIER, G. (2007): I decapodi dell’Eocene inferiore di Contrada Gecchelina (Vicenza – Italia settentrionale) (Anomura e Brachiura). – *Museo di Archeologia e Scienze Naturali “G. Zannato”*, Montecchio Maggiore (Vicenza), **14**: 9–76.
- BESCHIN, C., BUSULINI, A., FORNACIARI, E., PAPAZZONI, C.A. & TESSIER, G. (2018): La fauna di crostacei associati a coralli dell’Eocene superiore di Campolongo di Val Liona (Monti Berici, Vicenza, Italia nordorientale). – *Bollettino del Museo di Storia naturale di Venezia*, **69**: 129–215.
- BESCHIN, C., BUSULINI, A. & TESSIER, G. (2015): Nuova segnalazione di crostacei associati a coralli nell’Eocene inferiore dei Lessini orientali (Vestenanova–Verona). – *Lavori Società veneziana di Scienze naturali*, **40**: 47–109.
- BESCHIN, C., BUSULINI, A., TESSIER, G. & ZORZIN, R. (2016): I crostacei associati a coralli nell’Eocene inferiore dell’area di Bolca (Verona e Vicenza, Italia nordorientale). – *Memorie del Museo civico di Storia naturale di Verona, Serie 2, Sezione Scienze della Terra*, **9**: 1–189.
- BESCHIN, C., DE ANGELI, A., CHECCHI, A. & ZARANTONELLO, G. (2005): Crostacei eocenici di Grola presso Spagnago (Vicenza, Italia settentrionale). – *Studi e Ricerche, Associazione Amici del Museo, Museo Civico “G. Zannato”*, Montecchio Maggiore (Vicenza), **12**: 5–35.
- BESCHIN, C., DE ANGELI, A., CHECCHI, A. & ZARANTONELLO, G. (2012): Crostacei del giacimento eocenico di Grola presso Spagnago di Cornedo Vicentino (Vicenza, Italia settentrionale) (Decapoda, Stomatopoda, Isopoda). – 100 pp.; Montecchio Maggiore (Museo di Archeologia e Scienze naturali “G. Zannato”).
- BITTNER, A. (1875): Die Brachyuren des vicentinischen Tertiärgebirges. – *Denkschriften der kaiserlichen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Klasse*, **34**: 63–105.
- BRÖSING, A. (2008): A reconstruction of an evolutionary scenario for the Brachyura (Decapoda) in the context of the Cretaceous-Tertiary boundary. – *Crustaceana*, **81** (3): 271–287. doi: [10.1163/156854008783564091](https://doi.org/10.1163/156854008783564091)
- BUSULINI, A., TESSIER, G. & BESCHIN, C. (2006): The genus *Phlyctenodes* Milne Edwards, 1862 (Crustacea: Decapoda: Xanthidae) in the Eocene of Europe. – *Revista Mexicana de Ciencias geológicas*, **23** (3): 350–360.
- CANUDO, J.I. (2018): The collection of type fossils of the Natural Science Museum of the University of Zaragoza (Spain). – *Geoheritage*, **10**: 385–392. doi: [10.1007/s12371-017-0228-1](https://doi.org/10.1007/s12371-017-0228-1)
- CANUDO, J.I., MALAGON, J., MELENDEZ, A., MILLÁN, H., MOLINA, E. & NAVARRO, J.J. (1991): Las secuencias deposicionales del Eoceno medio y superior de las Sierras externas (Prepirineo meridional aragonés). – *Geogaceta*, **9**: 81–84.
- CANUDO, J.I., MOLINA, E., RIVELINE, J., SERRA-KIEL, J. & SUCUNZA, M. (1988): Les événements biostratigraphiques de la zone prépyrénéenne d’Aragon (Espagne), de l’Eocène moyen à l’Oligocène inférieur. – *Revue de Micropaléontologie*, **31**: 15–29.

- CASTELLORT, S., GUILLOCHEAU, F., ROBIN, C., ROUBY, D., NALPAS, T., LAFONT, F. & ESCHARD, R. (2003): Fold control on the stratigraphic record: a quantified sequence stratigraphic study of the Pico del Aguila anticline in the south-western Pyrenees (Spain). – *Basin Research*, **15**: 527–551. doi: [10.1111/j.1365-2117.2003.00218.x](https://doi.org/10.1111/j.1365-2117.2003.00218.x)
- CHECCHIA-RISPOLI, G. (1905): I crostacei dell'Eocene dei dintorni di Monreale in provincia di Palermo. – *Giornale della Società Scienze naturale e economiche di Palermo*, **25**: 309–325.
- DE ANGELI, A. & CECCON, L. (2012): *Eouropycthus montemagrensis* n. gen., n. sp. (Crustacea, Decapoda, Anomura, Chirostylidae) dell'Eocene inferiore (Ypresiano) di Monte Magrè (Vicenza, Italia settentrionale). – *Lavori Società veneziana di Scienze naturali*, **37**: 19–24.
- DE ANGELI, A. & CECCON, L. (2013a): Tetraliidae and Trapeziidae (Crustacea, Decapoda, Brachyura) from the Early Eocene of Monte Magrè (Vicenza, NE Italy). – *Natural History Sciences*, **154** (1): 25–40. doi: [10.4081/nhs.2013.25](https://doi.org/10.4081/nhs.2013.25)
- DE ANGELI, A. & CECCON, L. (2013b): *Latheticocarcinus italicus* sp. nov. (Decapoda, Brachyura, Homolidae) dell'Eocene inferiore (Ypresiano) di Monte Magrè (Vicenza, Italia settentrionale). – *Lavori Società veneziana di Scienze naturali*, **38**: 103–109.
- DE ANGELI, A. & CECCON, L. (2014): Nuovi brachiuri (Decapoda) dell'Eocene inferiore di Monte Magrè (Vicenza, Italia settentrionale). – *Lavori Società veneziana di Scienze naturali*, **39**: 77–92.
- DE ANGELI, A. & CECCON, L. (2015): Nuovi crostacei brachiuri dell'Eocene di Monte Magrè (Vicenza, Italia settentrionale). – *Lavori Società veneziana di Scienze naturali*, **40**: 119–138.
- DE ANGELI, A. & CECCON, L. (2016): Contributo ai crostacei decapodi dell'Eocene inferiore dei Monti Lessini orientali (Italia nordorientale). – *Natura Vicentina*, **20**: 5–38.
- DE ANGELI, A. & GARASSINO, A. (2002): Galatheid, chirostylid and porcellanid decapods (Crustacea, Decapoda, Anomura) from the Eocene and Oligocene of Vicenza (N Italy). – *Memorie della Società italiana di Scienze naturali e del Museo civico di Storia naturale in Milano*, **30**: 1–40.
- DE ANGELI, A. & GARASSINO, A. (2014): *Palinurellus bericus* n. sp. (Crustacea, Decapoda, Palinuridae) from the late Eocene (Priabonian) of San Feliciano (Orgiano, Vicenza, northeastern Italy). – *Natural History Sciences*, **1**: 7–12. doi: [10.4081/nhs.2014.58](https://doi.org/10.4081/nhs.2014.58)
- DE ANGELI, A., GARASSINO, A. & CECCON, L. (2010): New report of the coral-associated decapods from the “Formazione di Castelgomberto” (early Oligocene) (Vicenza, NE Italy). – *Atti della Società italiana di Scienze naturali e del Museo civico di Storia naturale in Milano*, **151** (2): 145–177.
- DE HAAN, W. (1833–1850): Crustacea. – In: SIEBOLD, P.F. v. (ed.): *Fauna Japonica sive descriptio animalium, quae in itinere per Japoniam, jussu et auspiciis superiorum, qui summum in India Batava imperium tenent, suscepto, annis 1823-1830 collegit, notis, observationibus et adumbrationibus illustravit: i–xvii, i–xxxix, ix–xvi, 1–243; Lugduni Batavorum (J. Müller et Co.)*.
- DE SAINT LAURENT, M. (1980): Sur la classification et la phylogénie des crustacés décapodes brachyours. I. Podotremata Guinot, 1977, et Eubrachyura sect. nov. – *Comptes Rendus hebdomadaires des Séances de l'Académie des Sciences, Paris*, **D290**: 1265–1268.
- DI SALVO, G. (1933): I crostacei del Terziario Inferiore della Provincia di Palermo. – *Giornale di Scienze naturale ed economiche*, **37** (3): 1–46.
- DOMÍNGUEZ, J.L. & OSSÓ, A. (2016): New decapod fauna at midway of the Tethys Sea and Atlantic Ocean; central Pyrenees of Huesca (Aragon, Spain). – In: CHARBONNIER, S. (ed.): *6th Symposium on Mesozoic and Cenozoic decapod crustaceans: 23–24; Villers-sur-Mer, Normandy, France*.
- DREYER, T., CORREGIDOR, J., ARBUÉS, P. & PUIGDEFABREGAS, C. (1999): Architecture of the tectonically influenced Sobrarbe deltaic complex in the Ainsa Basin, northern Spain. – *Sedimentary Geology*, **127**: 127–169. doi: [10.1016/S0037-0738\(99\)00056-1](https://doi.org/10.1016/S0037-0738(99)00056-1)
- FABIANI, R. (1908): *Paleontologia dei Colli Berici*. – *Memorie di Matematica e di Fisica della Società Italiana delle Scienze*, **15**: 45–248.
- FELDMANN, R.M., SCHWEITZER, C.E., BENNETT, O., FRANȚESCU, O.D., RESAR, N. & TRUDEAU, A. (2011): New Eocene Brachyura (Crustacea: Decapoda) from Egypt. – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **262** (3): 323–353. doi: [10.1127/0077-7749/2011/0202](https://doi.org/10.1127/0077-7749/2011/0202)
- FERRATGES, F.A., ZAMORA, S. & AURELL, M. (2019): A new genus and species of Parthenopidae MacLeay, 1838 (Decapoda: Brachyura) from the lower Eocene of Spain. – *Journal of Crustacean Biology*, **39** (3): 303–311. doi: [10.1093/jcbiol/ruz014](https://doi.org/10.1093/jcbiol/ruz014)
- FRAAIJE, R.H.B. (2003): Evolution of reef-associated decapod crustaceans through time, with particular reference to the Maastrichtian type area. – *Contributions to Zoology*, **72** (2–3): 119–130. doi: [10.1163/18759866-0720203010](https://doi.org/10.1163/18759866-0720203010)
- GATT, M. & DE ANGELI, A. (2010): A new coral-associated decapod assemblage from the Upper Miocene (Messinian) Upper Coralline Limestone of Malta (central Mediterranean). – *Palaeontology*, **53** (6): 1315–1348. doi: [10.1111/j.1475-4983.2010.01008.x](https://doi.org/10.1111/j.1475-4983.2010.01008.x)
- GLAESSNER, M.F. (1929): Crustacea Decapoda. – In: POMPECKJI, F.J. (ed.): *Fossilium Catalogus 1, Animalia*, **41**: 464 pp.; Berlin (Junk).
- GUINOT, D. (1977): Propositions pour une nouvelle classification des crustacés décapodes brachyours. – *Comptes Rendus hebdomadaires des Séances de l'Académie des Sciences, Paris*, **D285**: 1049–1052.
- GUINOT, D., TAVARES, M. & CASTRO, P. (2013): Significance of the sexual openings and supplementary structures on the phylogeny of brachyuran crabs (Crustacea, Decapoda, Brachyura), with new nomina for higher-ranked podotreme taxa. – *Zootaxa*, **3665** (1): 1–414. doi: [10.11646/zootaxa.3665.1.1](https://doi.org/10.11646/zootaxa.3665.1.1) PMID: [26401537](https://pubmed.ncbi.nlm.nih.gov/26401537/)
- HALLOCK, P. & POMAR, L. (2008): Cenozoic evolution of larger benthic foraminifers: paleoceanographic evidence for changing habitats. – *Proceedings of the 11th International Coral Reef Symposium, Fort Lauderdale, Florida*: 16–20.

- HALLOCK, P., PREMOLI-SILVA, I. & BOERSMA, A. (1991): Similarities between planktonic and larger foraminiferal evolutionary trends through Paleogene paleoceanographic changes. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, **83**: 49–64. doi: [10.1016/0031-0182\(91\)90075-3](https://doi.org/10.1016/0031-0182(91)90075-3)
- HAY, W.W., DE CONTO, R., WOLD, C.N., WILSON, K.M., VOIGT, S., SCHULZ, M., WOLD-ROSSBY, A., DULLO, W.C., RONOV, A.B., BALUKHOVSKY, A.N. & SOEDING, E. (1999): Alternative global Cretaceous paleogeography. – In: BARRERA, E. & JOHNSON, C. (eds.): *The evolution of Cretaceous ocean/climate systems*. – Geological Society of America, Special Papers, **332** : 1–47. doi: [10.1130/0-8137-2332-9.1](https://doi.org/10.1130/0-8137-2332-9.1)
- HERBST, J.F.W. (1782–1804): Versuch einer Naturgeschichte der Krabben und Krebse nebst einer systematischen Beschreibung ihrer verschiedenen Arten, 1–3: 515 pp.; Berlin & Stralsund) (Lange).
- HOGAN, P.J. (1993): Geochronologic, tectonic and stratigraphic evolution of the Southwest Pyrenean foreland basin, northern Spain. – Unpubl. PhD thesis, University of southern California, Los Angeles: 219 pp.
- HUYGHE, D., MOUTHEREAU, F., CASTELLORT, S., FILLEAUDEAU, P.Y. & EMMANUEL, L. (2009): Paleogene propagation of the southern Pyrenean thrust wedge revealed by finite strain analysis in frontal thrust sheets: implications for mountain building. – *Earth and Planetary Science Letters*, **288**: 421–433. doi: [10.1016/j.epsl.2009.10.002](https://doi.org/10.1016/j.epsl.2009.10.002)
- JAGT, J.W.M., VAN BAKEL, B.W.M., GUINOT, D., FRAAIJE, R.H.B. & ARTAL, P. (2015): Fossil Brachyura. – *Treatise on Zoology - Anatomy, Taxonomy, Biology, The Crustacea*, **9**: 847–920.
- KARASAWA, H., SCHWEITZER, C.E. & FELDMANN, R.M. (2011): Phylogenetic analysis and revised classification of podotrematous Brachyura (Decapoda) including extinct and extant families. – *Journal of Crustacean Biology*, **31** (3): 523–565. doi: [10.1651/10-3423.1](https://doi.org/10.1651/10-3423.1)
- KLOMPMAKER, A.A. (2013): Extreme diversity of decapod crustaceans from the mid-Cretaceous (late Albian) of Spain: implications for Cretaceous decapod paleoecology. – *Cretaceous Research*, **41**: 150–185. doi: [10.1016/j.cretres.2012.12.003](https://doi.org/10.1016/j.cretres.2012.12.003)
- KLOMPMAKER, A.A., HYŽNÝ, M. & JAKOBSEN, S.L. (2015): Taphonomy of decapod crustacean cuticle and its effect on the appearance as exemplified by new and known taxa from the Cretaceous-Danian crab *Caloxanthus*. – *Cretaceous Research*, **55**: 141–151. doi: [10.1016/j.cretres.2014.11.011](https://doi.org/10.1016/j.cretres.2014.11.011)
- KLOMPMAKER, A.A., JAKOBSEN, S.L. & LAURIDSEN, B.W. (2016): Evolution of body size, vision, and biodiversity of coral-associated organisms: evidence from fossil crustaceans in cold-water coral and tropical coral ecosystems. – *BMC Evolutionary Biology*, **16** (1): 132. doi: [10.1186/s12862-016-0694-0](https://doi.org/10.1186/s12862-016-0694-0) PMID: 27311756
- KLOMPMAKER, A.A., SCHWEITZER, C.E., FELDMANN, R.M. & KOWALEWSKI, M. (2013): The influence of reefs on the rise of Mesozoic marine crustaceans. – *Geology*, **41**: 1179–1182. doi: [10.1130/G34768.1](https://doi.org/10.1130/G34768.1)
- KROBICKI, M. & ZATON, M. (2008): Middle and Late Jurassic roots of brachyuran crabs: Palaeoenvironmental distribution during their early evolution. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, **263**: 30–43. doi: [10.1016/j.palaeo.2008.01.025](https://doi.org/10.1016/j.palaeo.2008.01.025)
- LINNAEUS, C. (1758): *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis* (Editio 10), 1: 1–824; Holmiae (Laurentius Salvius).
- LÓPEZ-HORGUE, M.A. & BODEGO, A. (2017): Mesozoic and Cenozoic decapod crustaceans from the Basque-Cantabrian Basin (western Pyrenees): new occurrences and faunal turnovers in the context of basin evolution. – *Bulletin de la Société géologique de France*, **188** (3): 1–14. doi: [10.1051/bsgf/2017180](https://doi.org/10.1051/bsgf/2017180)
- LÖRENTHEY, E. (1898): Beiträge zur Decapodenfauna des ungarischen Tertiärs. – *Természetráji Füzetek*, **21**: 1–133.
- MADIN, J.S., HUGHES, T.P. & CONNOLLY, S.R. (2012): Calcification, storm damage and population resilience of tabular corals under climate change. – *PLoS ONE*, **7** (10): 1–10. doi: [10.1371/journal.pone.0046637](https://doi.org/10.1371/journal.pone.0046637) PMID: 23056379
- MCCOY, F. (1849): On the classification of some British fossil Crustacea, with notices of the new forms in the University Collection at Cambridge. – *The Annals and Magazine of Natural History*, (2), **4** (21): 161–179. doi: [10.1080/03745486009494810](https://doi.org/10.1080/03745486009494810)
- MEYER, H. v. (1842): Ueber die in dem dichten Jurakalk von Aalen in Württemberg vorkommenden Spezies des Crustaceengenus *Prosopon*. – *Beiträge zur Petrefaktenkunde*, **5**: 70–75.
- MEYER, H. v. (1862): Tertiaere Decapoden aus den Alpen, von Oeningen und dem Taunus. – *Palaeontographica*, **10**: 147–178.
- MIERS, E.J. (1886): Part II. Report on the Brachyura collected by H.M.S. Challenger during the years 1873–76. – In: Report on the Scientific Results of the Voyage of H.M.S. Challenger during the years 1873–1876 under the command of Captain Frank Tourle Thomson, R.N. prepared under the Superintendence of the late Sir C. Wyville Thomson, Knt., F.R.S. & c. Regius Professor of Natural history in the University of Edinburgh of the civilian scientific staff on board and now of John Murray one of the naturalists of the Expedition. Zoology, Published by Order of Her Majesty's Government, London, Edinburgh and Dublin, HMSO, **17**: 1–29.
- MILLÁN, H., AURELL, M. & MELÉNDEZ, A. (1994): Synchronous detachment folds and coeval sedimentation in the Prepyrenean External Sierras (Spain): a case study for a tectonic origin of sequences and systems tracts. – *Sedimentology*, **41** (5): 1001–1024. doi: [10.1111/j.1365-3091.1994.tb01437.x](https://doi.org/10.1111/j.1365-3091.1994.tb01437.x)
- MILLÁN, H., PUEYO, E.L., AURELL, M., LUZÓN, A., OLIVA, B., MARTÍNEZ, M.B. & POCOVÍ, A. (2000): Actividad tectónica registrada en los depósitos terciarios del frente meridional del Pirineo central. – *Revista de la Sociedad Geológica de España*, **13**: 279–300.
- MILNE-EDWARDS, A. (1865): Monographie des Crustacés fossiles de la famille des Cancériens. – *Annales des Sciences naturelles*, (5), **3**: 297–351.
- MILNE-EDWARDS, A. (1872): Note sur quelques Crustacés fossiles appartenant aux genres *Ranina* et *Galenopsis*. – *Annales des Sciences géologiques*, **3**: 1–12.

- MILNE-EDWARDS, A. (1873–1881): Études sur les Xiphosures et les Crustacés podophthalmes. Mission scientifique au Mexique et dans l'Amérique centrale. – Recherches zoologiques pour servir l'histoire de la faune de l'Amérique centrale et du Mexique, **5**: 1–368.
- MORGAN, G.J. & BERRY, P.F. (1993): Decapod Crustacea of Ashmore Reef and Cartier Island. – Marine and Faunal Surveys of Ashmore Reef and Cartier Island North-western Australia, Western Australian Museum: 47–65.
- MORSILLI, M., BOSELLINI, F.R., POMAR, L., HALLOCK, P., AURELL, M. & PAPAZZONI, C.A. (2012): Mesophotic coral buildups in a prodelta setting (late Eocene, southern Pyrenees, Spain): a mixed carbonate–siliciclastic system. – Sedimentology, **59** (3): 766–794. doi: [10.1111/j.1365-3091.2011.01275.x](https://doi.org/10.1111/j.1365-3091.2011.01275.x)
- MÜLLER, P. & COLLINS, J.S.H. (1991): Late Eocene coral-associated decapods (Crustacea) from Hungary. – Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie, **28** (2/3): 47–92.
- MÜLLER, P., KROBICKI, M. & WEHNER, G. (2000): Jurassic and Cretaceous primitive crabs of the family Prosopidae (Decapoda: Brachyura) - their taxonomy, ecology and biogeography. – Annales Societatis Geologorum Poloniae, **70**: 49–79.
- MUÑOZ, J.A., MCCRAY, K. & POBLET, J. (1994): Synchronous extension and contraction in frontal thrust sheets of the Spanish Pyrenees. – Geology, **22**: 921–924. doi: [10.1130/0091-7613\(1994\)022<0921:SEACIF>2.3.CO;2](https://doi.org/10.1130/0091-7613(1994)022<0921:SEACIF>2.3.CO;2)
- MUTTI, E., REMACHA, E., SGAVETTI, M., ROSELL, J., VALLONI, R. & ZAMORANO, M. (1985): Stratigraphy and facies characteristics of the Eocene Hecho Group turbidite systems, south-central Pyrenees. – In: MILAM, D. & ROSELL, J. (eds.): IAS. 6th European Regional Meeting, Excursion Guidebook: 521–576; Lleida (Institut d'Estudis Ilerdencs).
- OPPENHEIM, P. (1900–1901): Die Priabonaschichten und ihre Fauna, im Zusammenhange mit gleichalterigen und analogen Ablagerungen, vergleichend betrachtet. – Palaeontographica, **47**: 1–348.
- ORTMANN, A. (1892): Die Decapoden-Krebse des Strassburger Museums, mit besonderer Berücksichtigung der von Herrn Dr. Döderlein bei Japan und bei den Liu-Kiu Inseln gesammelten und zur Zeit im Strassburger Museum aufbewahrten Formen, V. Theil. Die Abtheilungen Hippidea, Dromiidea und Oxystomata. – Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere, **6**: 532–588. doi: [10.5962/bhl.part.26456](https://doi.org/10.5962/bhl.part.26456)
- ORTMANN, A. (1893): Die Decapoden-Krebse des Strassburger Museums. 7. Theil. Abtheilung: Brachyura (Brachyura genuina Boas) 2. Unterabtheilung: Cancroidea, 2. Section: Cancrinae, 1. Gruppe: Cyclometopa. – Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere, **7**: 411–495.
- OSSÓ, A. & DOMÍNGUEZ, J.L. (2017): A new genus and new species of decapod crustacean (Decapoda: Brachyura: Panopeidae) from the early Priabonian (Late Eocene) of the central Pyrenees of Huesca (Aragón, Spain), with remarks on its habitat and ecology. – Journal of Crustacean Biology, **37** (5): 602–607. doi: [10.1093/jcbiol/rux072](https://doi.org/10.1093/jcbiol/rux072)
- OSSÓ, A., DOMÍNGUEZ, J.L. & ARTAL, P. (2014): *Pyreneplax basaensis* new genus, new species (Decapoda, Brachyura, Vultocinidae) from the Priabonian (Late Eocene) of the Pyrenees of Huesca (Aragón, Spain), and remarks on the genus *Lobonotus* A. Milne-Edwards, 1863. – Treballs del Museu de Geologia de Barcelona, **20**: 33–43. doi: [10.32800/tmgb.2014.20.0033](https://doi.org/10.32800/tmgb.2014.20.0033)
- PATTON, W.K. (1994): Distribution and ecology of animals associated with branching corals (*Acropora* spp.) from the Great Barrier Reef, Australia. – Bulletin of Marine Science, **55** (1): 193–211.
- PEYROT-CLAUDE, M. (1989): Crab cryptofauna (Brachyura and Anomura) of Tikehau, Tuamotu Archipelago, French Polynesia. – Coral Reefs, **8** (3): 109–117. doi: [10.1007/BF00338266](https://doi.org/10.1007/BF00338266)
- POMAR, L., BACETA, J.I., HALLOCK, P., MATEU-VICENS, G. & BASSO, D. (2017): Reef building and carbonate production modes in the westcentral Tethys during the Cenozoic. – Marine and Petroleum Geology, **83**: 261–304. doi: [10.1016/j.marpetgeo.2017.03.015](https://doi.org/10.1016/j.marpetgeo.2017.03.015)
- PORTELL, R.W. & COLLINS, J.S.H. (2004): Decapod crustaceans of the Lower Miocene Montpelier Formation, White Limestone Group of Jamaica. – Cretaceous Research, **3** (1/2): 109–126.
- PUEYO, E., MILLÁN, H. & POCOVÍ, A. (2002): Rotation velocity of a thrust: a paleomagnetic study in the External Sierras (southern Pyrenees). – Sedimentary Geology, **146** (1–2): 191–208. doi: [10.1016/S0037-0738\(01\)00172-5](https://doi.org/10.1016/S0037-0738(01)00172-5)
- PUIGDEFABREGAS, C. (1975): La sedimentación molásica en la Cuenca de Jaca. – Pirineos, **104**: 1–188.
- RATHBUN, M.J. (1929): A new crab from the Eocene of Florida. – Proceedings of the United States National Museum, Bulletin, **75**: 1–4.
- RATHBUN, M.J. (1930): The Cancroid crabs of America of the families Euryalidae, Portunidae, Atelecyclidae, Cancridae and Xanthidae. – United States National Museum Bulletin, **152**: 1–609. doi: [10.5479/si.03629236.152.i](https://doi.org/10.5479/si.03629236.152.i)
- REMACHA, E., OMS, O., GUAL, G., BOLANO, F., CLIMENT, F., FERNÁNDEZ, L.P., CRUMEYROLLE, P., PETTINGILL, H., VICENTE, J.C. & SUAREZ, J. (2003): Sand-rich turbidite systems of the Hecho Group from slope to basin plain; facies, stacking patterns, controlling factors and diagnostic features. – AAPG International Conference and Exhibition, Barcelona, Spain, September 21–24. Geological Field Trip: 12.
- REMACHA, E., FERNÁNDEZ, L.P. & MAESTRO, E. (2005): The transition between sheet-like lobe and basin-plain turbidites in the Hecho basin (south-central Pyrenees, Spain). – Journal of Sedimentary Research, **75**: 798–819. doi: [10.2110/jsr.2005.064](https://doi.org/10.2110/jsr.2005.064)
- REUSS, A. (1871): *Phymatocarcinus speciosus*, eine neue fossile Krabbe aus dem Leithakalke des Wiener Beckens. – Sitzungsberichte der kaiserlichen Akademie der Wissenschaften in Wien, **63**: 325–330.
- SAMOUELLE, G. (1819): The entomologist's useful compendium, or an introduction to the British insects, etc. – 496 pp.; London (Boys).
- SCHWEITZER, C.E. & FELDMANN, R.M. (2015): Faunal turnover and niche stability in marine Decapoda in the Phanerozoic. – Journal of Crustacean Biology, **35**: 633–649. doi: [10.1163/1937240X-00002359](https://doi.org/10.1163/1937240X-00002359)

- SCHWEITZER, C.E., FELDMANN, R.M. & KARASAWA, H. (2018): Part R, Revised, volume 1, Chapter 8T2: Systematic descriptions: Superfamily Carpilioidea. – *Treatise Online*, **112**: 22 pp.
- SERÈNE, R. (1965): Guide for curators of brachyuran collections in southeast Asia. – Applied Scientific Research Corporation of Thailand: 1–65.
- SILVA-CASAL, R., AURELL, M., PAYROS, A., PUEYO, E.L. & SERRA-KIEL, J. (2019): Carbonate ramp drowning caused by flexural subsidence: the South Pyrenean middle Eocene foreland basin. – *Sedimentary Geology*, **393–394**: 105538. doi: [10.1016/j.sedgeo.2019.105538](https://doi.org/10.1016/j.sedgeo.2019.105538)
- SILVA-CASAL, R., PAYROS, A., MARTÍNEZ-BRACERAS, N. & AURELL, M. (2017): The Eocene marine sedimentation in the southern Pyrenean Basin: a basin-slope-platform transect. – International Meeting of Sedimentology 2017 (33rd IAS & 16th ASF Joint Meeting), Field Trip 1, Guidebook: 56 pp.; Toulouse.
- STICKLEY, C.E., ST JOHN, K., KOÇ, N., JORDAN, R.W., PASSCHIER, S., PEARCE, R.B. & KEARNS, L.E. (2009): Evidence for middle Eocene Arctic sea ice from diatoms and ice-rafted debris. – *Nature*, **460** (7253): 376–379. doi: [10.1038/nature08163](https://doi.org/10.1038/nature08163) PMID: [19606146](https://pubmed.ncbi.nlm.nih.gov/19606146/)
- STIMPSON, W. (1858): *Prodromus descriptionis animalium evertibratum, quae in expeditione ad oceanum Pacificum septentrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit. Pars VII. Crustacea Anomura.* – Proceedings of the Academy of Natural Sciences of Philadelphia, **10**: 225–252.
- STIMPSON, W. (1860): *Prodromus descriptionis animalium evertibratorum, quae in expeditione ad oceanum Pacificum septentrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit. Pars VIII. Crustacea Macrura.* – Proceedings of the Academy of Natural Sciences of Philadelphia, **12**: 22–47.
- STOLICZKA, F. (1871): Observations of fossil crabs from Tertiary deposits in Sind and Kutch. – *Memoirs of the Geological Survey of India, Palaeontologica Indica*, **1** (1): 1–16.
- TESSIER, G., BESCHIN, C. & BUSULINI, A. (2011): New evidence of coral-associated crustaceans from the Eocene of the Vicenza Lessini (NE Italy). – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **260** (2): 211–220. doi: [10.1127/0077-7749/2011/0168](https://doi.org/10.1127/0077-7749/2011/0168)
- TSANG, L.M., SCHUBART, C.D., AHYONG, S.T., LAI, J.C., AU, E.Y., CHAN, T.Y., NG, P.K. & CHU, K.H. (2014): Evolutionary history of true crabs (Crustacea: Decapoda: Brachyura) and the origin of freshwater crabs. – *Molecular Biology and Evolution*, **31** (5): 1173–1187. doi: [10.1093/molbev/msu068](https://doi.org/10.1093/molbev/msu068) PMID: [24520090](https://pubmed.ncbi.nlm.nih.gov/24520090/)
- VÍA, L. (1969): Crustáceos decápodos del Eoceno español. – *Pirineos*, **91–94**: 1–469.
- VÍA-BOADA, L. (1973): Datos para el estudio de los crustáceos decápodos del Eoceno circumpirenaico. – *Pirineos*, **107**: 55–70.
- VÍA-BOADA, L. (1991): Fauna carcínica del Eoceno Alicantino. – *Revista Española de Paleontología, Extraordinary Number*: 181–187.

Manuscript received: November 27th, 2019.

Revised version accepted by the guest editors and the Stuttgart editor: February 16th, 2020.

Addresses of the authors:

FERNANDO A. FERRATGES, MARCOS AURELL, Departamento de Ciencias de la Tierra-IUCA, Universidad de Zaragoza, Zaragoza 50009, Spain;
e-mails: fer.afk87@gmail.com, maurell@unizar.es

SAMUEL ZAMORA, Instituto Geológico y Minero de España, C/Manuel Lasala, 44/9B, Zaragoza 50006, Spain;
e-mail: s.zamora@igme.es