

An Aptian sponge-associated decapod crustacean assemblage from Cal Cassanyes (Catalonia, north-east Iberian Peninsula): Taxonomy and palaeoecological implications[☆]

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ABSTRACT

A highly diverse decapod crustacean fauna is described from the classic Aptian outcrop of Cal Cassanyes (Castellet i la Gornal) in Catalonia. Although decapod crustaceans are a minor component of the rich invertebrate assemblages at that locality, the just over fifty specimens collected comprise sixteen taxa assignable to the Macrura, Anomura and Brachyura. Of these, the last-named are the most prominent group, comprising eleven species, representing seven families, inclusive of one representative of the Eubrachyura. On the basis of this material, two new genera and five new species are erected, namely *Pagurus? garrafensis* sp. nov., *Garrafosopon* gen. nov. *angustus* (Wright and Collins, 1972) comb. nov., *Vectis blesai* sp. nov., *Mesodromilites prietoi* sp. nov., *Necrocarcinus mariae* sp. nov. and *Iberodorippe vinea* gen. nov., sp. nov. In addition, *Hoploparia* sp., an indeterminate axiid and one paguroid, as well as one indeterminate galatheid are recorded here. Material of *Distefania incerta* (Bell, 1863), the commonest species at the study site by far, of *Goniodromites laevis* (Van Straelen, 1940) and of *Etyxanthosia fossa* (Wright and Collins, 1972) represents the first Aptian and stratigraphically oldest records for these taxa. Added to this list are also *Eodromites* sp., *Paranecrocarcinus?* sp. and *Pseudonecrocarcinus?* sp. The high decapod crustacean diversity at Cal Cassanyes establishes this locality as the richest Aptian assemblage from the Iberian Peninsula, but also one of the richest in the world. The faunal assemblages here are dominated by sponges, and the varied composition of the decapod crustacean faunas can be linked to upwelling currents which provided abundant nutrients. In fact, the establishment of sponge communities played a crucial role in activating the food chain and functioned similarly to a patch reef, creating a relatively sheltered environment that facilitated the colonisation of other invertebrate communities, including decapod crustaceans. The latter occupied various trophic levels as both primary and secondary consumers. Current knowledge of Early Cretaceous decapod crustaceans is scant and hinders a thorough palaeobiogeographical analysis. The present study emphasises the challenges surrounding the identification of endemic taxa, thus impacting our understanding of decapod crustacean palaeobiogeography of the late Early Cretaceous.

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1. Introduction

The Cal Cassanyes property (Castellet i la Gornal, Alt Penedès) in Catalonia is situated on a horst of the south-western margin of the Garraf Massif (Figs. 1, 2A, B). This is a classic area of fossiliferous Aptian strata, well known since the works of, among others, [Almera \(1900\)](#) and [Lambert \(1927\)](#), who recorded numerous echinoids, ammonites, bivalves and, as a minor component, decapod crustaceans. One of the most iconic works on that locality is an extensive study by [Lagneau-Herenguer \(1962\)](#), who described rich faunas of siliceous sponges (see also [Moreno-Bedmar et al., 2009b](#) and references therein). As far as decapod crustaceans are concerned, [Vía \(1951\)](#) recorded a single chela that he attributed to *Homarus edwardsi* [Robineau-Desvoidy, 1849](#), as well as remains of a single carapace and chela assigned to *Distefania centrosa* [Van Straelen, 1940](#) [= *D. incerta* ([Bell, 1863](#))].

At the start of the 21st century, excavations on the hill slopes and clearance of land for planting new vineyards, expanded the pre-existing outcrops (Fig. 2) and allowed both *in-situ* and *ex-situ* collection of several specimens of decapod crustaceans, associated with sponges. [Moreno-Bedmar et al. \(2008\)](#) published preliminary notes and recorded the presence of decapod crustaceans. Subsequently, [Ossó et al. \(2022\)](#) presented a more detailed picture of those faunas.

With sixteen taxa documented in the present paper, the decapod crustacean assemblage of Cal Cassanyes represents the richest Aptian fauna currently known to date from the Iberian Peninsula and globally, not only on account of the relative abundance of the remains, but also of its diversity, particularly among brachyuran crabs. The remains collected from this relatively small outcrop (Fig. 2) comprise both fragmentary and near-complete carapaces, as well as isolated chelae. The taxonomic evaluation of these specimens forms the core of the present paper, in which two new genera and five new species are erected.

Furthermore, the palaeobiogeography of the Cal Cassanyes faunal assemblage is discussed and compared with other known Aptian decapod crustacean faunas from the Iberian Peninsula (e.g., [López-Horgue and Bodego, 2017](#); [Ossó et al., 2018, 2021](#); [Ossó and Moreno-Bedmar, 2020](#); [Ferratges et al., 2021](#); [García-Penas et al., 2023](#)) and other basins in the world (e.g., [Wright and Collins, 1972](#); [Van Bakel et al., 2021c](#)), as well as with both older and younger decapod crustacean communities (e.g., [Klomp maker, 2013](#); [Vega et al., 2019](#)).

The palaeoenvironment of the Cal Cassanyes site is also described and the palaeosynecology of its biota explored by comparison with similar extant communities. In the literature, settings with sponges have been shown, albeit less importantly than coralline environments, to have been sheltered habitats for decapod crustaceans, chiefly brachyurans, and to have played an important role in their diversification, for example, during the Late Jurassic (e.g., [Klomp maker et al., 2013, 2020](#)). Indeed, a large number of decapod crustaceans have been recorded from an Upper Jurassic sponge-microbial megafacies belt along the northern shelf of the Tethys Ocean (e.g., [Krautter, 1998](#)), also referred to as spongiolithic limestones, sponge microbialites or siliceous sponge-microbial buildups. These biohermal or sea mound structures usually form a slightly positive topography and include cryptic habitats (e.g., [Feldmann et al., 2006](#); [Schweitzer et al., 2007, 2017a](#); [Schweigert and Koppka, 2011](#); [Starzyk, 2015a](#); [Krobicki and Zatoń, 2008](#); [Klomp maker et al., 2020](#); [Schweigert, 2021](#)).

However, during the Early Cretaceous, following the decline of those sheltered habitats at the end of Jurassic, meiurans (Brachyura and Anomura) and axiid decapod crustaceans inhabited mainly siliciclastic-rich environments (e.g., [Klomp maker et al., 2013](#); [Schweitzer and Feldmann, 2015](#)). Accordingly, the Cal Cassanyes

assemblage has the potential of becoming a reference point for high-diversity decapod crustacean faunas from sponge-rich, siliciclastic settings during the Early Cretaceous.

2. Geological setting

The Aptian marine strata studied crop out at Cal Cassanyes and are situated in the Sitges Sub-basin, the most subsiding semigraben of the Upper Jurassic–Lower Cretaceous Garraf Basin of eastern Iberia (Salas et al. in [Martín-Chivelet et al., 2019](#)). The Garraf and Maestrat depocentres are neighbouring and related basins (Salas et al. in [Martín-Chivelet et al., 2019](#)). The Maestrat and Garraf basins were part of the Iberian-Catalan Rift System (Salas et al., 2001). Salas et al. in [Martín-Chivelet et al. \(2019\)](#) distinguished six syn-rift/post-rift phases that marked the evolution of the Iberian–Catalan Rift System. The Aptian rocks studied herein were deposited during the Early Cretaceous (Barremian–early Albian) Rifting Cycle 3 of Salas et al. in [Martín-Chivelet et al. \(2019\)](#), which recorded a peak of subsidence in the Garraf and Maestrat basins ([Bover-Arnal et al., 2010](#)). The Garraf Basin was inverted during the Alpine contraction (Paleogene); it currently forms the meridional part of the Catalan Coastal Chain, a system of fold-and-thrust belts (Salas et al. in [Martín-Chivelet et al., 2019](#)). Finally, an extensional episode, starting during the Late Oligocene, overprinted onto the Catalan Coastal Chain (Salas et al., 2001). This last phase was related to the opening of the València Trough ([Roca and Guimerà, 1992](#)).

In comparison to the related Maestrat Basin, previous work on the Aptian succession of the Garraf Basin is few and far between. For the former basin several papers, focused on a wide range of topics including basin analysis, stratigraphy, sedimentology and palaeontology (of different biotic groups) have been published during the last two decades (e.g., [Salas et al., 2001](#); [Vennin and Aurell, 2001](#); [Moreno-Bedmar et al., 2009a, 2010](#); [Embry et al., 2010](#); [Schlagintweit et al., 2010](#); [Skelton et al., 2010](#); [Bover-Arnal et al., 2010, 2015, 2016, 2022](#); [Peropadre et al., 2013](#); [García et al., 2014](#); [Baudouin et al., 2016](#); [González-León et al., 2016, 2017](#); [Ossó et al., 2018](#); [Salas et al. in; Martín-Chivelet et al., 2019](#); [García-Penas et al., 2022, 2023](#)). In contrast, contributions on the Garraf Basin during the last two decades have focused mainly on its palaeontology, in particular cephalopods ([Moreno-Bedmar and García, 2009](#); [Moreno-Bedmar et al., 2009b, 2016, 2017](#); [Baudouin et al., 2016](#); [Matamalas-Andreu and Moreno-Bedmar, 2017](#)).

Recent publications on the stratigraphy and basin analysis of the Garraf Basin include [Albrich et al. \(2006\)](#), [Salas and Moreno \(2008\)](#) and Salas et al. in [Martín-Chivelet et al. \(2019\)](#). A key contribution on Aptian stratigraphy of the Garraf Basin is the unpublished work by [Salas and Moreno \(2008\)](#), in which various units were informally defined. These lithostratigraphical units have subsequently been used in formal publications ([Moreno-Bedmar and García, 2009](#); [Moreno-Bedmar et al., 2009b, 2016, 2017](#); [Martín-Closas et al., 2018, 2021](#)). Strata exposed at the Cal Cassanyes outcrop belong to the Aptian Marls of Vallcarca Unit ([Moreno-Bedmar et al., 2009b](#)). As defined by [Salas and Moreno \(2008\)](#), the Vallcarca Unit consists of grey to bluish-grey and altered yellowish marls alternating with decimetre-thick marly limestone and limestone beds. These strata crop out at the Vallcarca quarry (Uniland Cementera S.A., Sitges), both along currently exploited and abandoned faces. Other localities where the Marls of Vallcarca Unit crop out include Jafra, Mas Ricard, Mas de l'Artís or the Pujol Florit-Cal Cassanyes-Casa Alta area (Fig. 1C). Biota from the Marls of Vallcarca Unit comprise mainly ammonites, nautiloids, planktic and benthic foraminifera, crustaceans, bivalves, echinoderms, brachiopods and siliceous and calcareous sponges. The unit was dated as early to late Aptian by means of ammonites (Salas and Moreno, 2008; [Moreno-Bedmar and García, 2009](#); [Moreno-Bedmar et al.,](#)

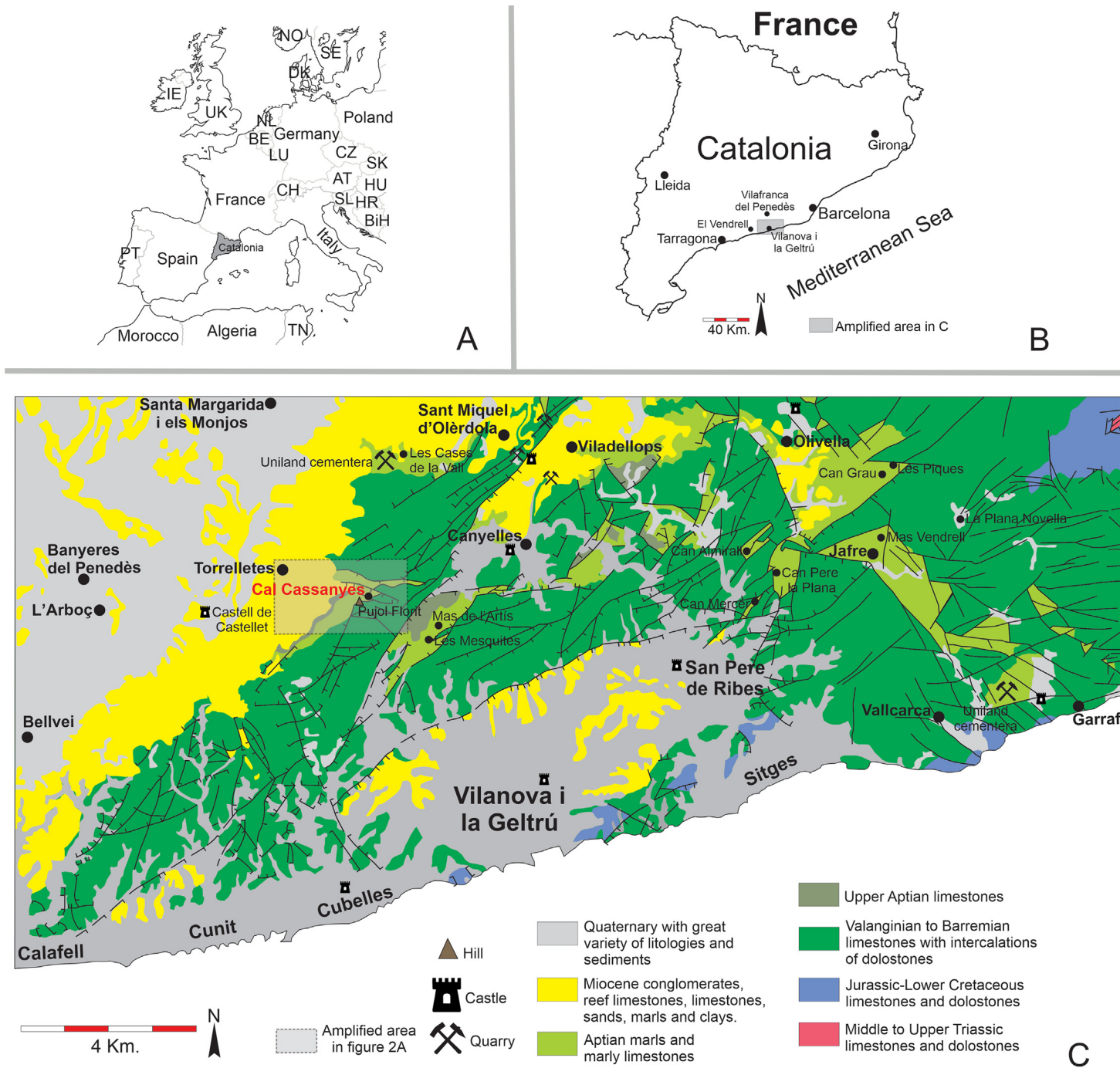


Fig. 1. A. Geographical position of Catalonia in relation to Europe and North Africa. B. Location of the study area indicated by grey rectangle. C. Geological map of the Garraf Basin; the Cal Cassanyes area is highlighted by grey rectangle (modified from 1:50,000 Geological Map of Catalonia by the Institut Cartogràfic i Geològic de Catalunya (https://betaportal.icgc.cat/visor/client_utfgrid_geo.html), accessed on July 4, 2023).

2009b, 2016; Matamalas-Andreu and Moreno-Bedmar, 2017). In the Cal Cassanyes area, Aptian marine strata crop out in several vineyards. The vineyard found in the highest topographical position located to the north-west of the study area is informally named “upper vineyard”; this is the one that has yielded the decapod crustacean assemblage described herein (Fig. 2). In this vineyard, the middle part of the Marls of Vallcarca Unit is exposed, consisting of yellowish to ochre-coloured marls, marly limestones and greyish limestones that range in age between the latest early to earliest late Aptian (Moreno-Bedmar et al., 2009b) and include the *Dufrenoyia furcata* and *Epicheloniceras martini* ammonite zones (Fig. 2C). This stratigraphical interval belongs to a subunit referred to as ‘Porifera marls’, on account of the extraordinary abundance of sponges (Moreno-Bedmar et al., 2009b). The levels at this small outcrop are locally extensively burrowed; it has yielded a large number of siliceous sponges but also nautiloids, ammonites, echinoids, bivalves, crinoids, brachiopods and the decapod crustaceans

described herein. Echinoids represented include rare cidaroids, *Hyposalenia* sp., *Tetragramma* sp., and abundant *Discoidea decoratus* (Desor, 1842) and *Platystrophia collegerii* (Sismonda, 1843) (Fig. 3).

3. Sedimentary evolution of the Cal Cassanyes section

The sequence exposed along the vineyards (Fig. 4A) attains a thickness of 50 m (Fig. 2C) and comprises a cyclic alternation of marls and limestones (Fig. 4B). In the lower first 37.5 m of the succession (Fig. 2C), limestones mainly exhibit packstone (Fig. 4C), rarely wackestone, textures, which contain sponge spicules (Fig. 4C, D), miliolids and other unidentified small benthic foraminifera, fragments of oysters and other undetermined molluscs, echinoids and decapod crustaceans, as well as sections of serpulids and non-skeletal components such as peloids. Completely preserved skeletons of siliceous sponges, fragments of crustaceans and ammonoid moulds and casts are also common (Fig. 2C). The deposition of silica

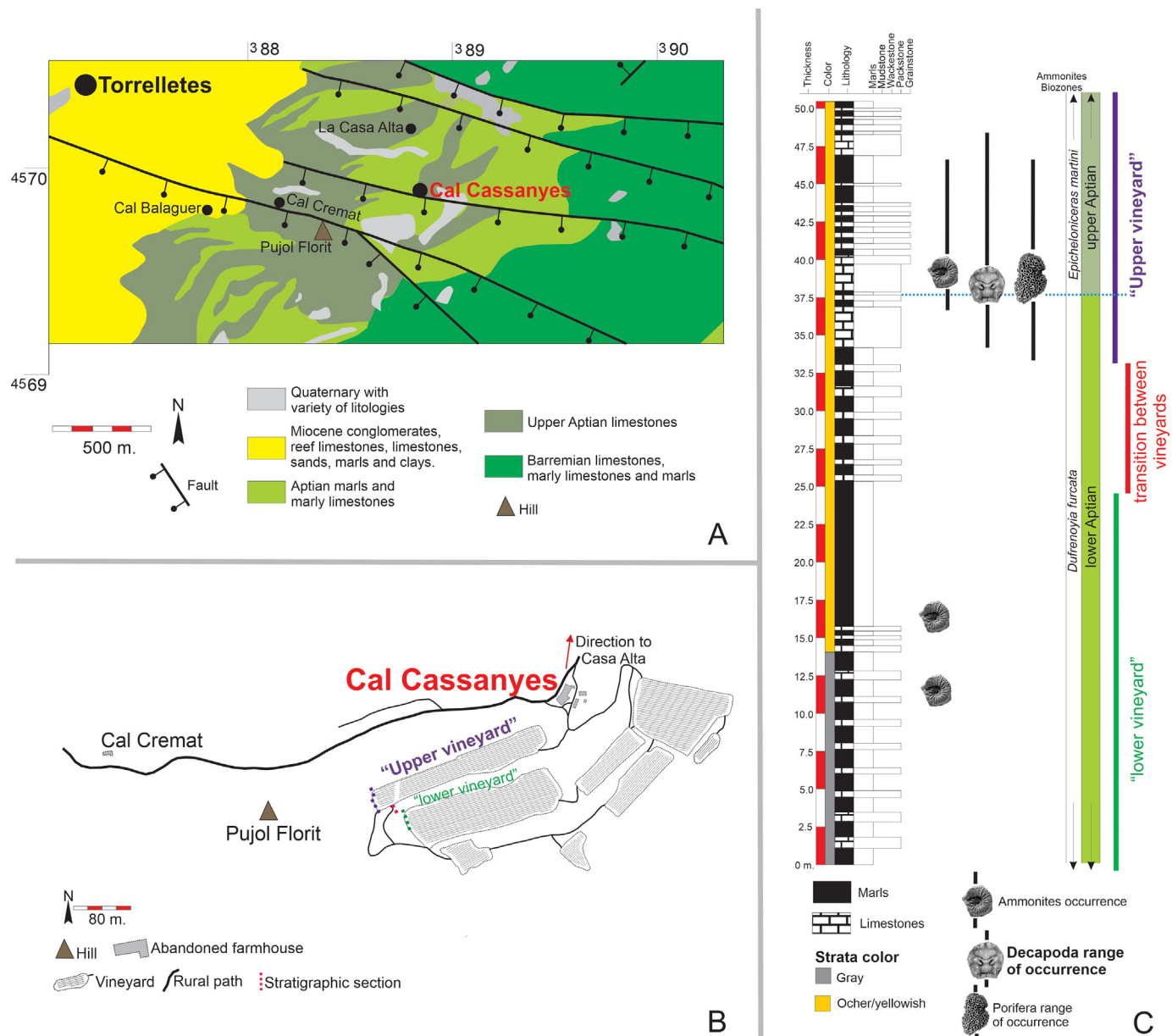


Fig. 2. A. Geological map of the Cal Cassanyes area, adapted from ICGC (2017). B. Illustration depicting roads, farms and vineyards in the study area, along with the location of the stratigraphical section. C. Stratigraphical section of Cal Cassanyes, highlighting the occurrences of decapod crustaceans, ammonites and sponges.

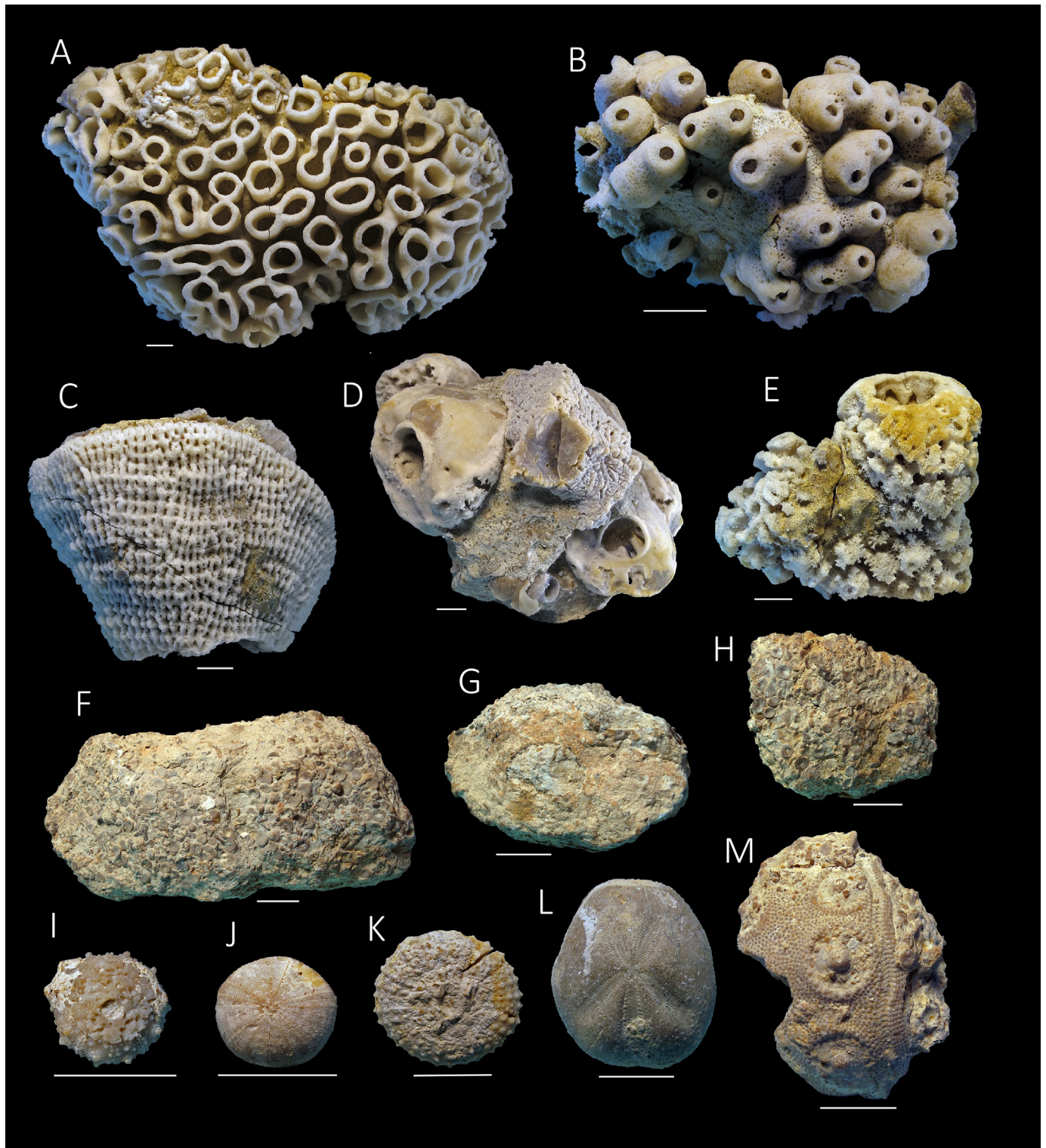


Fig. 3. Associated fauna from the uppermost lower Aptian to lowermost upper Aptian (*Dufrenoyia furcata* and *Epicheloniceras martini* ammonite zones, respectively) of Cal Cas-sanyes, Castellet i la Gornal (Alt Penedès, Catalonia). A–E. Siliceous sponges; A, *Exanthesis aptiensis* Hérengrer, 1942, MGSB88832; B, *Sarophora aptiensis* Hérengrer, 1942, MGSB88833; C, *Moretiella elegans* Lagneau-Hérengrer, 1962, MGSB88834; D, *Camerospongia asymetrica* Lagneau-Hérengrer, 1962, MGSB88835; E, *Linonema ramosa* Lagneau-Hérengrer, 1962, MGSB88836. F–H, decapod burrows with the walls reinforced with orbitolinids, F, H, MGSB88837; G, MGSB88838. I–M, echinoids, I, *Hyposalenia* sp., MGSB88839; J, *Discoides decoratus* (Desor, 1842), MGSB88840; K, *Tetragramma* sp., MGSB88841; L, *Pliotaxaster collegii* (Sismonda, 1843), MGSB88842; M, indeterminate cidaroid, MGSB88843. Scale bar equals 10 mm.

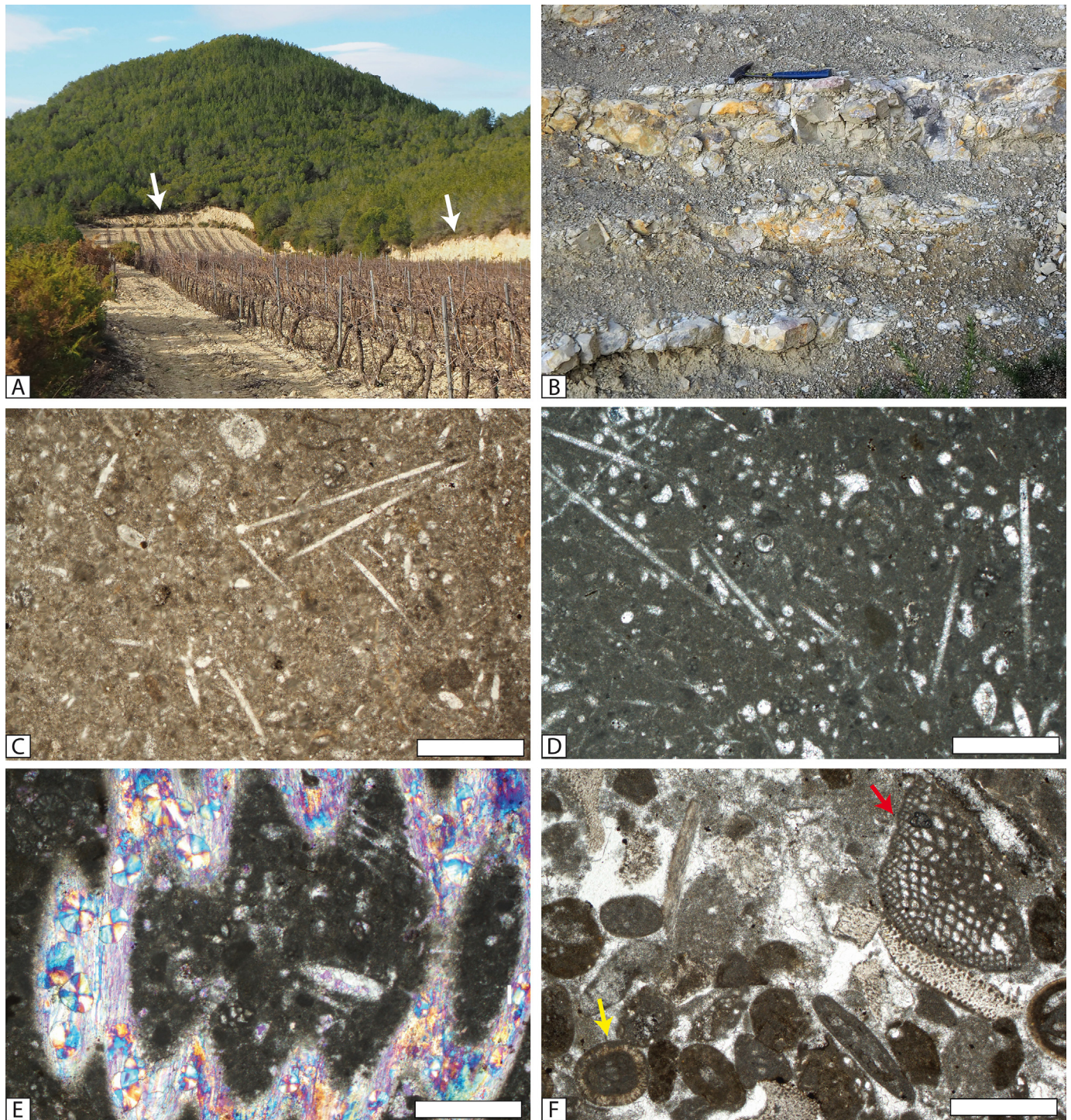


Fig. 4. A. Panoramic view of the upper vineyard (see Fig. 2B) with outcrop succession logged indicated by white arrows. B. Detail of alternating marls and limestone beds of the lower part of the succession studied. Hammer = 32 cm. C. Plane-parallel light photomicrograph of a sample from the lower part of the succession studied, exhibiting a fine-grained packstone texture with abundant sponge spicules. Scale bar equals 0.5 mm. D. Polarised-light microscope image showing a micrite-rich microfacies with sponge spicules. Scale bar equals 0.5 mm. E. Polarised-light microscope image combined with a retardation plate of a silicified bivalve exhibiting length-slow quartz (moganite) spherulites within a peloidal and foraminiferal packstone. Scale bar equals 0.5 mm. F. Grainstone texture sampled in the upper part of the succession studied showing an ooid (yellow arrow) and an orbitolinid (red arrow) together with peloids, foraminifera, fragments of molluscs and echinoids. Scale bar equals 0.5 mm.

by sponges led to local silicification of skeletal components during diagenesis (Fig. 4E).

The sponge- and decapod crustacean-rich deposits analysed here indicate deposition in an outer carbonate platform environment subjected to high nutrient inputs, likely brought in by upwelling. This distal platform succession is punctuated by local

limestone beds with packstone textures and exhibiting more proximal biotic associations including fragments of the calcareous alga *Permocalculus*, dayscladaceans, corals, bryozoans and orbitolinid skeletons that mark high-frequency regressions.

From 37.5 m to the top of the section logged, the limestone beds alternating with marls show grainstone textures (Figs. 2C, 4F), as

well as packstone textures, and contain non-skeletal components such as ooids (Fig. 4F), intraclasts and peloids. Skeletal components identified in the upper part of the succession include abundant orbitolinids (Fig. 4F), sponge spicules, miliolids and other benthic foraminifera, fragments of corals, oysters and other molluscs, bryozoans, echinoids, dasycladaceans and serpulids. Ammonites, decapod crustaceans, wholly preserved siliceous sponges and bacinellid fabrics (*sensu* Schlagintweit and Bover-Arnal, 2013) are also common constituents (Fig. 2C).

The presence of ooids, intraclasts, corals and dasycladaceans, together with the occurrence of grainstone textures, indicate shallower- and higher-energy water conditions. Accordingly, upwards from 37.5 m, the succession indicates regressive dynamics with reworking and shedding of platform top carbonates, prograding above marly distal outer platform settings.

4. Material and methods

Decapod crustacean specimens studied herein were collected from the surface, predominantly after plowing of the vineyard and subsequent rain falls. Specimens were prepared using a WEN Pneumatic Engraving pen, needles and/or chemicals, such as potassium hydroxide. Photographs were taken under cold light with a Canon PowerShot G11 camera; specimens were dry. Ten thin sections were produced from samples collected in the field for analysis of microfacies and micropalaeontological content. The repository of all specimens is the Museu de Geologia del Seminari de Barcelona (Barcelona, Catalonia), abbreviated as MGSB.

5. Systematic palaeontology (À. Ossó, B.W.M. van Bakel and P. Artal)

We follow the higher classification scheme of brachyurans proposed by Guinot (2019) (see also Guinot et al., 2013; Jagt et al., 2015), while for the systematics of the superfamily Palaeocorystoidea we adopt the scheme outlined by Van Bakel et al. (2012, 2021a).

Order Decapoda Latreille, 1802

Infraorder Astacidea Latreille, 1802

Superfamily Nephropoidea Dana, 1852

Family Nephropidae Dana, 1852

Genus *Hoplopatria* M'Coy, 1849

Type species. *Astacus longimanus* G.B. Sowerby, 1826, by the subsequent designation of Rathbun (1926).

Species included (in addition to the type, only Early Cretaceous species from Europe, after Tshudy and Sorhannus, 2003). *Hoplopatria aspera* Harbort, 1905, *H. dentata* (Roemer, 1841), *H. edwardsi* (Robineau-Desvoidy, 1849), *H. longimana* (Sowerby, 1826), *H. minima* de Tribolet, 1876; *H. pelseneeri* (Van Straelen, 1936) and *H. triboleti* Borissjak, 1904.

***Hoplopatria* sp.**

Fig. 5A, B

1951 *Homarus* (*Hoplopatria*) *edwardsi* Robineau-Desvoidy; Vía, pp. 161, 162, text-fig. IV, fig. 4.

1988 *Hoplopatria edwardsi*; Vía, p. 350.

1989 *Hoplopatria edwardsi* (Robineau-Desvoidy, 1849); Solé and Vía, p. 25.

2009a *Hoplopatria edwardsi* (Robineau-Desvoidy, 1849); Garassino et al., pp. 88, 92.

Locality. Cal Cassanyes-Casa Alta, Castellet i la Gornal (Alt Penedès, Catalonia).

Stratigraphical horizon. Uppermost lower Aptian to lowermost upper Aptian (*Dufrenoyia furcata* and *Epicheloniceras martini* ammonite zones, respectively).

Studied material and measurements. A single right palm of propodus, MGSB11942; length 18 mm, height 9 mm.

Description. Palm of right propodus subtrapezoidal, elongated, length almost twice height, higher in distal third. Outer surface slightly convex, granulated, coarsely in upper third; weak ridge paralleling lower margin. Inner surface vaulted medially. Upper margin almost straight, bearing two rows of seven or eight irregular spines. Lower margin slightly convex, blunt and with attenuate granulation. Fingers not preserved.

Remarks. Vía (1951) first recorded and described this propodus, assigning it to *Homarus* (*Hoplopatria*) *edwardsi*. We concur with the generic placement, but disagree with the species attribution. Robineau-Desvoidy (1849, pp. 108–111, pl. 4, fig. 1) noted that propodi of his new species, *H. edwardsi*, had a spiny upper margin and crenulated lower margin. This differentiates them from the Cal Cassanyes specimen which has a blunt lower margin. For the same reason, assignment to *H. dentata* is discarded (compare Roemer, 1841, pl. 16, fig. 24c; Woods, 1931, pl. 26, fig. 1). *Hoplopatria longimana* has a longer palm than the present specimen (see Woods, 1931, pl. 25, fig. 2.5; pl. 26, fig. 2a), whereas *H. minima* has a shorter one (de Tribolet, 1876, pl. 1, fig. 3). However, the Cal Cassanyes specimen strongly recalls chelae of *Hoplopatria collignoni* (Van Straelen, 1949) (= *H. intermedia* Secrétan, 1964), from the Albien of Madagascar, in having a spiny upper and a blunt lower margin (see Charbonnier et al., 2012, fig. 15G–I). In any case, the poor preservation of the chela and especially the absence of dactyli and associated carapace remains, preclude a specific assignment.

Infraorder Axiidea de Saint Laurent, 1979

Axiid; genus and species indeterminate

Fig. 5C

Locality. Cal Cassanyes, Castellet i la Gornal (Alt Penedès, Catalonia). *Stratigraphical horizon.* Uppermost lower Aptian to the lowermost upper Aptian (*Dufrenoyia furcata* and *Epicheloniceras martini* ammonite zones, respectively).

Studied material and measurements. A fragmentary left palm MGSB86072a, greatest length 6.25 mm, height 3.35 mm, plus three other incomplete remains of left palms of similar size (MGSB86072b–d).

Description. Left palm subrectangular, elongated, almost twice as long as high; cuticle smooth. Upper margin straight, ridged, a row of separated setal pits paralleling margin. Lower margin straight, subparallel with upper margin, with setal pits visible. Inner surface weakly convex medially. Pollex short.

Remarks. Vía (1951, pp. 165, 167, text-fig. VII, fig. 7) recorded the palm of an axiid from the Aptian of Viladellós (Olèrdola, Alt Penedès), a locality geographically close to Cal Cassanyes, as *Calianassa infracretacea* de Tribolet, 1874, a form originally described from the Hauterivian of France (see de Tribolet, 1874, pp. 353, 354, pl. 12, fig. 2; Hyžný and Klompmaker, 2015, fig. 13C, D). That assignment was based on the subrectangular shape of the palm, the smooth cuticle and the row of setal pits that run parallel to the upper cheliped margin. Although both specimens could be considered conspecific and similar to *C. infracretacea*, any generic and suprafamilial placement cannot be made with certainty given the fact that, according to Hyžný and Klompmaker (2015, p. 739) and Hyžný and Luque (2019, p. 87), *C. infracretacea* awaits revision. For this reason, we prefer to leave it as 'axiid' (M. Hyžný, pers. comm., September 1, 2021).

Infraorder Anomura MacLeay, 1838

Superfamily Paguroidea Latreille, 1802

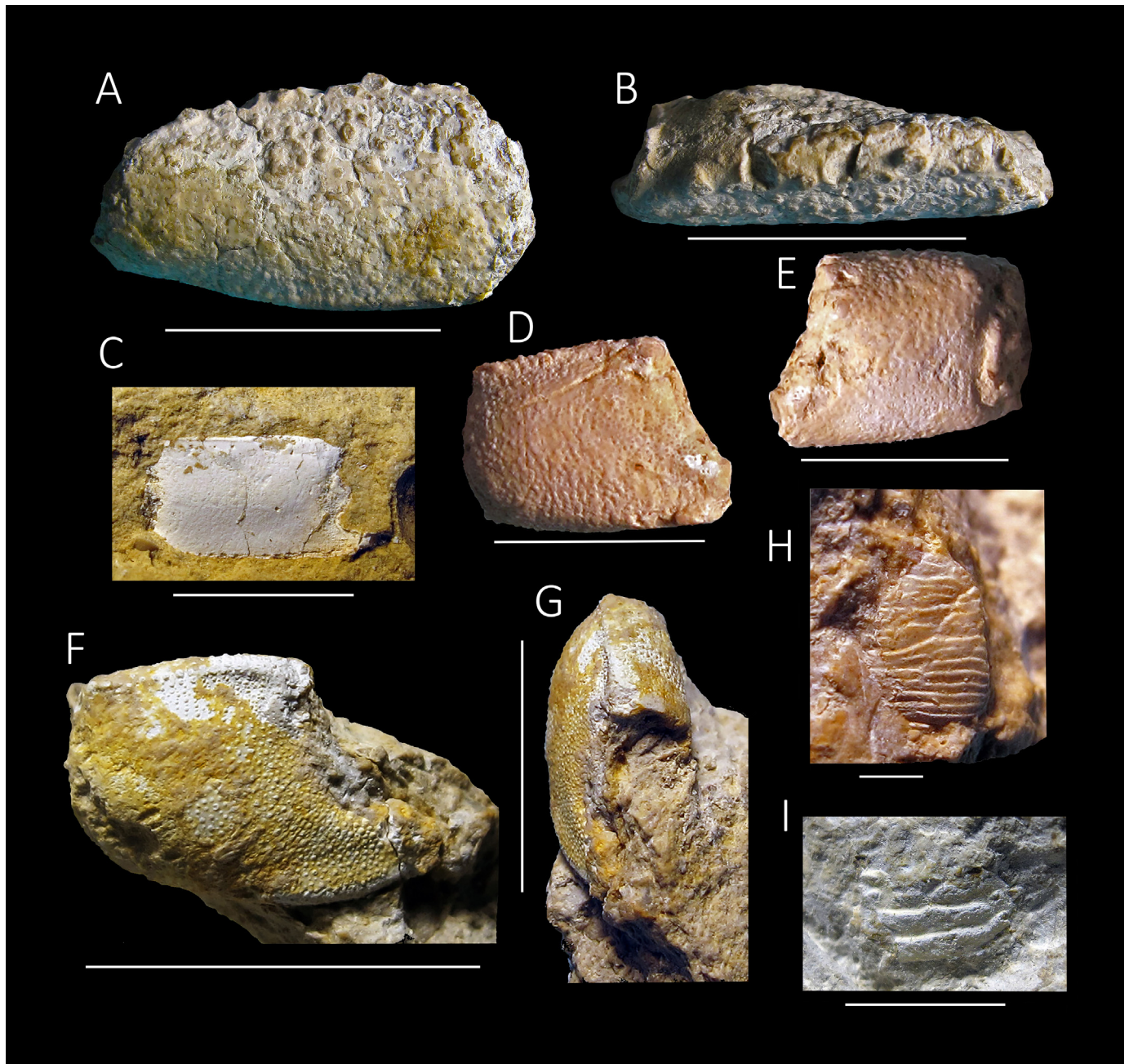


Fig. 5. Decapod crustaceans from the uppermost lower Aptian to lowermost upper Aptian (*Dufrenoyia furcata* and *Epicheloniceras martini* ammonite zones, respectively) of Cal Cassanyes, Castellet i la Gornal (Alt Penedès, Catalonia). A, B. *Hoploparia* sp. (MSG811942), right palm; outer margin and upper margin, respectively. C. Indeterminate axiid (MSG86072a), left palm, inner margin. D, E. Indeterminate paguroid (MSG86079a), right propodus; outer margin and inner margin, respectively. F, G. *Pagurus?* *garrafensis* sp. nov., **holotype** (MSG874530) outer margin and frontal view, respectively. H, I. Galatheoidea indeterminate, dorsal views (H, MSG86073a; I, MSG86073b). Scale bars equal 10 mm (A, B, F, G), 5 mm (C–E, I) and 1 mm (H).

Paguroid; genus and species indeterminate

Fig. 5D, E

Locality. Cal Cassanyes, Castellet i la Gornal (Alt Penedès, Catalonia). **Stratigraphical horizon.** Uppermost lower Aptian to the lowermost upper Aptian (*Dufrenoyia furcata* and *Epicheloniceras martini* ammonite zones, respectively).

Studied material and measurements. Two right propodi: MSG86079a, length 6.5 mm, height 4.7 mm; and MSG86079b, of similar size (not measured).

Description. Propodus subtrapezoidal, slightly higher distally, surface regularly granulated. Upper margin straight, flattened, double,

slightly spiny outer edge; lower margin faintly convex, blunt; outer margin of palm slightly convex; inner margin of palm gently convex, marked articulation bulge. Fixed finger broken, apparently originally short; dactylus not preserved.

Remarks. The specimens, just two incomplete right palms of propodi does not allow determination of either major or minor propodus of a paguroid. However, its straight and double spiny upper margin and the straight carpo-propodial articulation is reminiscent of the pagurid *Litorepagurus Fraaije, Van Bakel, Jagt, Wallaard and De Coninck, 2023*. However, in the absence of more complete specimens a more precise determination is impossible.

Family ?Paguridae Latreille, 1802

Genus ?*Pagurus* Fabricius, 1775

Type species. *Cancer bernhardus* Linnaeus, 1758, by the subsequent designation of Latreille (1817).

Species included. See Sasaki (2020, pp. 5995–6165).

Pagurus? garrafensis sp. nov.

Fig. 5F, G

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Derivation of name. From Garraf, the mountain massif along which the outcrop is located.

Type locality. Cal Cassanyes, Castellet i la Gornal (Alt Penedès, Catalonia).

Stratigraphical horizon. Uppermost lower Aptian to lowermost upper Aptian (*Dufrenoyia furcata* and *Epicheloniceras martini* ammonite zones, respectively).

Studied material and measurements. The sole known specimen is a right propodus embedded in a bioclastic limestone matrix; **holotype** MSGB 74530; length 9.72 mm, height 6.28 mm.

Diagnosis. Right propodus nearly subtrapezoidal, palm slightly higher than long. Surface granulated. Upper margin slightly convex, double-edged. Lower margin clearly convex, sharp edged. Outer upper margin of palm gently convex, with shallow longitudinal depression paralleling upper margin. Inner upper margin straight. Fixed finger robust, triangular in section, nearly half length of propodus, slightly curved inwards.

Description. Right propodus nearly subtrapezoidal, palm slightly higher than long, higher distally, slightly compressed in section. Surface regularly covered by fine granules of equal size, granules becoming spiny near occlusal margin of pollex. Upper margin slightly convex, flattened, double rimmed with rim at outer surface, ornate with row of bluntly rounded granules; inner edge straight, rounded. Lower margin clearly convex, sharp edged. Outer margin of palm gently inflated, becoming fairly concave longitudinally under rim of upper margin, forming shallow longitudinal depression. Fixed finger robust, inverted triangular in section, slightly curved inwards longitudinally, broken but apparently somewhat shorter than half propodus, proximally nearly half height of palm; dactylus not preserved.

Remarks. Placement in a family and genus of the this right chela is fraught with difficulties. Dealing with isolated chelae, rather than with complete, articulated material, makes precise systematic placement nearly impossible. This is a common trait in descriptions of extinct hermit crabs, as amply demonstrated Van Straelen (1925, p. 63), Schweitzer and Feldmann (2001, p. 193) and Schweitzer et al. (2017b, p. 95). The diagnostic keys provided by McLaughlin (2003) or Fraaije et al. (2017, 2022), based on elements that have not been preserved in the material studied herein, cannot be used. In our opinion, the present chela from Cal Cassanyes does not match any of the Cretaceous paguroid species known to date (see Sasaki, 2020, pp. 5260–6245). Below, we compare MSGB 74530 with all of these, irrespective of their current generic or familial placement, and with exclusion of genera that are solely based on shields.

The pagurid *Viapagurus avellanadai* (Vía, 1951), from the Iberian Peninsula, has a larger, more robust and thicker palm, with a spiny upper margin (see Ossó et al., 2018, figs 4A, B, 5A–J), while *Pagurus banderensis* Rathbun, 1935 from the Albian of Texas (USA) has a spiny upper margin and a concave lower margin to the palm and a coarser ornament (see Rathbun, 1935, pl. 9, figs 7, 8). *Pagurus convexus* Whetstone and Collins, 1982, from the Upper Cretaceous of Alabama (USA), has a more coarsely tuberculate ornament, distributed in longitudinal rows (see Whetstone and Collins, 1982,

pl. 1, figs 1–5, 7, 8), whereas in *Pagurus travisensis* Stenzel, 1945 from the Albian of Texas (USA) the palm has a globose cross section and a spiny upper margin (see Stenzel, 1945, pl. 45, figs 16–18). The Early Cretaceous *Palaeopagurus coultoni* (de Tribolet, 1874), from Switzerland, has a coarser ornament disposed in rows and a shorter index (see de Tribolet, 1874, pl. 12, fig. 3), while *P. cretaceus* Mertin, 1941, from the Upper Cretaceous of Germany, has a thicker and rounded propodus (see Mertin, 1941, pl. 5, figs 13, 14; text-fig. 17v, w) and *P. pilsbryi* Roberts, 1962, from the Campanian of Delaware and New Jersey (USA), has a palm with a convex upper margin and concave lower margin; it is thicker in cross section (see Roberts, 1962, pl. 85, figs 1–4). The right chela of *P. vandenengeli* Fraaije, 2003, from the Lower Cretaceous of Yorkshire (UK), appears to be very different to our specimen in spite of the fact that its left chela resembles ours in outline, by having rows of tubercles on the outer surface of propodus (see Fraaije, 2003; Collins et al., 2020, fig. 1B). *Paguristes florum* Collins, Fraaije and Jagt, 1995, from the upper Maastrichtian of the Netherlands and north-east Belgium, resembles the Catalanian form, but differs in having a longitudinal rim at the lower margin of the propodus (see Collins et al., 1995, fig. 4A–D), whereas *Paguristes ouachitensis* Rathbun, 1935, from the Upper Cretaceous of Arkansas (USA), has a different outline and ornament of the left propodus, but the right propodus is unknown (see Rathbun, 1935, pl. 6, figs 9–11) and *P. santamartaensis* Feldmann, Tshudy and Thompson, 1993, from the Upper Cretaceous of Antarctica, also recalls in shape our Catalanian form, but has a shorter palm and coarser and more tightly arranged granular ornament (see Feldmann et al., 1993, fig. 16.1, 2). ?*Paguristes* sp. from the Lower Cretaceous of Colombia has a more elongate propodus, with the palm ornamented with rows of granules (see Luque et al., 2017, fig. 8A), while *Paguristes liwinskii* Fraaije, Van Bakel, Jagt and Marchalski, 2015b, from the Albian of Poland, *Cretacocalcinus josaensis* Ferratges, Hyžný and Zamora, 2021 and *C. fortis* Ferratges and Zamora, in García-Penas et al., 2023, from the Aptian of Spain, have a much thicker, oval cross section, and a shorter pollex (in the former; see Fraaije et al., 2015a; Ferratges et al., 2021, pp. 9–11, fig. 8F–H; García-Penas et al., 2023, fig. 6A, B, D). *Parapaguristes tuberculatus* Bishop, 1986, from the Upper Cretaceous of the USA, differs in rounded cross sections of the propodus and a coarser, spiny ornament (see Bishop, 1983, figs 3–4; Bishop, 1986, figs 3D, 4A–F). *Paracapsulapagurus poponguinensis* Hyžný, Fraaije, Martin, Perrier and Sarr, 2016, from the Maastrichtian of Senegal, has a thicker propodus and coarser granulation (see Hyžný et al., 2016). The same holds true for *Capsulapagurus* spp., which are also characterised by spiny upper margins of the palm (see Fraaije et al., 2011; 2015a). *Annuntidiogenes sunuciorum* Fraaije, Van Bakel, Jagt and Artal, 2008, from the upper Maastrichtian of the Netherlands, has a right propodus that is covered by short transverse striae (see Fraaije et al., 2008, pp. 196–198, fig. 2D; pl. 1, figs 2–5), while *Palaeopetrochirus enigmus* Bishop, 1991, from the Maastrichtian of Mississippi (USA), has a thicker left propodus, only ornamented with granules in the lower half of the palm (see Bishop, 1991, pp. 11–15, fig. 5A–D) and *Striadiogenes frigerioi* Garassino, De Angeli and Pasini, 2009b, from the Cenomanian of Lebanon, has a corrugated dorsal margin on the left propodus (see Garassino et al., 2009b, figs 3–8; Charbonnier et al., 2017, figs 389–392, 394). *Litrepagurus wissantensis* Fraaije, Van Bakel, Jagt, Wallaard and De Coninck, 2023, from the Albian of Wissant (France), clearly differs from the studied propodus by its more convex outer surface and coarser ornament (see Fraaije et al., 2023). The paguroid chelae illustrated by Jagt et al. (2014a, pl. 1, figs 5, 6), from the upper Maastrichtian of the Netherlands and north-east Belgium, resemble our form in outline, but differ in their spiny upper margins and pitted cuticle of the outer margin of the palm.

In view of the above, we propose a new species to accommodate the propodus from Cal Cassanyes, despite the fact that its generic placement remains uncertain. This isolated right propodus, with a convex lower margin and straight upper margin of the palm, with a longitudinal depression paralleling it (probably of a major chela), vaguely recalls that of the extant *Pagurus bernhardus* and allied taxa (compare Sasaki, 2020). Thus, we place our new species tentatively within *Pagurus* (s. lat.).

Superfamily Galatheaidea Samouelle, 1819

Galatheid; genus and species indeterminate

Studied material and measurements. Two partially preserved specimens: MGSB86073a, length 3 mm, width 1.88 mm; MGSB 86073b, length 3.1 mm, width 5 mm.

Locality. Cal Cassanyes, Castellet i la Gornal (Alt Penedès, Catalonia). **Stratigraphical horizon.** Uppermost lower Aptian to lowermost upper Aptian (*Dufrenoyia furcata* and *Epicheloniceras martini* ammonite zones, respectively).

Description. Portion of right half of carapace (MSGB 86073a), crossed by transverse striae, gently vaulted transversely, lateral margin rounded; rostrum and lateral spines not preserved. Anterolateral margin very short, converging forwards. Posterolateral margin straight, gently rounded at posterolateral corner. Posterior margin slightly concave medially. Epigastric region crossed by two transverse striae. Mesogastric and protogastric regions confluent, delimited posteriorly by cervical groove. Urogastric region narrow, transversely elongated, delimited laterally by shallow branchiocardiac groove and anteriorly by cervical groove. Cardiac region appearing inverted subtriangular, faintly divided, separated from urogastric region by post-cervical groove. Intestinal region narrow transversely, crossed by two transverse striae. Hepatic region small. Epibranchial region subtriangular, delimited by anterior and posterior branches of cervical groove. Meso- and metabranchial groove slightly inflated. Cervical groove well marked, widely U-shaped. Ventral remains and appendages not preserved.

Remarks. The fragmentary condition of one of the studied specimens (MSGB 86073a), in particular the absence of a preserved rostrum, precludes a conclusive assignment to any particular systematic placement. However, the general outline and preserved features such as the branchial, protogastric, epigastric and hepatic regions, as well as the transverse striae, are morphologically reminiscent of the well-known Iberian galatheid *Eomunidopsis navarrensis* Van Straelen, 1940 (compare Van Straelen, 1940, pl. 1, figs 3, 4; Klompmaker et al., 2012a, fig. 4A–J). Remains of a second, larger specimen (MSGB 86073b) may be conspecific with the other, in spite of its large striae; the intraspecific variation of *E. navarrensis* was commented upon by Klompmaker et al. (2012a, p. 131). However, the lack of a rostrum precludes definite placement, given that the preserved portions of those dorsal carapaces could belong to either Galatheaidea or Munididae (see Ahlyong et al., 2010). Therefore, both specimens are left in open nomenclature.

Section Podotremata Guinot, 1977

Subsection Dynomeniformia De Haan, 1833

Superfamily Dromioidea De Haan, 1833

Family Dromiidae De Haan, 1833

Subfamily Goniodromitinae Beurlen, 1932

Genus *Distefania* Checchia-Rispoli, 1917

Type species. *Distefania himeraensis* Checchia-Rispoli, 1917, by original designation.

Species included (sensu Jagt et al., 2014b). *Distefania autissiodorensis* (Van Straelen, 1936) [as *Cyclothyreus autissiodorensis*]; *D. calva* Schweitzer and Feldmann, 2010a; *D. cryptica* (Jagt, Van Bakel & Fraaije, 2007) [as *Palaeodromites crypticus*], *D. dacia* Schweitzer

and Feldmann, 2010a; *D. himeraensis* Checchia-Rispoli, 1917; *D. incerta* (Bell, 1863) [as *Cyphonotus incertus*]; *D. lauginigeri* Feldmann, Schweitzer, Baltzly, Bennett, Jones, Mathias, Weaver and Yost, 2013; *D. oxythyreiformis* (Gemmellaro, 1869) [as *Prosopon oxythyreiforme*]; *D. renefraaijei* Klompmaker, Feldmann and Schweitzer, 2012b; *D. renevieri* (de Tribolet, 1876) [as *Prosopon renevieri*]; *D. sinuosulcata* (Wright and Collins, 1972) [as *Palaeodromites sinuosulcatus*]; *D. tangishirazensis* Jagt, Van Bakel, Fraaije and Neumann, 2014b; *D. transiens* (Wright and Collins, 1972) [as *Palaeodromites transiens*] and *D. vanrijsselti* Jagt, Fraaije and Van Bakel, 2014a.

Distefania incerta (Bell, 1863)

Fig. 6A–G

1863 *Cyphonotus incertus* Bell, p. 8, pl. 1, figs 17, 18 only.

1865 *Cyphonotus incertus* Bell, 1863; Woodward and Salter, fig. 17.

1875 *Cyphonotus incertus* Bell, 1863; de Tribolet, p. 80.

1877 *Cyphonotus incertus* Bell, 1863; Woodward, p. 1.

1887 *Cyphonotus incertus* Bell, 1863; Forir, p. 192.

1898 *Cyphonotus incertus* Bell, 1863; Carter, p. 20 (partim).

1929 *Cyphonotus incertus* Bell, 1863; Glaessner, p. 134.

1933 *Cyphonotus incertus* Bell, 1863; Glaessner, p. 584, pl. 28, figs 8–10.

1936 *Cyphonotus incertus* Bell, 1863; Van Straelen, p. 28.

1940 *Distefania centrosa* Van Straelen, p. 4, pl. 1, fig. 6.

1944 *Distefania centrosa* Van Straelen, 1940; Van Straelen, p. 11.

1950 *Cyphonotus incertus* Bell, 1863; Wright and Wright, p. 20 (partim), text-fig. 7 only.

1951 *Distefania* sp.?; Vía, pp. 176, 177.

1969 *Cyphonotus incertus* Bell, 1863; Glaessner, p. R488, fig. 299/1.

1972 *Palaeodromites incertus* (Bell, 1863); Wright and Collins, p. 50, pl. 8, fig. 6; pl. 9, fig. 1a–c; text-fig. 9c.

1989 *Palaeodromites centrosus* (Van Straelen, 1940); Gómez-Alba, p. 26, pl. 1, figs 9, 10.

2012b *Distefania incerta* (Bell, 1863); Klompmaker et al., p. 783–787, figs 1, 2, table 2.

2014b *Distefania incerta* (Bell, 1863); Jagt et al., p. 39, pl. 2, figs 1, 2.

2016 *Distefania incerta* (Bell, 1863); Klompmaker et al., fig. 3A–C.

2020 *Distefania incerta* (T. Bell, 1863); Collins et al., p. 26, fig. 2C.

2020 *Distefania incerta* (Bell, 1863); Sasaki, p. 7460.

2022 *Distefania incerta* (Bell, 1863); López-Horgue et al., pp. 153, 155, pl. 1, fig. 8.

Locality. Cal Cassanyes, Castellet i la Gornal (Alt Penedès, Catalonia). **Stratigraphical horizon.** Uppermost lower Aptian to lowermost upper Aptian (*Dufrenoyia furcata* and *Epicheloniceras martini* ammonite zones, respectively).

Studied material and measurements. Five incomplete carapaces with cuticle preserved: MGSB74548a, length 30.6 mm, width 30.6 mm; MGSB 74548c, length 29.5 mm, width 26.9 mm; MGSB74548e, length 12.1 mm, width 16.7 mm, MGSB74548b and MGSB74548d not measured. Twenty-two cheliped remains, tentatively attributed to this species: MGSB74549a, length 21.3 mm, height 14.9 mm; MGSB74549b, length 19.9 mm, height 12.1 mm; MGSB74549d, length 19.7 mm, height 14.7 mm. Other cheliped remains (MGSB74549c, MGSB74549f–u) not measured.

Description. Carapace transversely ovate, slightly vaulted longitudinally and transversely. Maximum width posteriorly, at about two-thirds of length. Regions well marked, inflated, differentiated by grooves. Coarsely granulated. Rostrum bluntly triangular, strongly downturned, not visible from above, with strong, smooth rim; medially sulcate. Orbits ovoid, placed obliquely; outer orbital tooth subtriangular, strong; supraorbital margin rimmed; fold separating inner orbital angle from rostrum. Anterolateral margin slightly convex, armed with four flattened, subrectangular, subequal teeth

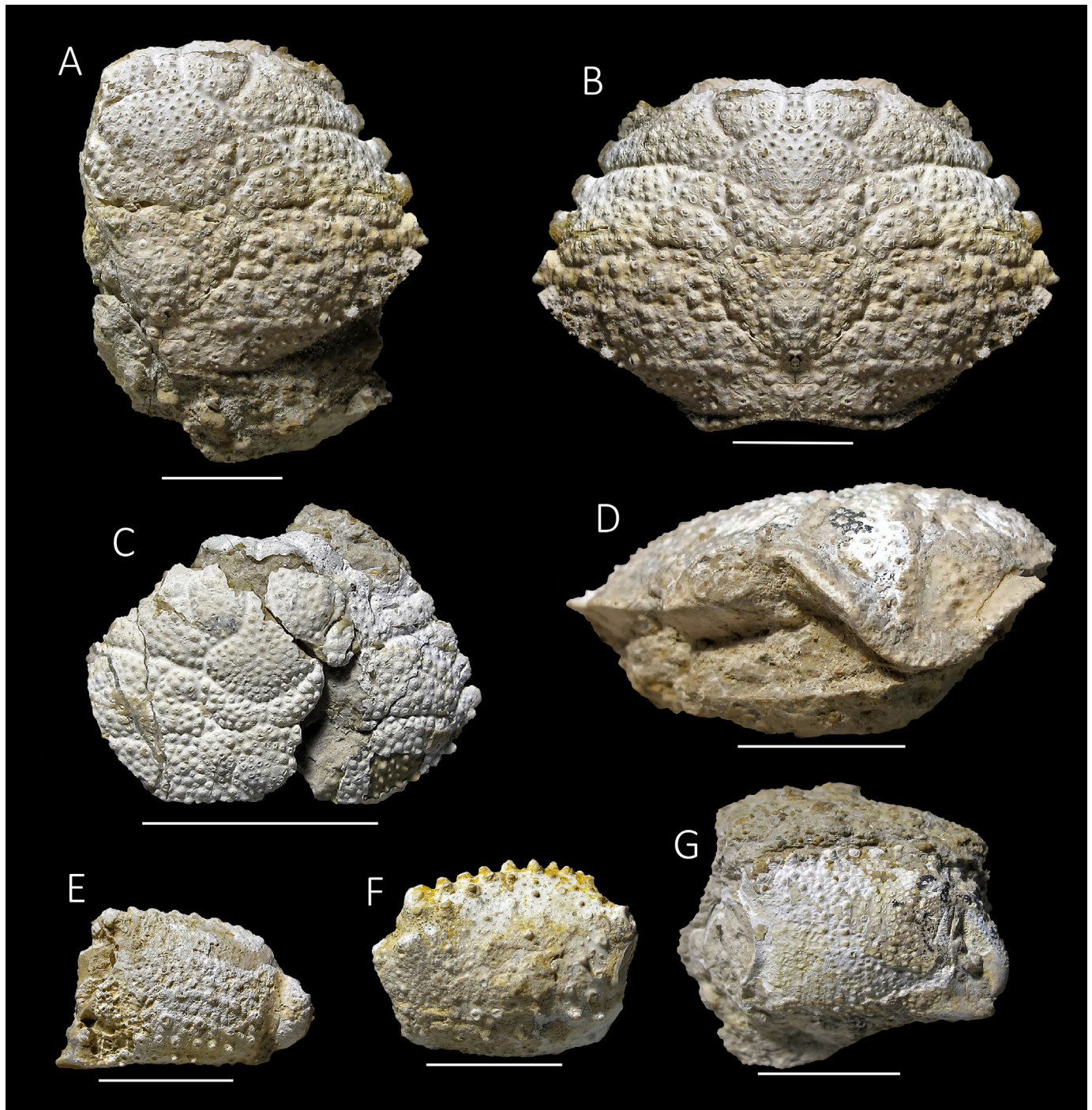


Fig. 6. Decapod crustaceans from the uppermost lower Aptian to lowermost upper Aptian (*Dufrenoyia furcata* and *Epicheloniceras martini* ammonite zones, respectively) of Cal Cassanyes, Castellet i la Gornal (Alt Penedès, Catalonia). A–G. *Distefania incerta* (Bell, 1863): dorsal view (A, B, MGSB 74548c, B being a digital composition), dorsal view (C, MGSB74548e), frontal view (MGSB74548a), right propodus, outer surface (E, MGSB74549b), left propodus, outer surface (F, MGSB74549d) and left propodus, inner surface (G, MGSB74549a). Scale bar equals 10 mm.

(excluding outer orbital tooth), last one usually bifid. Posterolateral margin convex, ornate with about six small teeth decreasing in size progressively backwards. Posterior margin short, slightly concave. Epigastric regions indistinct from protogastric lobes. Protogastric lobes inflated over entire length. Mesogastric region inverted T-shaped, swollen, posterior part wide, rhomboidal shaped, anterior part thin, elongate, overtaking half of protogastric lobes. Metagastric region small, weakly distinct from mesogastric posterior

portion. Urogastric region V-shaped, wide, bounding posterior part of mesogastric process along cervical groove, separating both regions anteriorly; medially divided by shallow depression below gastric pits. Cardiac region elongated, bounded by swollen lobes at both sides and separated from these by deep branchiocardiac grooves, giving area tripartite aspect. Intestinal region not well defined. Branchial region swollen; epi- and mesobranchial lobes separated from metabranchial lobe by branchiocardiac groove.

Cervical, branchial and branchiocardiac grooves deep, well marked; post-cervical groove less marked. Thoracic sternum and pleon not preserved.

Propodi of chelipeds longer than high, strong; articulating bulge about half of total height; outer surface convex with transverse rows of round tubercles, irregular granules scattered; inner surface faintly convex, strongly granulated; upper margin slightly convex, ornate with one or two rows of strong, blunt spines; lower margin convex. Index short, straight, about $0.15 \times$ total width of propodus; dactylus strongly curved downwards, upper edge granulated proximally, smooth distally.

Remarks. [Vía \(1951, pp. 176, 177\)](#) recorded *Distefania* sp.? from Casa Alta, the property adjacent to Cal Cassanyes, describing it as (translated), “a right manus, robust, granulose surface and with two rows of spiny teeth on the upper margin”. He also noted a fragment of a carapace, tuberculated and grooved, that reminded him of features of the genus *Distefania* or those of *D. centrosa* (= *D. incerta*). Specimens noted herein belong, beyond doubt, to *D. incerta*, as comparisons with the type specimen or with the Navarra material show, thus confirming Vía’s assumptions (compare [Wright and Collins, 1972, pp. 50, 51, text-fig. 9c, pl. 8, fig. 6; pl. 9, fig. 1a–c; Klompmaker et al., 2012b, pp. 783–787, figs 1, 2](#)). According to [Klompmaker et al. \(2012b, p. 787, table 1\)](#), *Distefania incerta* ranges from the Albian to the Cenomanian/Turonian. Therefore, *D. incerta* in the Aptian of the Cal Cassanyes outcrops represents the earliest record of this species and extends its range downwards. The species ranks among the longest-lived brachyurans.

Genus *Eodromites* [Patrulusius, 1959](#)

Type species. *Prosopon grande* von [Meyer, 1860](#), by monotypy.

Species included (sensu [Klompmaker et al., 2020](#)). *Eodromites bernchrisdomiorum* [Klompmaker, Starzyk, Fraaije and Schweigert, 2020](#); *E. cristinarobinsae* [Klompmaker, Starzyk, Fraaije and Schweigert, 2020](#); *E. depressus* (von [Meyer, 1860](#)) [as *Prosopon depressum*]; *E. dobrogea* ([Feldmann, Lazăr and Schweitzer, 2006](#)) [as *Cycloprosopon dobrogea*]; *E. grandis* (von [Meyer, 1860](#)) [as *Prosopon grande*]; *E. nitidus* ([A. Milne-Edwards, 1865](#)) [as *Ogydromites nitidus*]; *E. polyphemi* ([Gemmellaro, 1869](#)) [as *Prosopon polyphemi*]; *E. rostratus* (von [Meyer, 1840](#)) [as *Prosopon rostratum*] and *E. rotundus* [Starzyk, 2015b](#).

Remarks. Author attribution of *Eodromites depressus* and *E. grandis* should be von [Meyer \(1860\)](#), rather than von [Meyer \(1857\)](#); reference is made to [Van Bakel et al. \(2021b, p. 5\)](#) for an explanation. *Eodromites guenterii* [Starzyk, 2015b](#) was considered a junior synonym of *E. grandis* by [Klompmaker et al. \(2020, p. 5\)](#), while *Prosopon aequilatum* von [Meyer, 1860](#), often considered to belong to *Eodromites*, was transferred to *Tanidromites* by [Klompmaker et al. \(2020, p. 6\)](#).

***Eodromites* sp.**

Fig. 7A–C

Locality. Cal Cassanyes, Castellet i la Gornal (Alt Penedès, Catalonia). **Stratigraphical horizon.** Uppermost lower Aptian to lowermost upper Aptian (*Dufrenoyia furcata* and *Epicheloniceras martini* ammonite zones, respectively).

Studied material and measurements. Two partially preserved carapaces with cuticle: MGSB74542; length 19.1 mm, width 14.65 mm; MGSB74543, length 20.57 mm, width 21 mm.

Description. Carapace longitudinally ovate with tripartite appearance, slightly longer than wide, vaulted longitudinally and transversely; surface smooth, finely punctate; maximum width posterior to lateral cervical notch. Rostrum not preserved. Orbits elongate, gently oblique; blunt outer orbital tooth; infraorbital margin appearing projected beyond supraorbital margin. Lateral margins with three convex portions defined by cervical and branchial groove notches,

narrowing backwards at midlength of carapace; edge of anterior portion of lateral margin, between outer orbital tooth and cervical notch, weakly sharpened; edge of medial portion of lateral margin, between both cervical and branchial grooves, less acute; edge of posterior portion of lateral margin, between branchial groove and posterolateral corner rounded. Posterior margin incompletely preserved, appearing to have been straight and slightly concave medially. Epigastric regions with remains of swellings. Mesogastric region not well defined from protogastric lobes. Protogastric lobes undifferentiated from hepatic regions. Urogastric region wide, not well defined, delimited anteriorly by cervical groove and laterally by weak post-cervical grooves. Cardiac region weakly swollen, bounded laterally by branchiocardiac grooves. Intestinal region not defined. Branchial regions swollen. Subhepatic lobe strongly inflated and separated from upper lateral margin by concave depression. Cervical groove shallow, widely V-shaped, notching lateral margin and continuing onto lateral carapace walls. Branchial groove well marked, notching lateral margin and lateral walls, there converging forwards cervical groove. Post-cervical grooves, short, weakly marked, visible only axially. Branchiocardiac grooves deep. Ventral elements and appendages not preserved.

Remarks. The morphology of the Cal Cassanyes specimens matches the diagnosis of *Eodromites* perfectly (e.g., [Patrulusius, 1959, p. 254\(6\)](#); [Schweitzer et al., 2012a, p. 6](#); [Starzyk, 2015b, p. 5](#)), allowing assignment to this genus with confidence.

The absence of the frontal area, rostrum and orbits, preclude a detailed comparison with and reference to any of the species listed above. The material shows close morphological similarities to *Eodromites grandis* (compare e.g., [Schweitzer and Feldmann, 2007, pl. 1, fig. D](#); [pl. 4, figs A–C](#); [Starzyk, 2015b, fig. 4.1–8](#)). Specimens from Koskobilo (Navarra, northern Spain), initially recorded as *Eodromites grandis* ([Klompmaker et al., 2012b, p. 790, table 1](#)) and subsequently described as a new species, *E. cristinarobinsae* by [Klompmaker et al. \(2020, pp. 37, 38, fig. 4A–I\)](#), are smaller sized than the Cal Cassanyes individuals and have sharper lateral margin edges. *Eodromites* from Cal Cassanyes fills the stratigraphical gap between the Late Jurassic species described from different regions across mainland Europe and its youngest occurrence in the upper Albian of the Iberian Peninsula ([Klompmaker et al., 2012b, p. 790](#); [Starzyk, 2015b](#); [Klompmaker et al., 2020](#)). *Navarradromites pedroartali* [Klompmaker, Feldmann, Schweitzer, 2012b](#), also from Koskobilo, has a very similar cephalothorax to that of Cal Cassanyes specimens; however, the above-mentioned absence of the frontal area, rostrum and orbits, does not allow a proper comparison (see [Klompmaker et al., 2012b, pp. 796–799, fig. 8A–I](#)).

Genus *Goniodromites* [Reuss, 1858](#)

Type species. *Goniodromites bidentatus* [Reuss, 1858](#), by subsequent designation of [Glaessner \(1929\)](#).

Species included. *Goniodromites aliquantulus* [Schweitzer, Feldmann and Lazăr, 2007](#); *G. bidentatus* [Reuss, 1858](#); *G. cenomanensis* ([Wright and Collins, 1972](#)) [as *Pithonoton cenomanensis*], *G. dacica* (von [Mücke, 1915](#)) [as *Dromia dacica*]; *G. dentatus* [Lörenthey, in Lörenthey and Beurlen, 1929](#); *G. globosa* ([Remeš, 1895](#)) [as *Prosopon globosus*]; *G. hirotai* [Karasawa and Kato, 2007](#); *G. kubai* [Starzyk, Krzemińska and Krzemiński, 2012](#); *G. laevis* ([Van Straelen, 1940](#)) [as *Iberihomola laevis*]; *G. narinosus* [Frăntescu, 2010](#); *G. polyodon* [Reuss, 1858](#); *G. revili* [Van Straelen, 1925](#); *G. sakawense* [Karasawa and Kato, 2007](#); *G. serratus* [Beurlen, 1929](#) and *G. transsylvanicus* ([Lörenthey, in Lörenthey and Beurlen, 1929](#)) [as *Pithonoton Etalloni* var. *transsylvanica*].

***Goniodromites laevis* (Van Straelen, 1940)**

Fig. 7D, E

1940 *Iberihomola laevis* Van Straelen, p. 3, pl. 1, fig. 5.

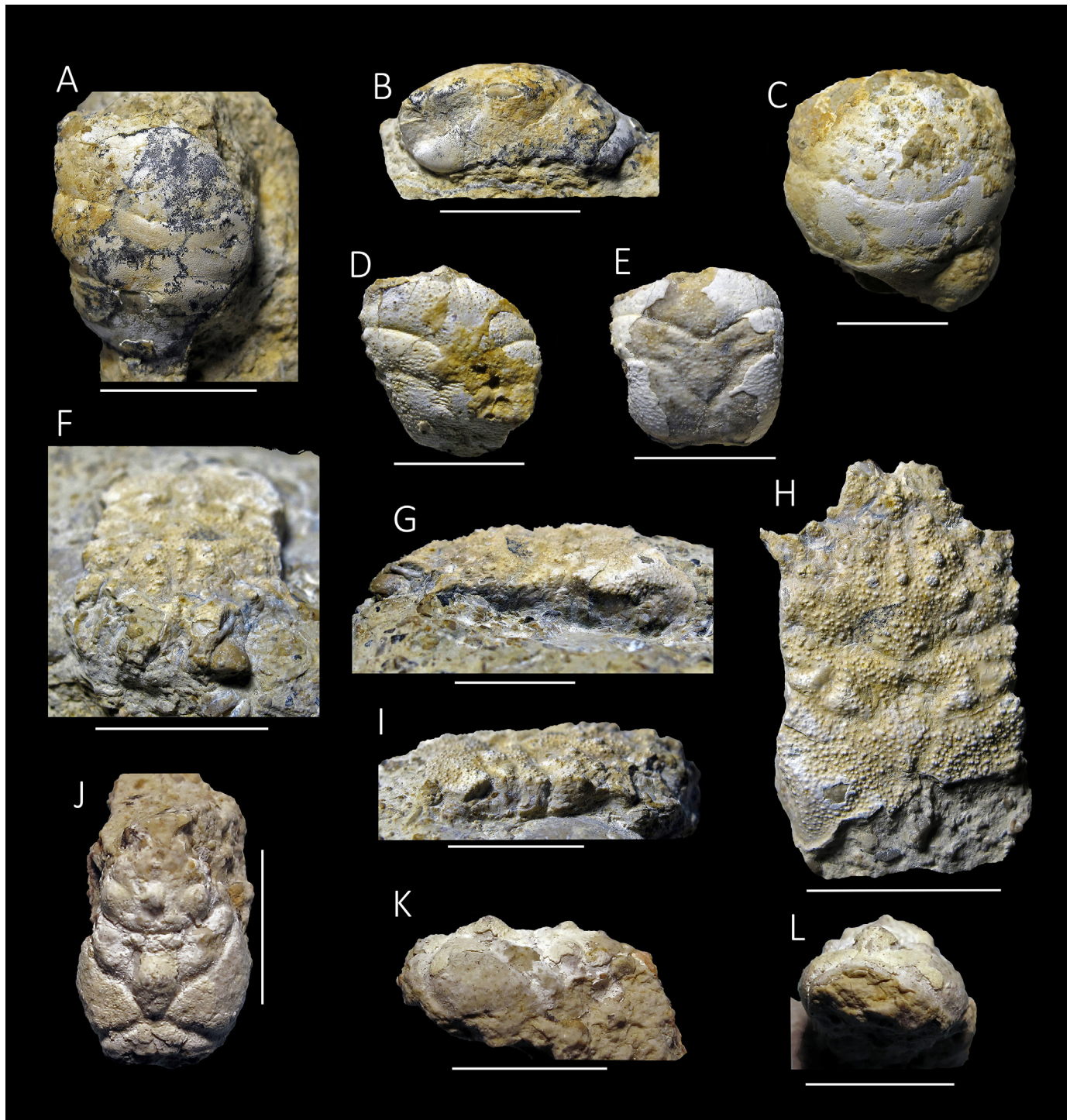


Fig. 7. Decapod crustaceans from the uppermost lower Aptian to lowermost upper Aptian (*Dufrenoyia furcata* and *Epicheloniceras martini* ammonite zones, respectively) of Cal Cassanyes, Castellet i la Gornal (Alt Penedès, Catalonia). A–C. *Eodromites* sp., dorsal and left lateral view (A, B, MGSB74542); dorsal view (C, MGSB74543). D, E. *Goniidromites laevis* (Van Straelen, 1940), dorsal views (D, MGSB86074a; E, MGSB86074b). F–I. *Garrafosopon angustus* (Wright and Collins, 1972) comb. nov. (MGSB86077a) in frontal, left lateral, right lateral and dorsal views, respectively. J–L. *Vectis blesai* sp. nov., **holotype** (MGSB86061), in dorsal, right lateral and posterior views, respectively. Scale bars equal 10 mm (A–C, F–I) and 5 mm (D, E, J–L).

1981 *Pithonoton laevis* (Van Straelen, 1940); Vía, p. 250.

1989 *Pithonoton laevis* (Van Straelen, 1940); Gómez-Alba, p. 26, pl. 1, fig. 8.

2006 *Goniidromites laevis* (Van Straelen, 1940); Feldmann et al., p. 9, table 4.

2007 *Goniidromites laevis* (Van Straelen, 1940); Schweitzer and Feldmann, p. 127, pl. 2, fig. B.

2012b *Goniidromites laevis* (Van Straelen, 1940); Klompaker et al., pp. 793–796, figs 1, 2, 6, 7.

2012a *Goniidromites laevis* (Van Straelen, 1940); Schweitzer et al., p. 4.

2015 *Goniidromites laevis* (Van Straelen, 1940); Jagt et al., pp. 868, 897.

2016 *Goniidromites laevis* (Van Straelen, 1940); Klompaker et al., pp. 91, 94–96, fig. 3D–G.

2019 *Goniodromites laevis* (Van Straelen); Vega et al., pp. 4, 5, figs. 4.7–4.26.

2020 *Goniodromites laevis* (Van Straelen, 1940); Sasaki, p. 7473.

2022 *Goniodromites laevis* (Van Straelen, 1940); López-Horgue et al., pp. 153, 155, pl. 1, fig. 8.

Locality. Cal Cassanyes, Castellet i la Gornal (Alt Penedès, Catalonia). **Stratigraphical horizon.** Uppermost lower Aptian to lowermost upper Aptian (*Dufrenoyia furcata* and *Epicheloniceras martini* ammonite zones, respectively).

Material and measurements. Two near-complete specimens, front not preserved in either, but cuticle partially present: MGSB86074a, length 7.44 mm, width 6.94 mm; and MGSB86074b, length 6.78 mm, width 6.12 mm.

Description. Carapace subpentagonal, slightly longer than wide, gently convex longitudinally and transversely; maximum width posterior to level of cervical groove; cuticle thick; surface sparsely granulated anteriorly and squamous posteriorly, coarser granules scattered along lateral sides. Rostrum not preserved, appearing to have been slightly downturned. Orbits wide, obliquely placed; outer orbital tooth prominent and triangular, forwardly directed. Anterior half of lateral margins slightly sharp edged, with laterally directed spines; two between outer orbital teeth and cervical groove, three between cervical and branchial grooves. Posterior half of lateral margins, from branchial groove to posterolateral corner, rounded, with few small spines nearbranchial groove. Posterior margin slightly concave, rimmed. Epigastric lobes slightly inflated. Mesogastric region pyriform, slender and more marked anteriorly, not delimited in posterior part from protogastric lobes. Protogastric lobes swollen, weakly marked. Urogastric region widely triangular, well separated from mesogastric region by cervical groove. Cardiac region subpentagonal, bounded laterally by branchiocardiac grooves. Intestinal region large, swollen, not well differentiated from branchial regions. Epibranchial regions gently swollen. Meso- and metabranchial regions not differentiated, swollen. Hepatic region small, depressed. Cervical groove deep, widely V-shaped, acute medially, notching lateral margins. Post-cervical groove, short, parallel to cervical groove, confluent with lower angles of urogastric lobe, only visible medially. Branchial grooves deep, parallel to cervical groove, notching lateral margins. Ventral parts and appendages not preserved.

Remarks. Although the two specimens reported here do not preserve important diagnostic structures such as the fronto-orbital margin, their dorsal carapaces present sufficient morphological similarities to assign them to *Goniodromites laevis* with confidence. *Goniodromites laevis* was originally described from upper Albian reef buildups of Monte Orobe (Navarra, northern Spain) (see Van Straelen, 1940) and subsequently recorded in great numbers from coeval reefal levels at the neighbouring Koskobilo quarry (Alsasua, Navarra) (e.g., Klompmaker et al., 2012b, pp. 793–796, fig. 6A–H). The present record of the Cal Cassanyes specimens might fill the temporal gap for this species between Barremian material from Mexico (see Vega et al., 2019) and late Albian individuals from Koskobilo.

When describing Barremian material from Puebla (Mexico) of *G. laevis*, Vega et al. (2019, p. 5) already noted that, besides subtle dorsal carapace differences, the ornament of the cuticle of the Mexican specimens was, ‘... more fine in size and distribution of ‘scales’ of cuticle’, in comparison with Spanish specimens, which have a more scabrous ornament (compare Klompmaker, 2012b, fig. 6A–H); we concur. Vega et al. (2019) attributed this difference to the fact that the Mexican specimens had preserved cuticles, in contrast to Spanish material which is usually preserved as internal moulds. Klompmaker (2012b, p. 795) also noted differences in

ornament in relation to ontogenetic variation. However, the Cal Cassanyes specimens are of small size, similar to the Mexican ones, but do preserve cuticle with a scabrous ornament. It would thus be interesting to revise the Mexican specimens in order to check if they might constitute new species of *Goniodromites*, different from *G. laevis*.

Family Longodromitidae Schweitzer and Feldmann, 2009a

Genera included. *Abyssophthalmus* Schweitzer and Feldmann, 2009a, *Cuchiadromites* Ossó, van Bakel and Ferratges, 2021, *Garrafosopon* gen. nov. (see below), *Levashidromites* Van Bakel, Mychko, Spiridonov, Jagt and Fraaije, 2021c, *Longodromites* Patruilius, 1959, *Pilidromia* Schweitzer, Feldmann, Lazăr, Schweigert and Franțescu, 2018a, *Planoprosopon* Schweitzer, Feldmann and Lazăr, 2007 and *Rosadromites* Schweitzer, Feldmann, Rader and Franțescu, 2016a.

***Garrafosopon* gen. nov.**

urn:lsid:zoobank.org:act:F024E4C6-9806-408F-81DD-F682CB8719FC

Type species. *Glaessneria angusta* Wright and Collins, 1972, by present designation (= *Glaessnerella angusta*; see Wright and Collins, 1975).

Etymology. From Garraf, the mountain massif in the Catalan Coastal Range, where the material was collected.

Diagnosis. Carapace elongated subrectangular, almost twice as long as wide, flattened dorsal surface, slightly convex transversely, nearly flat longitudinally; maximum width at metabranchial level. Regions well marked; dorsal surface profusely granulated. Front protruded, rostrum medially divided by a notch; bifid aspect. Orbits small, orbital fossae large, shallow; supraorbital margin with two notches separated by tooth; intra- and outer orbital teeth present, outer one robust, prominent, laterally directed. Fronto-orbital width equalling maximum carapace width. Lateral margins subparallel. Anterolateral margin short, sharp edged, with prominent elongate lobe. Posterolateral margin much longer than anterolateral margin, epibranchial portion sharp edged, with prominent elongate epibranchial lobe; rounded lobe in posterior portion. Lateral sides of carapace subvertical, perpendicular to dorsal surface; subhepatic lobe slightly inflated. Mesogastric region with posterior portion subrhomboidal; anterior mesogastric process elongate, longer than posterior portion, sides converging forwards. Cervical, post-cervical, branchial and branchiocardiac grooves shallow but well defined, post-cervical and branchiocardiac ones shallower; cervical and branchial grooves subparallel, making dorsal surface tripartite; grooves notching carapace laterally and converging at lateral carapace walls.

Remarks. *Glaessnerella angusta* was erected on the basis of a poorly preserved specimen from the upper Aptian of the Isle of Wight (UK); in view of this state of preservation, the description and definition of the sole specimen known remains incomplete. However, examination of the holotype by one of us (BWMvB) has demonstrated that the Cal Cassanyes specimen is conspecific, and this new material allows the description of the taxon to be completed. For instance, in the original description it was said that the branchial grooves were, ‘... more oblique than the cervical and curved.’ (see Wright and Collins, 1972, p. 35, text-fig. 6e; Collins et al., 2020, p. 28, fig. 3A), but this can be explained by the poor preservation of the holotype, which is decorticated. The newly collected specimen from Catalonia shows the branchial groove to run parallel to the cervical. In this respect, it is clear that *Glaessnerella angusta* differs morphologically from *Glaessnerella* in being much longer, rectangular, with less oblique orbital margins, shorter anterolateral margins, sharper lateral margins and a wider base of

the rostrum (see Wright and Collins, 1972, text-fig. 6a–j). Differences such as these were already pointed out by Schweitzer and Feldmann (2011, p. 7), who considered *Glaessnerella angusta* more similar to the longodromitid *Planoprosopon* than to *Glaesnerella*. Thus, we propose a new genus, *Garrafosopon*, to accommodate *Glaesnerella angusta*. *Garrafosopon* gen. nov. presents all the diagnostic characters that define members of the Longodromitidae sensu Van Bakel et al. (2021c). Comparisons with all the genera placed currently within that family (see above) are as follows: *Abyssophthalmus* Schweitzer and Feldmann, 2009a (type species: *Prosopon spinosus* von Meyer, 1842), from the Upper Jurassic of central Europe, differs from *Garrafosopon* gen. nov. in having a shorter carapace with the maximum width at mid-length, at the level of the epibranchial lobes which are laterally prominent, and with a narrower fronto-orbital margin with deeper orbital fossae, more inflated regions and better-developed subhepatic regions (see Schweitzer and Feldmann, 2009a, pp. 108–113, fig. 8.1–7). *Cuchiadromites* Ossó, Van Bakel and Ferratges, 2021 (type species: *C. jadeae* Ossó, Van Bakel and Ferratges, 2021), from the lower Aptian of northern Spain, differs clearly from *Garrafosopon* gen. nov. by its shorter carapace, shorter anterolateral margins and overall by its profuse dorsal ornament of fungiform granules (see Ossó et al., 2021). *Levashidromites* Van Bakel, Mychko, Spiridonov, Jagt and Fraaije, 2021c (type species: *L. cornutus* Van Bakel, Mychko, Spiridonov, Jagt and Fraaije, 2021c), from the Aptian of Dagestan, has a relatively shorter carapace than *Garrafosopon* gen. nov., as well as shorter anterolateral margins, more inflated regions and blunt lateral margins; in the new genus, these are sharp edged (see Van Bakel et al., 2021c, p. 5, figs 4A–D, 7D). *Longodromites* (type species: *Pithonotus angustus* Reuss, 1858), from the Upper Jurassic of central Europe, differs from *Garrafosopon* gen. nov. by its narrower carapace, wider at mid-length, convex lateral margins with bluntly rounded edges instead of parallel and sharp edged as in the new genus, as well as an obliquely directed branchial groove, whereas this is subparallel with the cervical groove in the new genus (see Reuss, 1858, p. 11; Schweitzer and Feldmann, 2009a, pp. 101–108, fig. 7.1–10). *Pilidromia* Schweitzer, Feldmann, Lazăr, Schweigert and Franțescu, 2018 (type species: *Planoprosopon thiedeae* Schweigert and Koppka, 2011), from the Upper Jurassic of northern Europe, is distinct from *Garrafosopon* gen. nov. in having a longitudinally and transversely strongly vaulted carapace, posteriorly strongly deflexed, instead of flattened in both directions as in the new genus; moreover, the lateral margins in *Pilidromia* are rounded whereas in *Garrafosopon* gen. nov. these are distinctly sharp edged (Schweitzer et al., 2018a, pp. 325, 326, fig. 12.1, 2). *Planoprosopon* Schweitzer, Feldmann and Lazăr, 2007 (type species: *Prosopon heydeni* von Meyer, 1857), from the Middle–Upper Jurassic of central Europe and Japan, presents some similarities to *Garrafosopon* gen. nov. in its dorsal morphology; however, the more inflated regions, shorter anterolateral margins and blunt lateral margins distinguishes *Planoprosopon* from the new genus (see von Meyer, 1842, p. 556; Schweitzer et al., 2007, pp. 104–106, fig. 3.1–4; Schweitzer and Feldmann, 2009b, pp. 10–12, fig. 3.1–7). *Rosadromites* from the Lower Cretaceous of the USA, also shows dorsal similarities to *Garrafosopon* gen. nov., but it differs from it by having a shorter carapace, much shorter anterolateral margins and a carapace surface that is moderately vaulted transversely instead of flattened (see Schweitzer et al., 2016a, pp. 8, 9, fig. 5). Lastly, *Antarctiprosopon* Schweitzer and Feldmann, 2011, with the sole species *A. chaneyi* (Feldmann and Wilson, 1988) from the Eocene of Antarctica, recently excluded from the Longodromitidae by Van Bakel et al. (2021c) on the basis of phylogenetic analyses and assessment of phylomorphospace, presents striking dorsal similarities to *Garrafosopon* gen. nov. However, it differs in having a shorter carapace, moderately vaulted longitudinally and

transversely, whereas in the new genus, the carapace is flattened in both directions, the maximum width being at epibranchial level; also, *Antarctiprosopon* presents shorter anterolateral margins and metabranchial region, and less subvertical and less sharp-edged lateral margins than *Garrafosopon* gen. nov. (see Feldmann and Wilson, 1988, pp. 473–477, figs 6.1–10; Schweitzer and Feldmann, 2011, pp. 10–12, fig. 5).

***Garrafosopon angustus* (Wright and Collins, 1972) comb. nov.**
Fig. 7F–I

- 1972 *Glaessnerella angusta* Wright and Collins, pp. 35, 36, text-fig. 6e; pl. 3, fig. 9.
1975 *Glaessnerella angusta* (Wright and Collins, 1972); Wright and Collins, p. 441.
2011 *Glaessnerella angusta* Wright and Collins, 1972; Schweitzer and Feldmann, pp. 6, 7.
2020 *Glaessnerella angusta* Wright and Collins, 1972 [sic]; Collins et al., p. 28; fig. 3A.

Material and measurements. A single, complete specimen preserving cuticle: MGSB86077a, length 27.27 mm, width 16.52 mm; and a carapace fragment (MGSB86077b).

Locality. Cal Cassanyes, Castellet i la Gornal (Alt Penedès, Catalonia). **Stratigraphical horizon.** Uppermost lower Aptian to lowermost upper Aptian (*Dufrenoyia furcata* and *Epicheloniceras martini* ammonite zones, respectively).

Description. Carapace medium sized, subrectangular, elongated, almost twice as long as wide; flattened longitudinally and transversely; dorsal surface with cuticle profusely ornamented by coarse granules of different sizes; maximum width at metabranchial level. Regions well marked. Front protruded, about half of carapace width; rostrum forwardly directed, medially divided, bifid. Orbits oblique, orbital fossae large, shallow; supraorbital margin gently oblique and concave in dorsal view, with two notches separated by blunt tooth; intra-orbital tooth blunt, weakly prominent; outer orbital teeth robust, prominent, forwardly/laterally directed. Lateral margins subparallel. Anterolateral margin short, straight, sharp edged, with prominent and granulated posterior lobe upwardly directed. Posterolateral margin about three times longer than anterolateral margin, epibranchial portion sharp edged, with prominent, granulated, epibranchial lobe; edge of anterior portion of posterolateral margin sharp, posterior portion of margin slightly convex and somewhat rounded. Lateral sides of carapace subvertical, perpendicular to dorsal surface, tripartite. Posterior margin not preserved, but apparently concave. Frontal region granulated. Mesogastric region slightly swollen, well delineated, posterior portion subrhomboidal, with coarse prominent granules; anterior mesogastric process elongate, longer than posterior portion, well delineated, granulated, with prominent granulated tubercle medially. Protogastric region lobes slightly swollen, granulated, with three prominent granulate tubercles in central and lateral portions and scattered granulate tubercles and granules in anterior portion adjacent to anterior mesogastric process. Urogastric region wider than posterior margin of mesogastric region, separated from metagastric region by cervical groove, and confluent laterally with epibranchial region. Cardiac region elongated, diamond shaped, laterally bounded by shallow branchiocardiac grooves. Epibranchial region narrow, delimited by cervical groove anteriorly and post-cervical groove posteriorly; weakly swollen, confluent with urogastric lobe, ending in a slightly upraised and prominent epibranchial tooth. Mesobranchial region narrow, delimited anteriorly by post-cervical groove and posteriorly by branchial groove; slightly swollen, medially more prominent, ending laterally in lobe. Metabranchial region slightly swollen, large, flattened, ornate with scattered coarse granules of different sizes. Hepatic region weakly

differentiated from protogastric lobes, slightly swollen and defined by slightly raised granulated tubercle. Cervical groove shallow, forming obtuse angle, somewhat more acute and deeper medially; post-cervical groove weakly defined, discontinuous; branchial grooves shallow, subparallel with cervical and post-cervical grooves; cervical, post-cervical and branchial grooves notching carapace lateral margins. Sternopleonal elements and appendages not preserved.

Remarks. See the diagnosis of the genus.

Family Vialiidae Artal, Van Bakel, Fraaije, Jagt and Klompmaker, 2012

Genus *Vectis* Withers, 1946

Type species. *Vectis wrighti* Withers, 1946, by monotypy.

Species included. *Vectis atherfieldensis* (Wright, 1997) [as *Rathbunopon? atherfieldense*]; *V. blesai* sp. nov., *V. caseyi* Wright and Collins, 1972; *V. collinsi* Van Bakel, Mychko, Spiridonov, Jagt and Fraaije, 2021c; *V. echinorum* Wright and Collins, 1972 and *V. wrighti* Withers, 1946.

***Vectis blesai* sp. nov.**

Fig. 7J–L

urn:lsid:zoobank.org:act:31895D6E-563B-4220-84A0-ACE4E8ADD232

Studied material and measurements. A single specimen: **holotype** MGSB86061, length 7.74 mm, width 5.61 mm.

Etymology. In honour of Mr Eduard Blesa, who found and donated the type specimen.

Type locality. Cal Cassanyes, Castellet i la Gornal (Alt Penedès, Catalonia).

Stratigraphical horizon. Uppermost lower Aptian to lowermost upper Aptian (*Dufrenoyia furcata* and *Epicheloniceras martini* ammonite zones, respectively).

Diagnosis. Carapace small, pyriform, about three-quarters longer than wide, maximum width at metabranchial region about three quarters posteriorly; cuticle smooth; dorsal regions well marked, swollen, well defined by deep grooves; slightly arched longitudinally, strongly convex transversely. Orbits deep, directed anterolaterally; prominent outer orbital tooth. Rostrum truncated, slightly downturned. Lateral margins undefined, rounded branchial flank. Posterior margin concave in dorsal view, strongly concave in posterior view, rimmed. Protogastric regions strongly swollen. Mesogastric region with prominent tubercle posteriorly, and less prominent tubercle anteriorly. Metagastric region slightly swollen, narrow transversely. Urogastric region narrow, separated from metagastric region by deep cervical groove. Cardiac region inverted subpentagonal, elongated longitudinally, with two weakly defined medial tubercles closely spaced, and one posterior. Intestinal region subtriangular, conspicuously wide. Hepatic region subtriangular, swollen. Epibranchial region reniform, swollen; mesobranchial region subtriangular, swollen, separated from epibranchial region by shallow depression and from metabranchial region by deep branchial groove; metabranchial region large, swollen, well defined by branchial groove and deep intestinal groove. Cervical groove wide, U shaped, deep; branchial groove deep, long, sinuous; both cervical and branchial grooves extending onto flanks; intestinal groove deep, bounding intestinal region and forming characteristic triangle.

Description. As for genus.

Discussion. The elongate pyriform shape of the carapace, which is about three quarters longer than wide, the swollen regions well defined by deep grooves, and overall, the typical subtriangular intestinal region bounded by a groove, allows to place the present carapace in the genus *Vectis* with confidence. It is noteworthy that

the sole specimen of *Vectis blesai* sp. nov. preserves, in part, both exo- and endocuticle layers, which appears completely smooth even though some remains of miniscule, scattered granules may be observed. In spite of the strong morphological similarities of *Vectis blesai* sp. nov. to congeners, in particular to those from the Aptian of the Isle of Wight, United Kingdom (i.e., *V. atherfieldensis*, *V. echinorum* and *V. wrighti*), some differences may be observed.

Vectis wrighti, the type species, differs from *V. blesai* sp. nov. in having a uniformly granulated cuticle, whereas in the new species this appears to be almost smooth; in addition, *V. wrighti* possesses a lateral row of tubercles that forms an incipient posterolateral margin; these are absent from the new species (see Withers, 1946; Wright and Collins, 1972, pp. 18, 19, pl. 1, fig. 1a–c; Collins et al., 2020, p. 30, fig. 3C). *Vectis echinorum* differs from *V. blesai* sp. nov. by its larger size and coarser dorsal granulation (see Wright and Collins, 1972, p. 19, pl. 1, figs 2, 3; Collins et al., 2020, p. 30). *Vectis atherfieldensis* differs from *V. blesai* sp. nov. in having a uniformly granulated carapace surface (vs almost smooth in the new species), a wider and less elongated cardiac region and a much shallower cervical groove separating the metagastric and urogastric regions (see Wright, 1997, pp. 137, 138, figs 9, 14; Van Bakel et al., 2021c, p. 10). The Russian *Vectis collinsi*, also of Aptian age, differs clearly from the new species by its strongly granulate regions and spiny lateral margins (vs unarmed in *V. blesai* sp. nov.; see Van Bakel et al., 2021c, p. 10, figs 4E, F, 7C). The Albian *Vectis caseyi*, morphologically the most closely similar form, differs from *V. blesai* sp. nov. in having a wider cardiac lobe with eight tubercles, tubercles in branchial regions, and in the absence of the prominent posterior rounded swelling that is seen in *V. blesai* sp. nov. (see Wright and Collins, 1972, p. 19, pl. 1, fig. 4; Collins et al., 2020, p. 30). As pointed out by Van Bakel et al. (2021c, p. 10), a re-examination of the type material of species of *Vectis* from the Isle of Wight would be needed, since these, with the exception of *V. wrighti*, had been erected on the basis of fragmentary material. Even though the specimen from Cal Cassanyes is not perfectly preserved, it retains enough characters to consider it as a separate species.

Family *incertae sedis*

Genus *Mesodromilites* Woodward, 1900

Type species. *Necrocarcinus glaber* Woodward, 1898, by original designation.

Species included. In addition to the type species, only *M. prietoi* sp. nov. (see below).

***Mesodromilites prietoi* sp. nov.**

Fig. 8A–D

urn:lsid:zoobank.org:act:8FB04B4F-247D-4392-ABD4-6484C6A324CD

Derivation of name. In memory of Lluís Prieto, a passionate collector whose remarkable generosity led to the donation of the holotype.

Type locality. Cal Cassanyes, Castellet i la Gornal (Alt Penedès, Catalonia).

Stratigraphical horizon. Uppermost lower Aptian to lowermost upper Aptian (*Dufrenoyia furcata* and *Epicheloniceras martini* ammonite zones, respectively).

Material studied and measurements. Two near-complete carapaces preserving cuticle: **holotype** MGSB74540, length 14.6 mm, width 13.7 mm; **paratype** MGSB86064a, length 11.35 mm, width 9 mm; as well as a fragment of a carapace (MGSB86064b).

Diagnosis. Small-sized carapace, longitudinally subelliptical in outline, only slightly longer than broad, maximum width in posterior portion; carapace convex in both directions; front bilobed, with rounded tips, axial portion downturned; orbits large, directed forwards; anterolateral margins long, arched, bearing three spines,

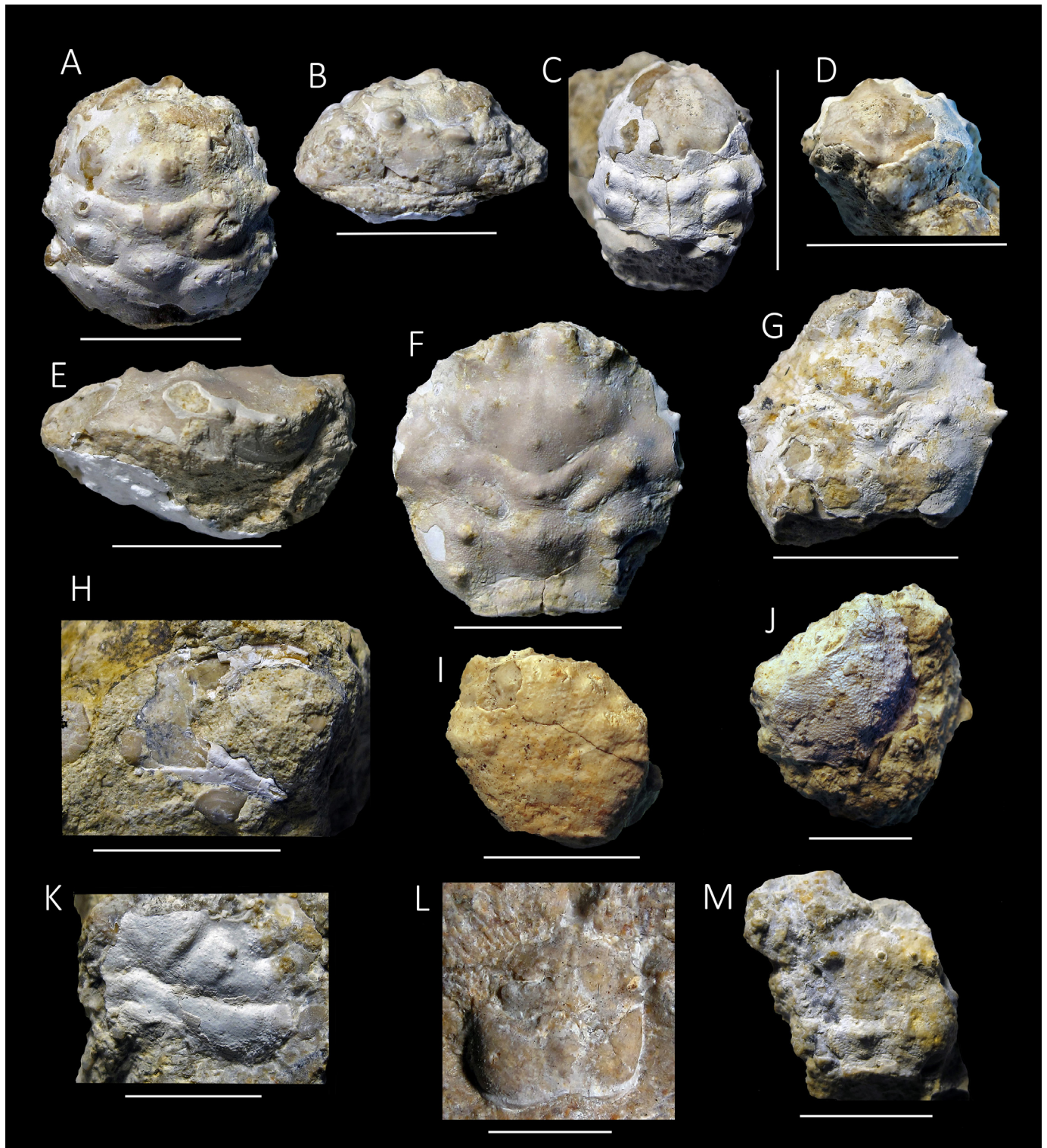


Fig. 8. Decapod crustaceans from the uppermost lower Aptian to lowermost upper Aptian (*Dufrenoyia furcata* and *Epicheloniceras martini* ammonite zones, respectively) of Cal Cassanyes, Castellet i la Gornal (Alt Penedès, Catalonia). A, B. *Mesodromilites prietoi* sp. nov., **holotype** (MGSB74540) in dorsal and right lateral views, respectively. C, D. *Mesodromilites prietoi* sp. nov., **paratype** (MGSB86064a) in dorsal and frontal views, respectively. E–H. *Necrocarcinus mariae* sp. nov., **holotype** (E, F; MGSB74538), in right lateral and dorsal views (E, F), respectively; **paratype** (G, MGSB74539), in dorsal view; propodus (H, MGSB86063a). I. *Paranecrocarcinus?* sp. (MGSB86076), dorsal view. J. *Pseudonecrocarcinus?* sp. (MGSB86075), dorsal view. K. *Etyxanthosia fossa* (Wright and Collins, 1972) (MGSB74550), dorsal view. L, M. *Iberodorippe vinea* gen. nov., sp. nov., **holotype** (L, MGSB86062), in dorsal view; **paratype** (M, MGSB86078a) in dorsal view. Scale bars equal 10 mm (A–H, J) and 5 mm (I, K–M).

posterior one being largest; posterolateral margins very short, with salient node; posterior margin nearly straight; dorsal regions with thirteen notable swellings, four in gastric area, two in hepatic areas, two in urogastric region, one in cardiac region and four in branchial regions; cervical and branchial grooves continuous, arched, relatively deep; dorsal surface of carapace smooth, without granules or tips, metabranchial region bearing row of small granules.

Remarks. The new species shares with *Mesodromilites glaber* the general outline of the carapace, which is longitudinally elongate; the orbital and frontal construction, the front being bilobed and a dorsal carapace surface with well-defined regions, bearing notable protuberances. Being close to the type species, from the Albion of the United Kingdom, it differs in having a less raised carapace, with dorsal regions having more numerous and less salient protuberances, a more strongly marked cervical and a row of tubercles in the metabranchial area (see Woodward, 1898, 1900; Wright and Collins, 1972).

Description. Small-sized carapace, longitudinally subelliptical in outline, only slightly longer than wide; maximum width in posterior portion, at position of metabranchial region; carapace fairly convex in both directions. Front notably projecting beyond orbits, narrow, bilobed, with rounded tips, axial portion depressed and downturned. Orbits large, directed forwards. Anterolateral margins broadly arched, bearing three notable teeth, posterior one being largest. Posterolateral margins very short, converging backwards, bearing conspicuously strong node. Posterior margin narrow, nearly straight. Dorsal surface of carapace with well-defined regions, bearing numerous protuberances and bounded by fairly marked grooves. Gastric regions clearly differentiated, mesogastric region bearing two notable protuberances and bounded posteriorly by marked cervical groove; protogastric regions bearing two subtle swellings. Hepatic region large, defined by strong subcircular swellings. Urogastric region narrow, swollen, bearing two subtle protuberances. Cardiac region large, swollen, transversely rhombus shaped. Epibranchial region large, defined by two strong subcircular swellings, vertically distributed; posterior one being larger. Metabranchial regions large, anteriorly bounded by well-marked branchial groove; lateral portions bearing transverse row of tubercles. Intestinal region small, flat. Branchial groove relatively deep, arched, bounded posteriorly by subtle ridge covered by small granules.

Discussion. The nearly complete dorsal features in the new species exhibit primary characters that permit assignment to the genus *Mesodromilites* (compare Wright and Collins, 1972, pp. 59–61, pl. 3, figs 5a–d, 6a–c). The main features of *Mesodromilites prietoi* sp. nov. warrant placement in this genus; these include the general carapace outline, being longitudinally subelliptical; the narrow, bilobed and projected front; large orbits, directed forwards; the shape and distribution of dorsal regions, with notable swellings defining the gastric, branchial and cardiac areas; the presence of arched lateral carapace margins, bearing nodes or teeth and the narrow posterior margin. However, a set of distinctive features defines the new species, including the more numerous dorsal protuberances, being distinct in number and distribution, but especially distinct because of less protuberant swellings. In addition, the deep and pronounced cervical groove distinguishes *Mesodromilites prietoi* sp. nov. from *M. glaber*. The English species presents an extremely raised dorsal carapace, with notably larger conical protuberances. The front is characterised by acute lateral lobes; the orbits exhibit long and acute outer orbital teeth and a strong subtriangular tooth is seen on the infraorbital margin. The cervical groove is scarcely defined, being shallow and with notable indentations in the lateral margins. The branchial groove is bounded by a somewhat stronger ridge, and the posterior metabranchial area is smooth, without rows of tubercles. The dorsal regions also present some differences in the English species, mainly the two

mesogastric and two urogastric protuberances, which are extremely raised. The hepatic area is flat, without protuberances; the gastric area is characterised by two small epigastric swellings, two notable protogastric swellings and two extremely salient mesogastric nodes; the urogastric region bears two close-set, strong protuberances; the cardiac region is rhombus shaped, not very large and swollen; the epibranchial region is characterised by notable oblique swellings. The dorsal carapace surface is densely covered by small granules. *Mesodromilites prietoi* sp. nov. constitutes the earliest record of the genus.

Subsection Gymnopleura Bourne, 1922

Superfamily Palaeocorystoidea Lörenthey, in Lörenthey and Beurlen, 1929

Family Necrocarcinidae Förster, 1968

Subfamily Necrocarcininae Förster, 1968

Genus *Necrocarcinus* Bell, 1863

Type species. *Orithyia labeschei* Eudes-Deslongchamps, 1835, by the subsequent designation of Glaessner (1929).

Species included (sensu Van Bakel et al., 2022a). *Necrocarcinus bod-rakensis* Levitskyi, 1974; *N. christinae* Van Bakel, Ossó and Jackson, 2022a; *N. davisii* Bishop, 1985; *N. inornatus* Breton and Collins, 2011; *N. labeschei* Eudes-Deslongchamps, 1835 [as *Orithyia labeschei*]; *N. mariae* sp. nov. (see below); *N. olsonorum* Bishop and Williams, 1991; *N. rathbunae* Roberts, 1962; *N. senonensis* Schlüter, in von der Marck and Schlüter, 1868; *N. tauricus* Ilyin and Alekseev, 1998; *N. texensis* Rathbun, 1935; *N. undecimtuberculatus* Takeda and Fujiyama, 1983 and *N. woodwardii* Bell, 1863.

***Necrocarcinus mariae* sp. nov.**

Fig. 8E–H

urn:lsid:zoobank.org:act:2C428D14-0758-4D9C-8E5D-F658A2106A22

Derivation of name. In honour of Mrs Maria Sánchez, who donated the holotype.

Type locality. Cal Cassanyes, Castellet i la Gornal (Alt Penedès, Catalonia).

Stratigraphical horizon. Uppermost lower Aptian to lowermost upper Aptian (*Dufrenoyia furcata* and *Epicheloniceras martini* ammonite zones, respectively).

Studied material and measurements. Two complete carapaces preserving cuticle and a single propodus embedded in matrix: **holotype** MGSB74538, length 17.8 mm, width 17.7 mm; **paratype** MGSB74539, length 13.8 mm, width 14.4 mm. Propodus tentatively attributed to this species L MGSB86063a, length 12 mm, height 7.25 mm. In addition, a similar-sized fragment of a propodus (MGSB86063b).

Diagnosis. Small-sized carapace, subpentagonal in outline, wider than long; maximum width in anterior portion, at position of epibranchial region; carapace weakly convex in both directions; front fairly widely projecting beyond orbits, with notably acute spines at lateral corners of orbits; orbits small, directed forwards, supraorbital margins with two slight incisions; anterolateral carapace margins broadly arched, with five spines, last one being largest; posterolateral carapace margins nearly straight, converging backwards, bearing very small tubercle in anterior portion; posterior margin large, strongly concave; dorsal carapace surface with eleven small tubercles; three gastric, six branchial, one urogastric and one cardiac; gastric regions broad, slightly swollen, with three small tubercles; urogastric region narrow, slightly inflated, bounded anteriorly by short cervical groove; epibranchial region characterised by small tubercle at lateral portion, and slightly swollen inner portion bounded by well-marked grooves; mesobranchial and metabranchial regions large, bearing two notable tubercles;

cardiac region large, subelliptical in shape; intestinal region flat; dorsal carapace surface densely covered by small granules.

Description. Small-sized carapace, subpentagonal in outline; equally wide as long, maximum width in anterior carapace portion, at position of epibranchial region; carapace scarcely convex in both directions. Front projected, with acute spines in orbital corners. Orbits small, directed forwards, supraorbital margin with two fissures, outer orbital spine strong, acute. Anterolateral margins arched, bearing five acute teeth of different sizes, excluding outer orbital; three teeth of similar size at level of hepatic region; following notable indentation, two teeth at level of epibranchial region, posterior one being longer. Posterolateral margins nearly straight, lateral sides converging backwards, with small tubercle in first portion of margins. Posterior margin broad, strongly convex. Dorsal regions of carapace well defined by swellings and grooves, most regions bearing small tubercles. Hepatic region flat, small. Gastric region very broad, with three small tubercles; protogastric portions inflated, with swollen lateral extensions, mesogastric region bounded posteriorly by deep groove; gastric pits present. Urogastric region narrow, arched, swollen, with small axial tubercle. Cardiac region transversely subelliptical in shape, swollen, with small axial tubercle. Epibranchial region defined by short, oblique swelling, bearing strong tubercle in lateral portion; inner portion of epibranchial region bounded by relatively deep grooves. Mesobranchial and metabranchial regions large, bearing two notable tubercles. Intestinal small, depressed. Dorsal surface of carapace densely covered by small granules.

Remarks. The new species can be assigned to *Necrocarcinus* with confidence. The main shared features are the general carapace outline, the frontal and orbital construction, the dorsal regions bearing tubercles and more or less marked grooves; the lateral margins bearing several teeth or nodes. The dorsal regions are similarly defined and distributed, with extremely broad gastric regions, a small hepatic region, the epibranchial region defined by an oblique swelling, the mesobranchial and metabranchial regions large, bearing two tubercles, one below the other. The most similar species is the type species, *N. labeschii*, which has main features in common with the new form. However, in *N. labeschii* the main difference is the stronger carapace convexity; moreover, dorsal tubercles are stronger and more notably developed. The anterolateral margin bears only four teeth, instead of five, the lateral indentation between the hepatic and epibranchial being less pronounced. The posterolateral margin does not exhibit a small granule in the first portion, but bears several small granules in the posterior portion. The dorsal regions also present some peculiarities, the protogastric regions having four tubercles instead of two; the epibranchial region exhibiting a longer oblique inflation, a stronger tubercle and an additional small tubercle situated at the lateral portion, close to the second spine of the anterolateral margin. In *N. labeschii*, the tubercle of the metabranchial region is situated posteriorly, really close to the posterolateral margin (compare Guinot et al., 2008, fig. 8E, F; Schweitzer et al., 2012b, fig. 2C, D).

Schweitzer et al. (2010) listed 21 species for the genus *Necrocarcinus*. The number of superficially similar characters was too high to be acceptable, which is why in some recent papers these have interpreted differently (see e.g., Luque et al., 2012; Schweitzer et al., 2012b; Karasawa et al., 2014). The most recent papers (Schweitzer et al., 2016b, p. 349; Sasaki, 2020, p. 7956), listed only 7 and 8, respectively, valid species of *Necrocarcinus*. Van Bakel et al. (2022a) reviewed the genus and reassigned to *Necrocarcinus* a number of species that had been transferred to *Elektrocarcinus* Schweitzer, Karasawa, Luque and Feldmann, 2016b by Schweitzer et al. (2016b).

As indicated below, all species now included in the genus present similar differences to the new species, mainly in the number, development and shape of dorsal tubercles, the number, position

and shape of nodes on the lateral carapace margins and differences in dorsal grooves.

Necrocarcinus bodrakensis from the Albian of Crimea presents a more subcircular carapace outline, a deeper, much more marked cervical groove, anterolateral margins without numerous spines, a strongly concave posterior margin, dorsal regions with more numerous and stronger tubercles and a dorsal carapace surface with numerous granules, setting it apart from the new species (see Levitskyi, 1974, pl. 2, fig. 4; pl. 3, fig. 3). *Necrocarcinus christinae* from the Cenomanian of Texas (USA) differs from *N. mariae* sp. nov. in having a more subcircular carapace outline, which is convex in transverse direction, as well as taller and larger tubercles in protogastric, hepatic and epibranchial regions (see Van Bakel et al., 2022a). *Necrocarcinus davisii* from the Campanian of South Dakota (USA) presents a more subcircular carapace outline, with anterolateral margins bearing fewer spines or denticles, a narrower posterior margin and dorsal carapace regions with more numerous and more protruding tubercles and a slightly ridged epibranchial region (see Bishop, 1985, p. 169, figs 3.6, 10, 12; Schweitzer et al., 2016b, fig. 6C–E). The Cenomanian (Paris Basin, France) *N. inornatus* is differentiated from *N. mariae* sp. nov. by the strong convexity of the dorsal surface, the notable concavity of the posterior margin and the shape and distribution of dorsal tubercles (see Breton and Collins, 2011, p. 147, fig. 6). *Necrocarcinus olsonorum*, from the Turonian of South Dakota (USA), presents a more subcircular carapace outline, strongly convex in both directions, plus anterolateral margins with scarce spines or denticles, dorsal carapace regions with more numerous and somewhat larger tubercles than in *N. mariae* sp. nov. (see Bishop and Williams, 1991, fig. 2A–D). *Necrocarcinus rathbunae* from the Campanian of New Jersey (USA) exhibits a strongly convex dorsal carapace, a different shape and distribution of dorsal regions than in *N. mariae* sp. nov., being more raised and swollen (see Roberts, 1962, pl. 85, fig. 12; pl. 87, figs 1, 2). *Necrocarcinus senonensis* from the Danian of Denmark and northern Germany has a more convex carapace, dorsal tubercles are more salient and acute than in *N. mariae* sp. nov., and lateral carapace margins have a strong tooth in the middle of the posterolateral margin and the anterolateral margin lacks nodes or teeth (compare Schweitzer et al., 2016b, fig. 5C, D). *Necrocarcinus tauricus* from the Albian of Crimea has a more convex carapace, deeper dorsal grooves and a different shape and distribution of dorsal tubercles and nodes on the lateral margins than *N. mariae* sp. nov. (compare Ilyin, 2005, pl. 9, fig. 4). *Necrocarcinus texensis* from the Albian of Texas (USA) differs from *N. mariae* sp. nov. in having a more subhexagonal carapace outline, the anterolateral margin having rare spines or denticles, dorsal carapace regions with more numerous tubercles, some of them arranged in vertical ridges (see Rathbun, 1935, pp. 45, 46, pl. 11, figs 20–22). *Necrocarcinus undecimtuberculatus*, from the upper Aptian of Japan, presents more swollen dorsal regions, with larger and more numerous gastric tubercles than seen in *N. mariae* sp. nov.; moreover, the lateral carapace margins are broadly arched and the posterior margin extremely concave (see Takeda and Fujiyama, 1983, fig. 3, pl. 1, figs 1, 2, 3E). *Necrocarcinus woodwardii* from the Albian of the United Kingdom and the Cenomanian of France can be differentiated from *N. mariae* sp. nov. in that the dorsal surface exhibits more numerous, salient tubercles and well-marked longitudinal grooves occur all over the carapace (e.g., Bell, 1863, pp. 20, 21, pl. 4, figs 1–3; Breton and Collins, 2011, pp. 146, 147, fig. 5A, B). *Necrocarcinus mariae* sp. nov. constitutes the second record of the genus from the Iberian Peninsula, *N. woodwardii* having been previously recorded by Ossó (2017, pp. 278, 279, fig. 4A–C).

The three other valid genera within the Necrocarcininae (Schweitzer et al., 2018b; Sasaki, 2020) exhibit additional notable differences. *Hadrocarcinus* Schweitzer, Feldmann and Lamanna,

2012b presents characters that easily set it apart from the new taxon, such as more swollen dorsal regions, larger dorsal tubercles, deeper dorsal grooves, a front with notably elongate inner orbital spines, orbits with two small intra-orbital spines and a long outer-orbital spine, and a fairly concave posterior margin (see Schweitzer et al., 2012b, fig. 3A–F; 2016b, fig. 5E, F).

Artiocarcinus Schweitzer, Karasawa, Luque and Feldmann, 2016b exhibits a subhexagonal carapace outline, with fairly straight and convergent posterolateral margins, larger epibranchial and meso-branchial spines on the lateral margins and a different shape and distribution of dorsal tubercles (Schweitzer et al., 2016b, fig. 6A; 2018b, fig. 4.2).

Elektrocarcinus, represented by the type species, *Necrocarcinus pierrensis* Rathbun, 1917 only, has a more elongate subelliptical carapace outline, with axial, epibranchial and metabranchial ridges in dorsal regions, and a different shape and distribution of dorsal tubercles and spines on the lateral margins (see Schweitzer et al., 2016b, fig. 6B; 2018b, fig. 4.3; Van Bakel et al., 2022a).

Subfamily *Paranecrocarcininae* Fraaije, Van Bakel, Jagt and Artal, 2008

Genus *Paranecrocarcinus* Van Straelen, 1936

Type species. *Paranecrocarcinus hexagonalis* Van Straelen, 1936, by original designation.

Species included. *Paranecrocarcinus balla* Van Bakel, Guinot, Artal, Fraaije and Jagt, 2012; *P. hexagonalis* Van Straelen, 1936; *P. libanoticus* Förster, 1968 and, possibly, *P. mozambiquensis* Förster, 1970.

***Paranecrocarcinus*? sp.**

Fig. 8I

Locality. Cal Cassanyes, Castellet i la Gornal (Alt Penedès, Catalonia). *Stratigraphical horizon.* Uppermost lower Aptian to lowermost upper Aptian (*Dufrenoyia furcata* and *Epicheloniceras martini* ammonite zones, respectively).

Studied material and measurements. A single carapace, preserving cuticle: MSGB86076, length 6.5 mm, width 6.6 mm.

Description. Carapace small, subhexagonal, slightly vaulted transversely; regions vaguely defined. Fronto-orbital margin not preserved. Anterolateral margins slightly convex in dorsal view, strongly concave in lateral view, finely dentate; blunt epibranchial node. Posterolateral margins straight, with row of small granules, giving finely serrate aspect, and smaller node posterior to epibranchial node. Posterior margin wide, rimmed, slightly concave. Weak tubercles in protogastric and epibranchial regions. Cervical groove faintly marked; branchiocardiac groove barely visible.

Remarks. The poor preservation of this specimen, and in particular the missing portions of the fronto-orbital area, precludes a more precise generic assignment. The lateral margins are finely dentate, ruling out that this carapace is a juvenile specimen of *Necrocarcinus*. Instead, it strongly recalls lateral margins seen in *Paranecrocarcinus balla*, *P. mozambiquensis* or *P. libanoticus*, which also have an attenuated dorsal ornament (see Van Straelen, 1936, pl. 4, figs 6, 7; Förster, 1968, pl. 13, fig. 1; Van Bakel et al., 2012, fig. 19A, C, E, G; Schweitzer et al., 2018b, fig. 7.1). Therefore, in the absence of better-preserved material, we assign it, with a query, to *Paranecrocarcinus*.

Genus *Pseudonecrocarcinus* Förster, 1968.

Type species. *Necrocarcinus quadricissus* Noetling, 1881, by original designation.

Species included. *Pseudonecrocarcinus biscissus* (Wright and Collins, 1972) [as *Paranecrocarcinus* (*Pseudonecrocarcinus*) *biscissus*]; *P. digitatus* (Wright and Collins, 1972) [as *Paranecrocarcinus* (*Paranecrocarcinus*) *digitatus*]; *P. eichhorni* Nyborg, Garassino, Pasini and Vega, 2021; *P. foersteri* (Wright and Collins, 1972) [as

Paranecrocarcinus (*Paranecrocarcinus*) *foersteri*]; *P. gamma* (Roberts, 1962) [as *Paranecrocarcinus gamma*]; *P. graysonensis* (Rathbun, 1935) [as *Necrocarcinus graysonensis*]; *P. milbournei* (Collins, 2010) [as *Paranecrocarcinus milbournei*]; *P. moseleyi* (Stenzel, 1945) [as *Necrocarcinus moseleyi*]; *P. pusillus* (Breton and Collins, 2011) [as *Paranecrocarcinus pusillus*]; *P. scotti* Stenzel, 1945 [as *Necrocarcinus scotti*] and *P. vanbirgeleni* Fraaije, 2002.

***Pseudonecrocarcinus*? sp.**

Fig. 8J

Locality. Cal Cassanyes, Castellet i la Gornal (Alt Penedès, Catalonia). *Stratigraphical horizon.* Uppermost lower Aptian to lowermost upper Aptian (*Dufrenoyia furcata* and *Epicheloniceras martini* ammonite zones, respectively).

Studied material and measurements. A single incomplete carapace: MGSB86075, length 16.1 mm.

Description. Carapace apparently subpentagonal, slightly vaulted transversely; surface rugose, with scattered granules anteriorly and rows of granules forming short crests giving squamous aspect posteriorly. Front not preserved. Anterolateral margin convex, with granulated teeth or nodes. Posterolateral margin arched, rugose, with granules. Posterior margin slightly convex. Protogastric lobe inflated. Hepatic region depressed. Urogastric, cardiac, and intestinal regions undefined. Epibranchial region defined by an irregular row of granules. Meso- and metabranchial regions not well defined. Cervical groove shallow, faintly marked.

Remarks. Due to its incompleteness, an exhaustive description of this carapace is not possible. However, its apparent outline, rugose dorsal surface and shape of the lateral margins recalls *P. foersteri* from the Cenomanian of Wilmington (UK), and *P. vanbirgeleni* from the Maastrichtian of Maastricht (the Netherlands). The specimen is here placed within the *Paranecrocarcininae* and tentatively assigned to *Pseudonecrocarcinus*, even though the absence of frontal characters precludes verification of the presence of the diagnostic post-frontal slits (see Wright and Collins, 1972, pl. 22, fig. 5a–c; Fraaije, 2002, figs 1.3, 3.1, 3.2; Jagt et al., 2010, fig. 2C).

Incertae sedis

Superfamily Etyoidea Guinot and Tavares, 2001

Family Etyidae Guinot and Tavares, 2001

Genus *Etyxanthosia* Fraaije, Van Bakel, Jagt and Artal, 2008

Type species. *Xanthosia fossa* Wright and Collins, 1972, by original designation.

Species included. *Etyxanthosia fossa* (Wright and Collins, 1972) [as *Xanthosia fossa*]; and *E. inflata* López-Horgue and Bodego, 2017.

***Etyxanthosia fossa* (Wright and Collins, 1972)**

Fig. 8K

1972 *Xanthosia fossa* Wright and Collins, p. 100, text-fig. 14f; pl. 20, figs 4–6.

1999 *Xanthosia fossa* Wright and Collins; Schweitzer Hopkins et al., p. 80, fig. 11.

2008 *Etyxanthosia fossa* (Wright and Collins, 1972); Fraaije et al., pp. 200, 201, pl. 2, fig. 4.

2011 *Etyxanthosia fossa* (Wright and Collins, 1972); Breton and Collins, p. 144, fig. 2.

2011 *Etyxanthosia fossa* (Wright and Collins, 1972); Klompmaker et al., 2011, pp. 1205, 1206, text-fig. 5.

2012b *Etyxanthosia fossa* (Wright and Collins, 1972); Schweitzer et al., p. 137, fig. 5.

2017c *Etyxanthosia fossa* (Wright and Collins, 1972); Schweitzer et al., p. 3, fig. 1.2.

2020 *Etyxanthosia fossa* (Wright and Collins, 1972); Collins et al., p. 34, fig. 4J.

2020 *Etyxanthosia fossa* (Wright and Collins, 1972); Sasaki, p. 8070.

Locality. Cal Cassanyes, Castellet i la Gornal (Alt Penedès, Catalonia).
Stratigraphical horizon. Uppermost lower Aptian to lowermost upper Aptian (*Dufrenoyia furcata* and *Epicheloniceras martini* ammonite zones, respectively).

Studied material and measurements. A single portion (right-hand side) of carapace, with preserved cuticle: MGSB74550, length 7.6 mm, width 9.5 mm.

Description. Small carapace, much wider than long; transversely ovate; cuticle finely granulated. Front and orbits not preserved. Anterolateral margin with large spines, rectangular at bases, outer-orbital spine preserved, pointed. Posterior portion of mesogastric region preserved, rhombus shaped, large. Protogastric region swollen. Hepatic region flattened, subtriangular, clearly separated from protogastric lobe by well-marked gastrohepatic groove and bearing prominent tubercle. Urogastric region slightly swollen; cardiac region wide; intestinal region not preserved. Epibranchial region subdivided by groove, swollen medially, more flattened near posterolateral margin. Mesobranchial region swollen, bounded by two oblique grooves. Metabranchial region not preserved. Cervical groove sinuous, complete, notching lateral carapace margins.

Remarks. The single specimen from Cal Cassanyes corresponds fully with a carapace of the present species illustrated by Fraaije et al. (2008, pl. 2, fig. 4), but is incomplete, lacking the front, posterior margin and large portions of the central carapace regions. A comparison with the diagrammatic figure presented by Wright and Collins (1972, text-fig.14f) and to photographs of the types supplied by Collins et al. (2020, fig. 4j) do not show significant morphological differences. Compared with the specimen of *E. fossa* from Koskobilo (Navarra, northern Spain), illustrated by Fraaije et al. (2008, pl.2, fig. 4), the Cal Cassanyes carapace shows all typical features and can thus be assigned to *E. fossa* with confidence (see also; Klompmaker et al., 2011, text-fig. 5; Schweitzer et al., 2012c, p. 136). The Cal Cassanyes specimen constitutes the earliest record of the genus, and one of the earliest of the family (see Schweitzer et al., 2017c, p. 2).

Another species of *Etyxanthosia* from the Iberian Peninsula is *E. inflata*, from the upper Albian (Zufia Formation) near Allotz (Navarra), which differs from the Cal Cassanyes specimen in lacking a tubercle in the hepatic region and by having more inflated protogastric regions (compare López-Horgue and Bodego, 2017, pp. 13, 14, fig. 8F–H).

Section Eubrachyura de Saint Laurent, 1980

Subsection Heterotremata Guinot, 1977

Superfamily Dorippoidea MacLeay, 1838

Family Telamonocarcinidae Larghi, 2004

Type genus. *Telamonocarcinus* Larghi, 2004

Other genera included. *Eodorippe* Glaessner, 1980, *Iberodorippe* gen. nov. (see below), *Navarrara* Klompmaker, 2013, *Personadorippe* Van Bakel, Mychko, Spiridonov, Jagt and Fraaije, 2021c and *Withersella* Wright and Collins, 1972.

Diagnosis. See Luque (2014).

***Iberodorippe* gen. nov.**

urn:lsid:zoobank.org:act:F277A86B-334B-4A55-AD0A-DB2986119459

Type species. *Iberodorippe vinea* sp. nov., by monotypy.

Species included. Only the type species is currently known.

Derivation of name. Alluding to a fossil dorippoid crab from the Iberian Peninsula.

Diagnosis. Carapace subpentagonal in outline, length slightly exceeding width; flattened in longitudinal and transverse cross sections; regions weakly defined, flattened; front strongly

projected, subtriangular with bifid tip, with two subdistal spines; orbitofrontal margin occupying entire carapace width; orbital margin oblique, sinuous, without notches; outer orbital spine strong, pointed, forwardly and outwardly directed; lateral carapace margins subvertical, blunt, with strong, outwardly directed hepatic spine; carapace surface smooth, with tubercles on cardiac, protogastric and hepatic region; cardiac region narrow, oval; cervical groove wide, V-shaped, reaching lateral carapace margin; branchial groove well defined. Posterior carapace margin with thin rim, concave.

Remarks. *Iberodorippe* gen. nov. is morphologically closest to *Withersella*, which is known exclusively from the Aptian of the United Kingdom (see Wright and Collins, 1972; Van Bakel et al., 2021c). *Withersella* differs in lacking the robust hepatic lateral spine, in having a granular carapace surface structure (vs smooth in *Iberodorippe* gen. nov.) and a triangular cardiac region with three tubercles (vs oval, with two axial and two admedial tubercles, in *Iberodorippe* gen. nov.).

Eodorippe comprises the Campanian–Maastrichtian type species, *E. spedeni* Glaessner, 1980 from New Zealand and the Cenomanian *E. binodosa* Collins, Kanie and Karasawa, 1993 from Japan. The former can be differentiated from *Iberodorippe* gen. nov. in having a relatively wider carapace and a more sinuous lateral carapace margin and in lacking the hepatic lateral spine. The monotypic *Navarrara* (type: *N. betsieae* Klompmaker, 2013, from the upper Albian of northern Spain) has a relatively narrow dorsal carapace, with spines along the anterolateral and posterolateral margins, an elongated anterior mesogastric process, a very short posterior mesogastric region and a granular dorsal surface. These characters set it apart from *Iberodorippe* gen. nov. The new genus is morphologically reminiscent of *Personadorippe*, which comprises three species: the type species, *P. kalashnikovii* Van Bakel, Mychko, Spiridonov, Jagt and Fraaije, 2021c (lower Cenomanian, Moscow region, Russia), *P. connori* (Nyborg, Garassino, Vega and Kovalchuck, 2019; as *Eodorippe connori*) (Albian of Oregon, USA) and *P. levashiensis* Van Bakel, Mychko, Spiridonov, Jagt and Fraaije, 2021c (middle Aptian, Levashinsky region, Dagestan). This genus differs from *Iberodorippe* gen. nov. in lacking the prominent hepatic lateral carapace spine and a central cardiac tubercle, and in having an overall evenly granular (vs smooth in *Iberodorippe* gen. nov.) carapace and the posterior branchial region expanded.

***Iberodorippe vinea* sp. nov.**

Fig. 8L, M

urn:lsid:zoobank.org:act:22384E3C-4562-42F5-BA53-F8BF3EBB88D2

Derivation of name. From the Latin *vinea*, meaning vineyard, with reference to the type locality.

Locality. Cal Cassanyes, Castellet i la Gornal (Alt Penedès, Catalonia).
Stratigraphical horizon. Uppermost lower Aptian to lowermost upper Aptian (*Dufrenoyia furcata* and *Epicheloniceras martini* ammonite zones, respectively).

Studied material and measurements. Four specimens; **holotype**, MGSB86062, length 8 mm, width 7.2 mm; **paratypes**, MGSB86078a, length 6.7 mm, width 6.6 mm; MGSB86078b, length 6.7 mm, width 6.6 mm; MGSB86078c, length 6.7 mm, width 6.6 mm.

Diagnosis. As for genus.

Description. Carapace small, subpentagonal in outline, length slightly exceeding width, about 1.1 CL/CW ratio, widest at hepatic lateral spine, and halfway branchial region; regions barely inflated; carapace flattened in longitudinal and transverse sections. Front prominent, strongly projected, subtriangular with bifid tip, with two acute subdistal spines slightly projected, axially weakly sulcate. Orbital margin oblique, sinuous, without notches; outer orbital

spine strong, pointed, directed forwards and outwards. Lateral carapace margins subvertical, blunt in cross section; anterolateral margin with strong, outwardly directed hepatic spine; posterolateral margin longer, slightly convex at branchial region. Posterior margin medially concave, inverted V-shaped, with thin rim in central portion; lateral portions rounded, with thick rim, curved around posterior corner. Mesogastric region narrow, elongate, posterior part subtriangular, anterior process with vertical lateral margins; epigastric regions flat. Protogastric region large, suboval, bearing central tubercle; hepatic region weakly differentiated, subrectangular, with central tubercle. Urogastric region poorly preserved, apparently low. Epibranchial region low, obliquely oriented; posterior branchial region large, pyriform, surface flattened. Cardiac region narrow, oval, anteriorly slightly wider, region bearing two axial tubercles, anterior one being larger, and single pair of admedial tubercles, smaller than axial pair and positioned anterior to anteriormost axial tubercle. Intestinal region weakly defined, as subtrapezoidal strip. Cervical groove shallow, widely V-shaped, with deflected lateral portion arched under hepatic spine and reaching lateral carapace margin. Branchial groove shallow, oblique, straight. Branchial groove shallow, not clearly defined. Grooves enclosing anterior mesogastric process and epibranchial region well defined, branchiocardiac grooves shallower. Carapace surface smooth, with tubercles on cardiac, protogastric and hepatic region. Ventral surface and appendages not preserved.

Remarks. It is worth noting that the swelling in the left branchial chamber that present one of the reported specimens, the holotype MGSB86062 (Fig. 8L), could be due to a parasitic infestation by a bopyrid isopod, likely representing the ichnofossil taxon *Kant-hyloma crusta* Klompmaker et al., 2014.

6. Discussion

6.1. Comparative discussion of Early Cretaceous decapod crustacean communities across basins

The decapod crustacean assemblage from Cal Cassanyes is characterised by a high diversity, especially so when considering the small extent of the outcrop and the comparatively paucity of crustacean remains. Taxa recognised include representatives of the Macrura, Axiidae, Anomura and Brachyura. Brachyurans clearly dominate the assemblage with eleven species, representing seven families. Dromioids and palaeocorystoids are commonest, both in number of species and specimens, with *Distefania incerta* being most abundant. In fact, this species accounts for five carapace remains and twenty-two isolated chelae, being fifty percent of samples studied (Fig. 9).

Other Aptian decapod crustacean assemblages from the Iberian Peninsula have been recorded from the neighbouring Maestrat Basin; García-Penas et al. (2023) have recently published an extensive compilation, with special emphasis on the Oliete and Galve sub-basins of the Maestrat Basin (see Salas et al. in Martín-Chivelet et al., 2019), linking the peak of decapod crustacean diversity to transgressive events. According to García-Penas et al. (2023), diversity peaks in these sub-basins occur in the lower Aptian Forcall Formation, which is in part correlatable with the Vallcarca Marls Unit (see Moreno-Bedmar et al., 2009b, 2016), the source of the Cal Cassanyes assemblage. Decapod crustacean faunas from the Oliete and Galve sub-basins are clearly dominated in number by the mecochirid lobster *Atherfieldastacus magnus* (M'Coy, 1849); to date, only four brachyuran taxa have been recorded (García-Penas et al., 2023, fig. 8). However, in the open-marine platform of the Morella and Salzedella sub-basins (see Salas et al. in Martín-Chivelet et al., 2019), varied faunules of decapod crustaceans are known (À.O. pers. obs.) from the marly limestones with

fragments of rudists and corals at the top of the Forcall Formation (see Bover-Arnal et al., 2022, figs 5C, D, 15B). These faunules comprise indeterminate axiids, squat lobsters such as *Galatheites royo* Van Straelen, 1927 and other indeterminate galatheoids, as well as paguroids, dromiids such as *Distefania* spp. (= *Dromiopsis* sp. of Van Straelen, 1927, pl. 2, fig. 3), prosopids (*Rathbunopon tarraconensis* Ossó, Van Bakel, Ferratges-Kwekel and Moreno-Bedmar, 2018) and etyids (*Xanthosia* sp.). All of these have been documented from the Morella la Vella Member of the Forcall Formation (see Moreno-Bedmar et al., 2010 for the stratigraphy of the different members of the Forcall Formation). Additionally, the common *Mithracites vectensis* Gould, 1859, has been collected in the underlying Barra de Morella Member of the same formation (O. Ferrer, pers. comm.). In the eastern part of the Morella Sub-basin, the marly limestones of the Forcall Formation yielded a faunule that includes paguroids, brachyurans such as the dromiid *Pithonoton lluismariaorum* Ossó, Van Bakel, Ferratges-Kwekel and Moreno-Bedmar, 2018 and *Rathbunopon tarraconensis* (see Ossó et al., 2018). It is worth mentioning that remarkably similar, if not identical, to the Forcall Formation faunas have been observed in Aptian strata of the Urgonian Complex in the Sevlievo region of Bulgaria (À.O., pers. obs.).

In the northern Iberian Peninsula, decapod crustacean faunules have also been recorded from clayey marlstones of the lower Aptian Patrocinio Formation in Cantabria. Similar to assemblages from the Oliete sub-basin, that from the Patrocinio Formation is dominated by *Atherfieldastacus magnus*, although four brachyurans have been recorded as well (see González-León et al., 2016; Ossó and Moreno-Bedmar, 2020; Ossó et al., 2021; López-Horgue et al., 2022). In this regard, table 1 in García-Penas et al. (2023) provides a clear graphical representation of the abundance or paucity of various Iberian decapod crustacean assemblages based on their respective palaeoenvironments.

The Aptian decapod crustacean assemblage from clayey and sandy deposits of the Lower Greensand Group (Isle of Wight, UK; see Van Bakel et al., 2022b, and references therein), which also contain sponges and are dominated by the ubiquitous lobster *Atherfieldastacus magnus*, shows strong affinities with the Cal Cassanyes fauna, with several brachyuran taxa in common, e.g., *Garrasosopon angustus*, *Vectis*, *Xanthosia* as well as *Withersella*, similar to *Iberodorippe* gen. nov. (compare Wright and Collins, 1972; Klompmaker, 2013, table 6, appendices A, B). Although ongoing research by one of us (BWMvB), and co-workers, will shed new light on Aptian decapod crustacean faunas from the Isle of Wight, the currently available data reveal comprise a total of sixteen, eight of which are brachyurans (Klompmaker, 2013, appendices A, C). Faunules from sandy Aptian deposits in Dagestan (Russia) share longodromitids, viaiids and telamonocarcinids with the Cal Cassanyes assemblage (see Van Bakel et al., 2021c).

Younger and remarkably diverse assemblages from coral-reefal limestones of the upper Albian Eguino Formation in Alsasua (Navarra, Spain) (see Klompmaker, 2013) exhibit notable similarities to the Cal Cassanyes lot, despite the age difference. For instance, both assemblages have taxa at the family and genus level in common, such as galatheoids and the dromiid *Eodromites*. Furthermore, there are even shared taxa at the specific level, including *Distefania incerta*, *Goniodromites laevis* and *Etyxanthosia fossa*.

An older, geographically distant decapod crustacean assemblage from coral-sponge reefal limestones of the lower Barremian Zapotitlán Formation of Puebla (Mexico) presents strong faunal similarities to the Cal Cassanyes fauna, sharing galatheoids and dromiids (*Distefania* and *Goniodromites ?laevis*) (Vega et al., 2019; Klompmaker et al., 2022). However, no other taxa have to date been recorded from reefal environments in the Lower Cretaceous of

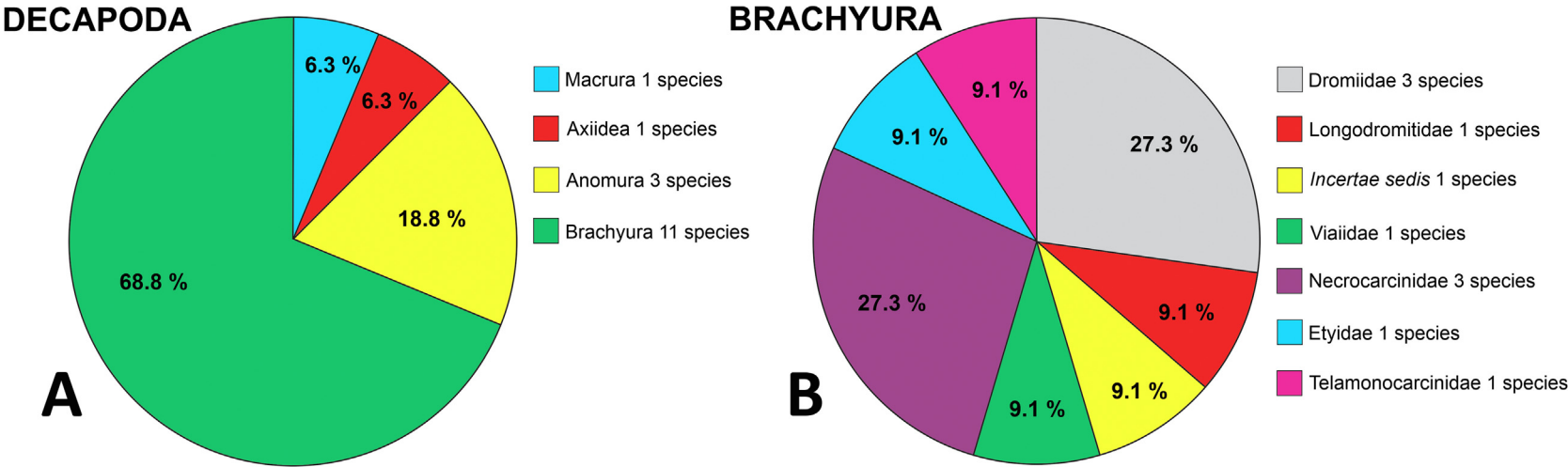


Fig. 9. A. Pie chart showing the composition of the Cal Cassanyes decapod crustacean assemblage according to main groups and number of taxa. B. Pie chart showing the composition of the main group, Brachyura, at the family level.

America. Instead, taxa found in non-reefal settings include in particular brachyurans, such as palaeocorystoids, raninoids, etyids and even eubrachiurans (dorippoids) and possibly eogeryonids. Nevertheless, the number of taxa at each locality is generally lower than at European localities (e.g., Klompmaker, 2013; appendices A–D; Luque et al., 2017; Prado et al., 2018). It has been suggested that species of *Distefania*, *Eodromites* and *Goniodromites*, mostly found in Upper Jurassic–Cretaceous coral-/sponge settings, like those of Cal Cassanyes outcrop, ensured the survival of that stock into the Paleocene (Klompmaker et al., 2012b, p. 780; Jagt et al., 2015, p. 868).

6.2. Preliminary palaeobiogeographical analysis

A proper palaeobiogeographical analysis of Early Cretaceous decapod crustaceans is frustrated by limited data, illustrating a need for further research. This is evidenced by the fact that even in recent literature, descriptions of new species or even genera remain commonplace (e.g., Artal et al., 2012; Klompmaker, 2013; Ossó et al., 2018; Ossó and Moreno-Bedmar, 2020; Ferratges et al., 2021; Van Bakel et al., 2021c; García-Penas et al., 2023). The present paper serves as an example, in that it introduces five new species and one new genus. Thus, palaeobiogeographical considerations of the Cal Cassanyes assemblage must be treated with caution. Paguroids, one of the most difficult groups for study, pose challenges to palaeobiogeographical analyses. Here we erect *Pagurus? garrafensis* sp. nov.; recent papers by Ferratges et al. (2021) and García-Penas et al. (2023) have introduced new genera, thus proving that our current understanding of this group is incomplete.

Galatheoids are notably rare at Cal Cassanyes, represented only by two remains. In contrast, dromioids are well represented at Cal Cassanyes, both in terms of specimens and diversity. *Distefania incerta*, the commonest representative, appears to have been a generalist, possibly opportunistic, with a wide geographical distribution and extensive stratigraphical range, with record from the Aptian to Cenomanian/Turonian of France, Germany, Spain and the United Kingdom. The term 'generalist' is used here to describe not only the dietary requirements of *Distefania incerta* but also its ability to tolerate various environmental conditions, such as water temperature. This is particularly relevant because the Cretaceous waters of Germany and the United Kingdom were slightly cooler than those of the Iberian Peninsula.

Goniodromites laevis, previously known only from the upper Albian in Spain, has its range extended downwards to the Aptian in the present study. Another rare species, *Garrafosopon angustus* comb. nov., first described from the upper Aptian of the Isle of Wight (*Parahoplites nutfieldensis* ammonite zone), is now recorded from Cal Cassanyes.

Among dromioids, two new species are here introduced: *Vectis blesai* sp. nov. and *Mesodromilites prietoi* sp. nov. Additionally, a new species of necrocarcinid, *Necrocarcinus mariae* sp. nov., is described. Of etyoids, *Etyxanthosia fossa* is recognised. Originally described from the Cenomanian (*Mantelliceras mantelli* ammonite Zone) of Devon, United Kingdom, it is now also known from the upper Albian of Spain and the Aptian of Cal Cassanyes. Lastly, among dorippoids, a new genus and species, *Iberodorippe vinea*, is described.

As noted above, conducting a proper palaeobiogeographical analysis is greatly restricted due to our inability to trace endemic taxa. The available data only allow us to establish connections with assemblages from the Aptian in the Maestrat Basin and the upper Albian in Navarra and Basque Country (Spain), as well as with assemblages from the United Kingdom, mainly the Isle of Wight, ranging in age from Aptian to Cenomanian. However, this is merely

a general overview, potentially influenced by biases such as the similarity between the studied assemblage and the most extensively researched assemblages of similar age. Additionally, the presence of generalist or opportunistic species may contribute to some degree of palaeobiogeographical affinity, which may not be truly significant.

6.3. Palaeoenvironment and palaeoecology of sponges and crabs at Cal Cassanyes

The sponge associations at Cal Cassanyes comprise Hexactinellida and 'Lithistida'. Such an association of siliceous sponges is typical of medium water depths, i.e., between 50 and up to 100 m below wave base, where low temperatures predominate (Keupp et al., 1989). Such depth range would be in agreement with an outer carbonate platform environment, as supported by observed lithologies, carbonate textures and accompanying biota (see above). Associations of this type have been widely recorded from the geological past (e.g., Hurcewicz, 1968; Sánchez-Beristain and Reitner, 2012, 2018).

Moreover, this association probably developed under low rates of sedimentation (compare Moreno-Bedmar et al., 2009b). A reduced sedimentation rate is generally considered as a precondition for establishment of sponge communities. However, some sponges can successfully adapt to higher rates of sedimentation. In these cases, tube-shaped morphotypes, as those of numerous species mentioned here (Fig. 3), are favoured (Krautter, 1998; Delecat and Reitner, 2005), since narrow oscula produce strong streams of water that protect the sponge from settling sediment.

Another possibility would be that the assemblage of siliceous sponges had received a continuous supply of sediments and food particles by means of cold upwelling currents (Hanz et al., 2019). This type of current is characterised by being rich in nutrients. Since deep water brought to the surface is normally rich in nutrients, coastal upwelling used to prop the growth of plankton and bacteria (Shannon and Nelson, 1996). These, in turn, sustain the marine food chain with a continuous supply of nutrients and may thus support diverse communities. This would explain the highly diverse assemblage of hexactinellids and 'lithistids', both of them well adapted to cold-water environments.

Changes in sedimentation are associated to variations in nutrient input (Tucker and Wright, 1990). Consequently, sedimentation represents a major controlling factor of morphological predominance and diversity of siliceous sponges (Krautter, 1996). Nevertheless, the fragile structure of hexactinellids is an important feature while assigning this association to any particular palaeoenvironment. We are inclined to consider either a low-energy environment or medium depths influenced by cold upwelling currents.

The tissue organisation of hexactinellid sponges allows them to absorb colloidal organic matter or dissolved amino acids through filtering mechanisms (Krautter, 1998), which constitutes their main feeding strategy. The currents formed by this type of feeding could favour the establishment of communities of crustaceans and siliceous sponges. For their part, lithistid sponges are known for being able to constitute aggregated solid clumps to form high mounds in modern seas (Maldonado et al., 2015). Siliceous sponges associated to crustaceans have been recorded from modern settings such as the Levantine zone of Turkey, where the demosponge *Sarcotragus muscarum* Schmidt, 1864, serves as habitation and perhaps provider of a nutrient medium for the alpheids *Synalpheus gambarelloides* (Nardo, 1847) and *Alpheus rapacida* (De Man, 1908; Özcan and Katakın, 2011). Based on these hypotheses, it is highly viable that the associations found at Cal Cassanyes reflect such a type of

community, which is of special interest for a palaeosynecological analysis of both crustaceans and siliceous sponges.

Dissolved organic matter (DOM) in seawater is a large and complex pool of carbon made up of a mosaic of molecules (Olinger et al., 2021). Sponges incorporate dissolved organic carbon (DOC) from these molecules. In this process, sponge symbionts play an important role (De Goeij et al., 2008). In spite of the fact that sponges feed on micro-organisms, a large quantity of extracellular bacteria inhabit the mesohyl of a considerable number of demersal sponges (Vacelet and Donadey, 1977), which have led to the denomination of these organisms as 'bacteriosponges' or 'high-microbial abundance sponges' (Hentschel et al., 2006).

It has been discovered that sponges can 'recycle' dissolved organic matter from corals (Rix et al., 2018). Additionally, it has been observed that the sponges themselves 'sneeze' mucus – which contains plenty of DOM – to shed particulate waste from their seawater inlet pore system (Kornder et al., 2022). In some sponges, such as *Aplysinia archeri* (Higgin, 1875), the particulate waste is trapped by the mucus secreted by the sponge and further aggregates on its surface. Both mucus and waste are either 'sneezed' into seawater or fed upon by associated fauna. This mucus is expelled against the direction of the internal flow of water of the sponge.

In modern times, cold-water coral reefs as well as sponge grounds are deep-sea biological hotspots (Bart et al., 2021). In such settings, DOM is incorporated into the sponge and is further released as particulate organic matter (POM) which sponges shed into seawater (Rix et al., 2018). In turn, this POM provides nutrients to associated fauna, which primarily encompasses some

crustaceans, annelids (serpulids?) and echinoids (Fig. 10), but also scleractinians, bryozoans, ascidians and demersal fish in addition to diverse sponge arrays. These sponges are usually represented by both 'lithistid' and hexactinellid forms in modern oceans (e.g., Maldonado et al., 2016; Meyer et al., 2019; Kornder et al., 2021; Morganti et al., 2022). Complex communities in which sponges are the main components, host a wide variety of invertebrates, such as corals, echinoderms, annelids, molluscs and crustaceans, among others (e.g., Braga-Henriques et al., 2012; Maldonado et al., 2015, and references therein; Ríos et al., 2020; Stratmann et al., 2021). Although decapod crustaceans have a wide spectrum of feeding habits (e.g., Davie, 2021), some of taxa recorded herein most certainly fed upon the remains of sponges, as the suspended particles surrounding them, which in turn most probably relied on the constant nutrient flow coming downslope. On the other hand, brachyurans likely scavenged or preyed upon the abundant fauna associated with the sponge aggregations at Cal Cassanyes (compare Hanz et al., 2022, figs 2, 4, 5). In turn, decapod crustaceans could have found protection from predators in such sheltered environments (e.g., Lavalli and Spanier, 2015). Therefore, it is highly likely that the associations described here exhibited ecological similarities to modern environments where both these groups coexist. Thus, we propose a comparable model for the diverse decapod-sponge communities found at Cal Cassanyes (Fig. 11).

Axiids could have served as primary consumers, acting as deposit feeders (e.g., Coelho and Rodrigues, 2001), while squat lobsters (Nicol, 1932) may have exhibited similar feeding behaviours, functioning as deposit feeders or scavengers, but also predators

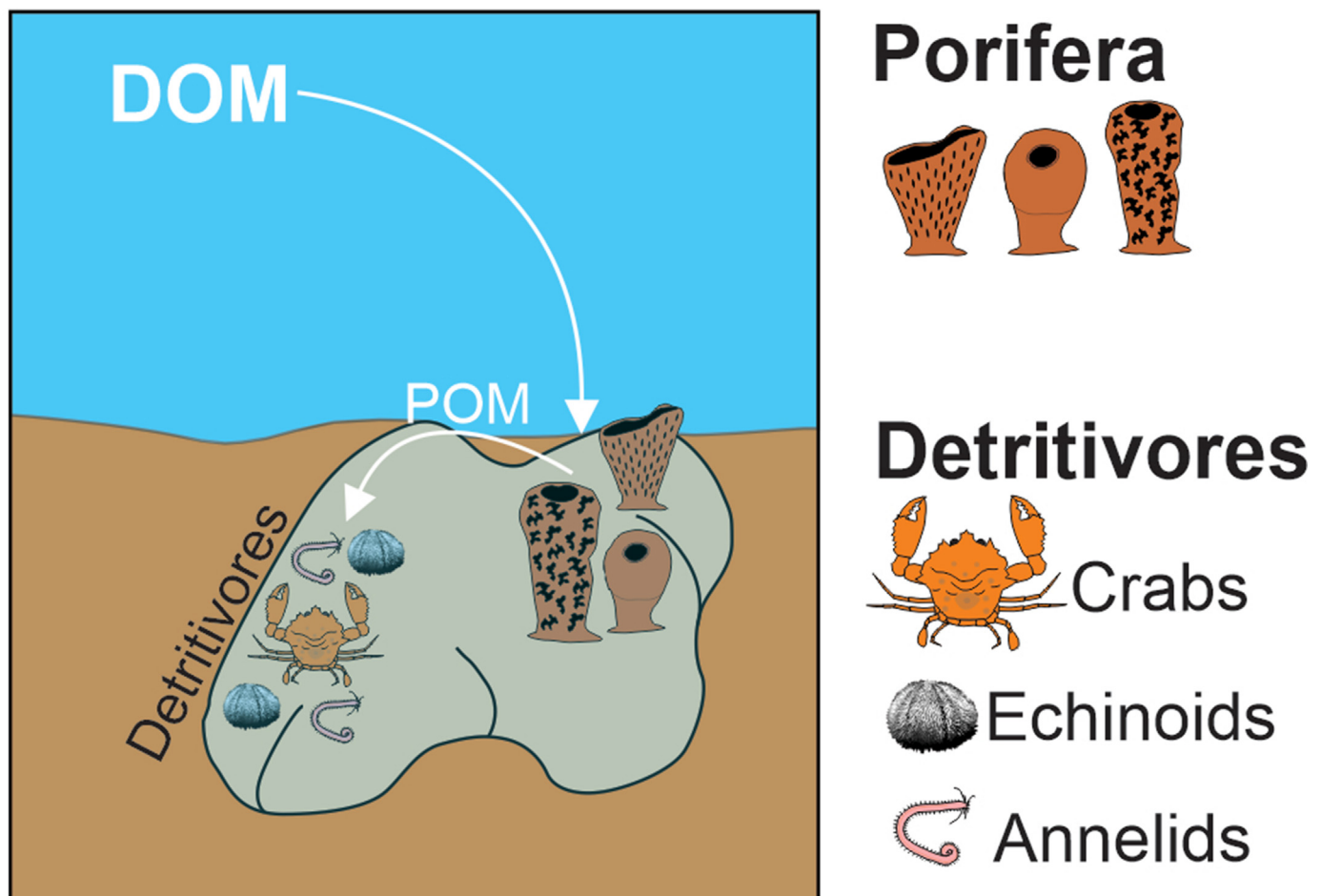


Fig. 10. An illustration depicting the flow of nutrients, Dissolved Organic Matter (DOM) and Particulate Organic Matter (POM) between the sponge community and various detritivores, including decapod crustaceans.

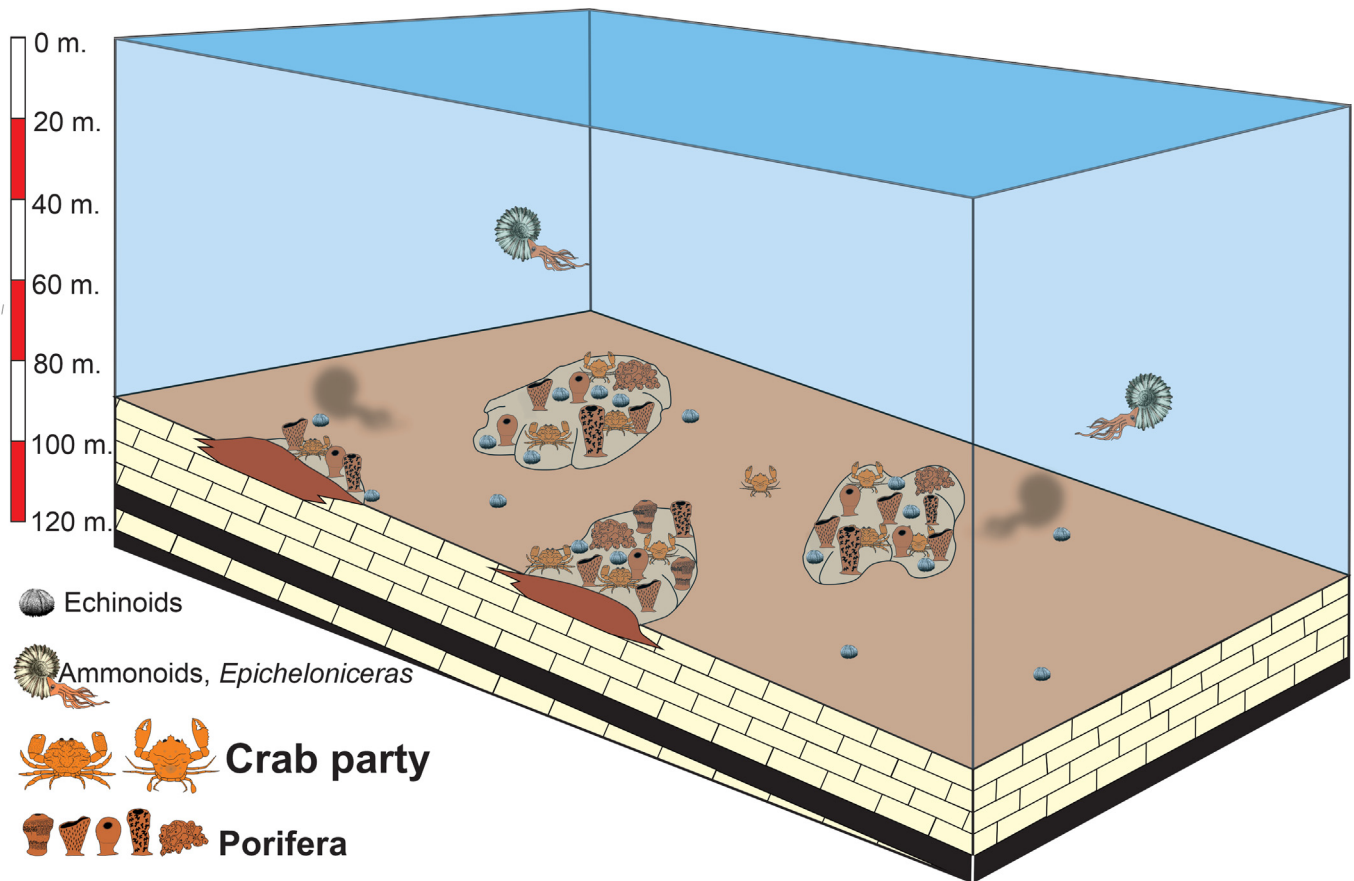


Fig. 11. An idealised reconstruction depicting sponge communities along with their associated fauna, such as decapod crustaceans and echinoids, as well as two ammonites.

(Hudson and Wigham, 2003). Paguroids exhibit a wide range of feeding styles (Davie, 2021), being even consumers of sponges. Chela shape (e.g., Schweitzer and Feldmann, 2010b) could infer that necrocarcinids (Fig. 8H) were opportunistic scavengers or predators, and that some dromiids such as *Distefania incerta* (Fig. 6E–G) could have foraged on worms, molluscs or on the extraordinary quantity of the sea urchin *Pliotoxaster collegnii*, similar to some extant dromiids (e.g., https://en.wikipedia.org/wiki/Dromia_dormia#/media/File:Sponge_crab_eating_a_sea_urchin.jpg accessed 01/06/2023). In any case, the feeding habits of decapods are not fully known, since many of them can be considered to have been almost omnivorous, sporting a broad variety of diet and multiple feeding strategies (e.g., Schweitzer and Feldmann, 2010b; Davie, 2021). However, given the feeding opportunities that the sponge aggregations of Cal Cassanyes offered, decapod crustaceans likely occupied different trophic levels in that biotic association (e.g., Hanz et al., 2022, figs 4, 5). Similarly, an example of abundance of decapod crustacean remains related to benthic food resources generated by upwelling has been recorded from Turonian siliciclastic rocks at localities in Colombia (see Feldmann et al., 1999). The incompleteness of the decapod crustaceans from there probably indicates that they represent disarticulated corpses in some cases or more likely moults, since it is in the moulting process that they are most vulnerable and sponges could provide a sheltered place to moult. The thin cuticle preserved in most of them could indicate that many remains constitute exuvia. One of the decapods recorded herein (Fig. 7C) was found inside the osculum of a tubular sponge, which could reinforce this notion.

Decapods have been found in both bioclastic sponge-rich limestones and adjacent marly limestones, suggesting that species of different lifestyles inhabited the Cal Cassanyes area. Some

taxa appear to have preferred hard or coarse sandy bottoms, such as dromiids (compare Klompmaker et al., 2012b) or on the sponges themselves, such as squat lobsters (see Maldonado et al., 2016; Robins and Klompmaker, 2019; Klompmaker et al., 2022). Others, for instance axiids, preferred to burrow into muddy soft sea floors (e.g., Kornienko, 2013) or burying, as seen in necrocarcinids (e.g., Van Bakel et al., 2021b).

7. Concluding remarks

The remarkable diversity of decapod crustaceans found in the Cal Cassanyes outcrop, especially brachyurans, establishes this locality as the most varied Aptian decapod site in the Iberian Peninsula, and one of the most diverse Aptian brachyuran localities globally to date. Furthermore, Cal Cassanyes constitutes an example of Early Cretaceous upwelling, crucial to the development of the Cal Cassanyes faunal assemblage. The abundant nutrients provided by upwelling currents from deeper, colder waters, allowed for the establishment of sponge aggregations in distal open-marine platform conditions. This, in turn, facilitated the flourishing of a rich associated fauna, including decapod crustaceans, occupying various trophic levels. Therefore, it can be concluded that decapod crustacean diversity at this locality was influenced by nutrient inputs resulting from upwelling.

The aggregation of sponges found at Cal Cassanyes, similar to coral-reef environments, provided a sheltered habitat for decapod crustaceans, enabling them to hide, forage and moult. Similar to the present day, sponge aggregations served as biodiversity hotspots in the past. Consequently, Cal Cassanyes displays notable faunal similarities to other assemblages associated with sponge or coral environments. Finally, the occurrence of *Distefania incerta*, *Mesodromilites*

and *Etyxanthosia fossa* in Aptian rocks at Cal Cassanyes represents the earliest record of these taxa. The new genus and species, *Iberodorippe vinea*, ranks among the earliest records of eubrachiurans.

A preliminary palaeobiogeographical analysis provides only a broad overview, revealing associations between the Cal Cassanyes fauna and assemblages from the Aptian of the Maestrat Basin and the upper Albian of Navarra and Basque Country in Spain, as well as the Aptian to Cenomanian of the United Kingdom, mainly the Isle of Wight.

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