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Fernando Ari Ferratges Kwekel

Sistemática, diversidad y distribución paleoambiental de los crustáceos decápodos del Eoceno de la zona surpirenaica central

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SISTEMÁTICA, DIVERSIDAD Y DISTRIBUCIÓN PALEOAMBIENTAL DE LOS CRUSTÁCEOS DECÁPODOS DEL EOCENO DE LA ZONA SURPIRENAICA CENTRAL

Autor

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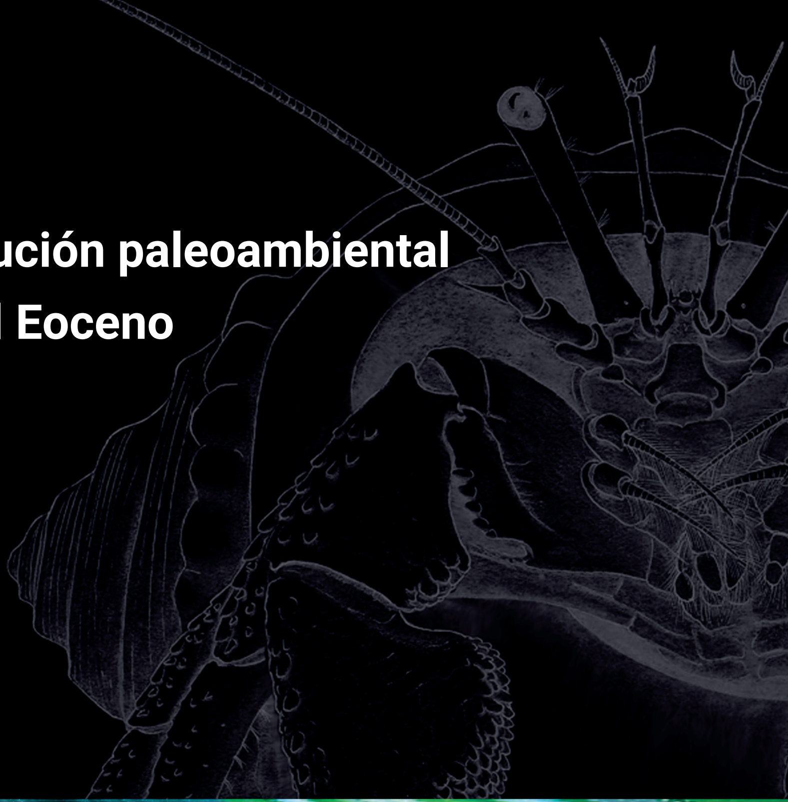

Fernando Ari Ferratges Kwekel

Departamento de Ciencias de la Tierra
Áreas de Estratigrafía y Paleontología
Zaragoza, 2022

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Portada:

Phrynolambrus sagittalis (nueva especie) del Eoceno superior de Huesca. Reconstrucción de Hugo Saláis.

Contraportada:

Aragolambrus collinsi Ferratges, Zamora y Aurell, 2019, del Eoceno inferior de Huesca. Reconstrucción del autor.

“En la larga historia de la humanidad (y de los animales también) los que aprendieron a colaborar e improvisar de la manera más efectiva han prevalecido”

Charles Darwin

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Esta Tesis Doctoral no hubiera sido posible sin la ayuda, colaboración e influencia de muchas personas a las que estoy profundamente agradecido. Pero para poner en contexto estos agradecimientos considero necesario dar una breve explicación de los acontecimientos que me han llevado a estudiar un grupo tan particular como son los cangrejos.

Era el año 1993. Mi madre, que siempre ha sido de llevarnos a mi hermana y a mí a excursiones a la naturaleza, nos llevó a pasar el día en una playa cerca de Barcelona. En aquella época, era relativamente frecuente ver cangrejos en esas playas de arena fina, y casualmente encontramos lo que probablemente era un *Carcinus maenas*. Como curiosos críos que éramos, mi hermana y yo estuvimos jugando un buen rato con el pobre crustáceo. Mi madre, viendo el interés que despertaba en nosotros aquel pequeño animal, hizo fotos con una, entonces moderna, cámara Kodak, de esas que funcionaban con carrete. Yo, que ya manifestaba un marcado interés por la naturaleza y los animales, quedé enamorado de esa fascinante criatura. Tanto es así, que, al volver a casa, después de soltar al pobre cangrejo -aparentemente ileso-, quise ver las fotos de inmediato. Desgraciadamente, la tecnología de la época no ofrecía las ventajas que dan hoy en día las cámaras digitales, y en un arrebato de infantil ignorancia e impaciencia, abrí la tapa de la cámara pensando que vería las fotos en miniatura. Obviamente se estropearon todas.

Aún no lo sabía, pero ese día de playa marcó mi futuro y vocación (y además aprendí que no se debe abrir la tapa de una cámara analógica con el carrete sin revelar). Desde entonces, he tratado de aprender cuanto he podido sobre estos animales, intentando entender cómo y dónde viven y que papel desempeñan en su ecosistema, pero también como han evolucionado y de qué modo están relacionados unos con otros. Además, este interés en un grupo tan particular me impulsó a recolectar ejemplares de todo el mundo -preferiblemente ya muertos o mudas-, lo que me ha permitido disponer de una interesante y diversa colección, muy útil para comparar con las formas fósiles y ayudar a entender su evolución. Sin embargo, durante la adolescencia decidí que era más interesante la vida militar, por lo que me aparté (en cierta medida) de mis verdaderos intereses. No obstante, y nuevamente por influencia de mi madre, me apunté a la SAMPUZ (Sociedad de Amigos a la Paleontología de la Universidad de Zaragoza), un grupo de entusiastas de la paleontología en la ciudad donde tenía el cuartel al que me alisté. Fue en uno de los eventos organizados por este grupo donde conocí a Samuel, quien sería mi futuro director de tesis, y quien me insistió en que, si me gustaba la paleontología, debía retomar los estudios.

Por todo ello, quiero hacer constar en primer lugar mi más sentido agradecimiento hacia Aria, mi madre, que me llevó a numerosas salidas de campo y playa durante mi infancia y juventud, dando rienda suelta a mis inquietudes naturalistas. En segundo lugar, mi peculiar trayectoria y reconversión no habría sido posible de ninguna manera sin Samuel, quien fue capaz de transmitir su pasión por la paleontología, y hacerme dar un paso más allá del mero coleccionismo. Además, esta Tesis Doctoral no hubiera sido posible sin el inestimable apoyo y dirección de Marcos, que con su enorme paciencia y conocimientos ha sabido enseñarme tantas cosas tanto en el trabajo de campo como en el de despacho. Me siento afortunado de tener tan buenos directores; ambos han sido y son un referente para mí. Hacia ellos mantendré siempre una profunda gratitud.

A Vanessa que además de su amor, su apoyo y sus consejos, me ha ayudado en numerosas cuestiones estadísticas y lingüísticas, o haciéndome darle dos vueltas más a algunas de las hipótesis barajadas en esta tesis. Además, agradezco su creatividad en la planificación de los peculiares viajes en los que nos embarcamos en nuestras “*aventuras de crancs*”.

También expresar mi agradecimiento a mi hermana, Eloísa, y mi padre, Fernando, que siempre me han apoyado y empujado a ser mejor, ayudando en lo que estuviera en su mano, aportando su granito de arena.

Se reconoce con profundo agradecimiento a Andreu Velasco (titus), Gregorio Ortega, José M. Méndez, Eduvigis Moreno, Lluis Maza, Jesús García, y Josep Lluis Domínguez por su apoyo y compañía, y muy especialmente a Manuel Fernández (Manolo), a quien aprecio profundamente y ha sido para mí una de las personas más importantes en el "mundillo de las piedras", y con quien tan buenos ratos he pasado en el campo. A Joan Vilella, por cederme material bibliográfico incunable. Quiero dar las gracias también a todo el departamento de Ciencias de la Tierra de la Universidad de Zaragoza, y muy especialmente a mis compañeros Manuel Pérez, Álvaro García, Roi Silva, Cristina Sequero, Elisa Laita, Raquel Moya, Eduardo Medrano y Vicente Gilabert que tanto me han ayudado, y a Julia Galán y Carmen Núñez entre otras cosas, por las "enriquecedoras" y escatológicas charlas sobre los restos de cangrejos regurgitados por gaviotas. También agradecer a Asia y a Mirian por permitirnos usar su espléndido local (el *Louisiana Café*) para celebrar el inicio y clausura del congreso que organizamos.

A Juan Carlos García Pimienta ("Pimi") que con su incansable energía para muestrear y prospectar me ha brindado tanto material y nuevos afloramientos, además de muchas risas y entrañables jornadas de campo, tanto para lo fósil como para lo no tan fósil. A Isabel Pérez por sus magníficas fotografías, consejos estilísticos y por las divertidas conversaciones en el laboratorio fotográfico. A los técnicos de laboratorio: Felipe y Manolo (de la Universidad de Zaragoza), que tan maravillosas láminas preparan; a Belén Notario, (Técnico de Laboratorio Microscopia y Microtomografía Computarizada del CENIEH), quien amablemente ayudó con sus conocimientos de los modernos y complejos sistemas de CT scan.

Al "*Crustacean Research Group*" (o "*Crustacic Park*", cuyo logo extraoficial figuro al final de estos agradecimientos), con Maru Andrada, Álvaro G. Penas y Javi Luque que tan lúdicas y educativas charlas hemos tenido y especialmente a este último, con quien pese a que no pude llevar a cabo la estancia internacional que teníamos planeada (y concedida ya por el ministerio) en la Universidad de Harvard, debido a los problemas surgidos por el COVID-19, pero que igualmente tanto me ha enseñado de cangrejos, filogenias, carcinología y biología en general, ya sea en nuestras video-charlas, en correos o en persona.

Als meus professors de la Universitat Autònoma de Barcelona: Oriol Oms, Josep Maria Pons, Enric Vicens, Ricard Martínez i Esmeralda Caus i, els aleshores doctorands, Erzica Cruz i Jordi Pérez, que tant em van ensenyar i motivar. També als meus amics i companys Marc Guàrdia, Silvia Valenzuela, Amanda Garcia, Marc Riccetto i Alejandro Gil, l'ajuda i el suport dels quals des de l'inici del Grau en Geologia a la UAB (per allà al 2012) ha estat fonamental per arribar fins aquí (a més dels grats i divertits records que m'emporto de les nostres anades i vingudes). També m'agradaria agrair a l'Àlex Ossó i al Pere Artal, que amb la seva dilatada experiència i coneixements sobre l'estudi de la sistemàtica dels decàpodes fòssils i les seves ganes de transmetre els seus coneixements han estat tant una gran ajuda com un important punt de suport en aquest llarg camí.

I consider important to make a special mention and show my gratitude also to those reviewers who, with their critical reading, comments, suggestions and thoroughness, undoubtedly contributed to improving the scientific quality of the papers that make up this Thesis: John W.M. Jagt (Natuurhistorisch Museum Maastricht, the Netherlands); Carrie E. Schweitzet and Ronald Feldmann (Kent State University); Adiël Klompmaker (University of Alabama); René Fraaije (Oertijdmuseum Boxtel, The Netherlands); Barry van Bakel (Oertijdmuseum De Groene Poort, the Netherlands); Stephen Pates (University of Cambridge);

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I also want to thank to Ning Yang MS.c, of University of Westminster (London), who provided me with interesting modern material (both in photographs and taxidermy specimens) very useful to compare with fossil material.

Se agradece al Museo de Geología del Seminario de Barcelona (MGSB), el Museo Geominero (Madrid), el Museo di Archeologia e Scienze Naturali “G. Zannato” (Montecchio Maggiore, Italia) y el Museo cívico de Historia Natural de Verona (Italia) por poner a mi disposición todo el material de mi interés. A la Asociación Paleontológica Alcoyana Isurus (Alicante), (especialmente a Ángel Carbonell, María del Carmen Almahano y José Luis Giménez) y a Fernando Bravo que proporcionaron interesantísimo material del Eoceno alicantino (actualmente en estudio).

Agradezco también al Instituto Universitario de Ciencias Ambientales de Aragón (IUCA), cuyo servicio de prensa me ha hecho aparecer en repetidas ocasiones en la prensa, radio y televisión (pese a los nervios que esto me causa), optimizando de esta forma la divulgación de las diversas investigaciones realizadas durante mi Tesis. Agradecer también la ayuda económica por parte de la *International Association of Sedimentologists* (IAS), para su ayuda a la participación de congresos. A la Sociedad Española de Paleontología (SEP), la Diputación General de Aragón (DGA) y al IUCA (arriba mencionado), por su contribución para la organización del “8th Symposium on Fossil Decapod Crustaceans” que organizamos Samuel, Álvaro y yo en Zaragoza del 19 al 24 de junio de 2022, sin duda una experiencia muy gratificante y enriquecedora. Por último y no por ello menos importante, al PIF UNIZAR (y en especial a Alba Peiró) por su ayuda en tramitar y solucionar las diversas cuestiones burocráticas que me han surgido y a las que no hubiera sabido hacer frente por mí mismo.

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INDICE

1. TESIS COMO COMPENDIO DE PUBLICACIONES

La presente tesis doctoral, de acuerdo con el informe correspondiente, autorizado por los directores de Tesis y el Órgano Responsable del Programa de Doctorado, consiste en un compendio de artículos previamente publicados y cumple con la normativa establecida por el Reglamento sobre Tesis Doctorales (Título IV, Capítulo III, arts. 20 y 21). Esta tesis se compone de un total de 10 artículos publicados en revistas internacionales, 8 de ellos en revistas indexadas en el *Journal of Citation Reports* (JCR) (international peer-reviewed journals included in the SCI), que componen una unidad temática (el estudio de la sistemática, distribución y diversidad de crustáceos decápodos fósiles). Adicionalmente se incluyen 1 manuscrito recientemente sometido en una revista SCI pero que aún no ha sido publicado y otro en preparación. Todos los demás artículos han sido elaborados y aceptados durante los años de la realización de la tesis doctoral, entre los cursos 2018 y 2022. Las referencias completas de los artículos que constituyen el cuerpo de la tesis se presentan a continuación en orden cronológico de publicación:

I. **Ferratges, F.A**., Zamora, S. y Aurell, M. (2019). A new genus and species of Parthenopidae MacLeay, 1838 (Decapoda: Brachyura) from the lower Eocene of Spain. *Journal of Crustacean Biology*, 39(3), 303–311. https://doi.org/10.1093/jcbiol/ruz014; **IF: 1,254.**

II. **Ferratges, F.A**., Zamora, S. y Aurell, M. (2020). Systematics and distribution of decapod crustaceans associated with late Eocene coral buildups from the southern Pyrenees (Spain). *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen,* 79–100. https://doi.org/10.1127/njgpa/2020/0893; **IF: 0,95.**

III. **Ferratges, F.A**., Zamora, S. y Aurell, M. (2020). A new hermit crab out of its shell from the Eocene Arguis Formation, Huesca, Spain. *Acta*

Palaeontologica Polonica, 65(4), 787–792. https://doi.org/10.4202/app.00779.2020; **IF: 2,061.**

IV. Ossó, À., Domínguez, J.L., De Angeli, A. y **Ferratges, F.A**. (2020). First record of *Dynomene* (Brachyura, Dromioidea) from the Eocene of the Iberian Peninsula and remarks on the generic placement of *Eoacantholobulus oscensis* (Brachyura, Xanthoidea). *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, VIII, 185–192. https://doi.org/10.1127/njgpa/2020/0874; **IF: 0,95.**

V. **Ferratges, F.A**., Zamora, S. y Aurell, M. (2021). Unravelling the distribution of decapod crustaceans in the Lower Eocene coral reef mounds of NE Spain (Tremp-Graus Basin, southern Pyrenees). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 575, 110439. https://doi.org/10.1016/j.palaeo.2021.110439; **IF: 3,318.**

VI. **Ferratges, F.A**., Domínguez J.L. y Ossó, À. (2021). First record of a homolid crab (Crustacea: Decapoda: Homoloidea) from the early Eocene of the Iberian Peninsula. *Boletín de la Sociedad Geológica Mexicana*, 73(3), A311220. http://dx.doi.org/10.18268/BSGM2021v73n3a311220; **IF: 0,81.**

VII. **Ferratges, F.A**., Artal, P. y Zamora, S. (2021). New hermit crabs (Paguroidea, Anomura) from the Eocene of Huesca, Spain. *Boletín de la Sociedad Geológica Mexicana*, 73 (3) /A070121. http://dx.doi.org/10.18268/BSGM2021v73n3a070121; **IF: 0,81.**

VIII. Artal, P., **Ferratges, F.A.**, van Bakel, B.W.M. y Zamora, S. (2022). A highly diverse dromioid crab assemblage (Decapoda, Brachyura) associated with pinnacle reefs in the lower Eocene of Spain. *Journal of Paleontology*. 1–20. http://dx.doi.org/10.1017/jpa.2021.114; **IF: 1,471.**

IX. **Ferratges, F.A.**, Zamora, S. y Aurell, M. (2022). Systematics and palaeoecology of a new species of Varunidae H. Milne Edwards, 1853 (Decapoda: Brachyura) from the lower Eocene of Spain. *Journal of Crustacean Biology*. 42(2), 1–9. https://doi.org/10.1093/jcbiol/ruac013; **IF: 1,254.**

X. **Ferratges, F.A.**, Artal, P., van Bakel, B.W.M. y Zamora, S. (2022). Filling the early Eocene gap of paguroids (Decapoda, Anomura): A new highly diversified fauna from the Spanish Pyrenees (Serraduy Formation, Graus-Tremp Basin). *Journal of Paleontology*. 1–17. https://doi.org/10.1017/jpa.2022.67; **IF: 1,471.**

XI. **Ferratges, F.A.**, Luque, J., Ossó, À., Domínguez, J.L., Aurell, M. y Zamora, S. (en revisión). The oldest dairoidid crab (Decapoda: Brachyura: Parthenopoidea) from the Eocene of Spain.

XII. **Ferratges, F.A.,** Zamora, S., Klompmaker, A.A. y Aurell, M. (en preparación). Decapod crustacean diversity through time and space from a middle-upper Eocene carbonate-siliciclastic platform system (southern Jaca Basin, Pyrenees, Spain)

Además, algunos de los resultados preliminares han sido compartidos en reuniones científicas nacionales e internacionales a través de póster, comunicaciones orales y un capítulo de libro.

XIII. **Ferratges, F.A.**, Zamora, S. y Aurell, M. (2019). A new Parthenopidae MacLeay, 1838 (Decapoda, Brachyura) from the Lower Eocene of Spain. 7th Symposium on Mesozoic and Cenozoic Decapod Crustaceans. (Ljubljana, Slovenia). (Comunicación en póster).

XIV. **Ferratges, F.A.** y Zamora, S. (2019). Aptian Decapod assamblages from the Oliete Subbasin (North-east, Spain). 7th Symposium on Mesozoic and Cenozoic Decapod Crustaceans. (Ljubljana, Slovenia). (Comunicación oral).

XV. **Ferratges, F.A.**, Zamora, S. y Aurell, M. (2019). Eocene decapod crustaceans in time and space: an example from the Spanish Pyrenees. XVII Encuentro de Jóvenes Investigadores en Paleontología (EJIP). Zubía. (Nájera, La Rioja). (Comunicación oral).

XVI. **Ferratges, F.A.**, Zamora, S., Pueyo, E.L. y Aurell, M. (2019). Spatiotemporal fluctuations of decapod crustacean diversity from the Eocene of the south-central Pyrenees (Spain). 63rd Annual Meeting. The Palaeontological Association (PALASS). (Valencia, Spain). (Comunicación en póster).

XVII. **Ferratges, F.A.**, Zamora, S. y Aurell, M. (2019). Decapod crustaceans associated with coral reefs from the Lower Eocene (Huesca, Spain): paleoecological implications. International Association of Sedimentologists (IAS). 34th IAS Meeting of Sedimentology (Rome, Italy). (Comunicación en póster).

XVIII. **Ferratges, F.A.**, Zamora, S., Pueyo, E.L. y Aurell, M. (2020). Spatio-temporal variations in the diversity of decapod crustaceans during the Eocene in the Jaca-Pamplona Basin (South-central Pyrenees) Encuentro de Jóvenes Investigadores en Paleontología (EJIP). Novelties in Iberian Palaeontology. (Andorra, Teruel, Spain). (Comunicación en póster).

XIX. **Ferratges, F.A.** (2021). Paleoenvironmental influence on decapod crustaceans abundance and diversity from middle and upper Eocene at south-central Pyrenees, Spain. Geologists' Association (Virtual conference). (Comunicación oral).

XX. **Ferratges, F.A.**, Zamora, S. y Aurell, M. (2021). Paleoenvironmental influence on decapod crustaceans preservation, abundance and diversity from Eocene at south-central Pyrenees (Spain). International Association of Sedimentologists (IAS) 35th Meeting of Sedimentology. (Prague, Czech Republic). (Comunicación oral).

XXI. **Ferratges, F.A.**, Luque, J., Domínguez, J.L., Ossó, À., Aurell, M. y Zamora, S. (2022). The origin of dairoidid crabs (Decapoda, Brachyura, Parthenopoidea). 8th Symposium on Fossil Decapod Crustaceans. (Zaragoza, Spain). (Comunicación oral).

XXII. **Ferratges, F.A.**, García-Penas, Á., Aurell, M. y Zamora, S. (2022). Distribution of Decapod communities from the early Eocene of the South-Pyrenean Central Unit (Tremp-Graus Basin, Spanish Pyrenees) *En*: S. Zamora, **F.A. Ferratges**, A. García-Penas, y M. Aurell, (Eds.). 8th Symposium on Fossil Decapod Crustaceans. Field Guidebook. Palaeontological Publications, **1**, 113–136. (Capítulo de libro).

2.a. RESUMEN

Esta Tesis Doctoral presenta un conjunto de resultados obtenidos al combinar la estratigrafía y sedimentología, con el estudio sistemático y filogenético de los crustáceos decápodos encontrados en los materiales del Eoceno de la zona surpirenaica central (Huesca, Pirineo Español). Las cuencas incluidas en este sector ofrecen una excepcional oportunidad para estudiar la distribución espacio-temporal de un solo grupo sistemático en un área bien definida y permiten una mejor comprensión de los factores paleoambientales que controlaron su distribución. Los resultados obtenidos aportan datos que ayudan a comprender como se ha diversificado este grupo durante el Cenozoico, así como explorar la relación entre su diversidad y el desarrollo y declive de diferentes ambientes.

El trabajo de campo ha permitido recolectar más de 2000 ejemplares de crustáceos decápodos en diferentes litofacies. Este conjunto está compuesto por 163 especies (66 en el Ypresiense, 21 en el Luteciense, y 76 en el Bartoniense y Priaboniense inferior), con representantes de por lo menos 48 familias. Estos datos incrementan notablemente la diversidad de crustáceos decápodos previamente conocida para el Eoceno de toda la Península Ibérica. Este conjunto alberga importantes agrupaciones que no habían sido descritas hasta el momento y contiene numerosos taxones nuevos actualmente en estudio, mostrando que estas cuencas corresponden a un punto caliente de diversidad durante el Eoceno.

De todo este material, se han descrito 6 géneros y 22 especies nuevas. Entre las cuales, por un lado se han descrito 1 género y 9 especies de cangrejos ermitaños (Paguroidea): *Anisopagurus primigenius*, *Clibanarius isabenaensis*, *Dardanus balaitus*, *Diogenes augustinus*, *Eocalcinus veteris*, *Eocalcinus gerardbretoni*, *Parapetrochirus* robustus, *Parapetrochirus serratus*, *Paguristes perlatus*; y por otro lado, se han descrito 5 géneros y 13 especies de cangrejos verdaderos: *Basidromilites glaessneri*, *Dynomene collinsi*, *Gemmellarocarcinus riglosensis*, *Kromtitis isabenensis*, *Mclaynotopus longispinosus*, *Sierradromia gladiator*, *Torodromia elongata*, (Dromioidea), *Paromola bretoni* (Homoloidea), *Aragolambrus collinsi*, *Phrynolambrus sagittalis* (Parthenopoidea), *Daira corallina* (Dairidea), *Lobogalenopsis joei* (Pilumnoidea), *Asthenognathus fernandezi* (Grapsoidea). Entre estos nuevos taxones se encuentran los representantes más antiguos de los géneros *Anisopagurus*, *Asthenognathus*, *Basidromilites*, *Mclaynotopus* y *Parapetrochirus*, y el registro más antiguo y moderno del género *Eocalcinus*.

Algunos de los nuevos materiales recolectados corresponden a la primera cita en la Península Ibérica ampliando la distribución estratigráfica y paleobiogeográfica de varios géneros ya conocidos (*Daira*, *Dynomene*, *Galenopsis*, *Gemmellarocarcinus*, *Liopsalis*,

Lobogalenopsis, *Paromola*, *Phrynolambrus* y *Scultoplax*). Además, los resultados filogenéticos obtenidos indican que los géneros *Phrynolambrus* y *Aragolambrus* están estrechamente relacionados con el género moderno *Dairoides*, quedando incluidos en Parthenopoidea. Este descubrimiento hace retroceder los orígenes de los Dairoideos más de 40 millones de años. Estos conjuntos de decápodos asociados a diferentes ambientes constituyen una importante contribución al estudio de los decápodos conocidos en los Pirineos y en el Eoceno en general. Además, contienen la mayor asociación de dromioideos del Eoceno inferior, y una de las mayores diversidades de cangrejos ermitaños del Eoceno de todo el mundo. Todos estos datos ponen de manifiesto que el Eoceno corresponde a una época de rápida evolución para los crustáceos decápodos y arroja luz sobre los orígenes tempranos, la diversidad anatómica y las afinidades sistemáticas de ciertos grupos.

El excelente estado de los afloramientos ha permitido muestrear de forma intensiva diferentes paleoambientes, analizando así la distribución y abundancia relativa de diferentes grupos. Los análisis estadísticos realizados tanto en ambientes carbonatados como en siliciclásticos, apoyan los datos adquiridos por la observación de campo y los análisis sedimentológicos. Esto refuerza la hipótesis de que la mayor diversidad se encuentra en áreas con bioconstrucciones como biohermos de esponjas, briozoos, corales, y probablemente ambientes de praderas de fanerógamas marinas. Los resultados muestran una distribución desigual en diferentes ambientes, que varían drásticamente en abundancia y composición a través de diferentes intervalos estratigráficos.

Los arrecifes modernos se consideran importantes puntos calientes de biodiversidad, pero el análisis de la distribución de la fauna de invertebrados en diferentes dominios arrecifales en ecosistemas antiguos es un desafío, porque el registro fósil generalmente se ve afectado por fuertes sesgos tafonómicos. Sin embargo, la excelente exposición de estos afloramientos ha permitido concretar diferentes asociaciones dentro de un mismo arrecife. Los resultados obtenidos tanto en ambientes carbonatados como siliciclásticos indican que los cambios faunísticos se deben (por lo menos en parte) a cambios paleoecológicos, proporcionando un ejemplo extraordinario de zonificación ecológica de crustáceos decápodos dentro de transectos de escala kilométrica y batimetría variable.

2.b. ABSTRACT

This PhD Thesis presents a set of results obtained by combining stratigraphy and sedimentology, with the systematic and phylogenetic study of decapod crustaceans found in Eocene materials from the central southern Pyrenees (Huesca, Spanish Pyrenees). Three sedimentary basins, Tremp-Graus, Jaca and Ainsa are sampled in order to provide a spatio-temporal distribution of decapod crustaceans. Species are collected from different facies that represent a wide range of environments from shallow marine prodelta, to more distal carbonate platforms and reefs, and distal basins.The results obtained help understanding how decapods diversified during the Cenozoic, as well as to explore the relationship between diversity and facies.

More than 2000 specimens of decapod crustaceans have been collected from the fifferent facies. They include 163 species (66 in the Ypresian, 21 in the Lutetian, and 76 in the Bartonian and lower Priabonian), with representatives of at least 48 families.

They include, 6 genera and 22 new speciesthat include 1 genus and 9 species of hermit crabs (Paguroidea) have been described: *Anisopagurus primigenius*, *Clibanarius isabenaensis*, *Dardanus balaitus*, *Diogenes augustinus*, *Eocalcinus veteris*, *Eocalcinus gerardbretoni*, *Parapetrochirus robustus*, *Parapetrochirus serratus*, *Paguristes perlatus*; 5 genera and 13 species of true crabs: *Basidromilites glaessneri*, *Dynomene collinsi*, *Gemmellarocarcinus riglosensis*, *Kromtitis isabenensis*, *Mclaynotopus longispinosus*, *Sierradromia gladiator*, *Torodromia elongata*, (Dromioidea), *Paromola bretoni* (Homoloidea), *Aragolambrus collinsi* , *Phrynolambrus sagittalis* (Parthenopoidea), *Daira corallina* (Dairidea), *Lobogalenopsis joei* (Pilumnoidea), *Asthenognathus fernandezi* (Grapsoidea). Some of the new taxa are the oldest representatives of the genera *Anisopagurus*, *Asthenognathus*, *Basidromilites*, *Mclaynotopus*, and *Parapetrochirus*, and the oldest and most recent record of the genus *Eocalcinus*.

Some of the new materials collected correspond to the first record in the Iberian Peninsula, expanding the stratigraphic and paleobiogeographic distribution of several known genera (*Daira*, *Dynomene*, *Galenopsis*, *Gemmellarocarcinus*, *Liopsalis*, *Lobogalenopsis*, *Paromola*, *Phrynolambrus* and *Scultoplax*). Furthermore, the phylogenetic results obtained indicate that the genera *Phrynolambrus* and *Aragolambrus* are closely related to the modern genus *Dairoides*, being included in Parthenopoidea. This discovery pushes back the origins of Dairoids more than 40 million years.

Statistical analysis in both carbonate and siliciclastic environments reinforces the hypothesis that the greatest diversity is found in areas with bioconstructions such as sponge bioherms, bryozoans, corals, and/or seagrass environments. The results show an uneven

distribution in different environments, which vary dramatically in abundance and composition across different stratigraphic intervals; likely representing biological distributions respect to environmental conditions.

Taking together this study provides critic data on the distribution in time and space during the Eocene that shed light on the origin of modern biodiversities. The results obtained in both carbonate and siliciclastic environments indicate that faunal changes are due (at least in part) to paleoecological changes, providing an extraordinary example of ecological zonation of decapod crustaceans within transects of kilometer scale and variable bathymetry.

3. INTRODUCCIÓN GENERAL

Los crustáceos decápodos en general y los cangrejos en particular son uno de los grupos de invertebrados más característicos e icónicos, ya que forman parte importante de la cultura y del imaginario colectivo, juegan un papel fundamental en la pesca y acuicultura y son piezas fundamentales para el correcto funcionamiento de los ecosistemas marinos, dulceacuícolas e incluso terrestres. Pese a ello, son unos grandes desconocidos en muchos aspectos. Más aún si nos referimos a las especies fósiles, su diversidad en el registro geológico o las relaciones filogenéticas entre distintos grupos.

En las últimas décadas se ha visto un creciente interés tanto por estudio biológico como en el paleontológico de los crustáceos decápodos. Este reciente y renovado interés en tan singular grupo ha propiciado la compilación de una serie de conocimientos y datos que nos dejan entrever aspectos muy interesantes, como su diversificación en determinados momentos del pasado, coetáneamente al desarrollo de ambientes particulares. En este sentido, la zona surpirenaica central brinda una excepcional oportunidad de comprender la distribución y evolución de este grupo en un periodo clave de su evolución. Esta zona (que incluye las cuencas de Tremp-Graus, Ainsa y Jaca) presenta una sucesión Eocena casi completa, con una gran diversidad de ambientes sedimentarios desarrollados en un sistema marino mixto carbonatado-siliciclástico, que incluyen uno de los mejores registros de decápodos del Eoceno a nivel mundial. Estas sucesiones sedimentarias incluyen desde sistemas deltaicos proximales y ambientes someros en la cuenca oriental de Tremp-Graus, a sistemas de plataforma externa-talud-cuenca en la mayor parte de las cuencas de Ainsa y Jaca, progresivamente menos profundos hacia la parte superior de la serie y con una progradación de facies de Este a Oeste (p. ej., Puigdefàbregas, 1975; Millán *et al*., 1994; Morsilli *et al*., 2012; Pomar *et al*., 2017; Garcés *et al*., 2020; Canudo *et al*., 2021; Coll *et al*., 2022).

El estudio de los crustáceos decápodos, además de un amplio registro fósil que se reparte en un amplio abanico de facies, tiene el interés añadido de presentar una gran diversidad ecológica y morfológica. Esta gran diversidad y capacidad de adaptación con estrategias ecológicas especializadas a cada ambiente convierten a los decápodos en una herramienta de gran utilidad para realizar inferencias paleoecológicas. Por este motivo, comprender los factores que determinan su presencia, abundancia y distribución permiten precisar las características de los distintos ambientes dentro de diferentes sistemas sedimentarios siliciclásticos y carbonatados, empleando estas faunas como herramientas para el análisis paleoambiental.

Por todos estos motivos, el principal tema que se ha tratado de abordar durante el transcurso de esta investigación es el estudio de la distribución y diversidad de los crustáceos decápodos en los diferentes paleoambientes sedimentarios de las plataformas marinas del Eoceno de la zona surpirenaica central, además de aportar una visión general de la paleocarcinología realizando una revisión bibliográfica de los trabajos publicados en este campo, elaborando un estado de la cuestión como punto de partida al trabajo realizado. Algunos de los taxones encontrados han sido además tratados desde un punto de vista sistemático más completo, quedando todavía un ingente trabajo en este aspecto que por falta de tiempo no ha podido ser abordado. La diversidad de decápodos observada en el área de estudio está en parte relacionada con la variedad de facies marinas poco profundas, que están bien expuestas en afloramientos continuos, brindando una oportunidad única para comprender la distribución espacio-temporal en diferentes ambientes sedimentarios. De hecho, se han detectado sucesiones de diferentes comunidades de decápodos y se ha observado que las mismas facies pueden incluir diferentes asociaciones en diferentes intervalos. Esta condición permite estudiar las comunidades dentro de una misma región a lo largo de Eoceno, independientemente de los cambios de facies.

La Tesis Doctoral se ha realizado en la modalidad de compendio de artículos y consta de 10 artículos aceptados con una unidad temática. Además, en este manuscrito se han incluido datos de otros 2 artículos que se encuentra en proceso de revisión y preparación. La tesis se ha estructurado en 6 bloques principales. El primero de ellos es esta **introducción general**, en la que se describe por una parte el **estado de la cuestión**, donde se explica el trasfondo en el conocimiento de los crustáceos decápodos fósiles, centrándose en el Eoceno de la Península Ibérica; y, por otra parte, la **situación geológica**, donde se sitúa geológica y estratigráficamente las muestras que se han estudiado, y brevemente las condiciones paleoambientales del área de estudio, así como las condiciones climáticas de la época. En segundo lugar, se ha desarrollado un capítulo sobre los **objetivos de la investigación,** en el que se plantean cuestiones cuya respuesta puede ayudar a comprender la evolución, diversificación y distribución de este grupo de invertebrados. En tercer lugar, la **metodología**, en el que se describen las diferentes técnicas empleadas para dar respuesta a las cuestiones planteadas. El cuarto bloque corresponde a los **resultados**, en el que se exponen los diferentes estudios realizados y los nuevos avances en el campo mediante “compendio de artículos”; este apartado se ha subdividido a su vez en dos apartados: por una parte, se agrupan los trabajos que se centran en la paleontología sistemática y por otro, los trabajos que abordan la distribución de los taxones y la diversidad. En quinto lugar, se encuentra la **discusión** de los artículos en tres subcapítulos principales, uno en el que se resumen las principales discusiones sistemáticas, otro sobre la distribución de los taxones y un tercero en el que se discuten las posibles causas de los cambios en la diversidad. Por último, se ha realizado un capítulo de “**conclusiones y perspectivas futuras**”.

3.1. Estado de la cuestión

3.1.1. Evolución de los crustáceos decápodos

Los crustáceos decápodos se encuentran en un amplio pero disperso registro geológico que abarca desde rocas Paleozoicas ya en el Devónico medio (Schram *et al.*, 1978; Perrin, 2002; Schweitzer *et al.*, 2010) y han aumentado notablemente su diversidad a lo largo del tiempo (p. ej., Schwaitzer y Feldmann, 2015) (Fig. 1), encontrándose hoy en día ampliamente distribuidos. Concretamente, los grandes grupos de crustáceos decápodos que dominan los ecosistemas actuales comienzan a ser relevantes desde un punto de vista ecológico durante el Mesozoico (Klompmaker *et al*. 2013a; Schweitzer y Feldmann, 2015; Luque *et al.*, 2021), mostrando importantes picos de diversidad o radiaciones dentro del grupo (Guinot y Tavares, 2001; Karasawa *et al.*, 2011; Klompmaker *et al.*, 2013a; Schweitzer y Feldmann, 2015; Luque *et al.*, 2019) (Fig. 2) destacando por su diversidad los cangrejos verdaderos o braquiuros.

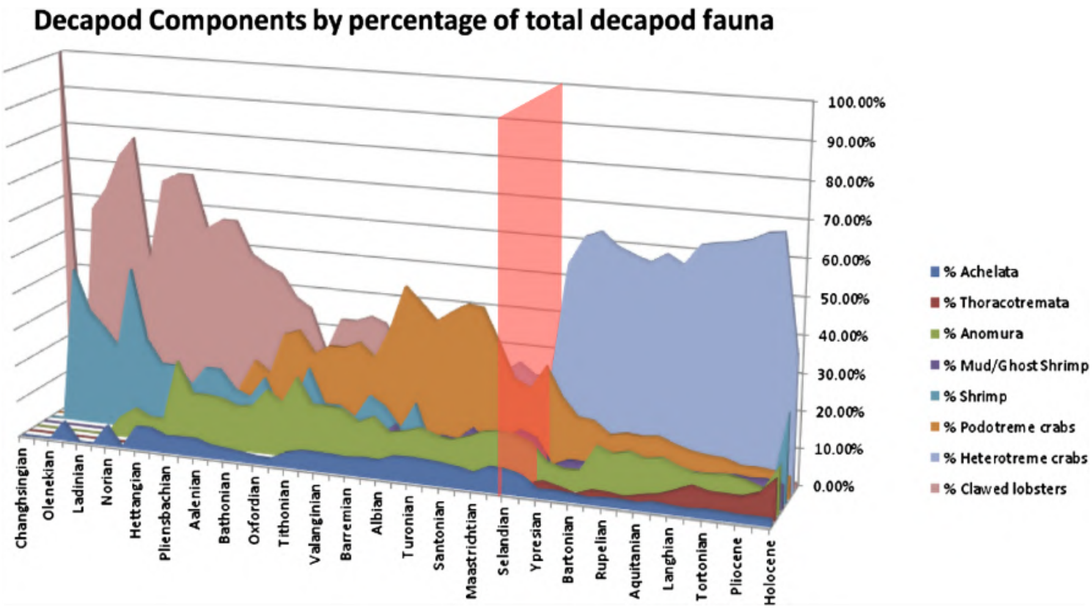

Figura 1: Variación de la diversidad de crustáceos decápodos a lo largo de los últimos 250 Ma. y dominio de los principales grupos de crustáceos decápodos (modificado de Schweitzer y Feldmann, 2015). La barra roja indica el inicio del Paleógeno.

Figure 1: Variation of diversity in decapod crustaceans over the last 250 Ma and dominance of the main groups of decapod crustaceans (modified from Schweitzer and Feldmann, 2015). Red bar indicates the Paleogene.

Algunos autores han sugerido que este éxito evolutivo pudo estar relacionado con la plasticidad morfológica del grupo (Števčić, 1971), caracterizados por presentar una morfología compacta y un pleón replegado ventralmente, lo que les confiere una gran versatilidad. La transición evolutiva de la forma alargada que presentan las formas menos derivadas como gambas y macruros (langostas), a la forma corta y compacta típica (de la mayoría) de los cangrejos se ha denominado carcinización (Fig. 3) o braquiurización (Borradaile, 1916; Števčić, 1971; McLaughlin y Lemaitre, 1997; McLaughlin *et al.*, 2004; Scholtz, 2014; Keiler *et al.*, 2017; Knotel *et al.*, 2018; Ostachuk, 2019; Wolfe *et al.*, 2021). No obstante, no todos los braquiuros están carcinizados (Scholtz, 2014; Luque *et al.*, 2019), y la carcinización también se puede observar en varios taxones incluidos en otros grupos como porcelánidos y lithódidos (Anomura) (p. ej., McLaughlin y Lemaitre, 1997; Morrison *et al.*, 2002; McLaughlin *et al.*, 2004; Reimann *et al.*, 2011; Tsang *et al.*, 2011; Scholtz, 2014; Keiler *et al.*, 2017), e incluso en algunas langostas (ver Wolfe *et al.*, 2021). Por este motivo, los estudios comparativos de las especies actuales de braquiuros y las especies fósiles son fundamentales para comprender el proceso de carcinización/descarcinización y evolución de diferentes planos corporales, así como su papel en el éxito evolutivo de estos animales (Scholtz, 2020).

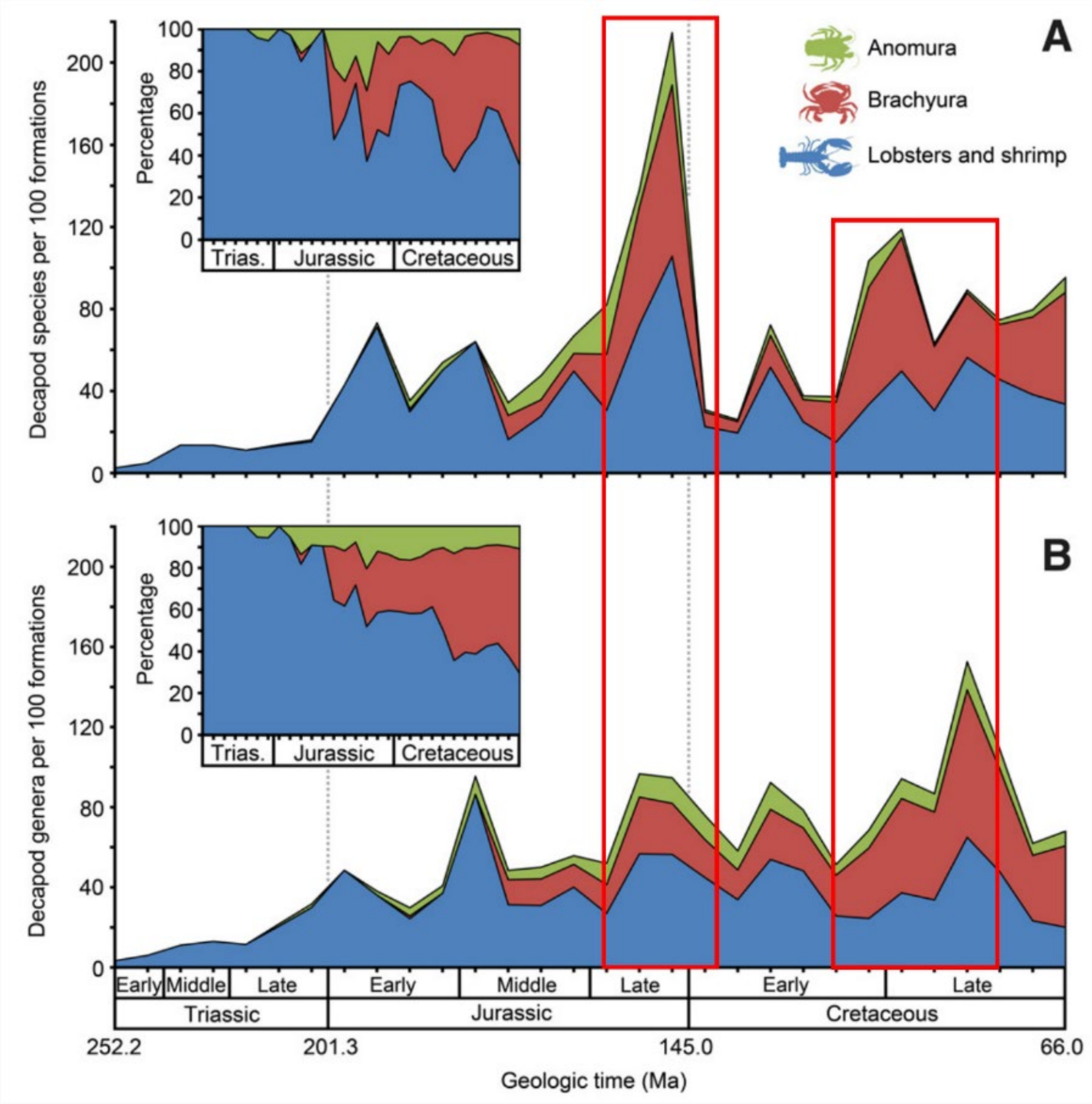

Figura 2: Incremento del número de géneros y especies a lo largo del Mesozoico (tomado de Klompmaker *et al*., 2013a).

Figure 2: Increase in the number of genera and species throughout the Mesozoic (taken from Klompmaker *et al*., 2013a).

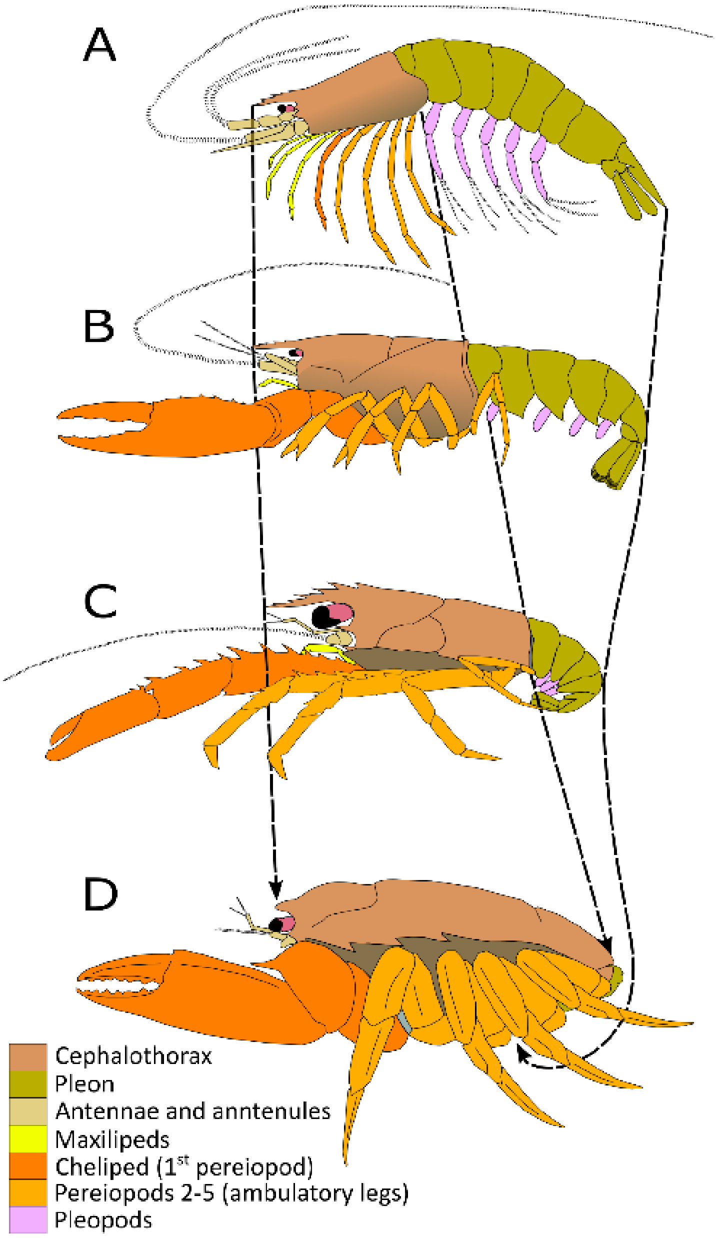

Figura 3: Esquema simplificado del proceso de carcinización, mostrando la reducción y repliegue del pleón (verde) bajo el cefalotórax (marrón), y el paso de un cefalotórax cilíndrico a comprimido dorsalmente. **A**: decápodo basal; **B**: Macruro; **C**: Anomuro; **D**: Braquiuro (Modificado de Glaessner, 1969).

Figure 3: Simplified diagram of carcinization process, showing the reduction and folding of the pleon (green) under the cephalothorax (brown), and the change from a cylindrical to a dorsally compressed cephalothorax. A: basal decapod; **B**: Macrur; **C**: Anomura; **D**: Brachiura (Modified from Glaessner, 1969).

Los "cangrejos verdaderos" o braquiuros (Brachyura), son sistemática y morfológicamente los más diversos de todos los decápodos, con más de 7000 especies en la actualidad (Ng *et al.*, 2008; Ahyong *et al.*, 2011; Tsang *et al.*, 2014) y más de 3000 conocidas a partir del registro fósil (p. ej., de Grave *et al.*, 2009; Schweitzer *et al.*, 2010; Jagt *et al.*, 2015; Luque *et al.*, 2017). El otro gran grupo tratado en la presente Tesis Doctoral corresponde a los cangrejos ermitaños (incluidos en el infraorden Anomura), y que junto a los anteriores conforma el gran grupo Meiura. Su diversidad es bastante menor a la de los braquiuros, con unas 1100 especies descritas en ecosistemas modernos (McLaughlin *et al.*, 2007, 2010) y unas 200 en el registro fósil (de Grave *et al.*, 2009). No obstante, hay muchos interrogantes en cuanto a las relaciones filogenéticas y el momento de aparición de múltiples grupos.

Los datos moleculares indican un origen pre-Jurásico para los braquiuros, con una divergencia entre podotremas y eubraquiuros entre el final del Pérmico y comienzos del Jurásico (ver Luque *et al*., 2021 y referencias). Por otra parte, los datos moleculares también indican que los heterotremas y los toracotremas (eubraquiuros) divergieron entre el final del Jurásico y el Cretácico inferior (Tsang *et al*., 2014; Wolfe *et al*., 2019) (Fig. 4A). Sin embargo, el registro fósil indica que los heterotremas más antiguos datan de finales del Cretácico inferior (p. ej., Luque, 2015; Prado *et al*., 2018; Guinot *et al*., 2019; Luque *et al*., 2019; van Bakel *et al*., 2021) y los toracotremas más antiguos corresponden al Eoceno (Luque *et al*., 2017; Beschin *et al*., 2007, 2016; Ferratges *et al*., 2022d). Reconciliar estas edades con el registro fósil es problemático debido a la naturaleza escasa y fragmentaria del material (Luque *et al*., 2021). Por este motivo, los fósiles son la única fuente fiable que permite anclar y calibrar las filogenias moleculares, permitiendo entender como han sido los procesos evolutivos y de qué forma aparecen los diferentes caracteres según la escala temporal.

El Meiuro más antiguo corresponde al anomuro *Platykotta akaina* Chablais, Feldmann y Schweitzer, 2011, del Triásico Superior (227-201 Ma) (Fig. 4B). Debido a que los anomuros y los braquiuros evolucionaron a partir de un ancestro común, algunos autores sugieren que los primeros cangrejos pueden tener una antigüedad similar (ver Davie, 2021). Sin embargo, en el caso concreto de los braquiuros, su primera aparición conocida en el registro fósil se produce en el Jurásico Inferior de Oxfordshire en el Reino Unido (Withers, 1932; Krobicki y Zatoń, 2008; Schweitzer y Feldmann, 2010; Schweigert y Koppka, 2011; Scholtz, 2020) con la especie *Eocarcinus praecursor* Withers (1932). Algunos autores (Guinot y Tavares, 2001; Karasawa *et al*., 2011; Klompmaker *et al*., 2013a) señalan que las primeras diversificaciones del grupo ocurrieron en el Jurásico medio y superior (Fig. 1).

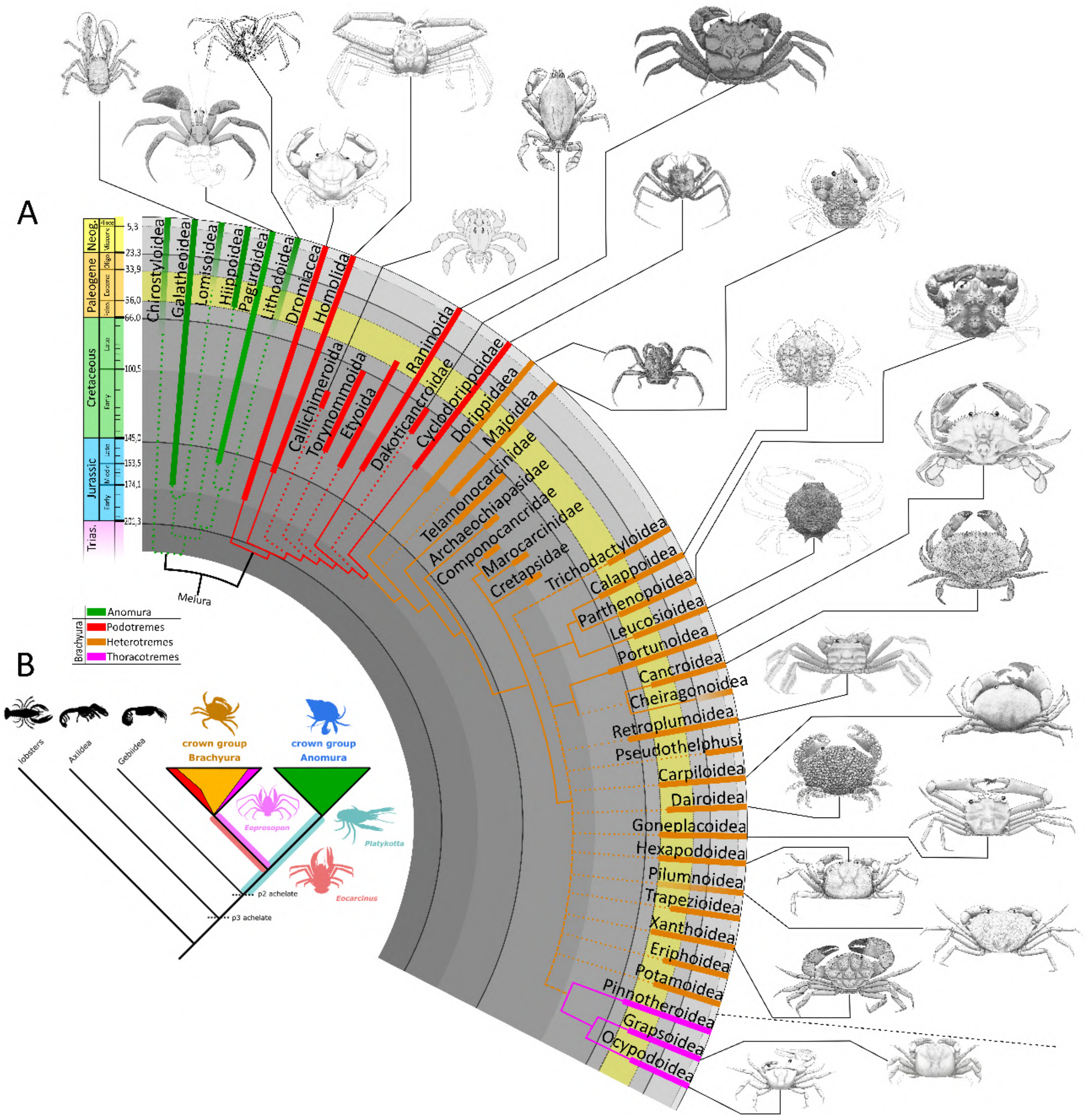

Figura 4: **A**: Correlación de análisis cladísticos con el registro fósil de Meiura; combina los datos aportados por Brösing, 2008; Luque *et al*., 2017, 2019, 2020; Wolfe *et al*., 2019, 2021 y los resultados propios. **B**: Afinidades de los primeros fósiles de cangrejos del grupo (modificado de Wolfe *et al*., 2021). Las abreviaturas p2, p3 se refieren al segundo y tercer pereiópodo.

Figure 4: **A**: Correlation of cladistic analisis with the Meiura fossil record; combines the data provided by Brösing, 2008; Luque *et al*., 2017, 2019, 2020; Wolfe *et al*., 2019, 2021 and own results. **B**: Diagnosing the affinities of early stem group crab fossils (modified from Wolfe *et al*., 2021). Abbreviations p2, p3 refer to the second and third pereopods.

Estas radiaciones dieron lugar a una expansión a nivel global, apareciendo gran cantidad de géneros y especies nuevas, con un amplio registro en Europa. Sin embargo, no empiezan a diversificarse anatómicamente de forma notable hasta el Cretácico medio (Luque *et al*., 2019). Esta etapa de diversificación, que corresponde a una de las más importantes en su historia evolutiva, es conocida como la “*Cretaceous Crab*

Revolution", en la que apareció el 80% de los clados principales de este grupo (ver Schweitzer y Feldmann, 2015; Luque, 2018; Luque *et al*., 2019; 2021). Esta "revolución evolutiva" coincide con el desarrollo de importantes arrecifes en el Albiense, como los descritos en Olazagutía (Navarra, España) (ver Klompmaker, 2013; Klompmaker *et al*., 2013b). En cualquier caso, a finales del Mesozoico ya habían aparecido la mayoría de las superfamilias que existen actualmente (Tsang *et al*., 2014, Luque *et al*., 2019; 2021), y cada vez más datos sugieren una diversificación temprana de los grupos principales (p.ej., Luque *et al*., 2021). Por otro lado, los primeros eubraquiuros -los cangrejos derivados más abundantes hoy en día- se han encontrado en el Cretácico Inferior y ya en el Albiense, este grupo presenta una diversidad de planos corporales que sugiere que se encontraban bien establecidos (Luque, 2015).

Después de la extinción asociada al límite Cretácico-Paleógeno se produce una sustitución de faunas en la que grupos basales (como los dromiáceos y raninidos entre otros) quedan relegados a un segundo plano, empezando a ser predominantes las formas más derivadas como las que vemos hoy en día de forma más habitual (Franțescu, 2013). Por otro lado, algunos de los representantes de estos grupos basales que sobreviven al límite Cretácico-Paleógeno, muestran un gradual descenso en su diversidad y acaban extinguiéndose al final del Eoceno (Hartzell, 2022). También es importante mencionar que el registro del Paleoceno marino es escaso en la Península Ibérica, por lo que puede existir un sesgo en este momento crucial en la sustitución de las faunas.

Sin embargo, según muestra el registro fósil, es durante el Cenozoico, y especialmente durante el Eoceno, cuando familias y géneros parecen experimentar un aumento en la diversidad más acelerado (Fig. 4A). En este sentido, el Eoceno está considerado como un periodo de diversificación y bajas tasas de extinción en los decápodos (Fraaije, 2003; Feldmann y Schweitzer, 2006) y muchos grupos muestran una rápida diversificación desde el Eoceno (p. ej., Fraaije, 2003; Brösing, 2008; Hartzell, 2022). Prueba de ello, es que se han descrito cerca de 1000 especies de decápodos procedentes de sucesiones sedimentarias de este periodo en todo el mundo, con la mayor diversidad concentrada en Europa (ver Franțescu, 2013).

Por este motivo, el Eoceno, cuyos factores externos y ecológicos probablemente afectaron a la diversificación de los crustáceos decápodos, parece ser un período crítico para su evolución, (p. ej., Brösing, 2008; Tsang *et al*., 2014; Schweitzer y Feldmann, 2015; Daniels *et al*., 2015; Pan *et al*., 2022) con la aparición en el registro fósil de muchos de los miembros más antiguos de formas modernas. Especialmente, los braquiuros heterotremas (p. ej., Goneplacidae, Xanthidae, Portunidae, Cancridae, y Parthenopidae) muestran una rápida diversificación en el Eoceno (Fig. 4A), que ha continuado hasta el presente (p.ej., Franțescu, 2013; Hartzell, 2022). Algunas de estas familias, como Xanthidae, han alcanzado las máximas diversidades del grupo en los ecosistemas actuales con más de 600 especies conocidas (Ng *et al.*, 2008).

3.1.2. Los crustáceos decápodos en las cuencas del oeste y sur de Europa

Algunos de los conjuntos de crustáceos decápodos estudiados en la zona surpirenaica tienen similitudes con el material encontrado en otros afloramientos clásicos del Eoceno: Islas Británicas (Via, 1969, 1991; Ferratges y Zamora, 2015), sur y nordeste de España (Via, 1959, 1969, 1991), Italia (De Angeli y Caporiondo, 2009; Busulini *et al.*, 2012; Beschin *et al.*, 1996, 2012, 2013; Domínguez y Ossó, 2016; Ossó *et al.*, 2020a); Eslovenia y Croacia (Schweitzer *et al.*, 2005, 2007); Hungría, Marruecos e Irán (Khodaverdi *et al.*, 2016; Ossó *et al.*, 2020b). Esto ayuda a enmarcar la relevancia de los crustáceos decápodos surpirenaicos a una escala regional (Fig. 5).

La distribución de diferentes conjuntos de decápodos con importantes similitudes en diversas cuencas europeas y diferentes momentos del Eoceno ha hecho proponer a algunos autores (p. ej., Via, 1969, 1991; Domínguez y Ossó, 2016, Ossó *et al.*, 2020a) que a finales del Eoceno medio se produjo una migración de faunas hacia el W y NW, llegando hasta la costa sur-oriental de Gran Bretaña (cuenca de Hampshire, ver Fig. 5). Por otra parte, si bien existen grandes similitudes entre las faunas del Eoceno del Tethys occidental y las cuencas pirenaicas (Domínguez y Ossó, 2016), la separación continental entre ambas áreas marinas que ya existió durante el Priaboniense, pudo favorecer la especiación alopátrica de ciertos taxones (Ossó *et al.*, 2020a). Sin embargo, el flujo “trans-pirenaico” propuesto por estos autores parece poco probable debido a la distribución de las masas contienentales de la época (ver Garcés *et al.*, 2020). Esta distribución faunística podría estar relacionada con los eventos climáticos de la época (explicados más adelante), que podrían haber permitido el flujo de faunas a latitudes más altas, como está sucediendo actualmente (p. ej., Galil y Zenetos, 2002; Raitsos *et al.*, 2010; Hoffman, 2014; Mannino *et al.*, 2017; Bianchi *et al.*, 2018;

Giangrande *et al*., 2020; Asakura, 2021). En cualquier caso, la polaridad de este flujo de fauna permanece desconocida, pero algunos de los descubrimientos de esta Tesis Doctoral sitúan los taxones más antiguos de algunos grupos en las cuencas Surpirenaicas.

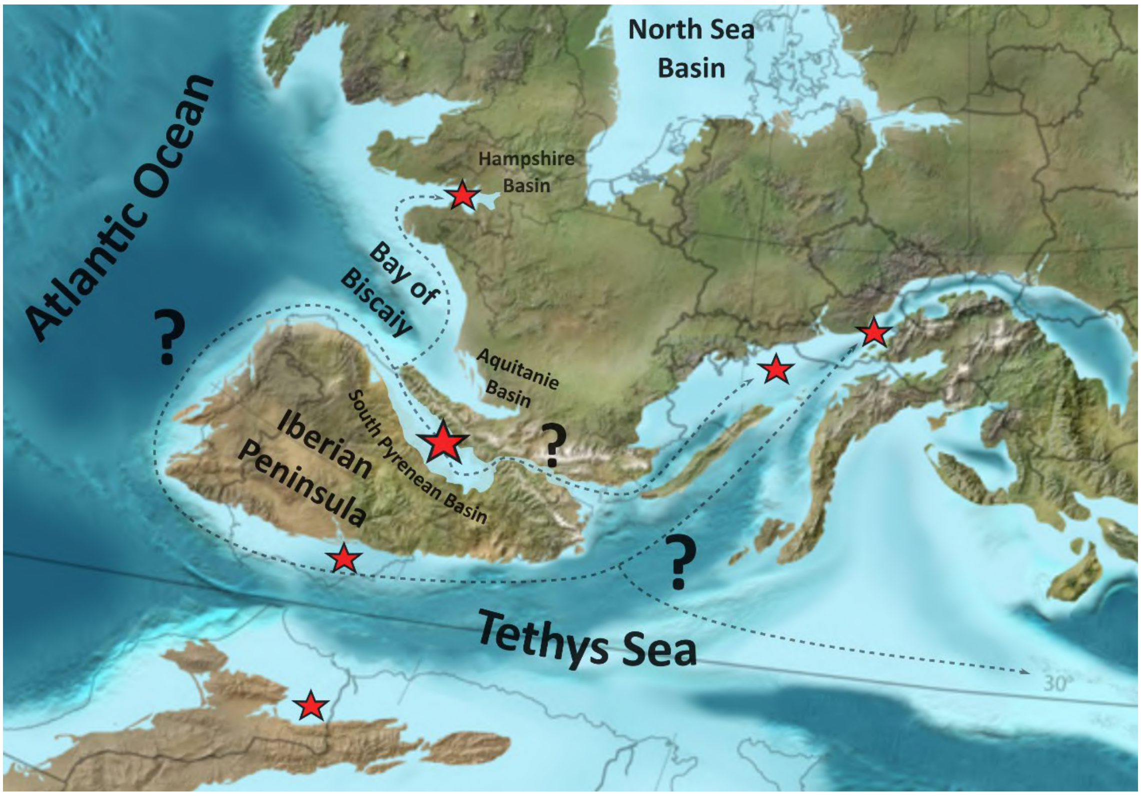

Figura 5: Reconstrucción paleogeográfica de Europa y norte de África durante el Eoceno (modificado de Ron Blakey y Colorado Plateau Geosystems, INC). Las estrellas rojas señalan diferentes agrupaciones carcínicas similares a las estudiadas.

Figure 5: Paleogeographic reconstruction of Europe and North Africa during the Eocene (modified from Ron Blakey and Colorado Plateau Geosystems, INC). Red stars indicate similar carcinic assemblages to those studied in the present work.

3.1.3. Los crustáceos decápodos de la zona surpirenaica

En la Península Ibérica se conocen diversas zonas fosilíferas que han aportado datos sobre la diversidad de crustáceos decápodos del Eoceno (ver compilación en Via, 1969; Franțescu, 2013). Estas se encuentran distribuidas entre Cantabria, Navarra, Cataluña, y Alicante, así como en los diferentes yacimientos del norte de la provincia de Huesca aquí estudiados. Son precisamente los afloramientos de esta última área, situados en el sector central de la zona Surpirenaica y distribuidos en tres cuencas sedimentarias distintas, los que preservan un registro más continuo y completo del Eoceno. Estos importantes afloramientos permiten entender la distribución en el tiempo y en el espacio de los decápodos fósiles, convirtiendo a las cuencas Surpirenaicas en un punto clave para el estudio de este grupo.

Las sucesiones de la zona Surpirenaica incluyen abundantes crustáceos decápodos fósiles, descritos en diferentes afloramientos. Los primeros registros de crustáceos decápodos fósiles en esta área corresponden a citas ocasionales de diferentes taxones (A. Milne-Edwards, 1862; Mallada, 1875, 1878; Dalloni, 1910, 1930, Via, 1932). Sin embargo, los primeros estudios rigurosos de decápodos fósiles en esta zona fueron realizados por Via a mediados del siglo XX en su importante revisión de los decápodos del Eoceno de España (Via, 1959, 1969). Estos estudios destacan la gran abundancia y el buen estado de conservación de los cangrejos fósiles en esta zona, especialmente de la especie *Zanthopsis dufourii*, así como algunas interpretaciones sobre su distribución y su relación con conjuntos carcínicos de otras cuencas europeas. Aunque Via hizo un trabajo exhaustivo y citó varios yacimientos en esta región, su trabajo se centró principalmente en la región catalana, y dejo un gran vacío en esta zona.

En las últimas décadas, el conocimiento de los crustáceos decápodos fósiles de la zona surpirenaica se ha incrementado sustancialmente (Fraaye, 1995; Artal *et al*., 2006, 2013a, b, 2021; Fraaije y Pennings, 2006; Schweitzer *et al*., 2007; van Bakel *et al*., 2012; Ossó *et al*., 2014; Domínguez y Ossó, 2016a, b; Artal y van Bakel, 2018a, b). No obstante, muchos de estos estudios han sido realizados por amateurs, y carecían en ocasiones de las bases geológicas adecuadas y necesitaban una revisión profunda, ya que muchas interpretaciones paleoambientales no estaban justificadas.

3.1.4. Algunas cuestiones planteadas

A pesar del extenso conocimiento que existe actualmente sobre los crustáceos decápodos, siguen quedando importantes cuestiones por resolver, como el origen de las diferentes familias y sus relaciones filogenéticas, el origen de la diversidad actual, la distribución en diferentes paleoambientes de un sistema sedimentario, o como afectaron los cambios ambientales a las comunidades de decápodos del Eoceno. De hecho, aunque los picos de diversidad parecen estar relacionados con la aparición/proliferación de ambientes arrecifales a lo largo del tiempo, existen pocos trabajos detallados que analicen el patrón de diversidad regional y global de los crustáceos decápodos y sus preferencias ambientales o que aporten datos acerca de la relación entre estos y los arrecifes durante el Cenozoico (ver Franțescu, 2013; Ferratges *et al*., 2020a, 2021c).

A menudo, el estudio de los crustáceos decápodos está condicionado por su reducido potencial de fosilización y la dificultad para localizar y procesar sus restos, así como por la presencia de afloramientos limitados y dispersos. Además, la dificultad de realizar muestreos sistemáticos implica que el estudio de los factores que condicionan la diversidad de este grupo sistemático a través de la misma formación litológica no sea una tarea sencilla. Todo esto impide en gran medida entender la distribución de los taxones según sus preferencias ambientales y las condiciones tafonómicas que han actuado a escala de afloramiento, nublando nuestra capacidad de entender cuándo y en qué condiciones se colonizaron determinados ambientes.

En la zona surpirenaica, a pesar del amplio conocimiento existente acerca de la estratigrafía y sedimentología de las diferentes unidades del Eoceno, la presencia de los crustáceos decápodos ha pasado casi inadvertida. Únicamente un pequeño conjunto de publicaciones de carácter sistemático ha reparado en este grupo en, y en ellas no se ha hecho hincapié de forma metódica en su distribución ni posibles preferencias ambientales, ni en los procesos tafonómicos sufridos. Por ello, existe un gran vacío en lo que respeta al estudio de los crustáceos decápodos en el Eoceno de estas cuencas.

Por otro lado, el origen de las familias modernas de cangrejos verdaderos y cómo se relacionan entre sí es actualmente tema de debate. Los análisis filogenéticos basados en datos moleculares y morfológicos ofrecen una buena oportunidad para comprender las relaciones entre diferentes grupos modernos más allá de la taxonomía alfa (Tsang *et al*., 2008; Wolfe *et al*., 2016; 2019; Luque *et al*., 2019, 2021), mientras que los fósiles son cruciales para calibrar los árboles moleculares. Sin embargo, existen pocos trabajos que combinen taxones fósiles y modernos en un contexto filogenético utilizando diferentes criterios de optimización (Luque *et al*., 2019, 2021). A este respecto, si bien algunos trabajos recientes señalan un posible origen y diversificación temprano de ciertos grupos, es en estratos del Eoceno donde encontramos los representantes más antiguos de muchas familias modernas (p. ej., Schweitzer y Feldmann, 2015; Luque *et al*., 2017). Por esta razón, comprender la diversidad de los braquiuros del Eoceno y cómo se relacionan con otros grupos actuales y extintos es fundamental para investigar los patrones espacio-temporales que conducen a la evolución de los grupos modernos que se ven hoy en día.

No obstante, muchas especies, géneros e incluso familias se conocen solo a partir de caparazones aislados y rara vez con quelípedos u otras extremidades asociadas con el cuerpo o el caparazón ventral, por lo que es necesario establecer ciertas bases y matrices de caracteres para poder contrastar los rasgos morfológicos de varios taxones de forma consistente, usando programas filogenéticos.

3.2. Situación geológica

Los materiales estudiados en esta Tesis Doctoral incluyen diversas formaciones en la provincia de Huesca (Fig. 6), que van desde el Eoceno inferior (formaciones Serraduy, Roda y Morillo) hasta el Eoceno medio y superior (formaciones Grustán, San Vicente, Arguis y Pamplona) (ver Fig. 7). Dichas unidades se depositaros en la zona surpirenaica central, en cuencas de antepaís paleógenas. Estas cuencas se desarrollaron en latitudes tropicales, aproximadamente a 35ºN de paleolatitud, en el límite sur de la zona axial de los Pirineos (Hay *et al*., 1999; Silva-Casal *et al*., 2017, 2019). La zona de estudio está dividida en una serie de cuencas (Fig. 6A): la cuenca Surpirenaica Oriental o Catalana (Sector Oriental), las cuenca de Tremp-Graus, Ainsa, y de Jaca (Sector Central), y la cuenca Vasco-Cantábrica (Sector Occidental). El área de estudio de esta tesis abarca materiales de las tres cuencas del Sector Central.

La sedimentación en las cuencas estudiades ha dado como resultado una sucesión eocena muy completa, depositada en un sistema sedimentario marino mixto carbonatado-siliciclástico. Estos afloramientos registran una amplia gama de ambientes sedimentarios, desde sistemas deltaicos proximales y ambientes someros a taludes profundos (p. ej., Puigdefabregas, 1975; Millán *et al*., 1994; Morsilli *et al*., 2012; Pomar *et al*., 2017; Canudo *et al*., 2021; Coll *et al*., 2022). Las llanuras abisales más distales se encuentran más al oeste, en la cuenca Vasco-Cantábrica (p. ej. Garcés *et al*., 2020).

La diversidad de ambientes marinos en el espacio y en el tiempo estuvo condicionada por la progradación de las facies costeras y continentales hacia el oeste, debido al levantamiento progresivo del orógeno pirenaico (Garcés *et al*., 2020 y referencias en el mismo; Coll *et al*., 2022). Este hecho, junto con la excepcional exposición de los afloramientos brinda una oportunidad única para estudiar la distribución espacio-temporal en diferentes ambientes sedimentarios de ciertos grupos de organismos (en este caso, de los crustáceos decápodos) y comprender su distribución. Pese a que en todas estas cuencas (Cuencas Surpirenaicas) existe un interesante registro de crustáceos decápodos fósiles (p. ej., Via, 1969, 1973; Franțescu, 2013; Ferratges, 2017; López-Horgue y Bodego, 2017), la presente tesis doctoral se centra en el estudio de las sucesiones situadas en el Sector Central de la zona Surpirenaica debido a su excelente exposición y gran variedad de facies y paleoambientes.

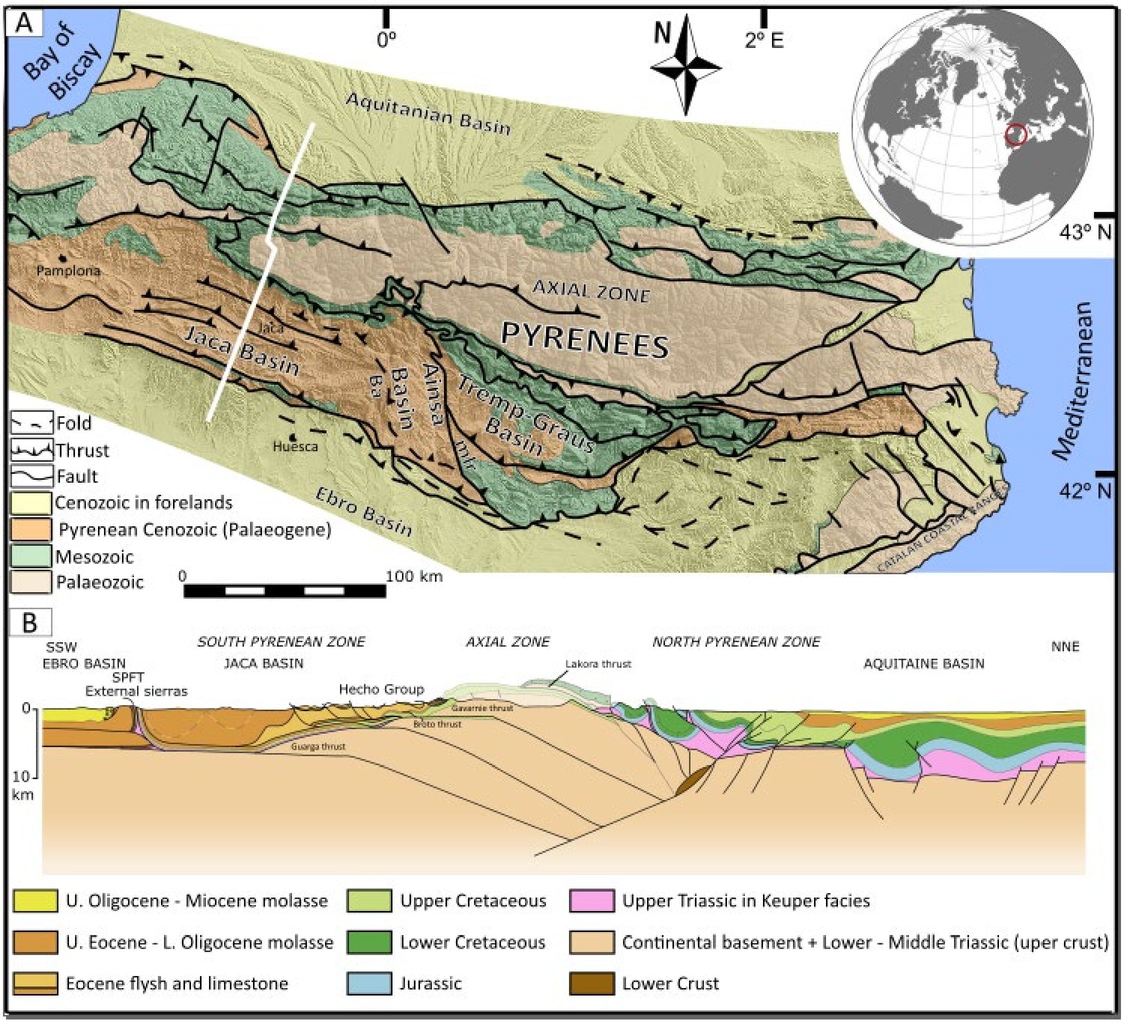

Figura 6: **A**: Mapa geológico simplificado del Pirineo, indicando la distribución de las cuencas Surpirenaicas objeto de estudio (modificado de Teixell *et al*., 2016). Ba: anticlinal de Boltaña; mlr: rampa lateral de Montsec. **B**: Corte transversal de los Pirineos centro-occidentales (simplificado de Teixell *et al*., 2016), mostrando tanto la Zona Sur Pirenaica como la Zona Nord Pirenaica.

Figure 6: **A**: Simplified geological map of the Pyrenees (modified from Teixell *et al*., 2016), showing the different basins and areas studied. Ba: Boltaña anticline; mlr: lateral ramp of Montsec. **B**: Cross-section of the central-western Pyrenees (simplified from Teixell *et al*., 2016), showing both the South Pyrenean Zone and the North Pyrenean Zone.

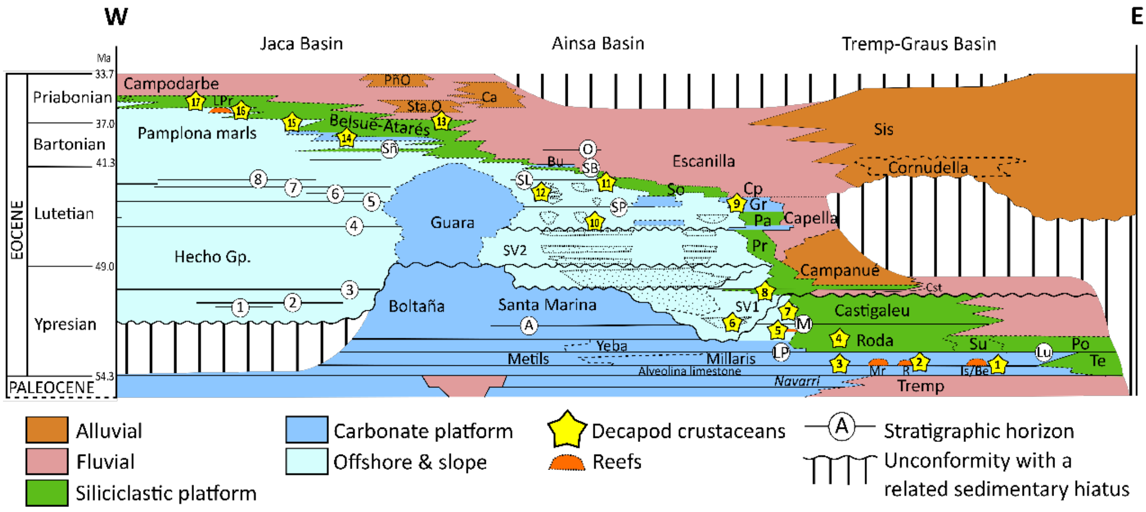

Figura 7: Panel cronoestratigráfico de las cuencas de Tremp-Graus, Ainsa y Jaca (Modificado de Garcés *et al*., 2020) con la indicación de las unidades litoestratigráficas donde se han encontrado decápodos fósiles. Unidades litoestratigráficas: Ca: Canciás; Cp, Capella; Cst, Castissent; Gr, Grustán; Is/Be: Iscles-Berganuy reefs; LPr: La Peña reef; Mr, Merli reef; Pa, Pano; PñO, Peña Oroel; Po, Porredó; Pr, Perarrúa; R: Ramals reef; So, Sobrarbe; Sta.O: Santa Orosia; Su, Suerri; SV1-2: diferent units making the San Vicente Formation; Te, Tendrui. **Horizons**: A, Ascaso; LP, La Puebla; Lu, Santa Llucia; M, Morillo limestone; O, Olsón; SB, Santa Bárbara; SL, San Lino; SÑ, Sabiñánigo; SP, San Pedro; 1 a 8 son diferentes niveles de megaturbiditas carbonatadas. **Estrellas amarillas**: 1: zona Suerri-Iscles; 2: Ramas; 3: zona baja de Bacamorta; 4: zona alta de Bacamorta; 5: Bacamorta; 6: Área de Atiart; 7-8: Morrillo; 9: Grustán; 10: Área de Mediano; 11: área de Lamata; 12: Sta. zona Mª de la Nuez; 13: Fanlillo; 14-17: Zona Belsué-La Peña.

Figure 7: A chronostratigraphic panel of the Tremp-Graus, Ainsa and Jaca basins (Modified after Garcés *et al*., 2020). **Lithostratigraphic units:** Ca: Canciás; Cp, Capella; Cst, Castissent; Gr, Grustán; Is/Be: Iscles-Berganuy reefs; LPr: La Peña reef; Mr, Merli reef; Pa, Pano; PñO, Peña Oroel; Po, Porredó; Pr, Perarrúa; R: Ramals reef; So, Sobrarbe; Sta.O: Santa Orosia; Su, Suerri; SV1-2: diferent units making the San Vicente Formation; Te, Tendrui. **Horizons**: A, Ascaso; LP, La Puebla; Lu, Santa Llucia; M, Morillo limestone; O, Olsón; SB, Santa Bárbara; SL, San Lino; SÑ, Sabiñánigo; SP, San Pedro; 1 to 8 are different carbonate megaturbidite beds. **Yellow stars**: 1: Suerri-Iscles area; 2: Ramals; 3: lower Bacamorta area; 4: upper Bacamorta area; 5: Bacamorta; 6: Atiart area; 7-8: Morillo; 9: Grustán; 10: Mediano area; 11: Lamata area; 12: Sta. Mª de la Nuez area; 13: Fanlillo; 14-17: Belsué-La Peña area.

3.2.1. Evolución tecto-sedimentaria

La formación de las cuencas Pirenaicas se remonta a la etapa de rift desarrollada en el Pérmico-Triásico. Durante gran parte del Mesozoico, la evolución de la cuenca estuvo relacionada con un régimen transtensivo, lo que derivó en la separación de la microplaca Ibérica del resto de Pangea (Rosenbaum *et al*., 2002). Este régimen extensivo, además, dio origen a la formación de mares epicontinentales desde el Triásico Medio al Jurásico (Meléndez y Aurell, 2004), y una segunda fase de rift durante el Cretácico Inferior, relacionada con la apertura del Golfo de Vizcaya.

El régimen tectónico, inicialmente distensivo o transtensivo cambió a partir del Cretácico Superior, entre el Santoniense y Maastrichtiense. En ese momento se inició la inversión de las cuencas Mesozoicas pirenaicas por la compresión alpina derivada del acercamiento entre África y Europa. Este cambio en el sentido de los esfuerzos tectónicos dio como resultado el comienzo del desarrollo de una cuenca de antepaís, a la vez que se producía el desarrollo del orógeno Pirenaico (Puigdefabregas *et al*., 1986, 1992; Puigdefabregas y Souquet, 1986). Especialmente notable es la transición hacia las cuencas de antepaís producida durante el Paleoceno, que dio como resultado la elevación de la zona axial en los Pirineos desde la zona oriental. Debido a esta elevación del orógeno, la cuenca Pirenaica quedó dividida en dos grandes dominios sedimentarios; las zonas Norpirenaica y la Surpirenaica (Barnolas *et al*., 2004) (Fig. 6B).

Durante el Eoceno inferior (Ypresiense) la actividad tectónica en la zona surpirenaica experimento un incremento, llegando hasta el Clímax Tectónico del Eoceno Medio. Como resultado de esta nueva etapa de actividad tectónica, se produjo el emplazamiento de la Unidad Surpirenaica Central (USPC) y el hundimiento de las plataformas carbonatadas. Estas últimas se formaron durante el Paleoceno y Eoceno basal gracias a la relativa calma tectónica anterior y la reducción de aporte siliciclástico que derivó de ello (ver Silva-Casal, 2017). Todo esto dio como resultado el avance de los sistemas sedimentarios hacia el antepaís y la compartimentación de la cuenca Surpirenaica, dando origen a la cuenca Surpirenaica Oriental, la cuenca de Tremp-Graus, la cuenca de Ainsa y la cuenca de Jaca comentadas anteriormente (ver Silva-Casal, 2017).

3.2.2. Contexto paleoclimático

El Paleoceno y el Eoceno temprano se caracterizaron por climas mucho más cálidos que el actual (Fig. 8A), pero ligeramente más fríos que los del Cretácico Superior (Witkowski *et al*., 2018; Baatsen *et al*., 2020). Las condiciones cálidas se mantuvieron durante casi todo el Paleógeno gracias a la gran concentración de gases de efecto invernadero (Pearson y Palmer, 2000; Zachos *et al*., 2008; Pomar *et al*., 2017), con condiciones similares a las del final del Cretácico durante parte del Eoceno (Zachos *et al*, 2001). Sin embargo, a lo largo del Eoceno se produjo una transición climática, pasando gradualmente a un clima frio, con presencia de casquetes polares al inicio del

Oligoceno (Zachos *et al*., 1993, 2001, 2008; Pekar *et al*., 2005; Tripati *et al*., 2005, 2008; Edgar *et al*., 2007; Jadwiszczak, 2010; Soták, 2010) (Fig. 8A).

Esta tendencia de enfriamiento general se vio interrumpida por una serie de episodios o eventos hipertermales que afectaron puntualmente al clima durante el Paleoceno y el Eoceno (Zachos *et al*., 1993; Bralower *et al*., 2002; Payros *et al*., 2012) (Fig. 8B-C). Estos episodios de calentamiento global de corta duración (alrededor de 100.000 años) quedaron registrados por excursiones negativas de los isótopos de oxígeno y carbono, y están relacionados con la emisión de gases de efecto invernadero (Zachos *et al*., 2008).

El primero de estos eventos es el Máximo Térmico del Paleoceno–Eoceno (PETM o Paleocene–Eocene Thermal Maximun) en el que las temperaturas del Cenozoico alcanzaron su estado más cálido (Zachos *et al*., 1993, 2001; Payros *et al*., 2015). En este evento, las temperaturas aumentaron abruptamente entre 5 y 6 °C y los gradientes de temperatura entre el ecuador y los polos volvieron a disminuir (Zachos *et al*., 1993). El calentamiento cesó después de 20ka y las temperaturas se estabilizaron después de solo 150-200ka (Zachos *et al*., 1993, 2001; Bice y Marotzke, 2002). Este evento parece estar relacionado con la proliferación de arrecifes coralinos de estilo moderno (Fig. 8C), cuyos requerimientos ecológicos cada vez se conocen mejor gracias a los estudios neontológicos (Pomar *et al*., 2017), y favoreció la gran diversificación de otros organismos bentónicos como los macroforaminíferos del Eoceno (Orue-Etxebarria *et al*., 2001; Pujalte *et al*., 2003, 2009; Scheibner *et al*., 2005; Scheibner y Speijer, 2008; Payros *et al*., 2010). Después del PETM, el Eoceno fue una época crítica en el desarrollo de muchas características modernas de la Tierra, como las configuraciones paleogeográficas, los patrones de circulación oceánica y diversas condiciones climáticas (p. ej., Hallock *et al*., 1991; Hallock y Pomar, 2008; Stickley *et al*., 2009).

Durante el resto de la primera etapa del Eoceno, el clima estuvo marcado por un aumento de la temperatura, llegando a su apogeo en el Óptimo Climático del Eoceno inferior (EECO o Early Eocene Climatic Optimum). Estas condiciones, sin embargo, cambiaron posteriormente, dando lugar a un enfriamiento gradual general, interrumpido por eventos de calentamiento de menor magnitud hasta el Eoceno medio. En este momento, se produce otra subida importante de temperatura, llamada Óptimo Climático del Eoceno medio (MECO o Middle Eocene Climatic Optimum) (Foster *et al*., 2013; Henehan *et al*., 2020). Después de este óptimo climático, se reinició la tendencia al enfriamiento global que desembocó en la glaciación del Oligoceno (Edgar *et al*., 2007; Baatsen *et al*., 2020) y la aparición de casquetes polares permanentes (Fig. 8A).

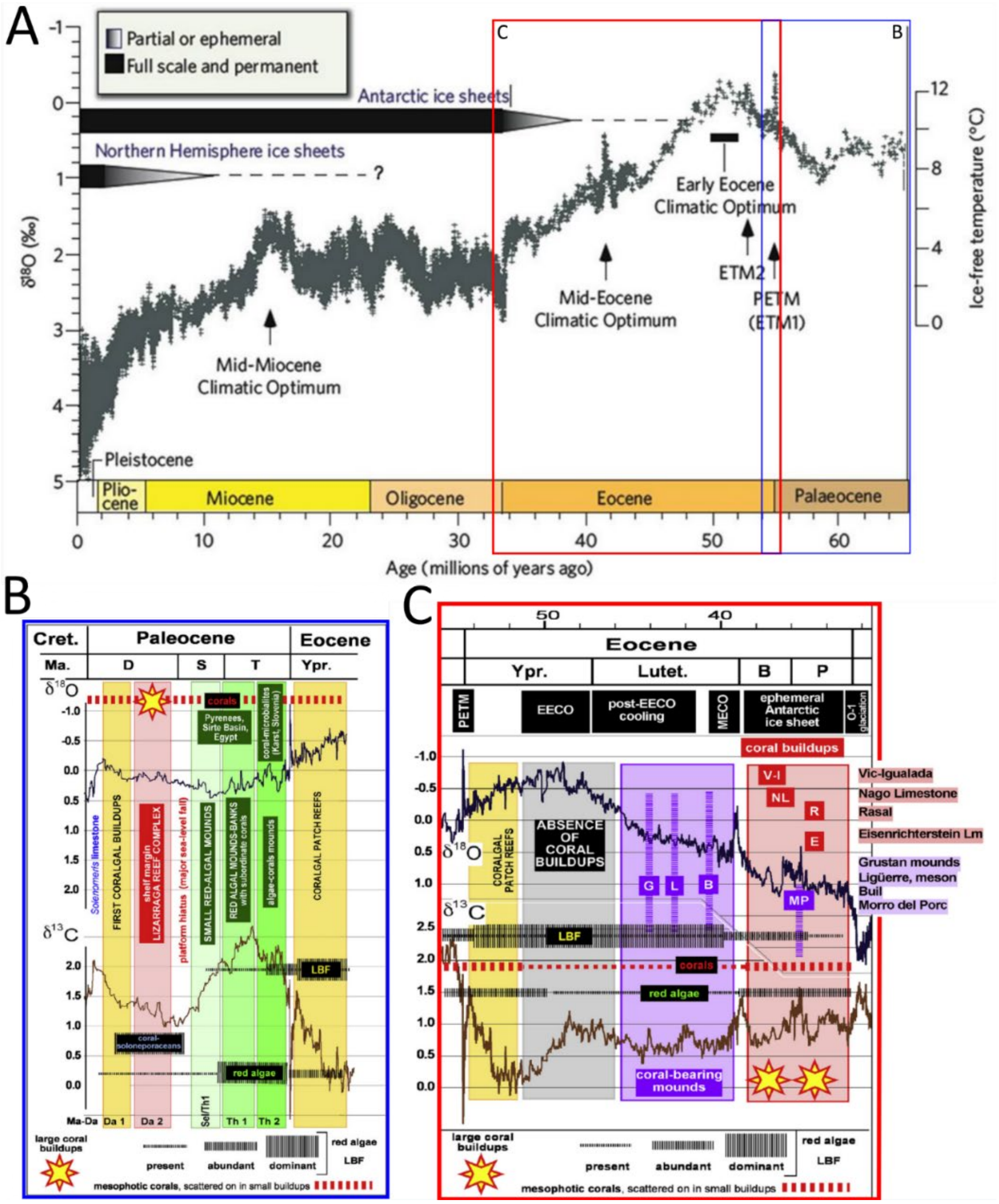

Figura 8: **A**: Evolución del clima global desde Paleoceno (hace 65 Ma) en base a isótopos de oxígeno de foraminíferos bénticos de aguas profundas (tomado de Zachos *et al*., 2008). **B**: Plataformas paleocenas y tipos de arrecifes predominantes; C: Detalle de los eventos climáticos durante el Eoceno y los tipos de arrecifes predominantes. LBF: Foraminíferos bentónicos grandes. (B y C tomados de Pomar *et al*., 2017).

Figure 8: **A**: Evolution of the global climate since the Paleocene (65 Ma) based on oxygen isotopes of deep-sea benthic foraminifera (taken from Zachos *et al*., 2008). **B**: Paleocene platforms and buildup types; **C**: Detail of the climatic events during the Eocene and the predominant buildup types. LBF: larger benthic forams. (B and C taken from Pomar *et al*., 2017).

3.2.3. Paleogeografía de la zona Surpirenaica

Durante el Eoceno, la zona Surpirenaica corresponde a un golfo alargado de este a oeste, por donde conectaba con el mar Cantábrico en el golfo de Vizcaya, y quedaba limitada al norte por la zona axial de los Pirineos (Plaziat, 1981; Garcés *et al.*, 2020) (ver Figs. 9, 10). El golfo estaba flanqueado por plataformas carbonatadas de aguas someras, sistemas siliciclásticos, y acumulaciones de sedimentos hemipelágicos en el fondo de la cuenca (ver Silva-Casal *et al.*, 2017; Silva-Casal, 2017; Garcés *et al.*, 2020) (Fig. 9). Hay que tener en cuenta que estas cuencas han sufrido un acortamiento tectónico de unos 114 km desde el Cretácico, especialmente activo en el Eoceno (ver Texiell *et al.*, 2016), estrechándose considerablemente.

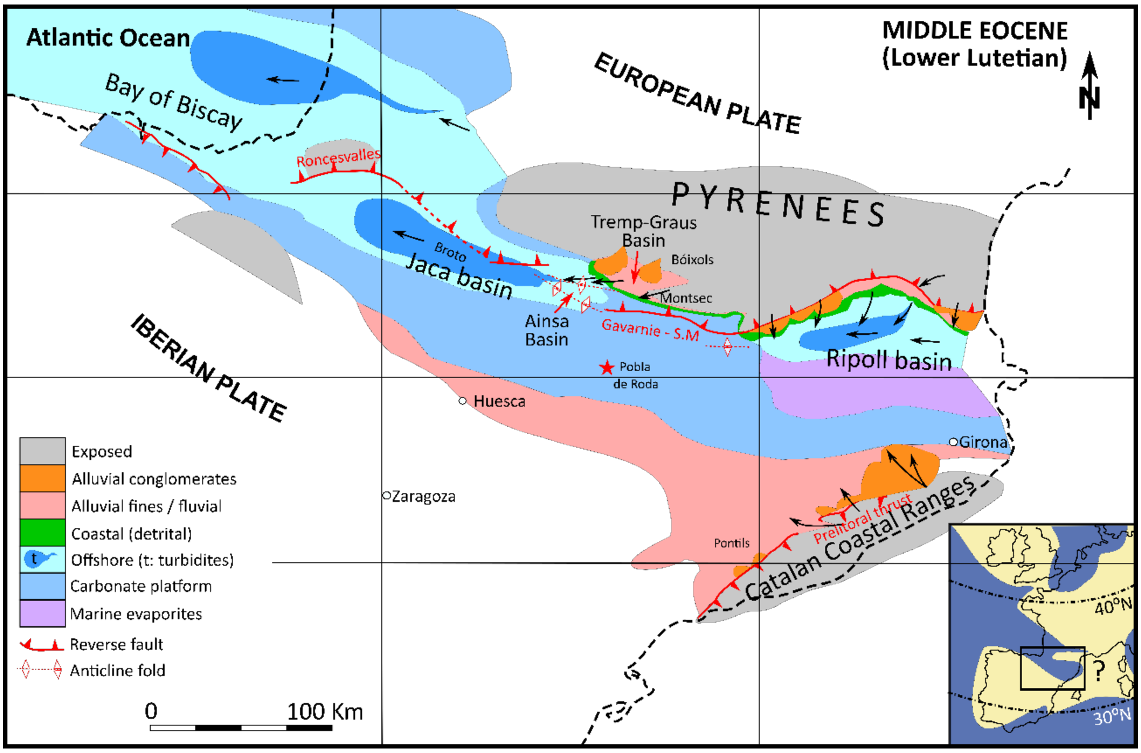

Figura 9: Reconstrucción paleogeográfica de los Pirineos y las cuencas de antepaís adyacentes durante el Eoceno inferior-medio (modificado de Garcés *et al.*, 2020).

Figure 9: Paleogeographic reconstruction of the Pyrenees and the adjacent foreland basins during the early-middle Eocene (modified after Garcés *et al.*, 2020).

A lo largo del Eoceno, la zona Surpirenaicas sufrió cambios significativos, tanto en la distribución de los medios sedimentarios, como en el tipo de sedimentación (Figs. 9-10). La parte más oriental o Cuenca Surpirenaica Oriental o Catalana, limitaba al oeste con la estructura del Segre (Barnolas, 1992) que corresponde con la rampa lateral de las láminas cabalgantes de la USPC (Muñoz *et al*., 2013). Al este, la cuenca Catalana quedaba limitada con el Mediterráneo, pero aún no hay consenso en si existía una conexión con este, pese a que existen algunas coincidencias faunísticas con otras cuencas mediterráneas del Eoceno (Via, 1969; Via y Cals, 1979; Via, 1980; Khodaverdi *et al*., 2016; y observación personal). A partir del Eoceno inferior, el emplazamiento de la USPC dio lugar al aislamiento parcial de esta cuenca, pero sin impedir que las condiciones marinas se mantuvieran durante casi todo el Eoceno (Barnolas y Gil-Peña, 2001). Al oeste, la cuenca Vasco-Cantábrica corresponde al límite occidental del sistema (Mengaud, 1920; Reguant y Truyols, 1968; Maldonado *et al*., 1970; Portero García y Ramirez del Pozo, 1977; Hines, 1985). Se trata de una zona de transición hacia condiciones cada vez más oceánicas, y queda separada de la cuenca de Jaca por la falla de Pamplona (Payros, 1997).

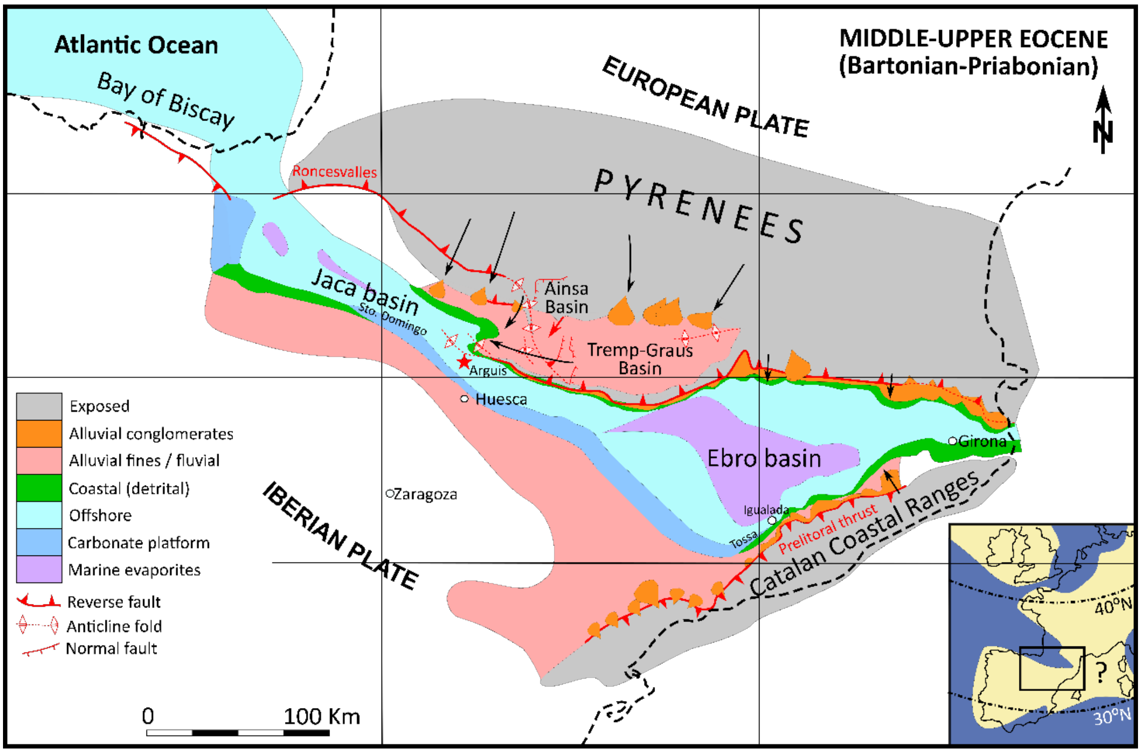

Figura 10: Mapa paleogeográfico del Eoceno medio y superior del área pirenaica, que muestra la ubicación de la cuenca Jaca (modificado de Garcés *et al*., 2020).

Figure 10: Mid-upper Eocene palaeogeographical map of the Pyrenean area, showing the location of the Jaca Basin (modified from Garcés *et al*., 2020).

A continuación, se explica de forma resumida las particularidades de las distintas cuencas del Sector Central de la Cuenca Surpirenaica durante el Eoceno. Con ello, se pretende dar un enfoque general de cada zona de estudio, para así comprender mejor el contexto paleogeográfico y paleoecológico.

3.2.3.1. La cuenca de Tremp-Graus

La Cuenca de Tremp-Graus corresponde a una cuenca de piggy-back, situada sobre la USPC (ver Fig. 6). En ella se formaron medios transicionales, con sistemas fluviales y deltaicos, en dirección SE-NO, alimentados por sistemas aluviales en dirección NE-SW, dando lugar a una sedimentación principalmente siliciclástica (Barnolas *et al*., 1991, 1992; Barnolas y Gil-Peña, 2001). Estos sistemas fluvio-deltaicos progradaron hacia el oeste debido a la actividad tectónica y abastecieron de sedimento al surco turbidítico de las cuencas de Ainsa y de Jaca durante el Ypresiense y Luteciense (Garcés *et al*., 2020 y referencias en el mismo).

De particular interés para esta Tesis es la unidad arrecifal del Eoceno inferior de la parte media de la Formación Serraduy, expuesta en el margen noroeste de la cuenca Tremp-Graus (Fig. 11). Alrededor del área de estudio conocida como Ramals (o “Font del Oro”, debido a las abundantes piritas de algunos niveles), la Formación Serraduy forma un afloramiento de dirección ESE-WNW casi continuo (Fig. 11A). Este afloramiento es conocido desde finales del siglo XIX (ver Cotteau, 1889). Sin embargo, únicamente se mencionó la alta diversidad y abundancia de otros organismos bentónicos como moluscos y equinodermos. Posteriormente, Via (1973) reporta los primeros ejemplares de braquiuros asociados a los equivalentes distales de estos materiales. Artal y Via (1989) pusieron de manifiesto por primera vez la gran diversidad de crustáceos en el intervalo arrecifal incluido en estos afloramientos. Desde entonces, varios estudios sistemáticos han descrito varias especies de crustáceos decápodos a partir de estos materiales (Artal y Castillo, 2005; Artal y Van Bakel, 2018a, 2018b; Ferratges *et al*., 2019; 2022a; Artal *et al*., 2022), con algunos representantes que ayudan a dilucidar el origen de algunas familias modernas.

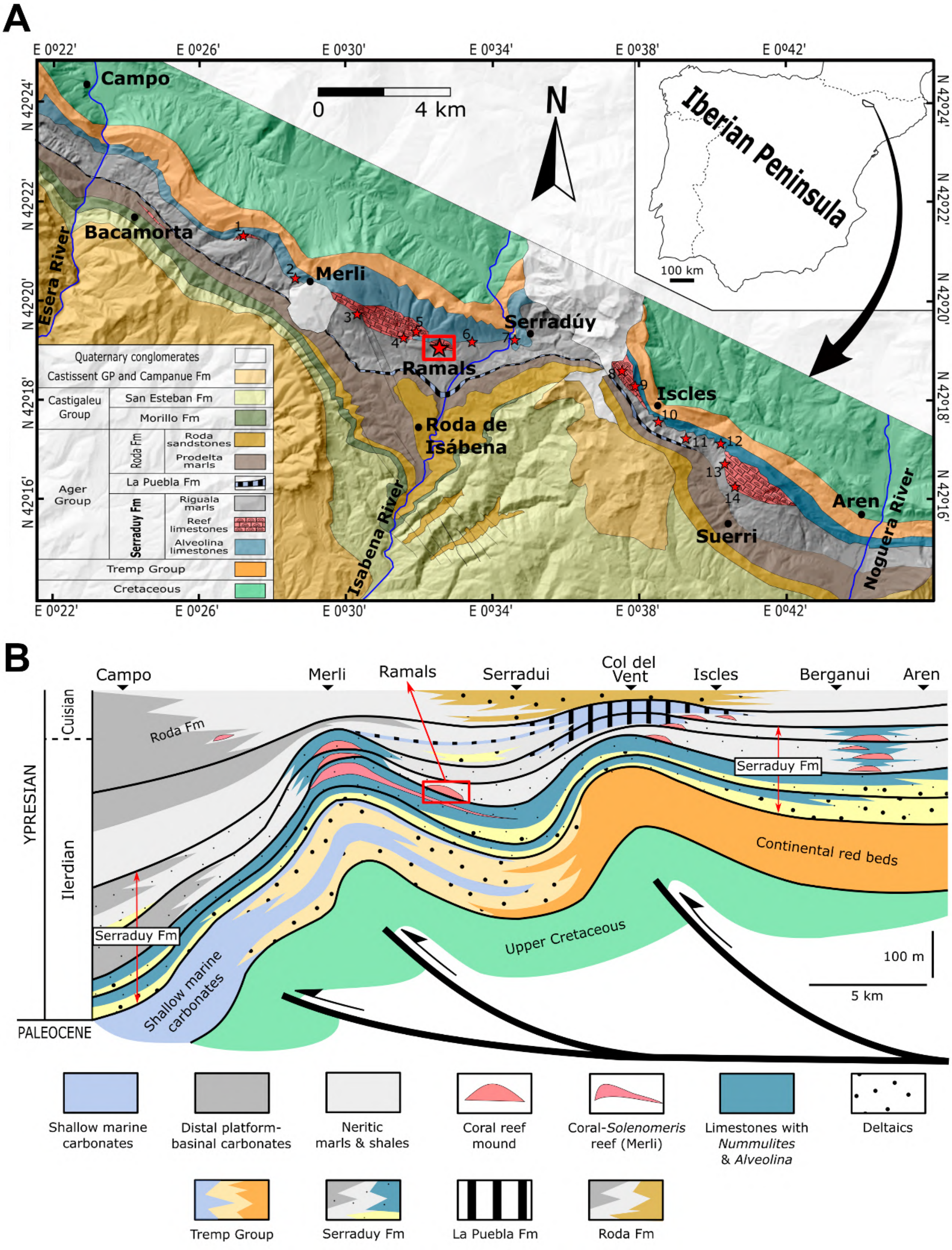

Figura 11: **A**: Marco geológico esquemático de la zona centro-sur de los Pirineos. **B**: Sección transversal estratigráfica sintética y modelo sedimentario del margen norte del área de Tremp durante el Eoceno inferior, con los principales tipos de facies y la ubicación de los principales complejos arrecifales indicados. Las áreas elevadas eran lugares de sedimentación carbonatada marina poco profunda frente a áreas más profundas con sedimentación fangosa. La equivalencia con las unidades litoestratigráficas utilizadas por Serra-Kiel *et al*. (1994) se indica en la leyenda de los diferentes tipos de facies. Modificado de Einchenseer (2003) y Pomar *et al*. (2017).

Figura 11: **A**: Schematic geological setting (south-central Pyrenean zone). **B**: Synthetic stratigraphic cross section and sedimentary model of the northern margin of the Tremp area during the lower Eocene, with main facies types and the location of the main reefal complexes indicated. Uplifted areas were places of shallow marine carbonate sedimentation facing deeper areas with muddy sedimentation. Equivalence with the lithostratigraphic units used by Serra-Kiel *et al*. (1994) is indicated in the legend of the different facies types. Modified from Einchenseer (2003) and Pomar *et al*. (2017).

Esta formación consta de tres intervalos litoestratigráficos (Serra-Kiel *et al*., 1994). El miembro inferior, de edad Ypresiense temprano, se conoce tradicionalmente como Calizas de Alveolina. Esta unidad se depositó tras la transgresión generalizada del inicio del Eoceno. La topografía, junto con las cálidas temperaturas, favoreció el establecimiento de una rampa carbonatada de bajo relieve a través de las zonas marginales de la cuenca de Tremp-Graus, en la que se depositaron las Calizas de Alveolina (Ferrer, 1971; Robador *et al*., 1991; Luterbacher *et al*., 1991, Eichenseer y Luterbacher, 1992; Payros *et al*., 2000; Miller *et al*., 2005; Zachos *et al*., 2008; Martinius, 2011; Garcés *et al*., 2020).

Las Calizas de Alveolina están cubiertas por una superficie de hard-ground, formada después de una inundación generalizada. Este evento de inundación alcanzó las áreas marginales de la cuenca Tremp-Graus y estuvo relacionado con la migración hacia el sur de la flexión de la placa (Fonnesu, 1984; Garcés *et al*., 2020). Las bajas tasas sedimentarias durante este período de aumento del nivel del mar favorecieron el desarrollo de una superficie endurecida que permitió el crecimiento de montículos arrecifales variables en tamaño y morfología (Eichenseer y Luterbacher, 1992). Estos arrecifes y las facies asociadas caracterizan el miembro medio de la Formación Serraduy (p.ej., el miembro de calizas arrecifales; Serra-Kiel *et al*., 1994). El análisis de este sistema arrecifal, combinado con la caracterización del conjunto de invertebrados asociado (p. ej., Zamora *et al*., 2018), indica que se desarrolló en profundidades eufóticas a mesofóticas, alrededor o por debajo de la base de las olas de tormenta (Gaemers, 1978; Eichenseer, 1988; Pomar *et al*., 2017).

El evento de profundización de mediados del Ypresiense dio como resultado la eventual inundación de la plataforma y el depósito de las margas de Riguala de la parte superior de la Formación Serraduy (Fig. 11B). Estas margas se depositaron en una plataforma marina abierta relativamente profunda, en transición a un entorno de talud, y sustentaron una menor concentración de comunidades bentónicas (Serra-Kiel *et al*., 1994). Las margas de Riguala fueron datadas como Ilerdiense inferior a medio, lo que corresponde al Ypresiense (Pujalte *et al*., 2009). A escala regional, la mayoría de los montículos arrecifales estudiados crecieron sobre la superficie de discontinuidad endurecida que se encuentra sobre la caliza Alveolina. Sin embargo, también se han encontrado arrecifes de coral aislados dentro de las margas de Riguala cerca de Suerri. También existe el registro local de arrecifes de coral más jóvenes en las margas de prodelta de la Formación Roda, en Bacamorta (Ferratges *et al*., 2021c y Fig. 11B).

La Formación Roda correspondiente al Ypresiense medio y superior (Samsó *et al*., 1990; Tosquella *et al*., 1990; Garcés *et al*., 2020) incluye niveles sucesivos ricos en crustáceos decápodos, preservados en un sistema deltaico progradante. La Formación Roda es una sucesión somerizante (Molenaar y Martinius, 1990) que muestra un patrón de progradación hacia el sur y el suroeste (ver Leren *et al*., 2010 y referencias en el mismo). Esta formación se divide en dos miembros: (1) el miembro inferior formado por gruesos cuerpos margosos de prodelta con intervalos detríticos, que sobre yace a la alternancia de areniscas y limolitas de la Formación La Puebla y miembro de margas Riguala de la Formación Serraduy; (2) el miembro superior, la Arenisca de Roda, corresponde a la facies deltaica influenciada por mareas. Las secuencias elementales consisten en cuerpos sedimentarios detríticos separados por intervalos margosos ricos en fauna, dispuestos en un conjunto de ciclos superpuestos de facies de progradación deltaica y de plataforma interna, respectivamente. Al oeste del río Isábena, la Formación Roda pasa rápidamente a prodelta y margas de plataforma abierta (ver detalles en Martinius y Molenaar, 1991).

Por encima se encuentra la Formación Morillo, del Ypresiense superior-inicio del Luteciense, que consta de dos niveles carbonatados ricos en macroforaminíferos, separados por un intervalo margoso. En esta formación destaca la abundancia y diversidad de equinodermos (ver Ferratges *et al*., 2022b), y una escasa pero diversa asociación de crustáceos decápodos (ver Ferratges *et al*., 2022b, d). El espesor de esta unidad aumenta en sentido E-O, alcanzando los 30 m en la zona del río Isábena (tramo Serraduy) y los 57 m en la zona del río Esera (tramo Campo). Se ha interpretado como un intervalo transgresivo cuyas facies más proximales (zona del río Isábena) están representadas por carbonatos de plataforma interna, y la facies distal (zona del río Esera) por limos carbonatados de plataforma media (Serra-Kiel *et al*., 1994). Tosquella (1988) interpretó la formación de estos niveles como un ambiente deposicional dentro de la zona fótica de una plataforma poco profunda.

Finalmente, desde el Luteciense superior, los sistemas fluvio-deltáicos progradaron y colmataron paulatinamente la cuenca de Tremp-Graus, alcanzando la cuenca de Jaca (de Federico, 1981; Bentham, 1992; Nijman, 1998; Barnolas y Gil-Peña, 2001; Montes-Santiago, 2002; Chanvry *et al*., 2018) (ver Fig. 10).

3.2.3.2. La cuenca de Ainsa

Al oeste de la cuenca de Tremp-Graus y limitada occidentalmente por el anticlinal de Boltaña, se encuentra la cuenca de Ainsa. Las unidades estudiadas en esta cuenca corresponden principalmente al Eoceno medio, y se enmarca mayoritariamente en el "Geoparque Sobrarbe-Pirineos" (ver Canudo *et al*., 2021). Las características sedimentológicas y estructurales que en ella se aprecian son en general distintas a la cuenca de Tremp-Graus y también difieren de la cuenca de Jaca, situada más al oeste. Desde el punto de vista estructural se conoce como Zona oblicua de Ainsa o AOZ-Ainsa fold and thrust Oblique Zone (Muñoz *et al*., 2013)].

Durante aproximadamente la primera mitad del Eoceno, esta cuenca correspondía a una región de transición. En ella se situaba el talud proximal de los sistemas turbidíticos que se acomodan en la cuenca de Jaca, alimentados por los sistemas fluvio-deltaicos de la cuenca de Tremp-Graus. Por otra parte, sobre el margen pasivo de la cuenca de antepaís en este sector, se encontraba la transición entre los sistemas siliciclásticos y costeros del margen de la cuenca de Tremp-Graus y las plataformas carbonatadas de la cuenca de Jaca (de Federico, 1981; Barnolas *et al*., 1991, 1992; Barnolas y Gil-Peña, 2001; Silva-Casal, 2017; Chanvry *et al*., 2018).

A medida que la lámina de Gavarnie se desplazaba, fue deformando progresivamente la cuenca de Ainsa a través de un sistema de pliegues y cabalgamientos. Esto complicó sustancialmente la relación entre los distintos sistemas sedimentarios, así como la paleogeografía general de este sector (Muñoz *et al*., 2013; Coll *et al*., 2022). La formación de los anticlinales de Boltaña y Balcés (en el Luteciense medio) dio lugar a la separación parcial de la cuenca de Jaca (Muñoz *et al*., 2013) y el surco creado entre estas estructuras y el anticlinal de Mediano aisló la cuenca de Ainsa. Finalmente, la progradación del delta del Sobrarbe durante el Luteciense superior reemplazó la sedimentación carbonatada por otra dominada por sedimentos siliciclásticos (de Federico, 1981; Dreyer *et al*., 1999; Mochales *et al*., 2012).

Los fósiles de decápodos en esta zona aparecen en diferentes intervalos, especialmente la Formación Grustán y su equivalente lateral, la Formación San Vicente, así como la Formación Sobrarbe (ver Canudo *et al*., 2021). En el flanco occidental del anticlinal de Mediano se formaron tres rampas carbonatadas sucesivas de la Formación Grustán (Arbués *et al*., 2011), que albergan invertebrados generalmente fragmentados en varios niveles. Según Arbués *et al*. (2011) y Pomar *et al*. (2017), las rampas inestables de la Fm. Grustán consisten en carbonatos bioclásticos de grano medio a fino ricos en foraminíferos bentónicos, moluscos, equinodermos, y algas rojas. Los corales ramificados y solitarios se encuentran en litofacies someras, pero también se encuentran biohermos discretos en posiciones más profundas. Fragmentos de estas plataformas carbonatadas fueron transportados durante la deformación del anticlinal de Mediano, produciéndose deslizamiento temprano y brechas. Sus restos se encuentran resedimentados en la Formación San Vicente, más profunda y equivalente lateral en la parte occidental del embalse de Mediano. Estos materiales contienen un rico y diverso conjunto de invertebrados, incluidos crustáceos decápodos, equinodermos y moluscos (ver Canudo *et al*., 2021). En el área de Paules de Sarsa, la Formación San Vicente también contiene una abundante (pero poco diversa) fauna de crustáceos decápodos autóctonos dominada por *Harpactoxanthopsis quadrilobata*, mencionado por primera vez por Garrido (1943). Otros componentes menores asociados a este último incluyen el dudosamente asignado "*Peltarion*" *pirenaicus* (Aguilar y Castillo, 2017), equinoideos y moluscos.

La Formación Sobrarbe suprayacente en el área de Mediano cerca de Ligüerre de Cinca representa una unidad carbonatada discreta (ver Fig. 7) compuesta de calcarenitas, pequeños montículos con corales y niveles numulíticos intercalados con limos laminados de prodelta y las arcillas del complejo de Sobrarbe (Pomar *et al*., 2017). Los niveles numulíticos en esta área han proporcionado algunos decápodos, incluidos paguridos y *Lophoranina*, así como equinoideos y moluscos. Hacia la parte superior de la secuencia se encuentran biostromas de coral, y según Mateu-Vicens *et al*. (2012), contienen una rica fauna de invertebrados que incluye celenterados, equinoideos, moluscos, briozoos, ostrácodos y decápodos.

3.2.3.3. La cuenca de Jaca

De particular interés para la Tesis son las unidades del Bartoniense-Priaboniense (Eoceno medio-superior) de las Sierras Exteriores, localizadas en el margen sur de la cuenca de Jaca, adosado al Cabalgamiento Frontal Surpirenaico (Fig. 12).

Las unidades del Eoceno medio y superior (Luteciense-Priaboniense) del margen sur de la cuenca de Jaca forman una sucesión de unos 2 km de espesor, que incluye las calizas marinas someras de la Formación Guara y los materiales de prodelta/margas/arcillas de rampa exterior de la Formación Arguis. Estos pasan lateralmente (hacia el este) y hacia techo hacia la Formación deltaica Belsué-Atares, y su equivalente lateral en facies siliciclásticas costeras de la Formación Yeste-Arres. Estas unidades están a su vez superpuestas a los materiales fluviales de la Formación Campodarbe (Puigdefabregas, 1975; Silva-Casal *et al.*, 2019). Este conjunto de unidades es diacrónico y registra el llenado tardío de la cuenca de antepaís de Jaca (Millán *et al.*, 1994, 2000; Coll *et al.*, 2022).

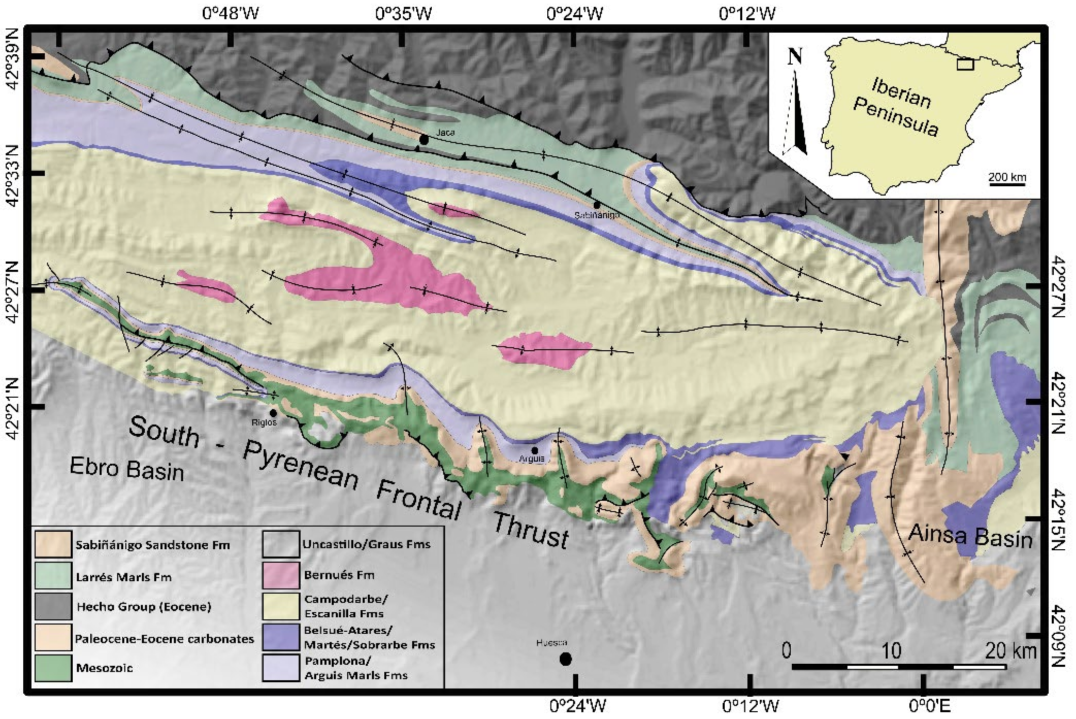

Figura 12: Mapa geológico de la Cuenca de Jaca (modificado de Puigdefàbregas, 1975).

Figure 12: Geological map of the Jaca Basin (modified after Puigdefàbregas, 1975).

La formación de la cuenca de Jaca se debió a la propagación hacia el sur de las estructuras cabalgantes y de deformación durante el Paleógeno (Millán *et al*., 1994; Muñoz *et al*., 1994; Castelltort *et al*., 2003; Huyghe *et al*., 2009). La propagación de estas estructuras resultó en la formación de un relieve coetáneo, actuando como un área fuente de sedimentos para los complejos deltaicos (p. ej., Plaziat, 1981; Dreyer *et al*., 1999; Pujalte *et al*., 2002; Barnolas *et al*., 2004). Estos complejos deltaicos progradaron hacia el oeste en la parte sur de la cuenca, cubriendo progresivamente los sistemas turbidíticos del Grupo de Hecho del Eoceno inferior y medio (Mutti *et al*., 1985; Remacha *et al*., 2003; 2005; Coll *et al*., 2022).

A nivel general, la evolución de la cuenca de Jaca durante el Eoceno se puede resumir en dos fases. La primera fase (Ypresiense superior–Luteciense terminal) se caracteriza por presentar rampas carbonatadas someras asociadas a su margen pasivo (sobre el antepaís), sistemas siliciclasticos en el margen activo y un surco turbidítico axial desarrollado paralelamente al orógeno (Barnolas y Gil-Peña, 2001; Barnolas *et al*., 2004). El avance de las láminas de cabalgamiento en el margen activo de la cuenca dio lugar una importante subsidencia flexural que la sedimentación aportada no pudo compensar (Barnolas y Teixell, 1994; Payros *et al*., 1999; Barnolas y Gil-Peña, 2001). La sedimentación deltaica en la cuenca de Jaca se derivó principalmente de las áreas orientales, ubicadas en los Pirineos centrales (Fig. 13A), en las que el basamento paleozoico contribuyó aportando componentes plutónicos (Coll *et al*., 2022). La segunda fase (Luteciense terminal–Priaboniense), se caracteriza por la progradación de los sistemas deltaicos axiales, que dio como resultado la colmatación de la cuenca (Barnolas and Gil-Peña, 2001; Montes-Santiago, 2002). La sedimentación carbonatada se redujo a plataformas puntuales a lo largo del Bartoniense inferior, quedando únicamente asociadas a episodios transgresivos (Puigdefàbregas, 1975; Millán *et al*., 1994; Morsilli *et al*., 2012). La progradación de estos sistemas deltaicos dio lugar la definitiva continentalización de la cuenca (Costa *et al*., 2010), cambiando a un contexto continental endorreico, en continuidad con los materiales de la cuenca del Ebro (Barnolas *et al*., 2004). Desde el final del Priaboniense hasta el Oligo-Mioceno, la Formación Campodarbe registra un cambio en el área de la fuente (Fig. 13B) que dio lugar a la evolución de una fuente paleozoica más rica en rocas metamórficas (Coll *et al*., 2022).

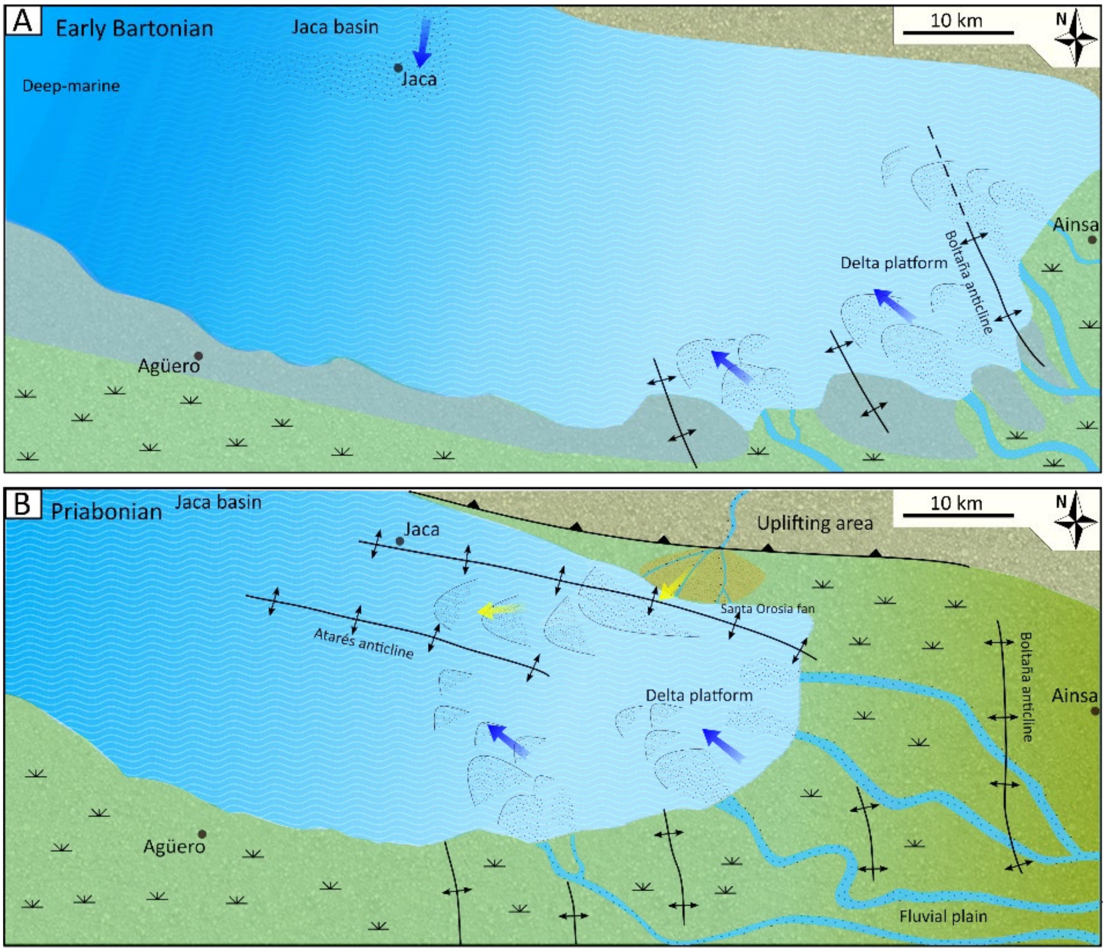

Figura 13: Esquema paleogeográfico de la cuenca de Jaca durante el Bartoniense-Priaboniense. **A**: Bartoniense temprano. **B**: Priaboniense (modificado de Coll *et al*., 2022).

Figura 13: Paleogeographic scheme of the Jaca basin during Bartonian–Priabonian times. **A**: Early Bartonian. **B**: Priabonian (modified from Coll *et al*., 2022).

En las Sierras Exteriores, situadas en el margen sur de la cuenca de Jaca objeto de estudio (sector de Bentue–La Peña), a partir del Luteciense comenzaron a desarrollarse una serie de rampas de cabalgamiento y anticlinales oblicuos con un eje norte-sur que se propagaron la deformación progresivamente hacia el oeste hasta el Priaboniense inferior, con tasas variables de acortamiento (Millán *et al*., 1994; Castelltort *et al*., 2003; Huyghe *et al*., 2009). En particular, los anticlinales de Gabardiella, Pico del Águila y Bentué de Rasal crearon un relieve e hicieron un efecto de compartimentación de la cuenca, actuando como barreras entre diferentes sectores del área de estudio. La presencia de estos anticlinales propició la proliferación de diferentes paleoambientes en un área relativamente pequeña, con marcadas diferencias en la sedimentación registrada en los sinclinales intermedios de Belsué, Arguis y Bentué de Rasal. Según Millán *et al*. (1994), las unidades sedimentarias depositadas coetáneamente al crecimiento de estos anticlinales están dispuestos en cuatro secuencias deposicionales de tercer orden I-IV (Formación Arguis) que tienen una evolución profundizante-somerizante. Estas secuencias presentan un intervalo superior dominado por facies carbonatadas y siliciclásticas poco profundas, depositadas por encima del nivel base de oleaje de tormenta (Millán *et al*. 1994, 2000; Morsilli *et al*., 2012).

La edad de estas secuencias se ha podido precisar mediante datos paleontológicos y magnetoestratigráficos (Canudo *et al*., 1988, 1991; Hogan, 1993; Pueyo *et al*., 2002; Silva-Casal *et al*., 2019; Garcés *et al*., 2020). La actividad tectónica tuvo un gran impacto en el registro sedimentario contemporáneo controlando la evolución sedimentaria y la entrada de terrígenos. Asimismo, los límites de secuencia están relacionados con pulsos tectónicos episódicos que implican la formación de discordancias angulares locales y de discontinuidades por ahogamiento (drowning unconformies) tras el hundimiento de las plataformas someras (Millán *et al*., 1994). Las cuatro secuencias deposicionales diferenciadas consisten en una unidad inferior pobremente fosilífera a arcillosa-margosa azoica, y una unidad superior siliciclástica o carbonatada somera con abundantes fósiles béntonicos. La extensión lateral de estas unidades marinas someras es progresivamente mayor en las secuencias más recientes, con una progradación que avanza de este a oeste (Millán *et al*., 1994; Ferratges *et al*., 2020a).

4. OBJETIVOS DE LA INVESTIGACIÓN

Esta Tesis Doctoral está compuesta por tres temas de investigación (sistemática; distribución de faunas; y cambios de diversidad) que comparten un objetivo común: el estudio de la influencia paleoambiental en la diversidad y distribución de los crustáceos decápodos durante el Eoceno en las Cuencas Surpirenaicas. Para este trabajo, se han seleccionado tres ejemplos clave de unidades litoestratigráficas del Eoceno de los Pirineos (NE de España), cada uno de los cuales registra diversos ambientes de plataformas marinas someras:

-Ambientes arrecifales y de prodelta de las formaciones Serraduy y Roda (Eoceno inferior) en la Cuenca de Tremp-Graus.

-Ambientes de prodelta de la Formación Arguis (Eoceno medio y superior) en la Cuenca de Jaca.

-Ambientes arrecifales de la Formación Arguis (Eoceno superior) en la Cuenca de Jaca.

De manera mucho más somera y para tener una comparativa completa se ha trabajado también las Formaciones Morillo (Cuenca de Tremp-Graus), San Vicente y Grustán (Cuenca de Ainsa).

Los ejemplos seleccionados comparten rasgos sedimentarios y faunísticos con otras áreas (ver apartado 3.1.2). Ello refuerza el interés de los resultados obtenidos en relación con la diversidad y el desarrollo de diferentes ambientes arrecifales y de prodelta. Con todo ello, se ha pretendido llenar el vacío de conocimiento acerca de la relación de diversos organismos bentónicos y el impacto que los cambios ambientales pueden tener sobre este tipo de organismos a lo largo del tiempo y el espacio. Todos estos datos han llevado a plantear ciertas cuestiones concretas sobre la distribución de los decápodos en distintas facies y paleoambientes a lo largo del tiempo, a las que se ha tratado de dar respuesta:

¿Qué relación existe entre la diversidad de crustáceos decápodos y los ambientes sedimentarios? O dicho de otro modo ¿hay relación entre el desarrollo de ciertos ambientes y el incremento/disminución de la diversidad?

¿Qué preferencias tienen determinados decápodos frente al tipo de substrato? ¿Es significativa la distribución de las diferentes agrupaciones?

¿Cómo influye en la diversidad cuando las condiciones ambientales cambian? En otras palabras ¿cómo se reflejan estos cambios ambientales en el registro fósil de crustáceos decápodos?

El objetivo general de la tesis doctoral es entender la relación entre la diversidad y distribución de los decápodos con los diferentes tipos de paleoambientes. Para ello se ha realizado un estudio sedimentológico y paleontológico integrado con los siguientes objetivos parciales:

- Definir y caracterizar los ambientes sedimentarios en los que se encuentran los crustáceos decápodos, mediante la correlación y análisis de facies en registros estratigráficos.

- Estudio sistemático de las facies con restos de crustáceos decápodos, partiendo de estudios previos, complementados con trabajos más específicos en determinadas facies de interés para el desarrollo de la investigación.

- Estudio de la paleodiversidad de los decápodos del Eoceno y su distribución en el tiempo, analizando cómo varían los distintos grupos a lo largo de la serie estratigráfica regional.

- Reconstrucción paleoambiental de arrecifes y ambientes asociados, así como ambientes prodelta con depósitos ricos en invertebrados en las formaciones estudiadas; incluyendo las interacciones de los organismos con los medios sedimentarios y sus implicaciones paleoecológicas.

- Determinar el contexto paleoecológico: en qué ambientes se encuentran actualmente los descendientes de estos taxones y en qué ambientes se encontraban en el pasado.

- Estudio sistemático completo de determinados grupos de decápodos que ayudan a entender el origen de taxones modernos.

5. METODOLOGÍA

Para cumplir los objetivos planteados se han llevado a cabo una serie de técnicas de trabajo, tanto de campo como de laboratorio y gabinete, utilizando un enfoque multidisciplinar paleontológico y sedimentológico-estratigráfico. De este modo, se han combinado la obtención de datos primarios (estudio de comunidades de decápodos durante el Eoceno, su morfología, etc.), con datos de geología a nivel regional (perfiles estratigráficos, análisis de facies, etc.) calibrados con escalas crono y biostratigráficas. Para ello, se ha realizado un muestreo exhaustivo de 42 yacimientos/localidades distribuidas en las zona central Surpirenaica, complementado con el análisis de facies, litoestratigráfico y bioestratigráfico.

Debido a la ausencia de colecciones previas de crustáceos decápodos del Eoceno en el área de estudio, parte del transcurso de la presente tesis se ha empleado en la prospección, recolección y preparación autónoma del material que la conforma. El material estudiado ha sido legalmente recogido bajo el permiso EXP: 032/2018 del *Servicio de Prevención, Protección e Investigación del Patrimonio Cultural* (Gobierno de Aragón), y se encuentra depositado en la colección paleontológica del *Museo de Ciencias Naturales de la Universidad de Zaragoza* bajo el acrónimo MPZ.

5.1. Trabajo básico

5.1.1. Trabajo de campo

- Levantamiento y correlación de perfiles estratigráficos. Se han realizado 8 perfiles estratigráficos de potencia variable. También se han empleado otros 12 perfiles levantados por otros autores para situar las nuevas muestras en su contexto estratigráfico. La interpretación de su relación lateral con diferentes facies ha sido fundamental para la comprensión de la distribución de los decápodos.

- Cartografía de detalle de arrecifes en diferentes yacimientos y caracterización de los mismos. Se realizó un muestreo detallado y un mapeo de los arrecifes y las áreas entre arrecifes alrededor de Ramals (Cuenca Graus-Tremp). Para el arrecife de Rasal (Cuenca Jaca) se partió de un trabajo previo (Morsilli *et al*., 2012). Esto proporcionó información sobre la geometría y la distribución de los diferentes tipos de facies arrecifales, necesaria para la reconstrucción de los diferentes medios sedimentarios, y para entender los modos de preservación de los fósiles. Estos yacimientos aportan información muy valiosa respecto a la paleoecología de los decápodos, aportando datos sobre su capacidad de adaptación a diferentes nichos, su evolución, su relación con miembros de su mismo grupo y con miembros de otros grupos.

- Recogida de material y prospecciones. Se ha realizado en afloramientos de potencial interés, en particular en zonas de plataforma equivalentes laterales a los sistemas arrecifales estudiados y en ambientes de prodelta. Para tratar de esclarecer la distribución de los diferentes grupos presentes en el área estudiada se han hecho diferentes muestreos exhaustivos, tanto en el Eoceno inferior, como en el medio y superior, teniendo en cuenta aspectos como el estado de conservación para tener en consideración los posibles procesos tafonómicos ocurridos tras la muerte (o muda) del animal.

- Campañas de excavación en yacimientos previamente conocidos. Necesario para obtener material complementario al ya publicado y poder así tener datos complementarios necesarios para realizar estudios estadísticos. Las diferentes técnicas de muestreo se explican en el apartado de estadística.

- Toma de muestras litológicas. Se han realizado laminas delgadas con el principal objetivo de poder estudiar los grupos de invertebrados (foraminíferos, briozoos, algas calcáreas, etc.) presentes en las formaciones estudiadas, y que puedan ser de ayuda para interpretar las condiciones paleoambientales, tafonómicas y precisar dataciones cuando estas sean necesarias.

5.1.2. Trabajo de laboratorio

- Estudio de láminas delgadas. Se han estudiado láminas delgadas de 4x2 cm para caracterizar las distintas facies sedimentarias (análisis de facies) a escala microscópica, y para identificar su contenido micropaleontológico. Estas láminas han sido preparadas por el Servicio de Preparación de Rocas y Materiales Duros de la Universidad de Zaragoza. Para ello, se ha utilizado una pulidora de mesa de giro excéntrico y de acción automática. La superficie de pulido ha sido preparada mediante una impregnación de carburo de silicio en polvo de grano 600 y agua.

- Limpieza y preparación de fósiles. Para poder estudiar adecuadamente el material a nivel sistemático, tafonómico y paleoecológico, ha sido necesaria la aplicación de diferentes técnicas mecánicas y químicas (explicadas en detalle en el apartado 5.2).

- Preparación de levigados. Incluye el lavado y tamizado de sedimento recogido en campo para recuperar ejemplares o fragmentos pequeños que puedan pasarse por alto en el campo, para aumentar la fiabilidad de los estudios estadísticos.

- Utilización de técnicas de visualización avanzadas. Mediante técnicas CT-scan se pueden visualizar rasgos morfológicos no visibles a simple vista o cuya preservación es tan delicada que es imposible su extracción por métodos mecánicos o químicos. Para ello se ha empleado el MicroCT, de Centro Nacional de Investigación sobre la Evolución Humana (CENIEH), modelo V|Tome|X s 240 de GE Sensing & Inspections

Technologies Phoenix X-Ray, así como softwares correspondientes de reconstrucción y análisis de imagen. En concreto el programa SPIERS que es de acceso libre.

5.1.3. Trabajo de gabinete

- Revisión bibliográfica. Para apoyar y completar la información obtenida, se ha realizado una revisión bibliográfica de trabajos realizados previamente en la zona de estudio (de estratigrafía, sedimentología, geología estructural y cronoestratigrafía). Además, se ha hecho una revisión de mapas y ortofotos, tanto del Instituto Geográfico Nacional (Serie PNOA) como de otras fuentes disponibles online como Sig-PAC (del MAGRAMA), Google Earth y la cartografía del plan nacional del IGME a escala 1:50000. La finalidad de esto ha sido seleccionar yacimientos de interés y estudiar sus accesos para realizar muestreos y prospecciones.

- Elaboración de mapas. Para ilustrar las publicaciones y situar los yacimientos, y para trazar rutas para su prospección. Para su elaboración, se ha utilizado software de edición fotográfica (Adobe Photoshop 2020) y dibujo vectorial (Adobe Illustrator 2020 e Inkscape). Para la construcción de mapas también se utilizó el programa QGIS 2.18.

- Estudio sistemático del material una vez preparado. Necesario para su encuadre en el conjunto y justificar su posición sistemática.

- Estudio de colecciones históricas. Se han visitado y revisado diferentes colecciones y museos con material de decápodos del Eoceno español, como el Museo paleontológico de Lamata (Huesca), Museo Paleontológico de Elche (Alicante), Museo Geológico del Seminario de Barcelona, y el Museo Geominero (Madrid). También se han revisado colecciones de fauna extranjera de la misma edad depositadas en el *Museo di Archeologia e Scienze Naturali "G. Zannato"* (Montecchio Maggiore, Italia) y el Museo cívico de Historia Natural de Verona (Italia).

- Realización de una base de datos bibliográfica del Eoceno a nivel mundial. Se ha hecho especial énfasis en el paleoambiente donde se han encontrado, aumentando considerablemente el conjunto de datos disponibles para la Península Ibérica en este período. Esto permite un análisis a nivel mundial para comprender la relación entre condiciones paleoambientales y crustáceos.

- Estudios morfológicos detallados y filogenéticos. Para codificar morfológicamente diferentes taxones y así incluir estos datos en filogenias. Para la obtención de estos datos, se han diseccionado y desarticulado numerosos especímenes actuales obtenidos por diferentes métodos (Fig. 14). En total se han codificado 46 especies diferentes (37 taxones actuales y 9 fósiles) a partir de aproximadamente 80 especímenes incluidos en 13 familias de braquiuros). Concretamente se han codificado 113 caracteres morfológicos adultos para cada taxón con el objetivo de obtener una filogenia lo más sólida posible. Estos datos se han codificado usando el programa Mesquite 3.70 (Fig. 14H). Los caracteres indeterminados y no conservados se marcaron como "?", y los caracteres inaplicables se marcaron como "–". Los estados de múltiples caracteres se marcaron como polimorfismos (valores de 0 a 3). El conjunto de datos final se analizó bajo Inferencia Bayesiana (BI), tal como se implementó en MrBayes v. 3.2.6. El conjunto de datos se analizó según el modelo Mk tradicional con una corrección de sesgo de determinación para tener en cuenta la puntuación de caracteres morfológicos variables únicamente. Cada análisis se realizó en dos tandas independientes de 3×10^7 generaciones cada una.

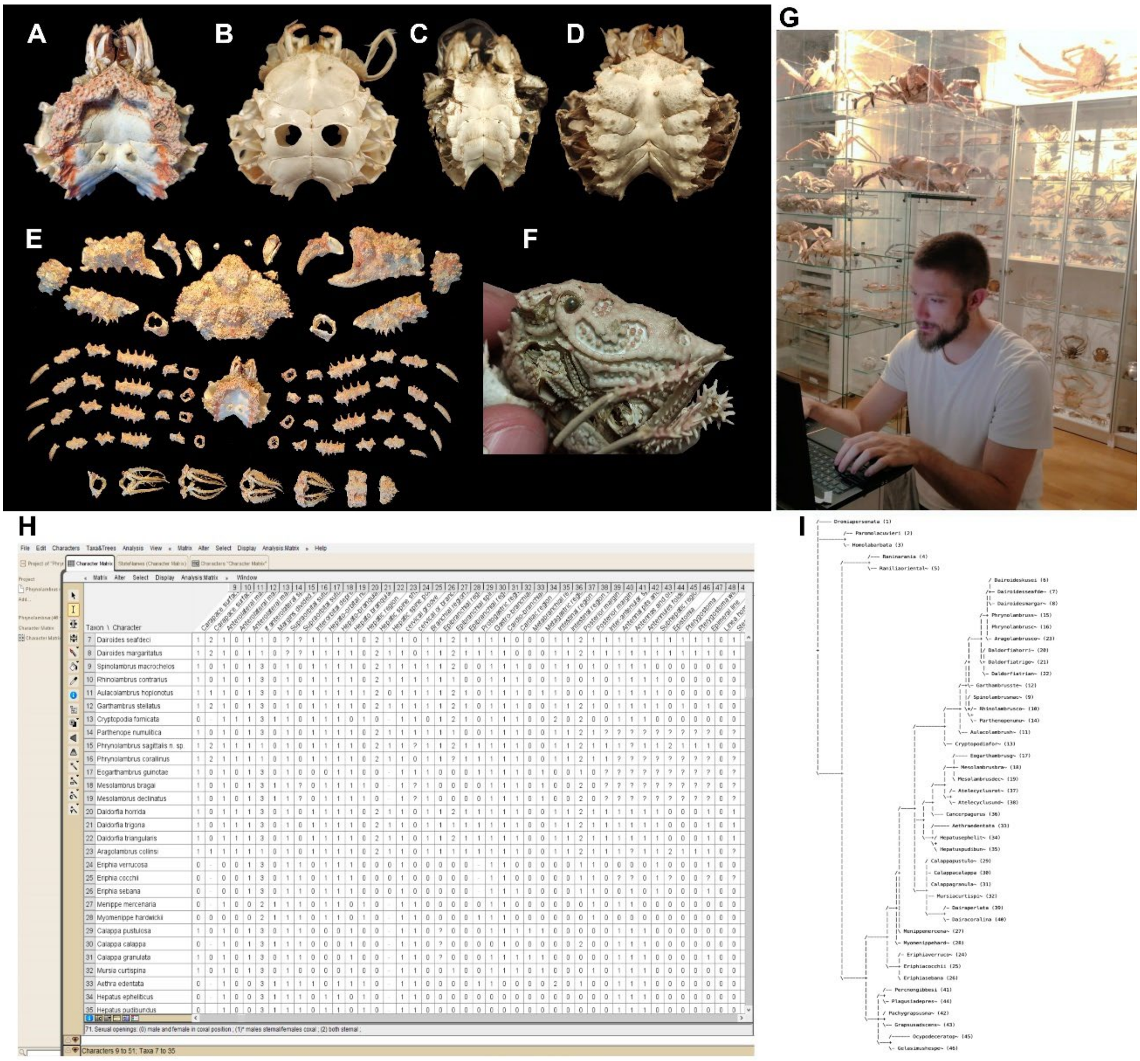

Figura 14: **A-F**: Ejemplos de diferentes taxones modernos desarticulados para la observación y codificación de caracteres; **G-H**: transcripción de los caracteres a una base de datos en Mesquite para su posterior análisis; **I**: resultado preliminar de las afinidades de los diferentes taxones analizados.

Figure 14: **A-F**: Examples of different modern taxa disjointed for observation and character coding; **G-H**: transcription of the characters to a database in Mesquite for later analysis; **I**: preliminary result of the affinities of the different taxa analyzed.

5.2. Preparación del material

El material recogido y posteriormente estudiado ha sido preparado en el laboratorio por diferentes técnicas mecánicas y químicas, o de forma mixta y se han consolidado con resina acrílica sólida (metilacrilato-etilmetacrilato o Paraloid B-72) disuelta en acetona.

La solución de Paraloid B-72 se ha empleado con una concentración entre el 2% al 15% de Paraloid en disolvente (2/15 de Paraloid B-72 respecto al 98/85 de disolvente). La aplicación de la solución se ha hecho con pincel de cerda suave, aplicando sobre la zona de interés y dejando que el producto sea absorbido por capilaridad a través de la porosidad natural, consolidando el fósil de manera uniforme. Los mejores resultados se obtienen tras sumergir el fósil en la solución, pero no en todas las ocasiones es viable, pues algunas matrices se disgregan al humedecerse (ya sea con agua o con el disolvente).

En algunos casos se ha considerado conveniente aplicar una solución más concentrada para consolidar el fósil durante el proceso de preparación tanto mecánica (para evitar roturas por la vibración) como química (para evitar abrasión química). Para eliminar posteriormente el exceso de resina, se ha pasado repetidas veces un pincel de cerda suave impregnado en acetona. Este proceso además es útil para evitar o reducir la formación de una película brillante y el ocultado de detalles como la porosidad.

Este producto, además de endurecer el fósil tiene ciertas propiedades interesantes para la conservación de estos fósiles: por un lado, evita la transformación del carbonato de calcio a sulfato de calcio, ya que aísla el fósil del anhídrido sulfuroso presente en el aire (ayudando a preservarlo); por el otro lado, reduce la absorción de agua, lo que es especialmente interesante en matrices higroscópicas.

Una vez consolidados los restos, se ha procedido a su preparación. Por un lado, algunos especímenes se han preparado mediante técnicas mecánicas de mayor o menor precisión (punzón, estilete y percutores de diferente potencia, cadencia y calibre). Por otro lado, para la preparación de determinados restos cuyas características así lo requerían, ha sido preciso la utilización de productos químicos con el objetivo de no dañar las delicadas estructuras que algunos taxones presentan, y que hubieran sido imposibles de extraer por métodos mecánicos. A continuación, se explican brevemente las dos principales metodologías empleadas:

5.2.1. Técnicas mecánicas

En cuanto al procesado del material, lo más usual es el rebajado de matriz mediante elementos mecánicos (generalmente neumáticos). Para las matrices más duras, o en los bloques de mayor tamaño, se ha empleado el percutor ME-9100 de la marca Paleotools con diferentes cabezales y aguja de carburo de tungsteno (calibre 3mm). Esta herramienta opera alrededor de 15.000 ciclos por minuto (CPM) a una presión de entre 6.9-8.2 bares. Adicionalmente, para trabajos de desbaste menos exigentes y aproximación al fósil se ha utilizado un percutor intermedio más versátil (modelo LAR-1209) de la marca Larwind (calibre 078" o 2mm), con una cadencia aproximada de 30.000 CPM a la misma presión que el anterior.

Para los trabajos más delicados, se ha usado la herramienta de micropercusión Micro Jack 2 de la marca Paleotools, mucho más fina que las anteriores. Esta herramienta opera alrededor de 55.000 CPM a una presión de 8 bares, con una afilada aguja de carburo de tungsteno (calibre 1,6mm (1/16" o 0.063")). Para el uso de esta herramienta se ha requerido el uso alternativo de dos lupas binoculares de hasta 40 aumentos progresivos de las marcas Optika Microscopes y Olympus. Además de las herramientas neumáticas (explicadas más abajo), en algunos casos ha sido necesario el uso de punzón y estilete para retirar pequeños encostramientos sin dañar la cutícula del fósil (Fig. 15).

5.2.2. Técnicas químicas

En algunos especímenes, debido a su naturaleza, la preparación mecánica no ha sido posible, o se ha tenido que combinar con procesos químicos para retirar adecuadamente la matriz. Para ello, se ha empleado hidróxido de potasio (KOH) en escamas. Esta técnica está especialmente indicada para fósiles calcáreos (como equinodermos y crustáceos). Sin embargo, este método debe ser tratado con cuidado y no todas las piezas han sido aptas para su aplicación.

Para su aplicación, se ha humedecido con agua la superficie de los fósiles a tratar y se han colocado sobre este las escamas de KOH. El tiempo que debe estar el fósil en este tratamiento es muy variable y oscila entre unos pocos minutos a varias horas, dependiendo de su naturaleza y cantidad de matriz a eliminar. Básicamente, el carbonato de la matriz reacciona con el hidróxido y genera portlandita ($Ca(OH)_2$) y carbonato de potasio (K_2CO_3) por la siguiente reacción:

$$CaCO_3 + 2KOH \rightarrow Ca(OH)_2 + K_2CO_3$$

Esta reacción afecta en especial el carbonato menos cristalizado, por lo que es especialmente indicado en matrices margosas y no es muy útil en caliza. Además, no es conveniente prolongar el tratamiento, pues también deteriora el fósil a medio y largo plazo.

Después del tratamiento, se ha eliminado el remanente de este producto para detener la reacción. Para neutralizar el hidróxido se han realizado repetidos y breves baños de ácido acético diluido en agua (aprox. al 3%), y finalmente inmersiones prolongadas en agua con cambios periódicos para eliminar los residuos. En el caso de que el fósil presentase partes expuestas delicadas previamente a la aplicación del hidróxido se ha procedido a la aplicación de Paraloid B-72 de forma localizada. Una vez seco y finalizado el tratamiento base-ácido, se ha eliminado el consolidante “sucio” con acetona, para luego volver a aplicar la solución de Paraloid limpio en una concentración menor por toda la superficie.

En algunos casos, para obtener un acabado uniforme de la matriz, se han aplicado baños sucesivos de ácido clorhídrico (HCl) diluido. Previamente a esto, el fósil se ha consolidado con una solución de paraloid B-72 concentrada (al menos al 20%) y en ningún caso el ácido se ha aplicado directamente sobre el fósil. Posteriormente se han aplicado generosos enjuagues y baños con agua para eliminar el ácido.

5.3. Métodos estadísticos

Para llevar a cabo los estudios estadísticos ha sido necesario realizar muestreos controlados en diferentes afloramientos. Para ello, se han seguido dos técnicas de muestreo intensivo: la primera, muestreando el afloramiento en superficie; la segunda, rompiendo bloques de roca. En ambas técnicas se ha dedicado un periodo de tiempo similar en las diferentes facies (cómo se señala en Klompmaker *et al*., 2013b), visitando los afloramientos de forma regular durante los años 2018 y 2021, con diferentes ángulos de luz (diferentes franjas horarias). La técnica de fragmentación de la matriz en el primer caso de estudio se descartó, porque resultó muy poco productiva ya que la matriz no se fragmenta adecuadamente para ver los fósiles (es necesario un periodo de meteorización). Por ese motivo se optó por un muestreo de superficie exhaustivo.

Los especímenes se contaron usando los siguientes criterios: (1) los caparazones asignables a un taxón específico (desde aprox. >30% conservado en los estudios llevados a cabo en áreas reducidas, y cualquier fragmento de caparazón asignable a un taxon en áreas extensas) se contaron como especímenes, ya sea a nivel de especie o en nomenclatura abierta; (2) las quelas se tomaron en cuenta solo para los taxones que conservan esta parte de la anatomía (p. ej., Axiidea y Paguridea). En el caso de Axiidea, solo se contaron las quelas izquierdas para evitar el sobredimensionar el conteo. En el caso de Paguroidea, solo se encontraron quelas izquierda o derecha para cada morfotipo, por lo que se contaron todos los especímenes. La revisión posterior de la colección del Museo de Geología del Seminario de Barcelona aportó ambas quelas de algunos taxones homoquelos (ambas quelas iguales o muy similares), y no varió el resultado final; (4) las quelas aisladas de braquiura (cangrejos verdaderos) no se incluyeron porque no se pudieron asignar con certeza a taxones específicos; (5) no se contaron los fragmentos o apéndices restantes por el mismo motivo que el caso anterior.

Para explorar la diversidad de la distribución de especies de crustáceos decápodos en cada dominio sedimentario, se realizaron pruebas de chi-cuadrado y análisis de componentes principales (PCA) utilizando el programa estadístico Past 4.03 (Hammer *et al.*, 2001). Se utilizaron grupos de decápodos como variables de cada ambiente. Al realizar PCA se redujo la dimensionalidad de estas variables para determinar cuáles eran las más características de cada ambiente. Para realizar estos cálculos no se han tenido en cuenta fósiles no asignables a ningún grupo (129 ejemplares correspondientes a quelas indeterminadas y fragmentos aislados). Los datos restantes se estandarizaron y representaron gráficamente en gráficos de PC1 frente a PC2 y PC1 frente a PC3. La información obtenida con este método se contrastó con los hábitos de taxones conocidos para deducir su origen más probable y así determinar si corresponden a restos transportados desde facies adyacentes (parautóctonos) o si son característicos de cada facies (autóctonos). La densidad de cada grupo de crustáceos decápodos se calculó dividiendo el número de ejemplares colectados por la superficie de la zona respectiva. Las áreas superficiales se calcularon con *Iberpix*.

Para investigar las diferencias en la diversidad entre las zonas dentro del afloramiento, se calcularon múltiples medidas de diversidad y se combinaron todas las muestras por sitio para crear un tamaño de muestra adecuado para las comparaciones entre sitios. Todos los especímenes identificados a nivel de especie se incluyeron en los análisis. Además, se incluyeron en el análisis todos los taxones que se identificaron como especies diferentes pero que quedaron en nomenclatura abierta (los fragmentos indeterminados no se usaron para el análisis). La diversidad por sitio se calculó utilizando la metodología descrita en Klompmaker *et al.* (2013b) con pequeñas variaciones en algún caso:

1. Riqueza taxonómica: el número de taxones encontrados en cada zona.
2. Se calcularon curvas de rarefacción individuales con intervalos de confianza del 95 % para cada una de las muestras usando PAST 4.03.
3. Índice de Shannon-Wiener o Índice de Shannon o Índice de Shannon-Weaver $H=-\Sigma pi(\ln(pi))$, donde pi es la proporción de la i-ésima especie, teniendo en cuenta además el número de especímenes por especie.
4. Índice de Margalev $d=(S-1)/\ln(N)$, donde S es el número de especies y N es el número de especímenes encontrados en el sitio para explicar el hecho de que más especímenes producen más especies en general.
5. Índice de diversidad de $Simpson=1-(\Sigma n(n-1))/(N(N-1))$, donde n es el número de especímenes de una especie y N nuevamente es el número total de especímenes encontrados en el sitio. Esta medida da cuenta no solo del número de especímenes involucrados, sino también del número de especímenes por especie.
6. El Índice de $Sorensen=SI=2c/a+b$, donde a es el número de especies de la zona 1, b es el número de especies de la zona 2 y c es el número de especies que comparten dos zonas. Esta medida se ha utilizado para determinar el grado de similitud entre zonas.
7. El Índice Chao1 (Chao, 1984) estimador del número absoluto de especies en un conjunto: $SChao1=Sobs+(F12/2F2)$, donde Sobs es el número de especies en la muestra, F1 es el número observado de especies representado por un espécimen, y F2 es el número observado de especies representadas por dos especímenes. Esta medida calcula el número teórico de especies si se hubieran recolectado un número infinito de ejemplares.
8. También se calculó el índice de uniformidad de Pielou: $E=H/\ln(S)$, donde E es el índice de uniformidad y H es el índice de Shannon (ver arriba).

Para probar si había una relación entre la distribución de las especies para cada facies, se realizó una prueba exacta de Fisher no paramétrica (debido a que el número de algunas especies es inferior a cinco), utilizando solo los grupos con mayor representación (ver detalles en Ferratges *et al*., 2020a). El análisis estadístico se computó con R (“RVAideMemoire” y la función “fisher.test”). Para analizar qué distribución de las especies está significativamente vinculada a una facies específica, se aplicó el comando "fisher.multcom" del mismo paquete R para aplicar una comparación por pares de la prueba exacta de Fisher.

5.4. Fotografía

Una vez preparados los especímenes estudiados se han cubierto con una capa de cloruro de amonio (NH_4Cl) sublimado (Fig. 15) mediante una pipeta de vidrio y una perilla de goma con el objetivo rociar uniformemente el fósil y así homogenizar la superficie. Para la sublimación del NH_4Cl se ha empleado un mechero Bunsen. La cámara empleada ha sido una Nikon D7100 con un objetivo macro de 60 mm.

El microfotografiado de las láminas delgadas de muestras de roca se ha hecho mediante luz transmitida en la lupa binocular Olimpus SZ7, del área de Estratigrafía del Departamento de Ciencias de la Tierra de la Universidad de Zaragoza.

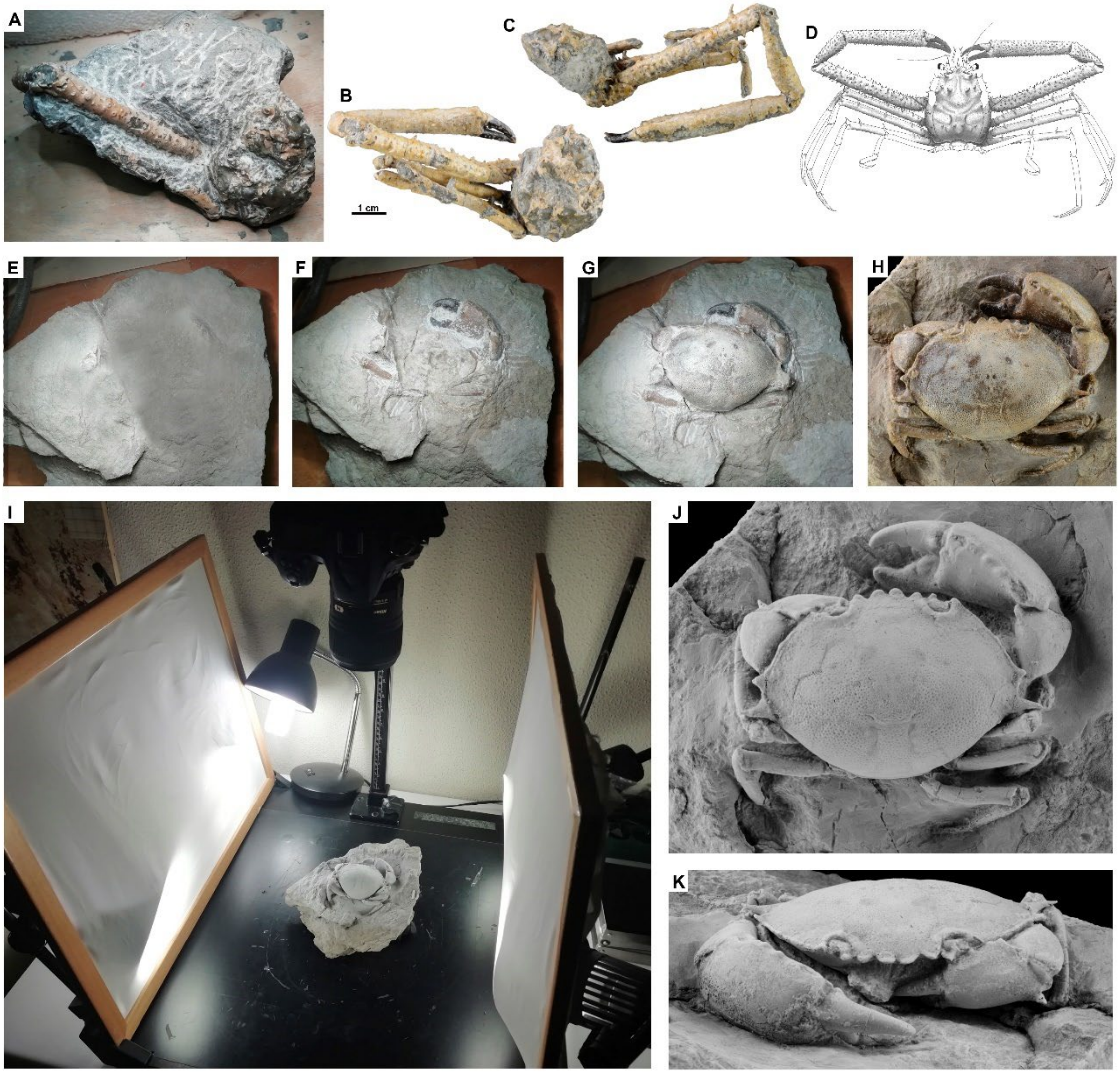

Figura 15: **A-C**: Proceso de preparación de *Paromola bretoni*, del Eoceno inferior (Ypresiense) de la cuenca de Tremp-Graus. **D**: Reconstrucción del espécimen a partir del holotipo. **E-H**: Proceso de preparación de *Harpactoxanthopsis quadrilobata* del Eoceno medio (Luteciense) de la cuenca de Ainsa. **I**: Fotografiado del ejemplar en el laboratorio fotográfico una vez se ha blanqueado con cloruro de amonio; **J-K**: Resultado.

Figure 15: **A-C**: Preparation process of *Paromola bretoni*, from the early Eocene (Ypresian) of the Tremp-Graus basin. **D**: Reconstruction of the specimen from the holotype. **E-H**: *Harpactoxanthopsis quadrilobata* preparation process from the middle Eocene (Lutecian) of the Ainsa basin. **I**: Photographed of the specimen in the photographic laboratory once it has been bleached with ammonium chloride; **J-K**: Result.

5.5. Micro-CT scan y modelos 3D

Debido a la importancia y fragilidad de ciertos especímenes, algunos fueron seleccionados para escanear en el Laboratorio de Microtomografía Computarizada del

Centro Nacional de Investigación sobre la Evolución Humana (CENIEH, Burgos, España, Micro-CT scan modelo V|Tome|X s 240 de GE Sensing & Inspections Technologies Phoenix X-Ray). Gracias al elevado contraste entre matriz y fósil, se han podido realizar modelos 3D del material estudiado de alta resolución (Fig. 16) empleando el software de reconstrucción y análisis de imagen SPIERS v3.1.0.

Durante esta tesis se han escaneado un total de 5 ejemplares, pero sólo uno se ha seleccionado para un procesado completo, quedando a la espera el resto para futuros trabajos de detalle. La matriz del ejemplar seleccionado fue cortada y alisada con un disco rotativo de diamante con el objetivo de reducir al máximo el grosor de roca circundante. Con ello se pretendió reducir las posibles interferencias ocasionadas por las irregularidades de la superficie de la muestra y mejorar el contraste del fósil. El espécimen en cuestión se escaneó juntamente con el molde, ya que tanto parte como contraparte preservaban elementos anatómicos.

Esta técnica, mediante el uso de Micro CT produce imágenes en 2D a partir de las diferentes densidades. Concretamente, el fósil (cortado en forma de cuadrado de 26 mm de lado) fue segmentado en 1680 secciones. Una vez obtenido el conjunto de datos de Micro-CT, se aplicó un umbral lineal invertido al conjunto de datos con el fin de visualizar y procesar los datos con el software SPIERS EDIT (Fig. 16D). Con esto, los píxeles que podían identificarse como partes del cangrejo se asignaron manualmente a un elemento anatómico determinado, pintando polígonos de diferentes colores (Fig. 16E). Luego, este conjunto de datos se exportó al software SPIERS VIEW, que es capaz de procesar y reconstruir los datos en 2D para formar un volumen en 3D. Con este programa se renderizaron isosuperficies para dar un modelo tridimensional interactivo del fósil, el cual podemos rotar, colocar en cualquier posición y aislar diferentes elementos (Fig. 16F-G).

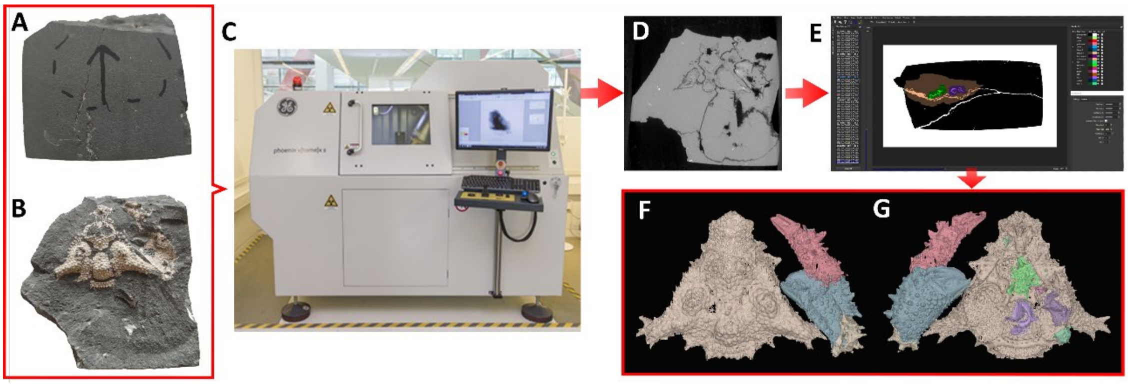

Figura 16: **A**-**B**: Espécimen sin preparar de *Phrynolambrus* sp. para escanear; **C**: Micro-CT scan modelo V|Tome|X s 240 de GE Sensing & Inspections Technologies Phoenix X-Ray (CENIEH, Burgos); **D**: resultado de una de las cerca de 2000 secciones realizadas; **E**: procesamiento de las secciones con el programa SPIERS-edit v3.1.0; **F**-**G**: reconstrucción del ejemplar a partir de las secciones realizadas en vista dorsal (F) y ventral (G), con los diferentes elementos anatómicos individualizados.

Figure 16: **A**-**B**: Specimen of *Phrynolambrus* sp. to be scanned; **C**: Micro-CT scan model V|Tome|X s 240 from GE Sensing & Inspections Technologies Phoenix X-Ray (CENIEH, Burgos); **D**: result of one of the nearly 2000 sections performed; **E**: section processing with the SPIERS-edit v3.1.0 program; **F**-**G**: reconstruction of the specimen from the sections made in dorsal (F) and ventral (G) views, with the different individualized anatomical elements.

6. RESULTADOS: PRESENTACIÓN DE LOS ARTICULOS CIENTÍFICOS

Este capítulo está compuesto por los diez artículos publicados en relación con el tema de la Tesis Doctoral, más uno actualmente en revisión y otro en preparación. Estos 12 artículos componen el cuerpo principal de la tesis. Para facilitar la comprensión del contenido, se ha dividido el capítulo en dos apartados principales.

En primer lugar, se muestran los resultados relacionados con la Paleontología sistemática de los nuevos taxones descritos (ocho artículos publicados y uno en revisión). En segundo lugar, se muestran los artículos relacionados con el estudio de la distribución y diversidad de decápodos en diferentes facies y paleoambientes (dos artículos publicados y uno en preparación). Los subcapítulos correspondientes se introducen con un breve texto. En los capítulos posteriores 7 y 8 se recuperarán los datos más relevantes contenidos en los artículos, y se expondrán en su caso otros datos y resultados obtenidos (que no han sido objeto de publicación), con objeto de enmarcar los resultados, interpretaciones y discusiones expuestas en esta Tesis Doctoral.

Dado que las publicaciones llevan una numeración independiente no correlativa a la del resto de la Tesis (correspondiente a la de las diferentes revistas donde se han publicado los estudios), la numeración de esta última se interrumpe antes y se retoma después de cada publicación.

6.1. Paleontología sistemática de los crustáceos decápodos del Eoceno

Para una correcta comprensión de la distribución, origen e implicaciones paleoecológicas y evolutivas de cada taxon es necesario un conocimiento sistemático detallado de cada uno de ellos. Por ello todos los taxones del área de estudio han sido clasificados sistemáticamente con el mayor detalle posible. Algunos de estos taxones han sido tratados en más detalle y publicados en revistas científicas, bien por su importancia para entender el origen de algunos grupos actuales o bien porque interesaba darles un tratamiento sistemático más adecuado. Obviamente, este ingente trabajo no ha terminado y abordarlo en su totalidad requeriría de varias décadas más.

Este subcapítulo se centra en el análisis y descripción de los nuevos taxones encontrados en las áreas de estudio durante el desarrollo de la Tesis Doctoral que han sido objeto de publicación. Para ello, se ha considerado necesario dividirlo a su vez en dos apartados menores: por un lado, el estudio y descripción de los nuevos cangrejos ermitaños (Anomura Macleay, 1838) y por el otro, el de los cangrejos verdaderos (Brachyura Latreille, 1802). Ambos grupos (los infraórdenes Anomura y Brachyura) están estrechamente emparentados y se consideran grupos hermanos dentro de los crustáceos decápodos, constituyendo el clado o subsección Meiura (Wang *et al*., 2021; Wolfe *et al*., 2021). Este conjunto contiene los grupos más derivados y representativos dentro del orden Decapoda. Al final de cada uno de estos subapartados se encuentran los diferentes artículos publicados.

Las diferencias generales más visibles entre braquiuros y anomuros son: la posición del plano de debilidad de la muda; la longitud de las antenas (más largas en los anomuros); y la posición de las antenas y anténulas con respecto a los ojos (un par al lado de los ojos en anomuros, ambos pares de antenas entre los ojos en braquiuros). Los anomuros tienen varios representantes totalmente carcinizados, con una apariencia externa muy parecida a los cangrejos verdaderos. Sin embargo, la totalidad de anomuros tratados a lo largo de esta tesis corresponden a cangrejos ermitaños. La mayor parte de este grupo tiene una morfología muy especializada y además de las diferencias que se acaban de explicar presentan un conjunto de características más obvias: plano corporal alargado (Fig. 17A); un escudo cefálico más mineralizado que la parte posterior del caparazón (Fig. 17B); pleon asimétrico, muy pobremente mineralizado y modificado para ocupar conchas de moluscos (Walker, 1992), u otras cavidades como esponjas, corales o restos de plantas (p. ej., de Forges *et al*., 2001; Lemaitre, 1989, 1990).

6.1.1. ANOMURA

Los pagúridos (Anomura) forman un grupo relativamente diverso de crustáceos decápodos con una morfología muy particular (Fig. 17) y un registro fósil fragmentario pero ampliamente distribuido (ver referencias en Ferratges *et al*., 2022a), que se remonta al Triásico superior (Chablais *et al*., 2012). En este grupo destacan por su abundancia y diversidad los cangrejos ermitaños (Superfamilia Paguroidea Latreille, 1802), empezando a ser relevantes desde el Jurásico (ver Fraaije *et al*., 2022) (ver Fig. 4).

El registro fragmentario de este grupo se debe en parte a su morfología altamente especializada (Fig. 17A y B) con pleones pobremente mineralizados adaptados a la vida dentro de conchas vacías u otras cavidades (p. ej., Lemaitre, 1989, 1990; Walker, 1992; de Forges *et al*., 2001). Después de la muerte, la desarticulación ocurre rápidamente por lo que el registro fósil de este grupo está representado principalmente por propodios y quelas aisladas (ver detalles en Ferratges *et al*., 2020b), que son las partes más duras y resistentes (ver Klompmaker *et al*., 2017). Estos elementos suelen presentar una morfología característica, siendo estas robustas, con sección generalmente triangular, con zonas aplanadas/deprimidas en la parte superior para encajar con el quelípedo opuesto en posición defensiva y dedos cortos de sección más o menos triangular a ovalada y un margen oclusal bien definido en el lado externo (Fig. 17C).

Los afloramientos del Eoceno en Europa han proporcionado cierta diversidad de cangrejos ermitaños, especialmente en el Eoceno medio y superior, concentrados en ambientes de prodelta y arrecifales de Italia y Hungría. Por el contrario, el material de la Península Ibérica es más escaso y previamente a esta Tesis Doctoral únicamente se conocían tres especies para el Eoceno (*Eocalcinus eocenicus* Via, 1959; *Pagurus marceti* Via, 1959; *Pagurus marini* Via, 1959). Por otro lado, el material del Eoceno temprano es en general más raro y solo se concentra en unas pocas localidades (ver Ferratges *et al*., 2022a y referencias). El conjunto de contribuciones realizado durante este estudio incluye representantes de cuatro familias (Annuntidiogenidae, Diogenidae, Calcinidae y Paguridae) que aumenta el conocimiento de los taxones conocidos con nueve especies nuevas (ver tablas 1, 2, 5). Los datos recopilados muestran una gran diversidad de paguroideos al comienzo del Eoceno, más rica que los registros del Paleoceno (ver Jakobsen *et al*., 2020 y referencias), y muestra que los arrecifes del Eoceno inferior fueron importantes puntos calientes de diversidad para los paguroideos, comparables a los ecosistemas modernos.

Algunos de los taxones estudiados muestran estrechas relaciones con varios géneros modernos (*Anisopagurus*; *Clibanarius*; *Dardanus*; *Diogenes; Paguristes*; *Pagurus*; *Petrochirus*) o corresponden a los representantes más antiguos de sus respectivos géneros (ver Ferratges *et al*., 2020b, 2022a). También se ha aumentado la distribución temporal del género *Eocalcinus* con el registro más antiguo (ver Ferratges *et al*., 2022a) y el más moderno (ver Ferratges *et al*., 2021a). Además, el material asignado a este género sugiere una tendencia evolutiva hacia formas más redondeadas. Esta tendencia podría estar relacionada con la progresiva adaptación de la quela mayor para realizar una función opercular (ver Ferratges *et al*., 2021a). La clasificación sistemática empleada en las publicaciones sigue a McLaughlin (2003), McLaughlin *et al*. (2007; 2010) y Fraaije *et al*. (2022).

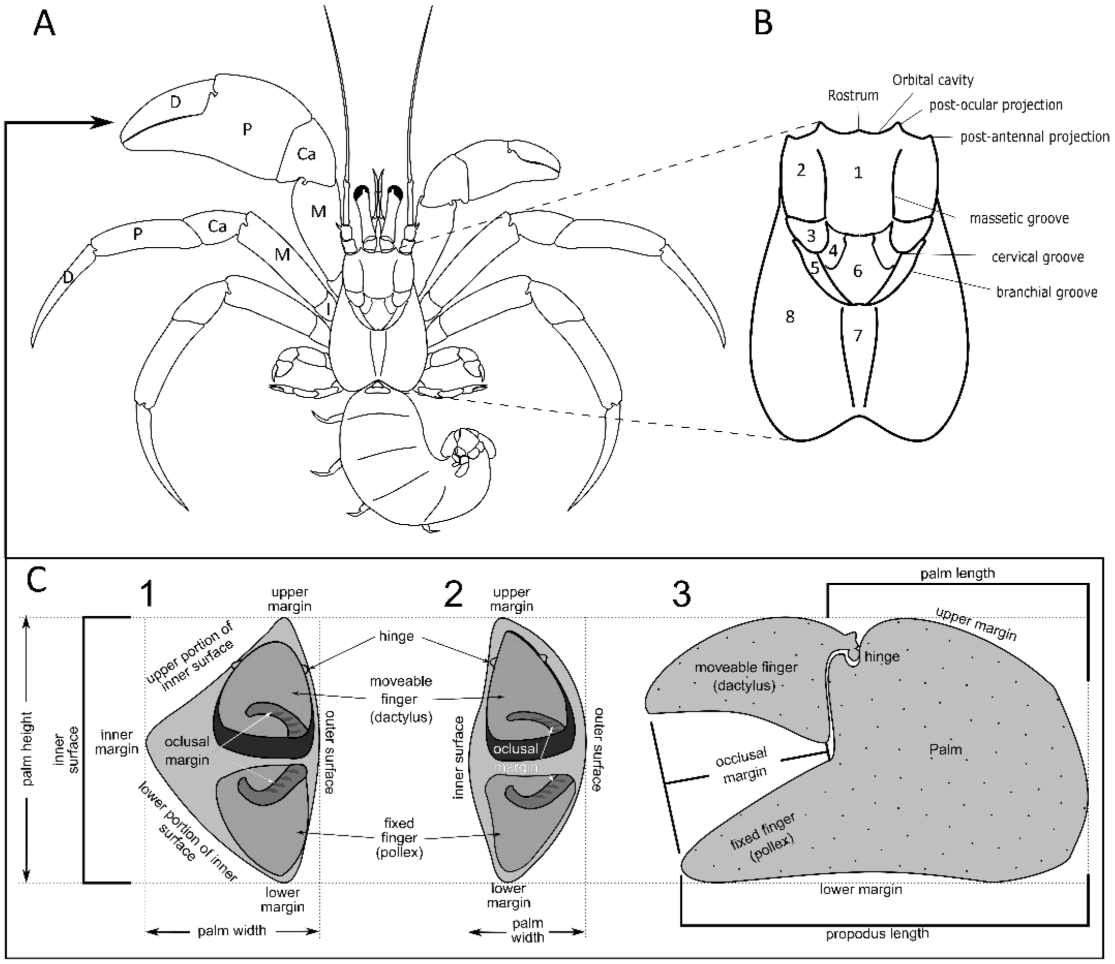

Figura 17: **A**: Esquema simplificado de un pagurido. Siglas: D: dactylus; P: propodio; Ca: carpo; M: mero; I: isquio. **B**) Cefalotórax con detalles de escudo: 1, región gástrica anterior; 2, región masética; 3, área branquial anterior; 4, región keraial; 5 branquial lateral; 5, mesobranquial; 6: region mesogástrica; 7, región cardíaca; 8, región branquial; 1-6: escudo cefálico. **C**) Esquema anatómico simplificado de morfotipos quelípedos de paguroides. (1-2) vista frontal de dos morfotipos diferentes; (3) vista lateral (C tomado de Ferratges *et al.*, 2022a).

Figure 17: **A**: Simplified scheme of a pagurid. Acronym: D: dactylus; P: propodus; Ca: carpus; M: merus; I: isquium. **B**: Cephalothorax with shield details: 1, anterior gastric region; 2, massetic region; 3, anterior branchial area; 4, keraial region; 5, lateral branchial; 5, mesobranchial; 6: mesogastric region; 7, cardiac region; 8, branchial region; **C**: Simplified anatomical scheme of cheliped morphotypes of paguroids. (1-2) frontal view of two different morphotypes; (3) lateral view (C taken from Ferratges *et al.*, 2022a).

A continuación se hace una exposición resumida de las principales aportaciones sistemáticas de esta Tesis. Al final de este apartado se incluyen una serie de tablas con todos los taxones reconocidos en esta tesis y clasificados hasta el mayor rango taxonómico posible. Los géneros indicados por una daga (†) solo se conocen a partir de representantes fósiles.

Orden Decapoda Latreille, 1802

Infraorden Anomura MacLeay, 1838

Superfamilia Paguroidea Latreille, 1802

Los cangrejos ermitaños articulados son fósiles raros; ya que en su mayoría, solo se conservan quelípedos aislados que ofrecen poca información sobre la estructura general de estos animales (ver detalles en Ferratges *et al*., 2020b). Por este motivo, el registro mundial de paguroideos del Paleógeno es pobre y a menudo fragmentario, lo que impide la descripción completa de los especímenes. Como resultado, la coincidencia entre las clasificaciones a partir de fósiles y/o de foras modernas es problemática, ya que la mayoría de las características taxonómicas para diferenciar entre géneros modernos no se conservan en el material fósil (p. ej., Jagt *et al*., 2006; Fraaije, 2014; Fraaije *et al*., 2014). Como consecuencia, la posición sistemática de los paguroideos fósiles está llena de dificultades (Fraaije y Polkowsky, 2016).

A pesar de estos inconvenientes, algunos autores (p. ej., McLaughlin, 2003; Fraaije *et al*., 2019) enumeraron importantes caracteres morfológicos útiles para distinguir entre diferentes taxones modernos que también pueden reconocerse en especies fósiles.

Familia Diogenidae Ortmann, 1892

Género *Diogenes* Dana, 1851a

Se ha descrito una nueva especie del género *Diogenes* a partir de un ejemplar excepcionalmente preservado y dos especímenes fragmentarios. El material estudiado, *Diogenes augustinus* Ferratges, Zamora y Aurell 2020, conserva delicadas características diagnósticas, como la morfología del escudo cefálico, ornamentación de los quelípedos, pedúnculos oculares y patas ambulatorias y representa uno de los pocos ejemplos en los que se dispone de toda la parte anterior del animal (Fig. 18). Esto permite su asignación a la familia Diogenidae. Los diogénidos del Eoceno incluyen nueve géneros que han sido descritos únicamente en base a quelas aisladas (Garassino *et al*. 2009a; De Angeli y Caporiondo, 2017), lo que dificulta la comparación con el material estudiado.

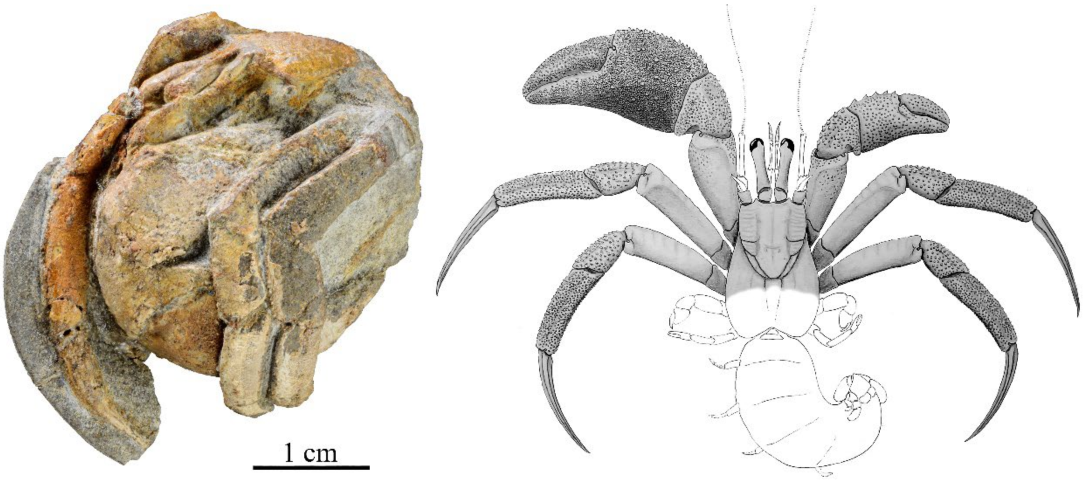

Figura 18: Holotipo de *Diogenes augustinus* Ferratges, Zamora y Aurell 2020 (MPZ2020/54), del Bartoniense superior de la Formación Arguís, Eoceno, Lúsera, Huesca, en vista lateral izquierda. Derecha: Reconstrucción de *Diógenes augustinus*; las partes que se muestran en gris son las conservadas en el material fósil. Otras partes se han reconstruido a partir de los taxones modernos más estrechamente relacionados.

Figure 18: Holotype of *Diogenes augustinus* Ferratges, Zamora & Aurell 2020 (MPZ2020/54), from the upper Bartonian of Arguís Formation, Eocene, Lúsera, Huesca, in left lateral view. Right: Reconstruction of *Diogenes augustinus*; parts shown in grey are those preserved in the fossil material available. Other parts have been reconstructed from the most closely related modern taxa.

Género *Clibanarius* Dana, 1852

También se ha descrito otra especie incluida en la familia Diogenidae, concretamente al género *Clibanarius*: *Clibanarius isabenaensis* Ferratges, Artal, van Bakel y Zamora, 2022 del Eoceno inferior (Ypresiense) de Ramals (Huesca). Esta especie presenta similitudes con otras especies fósiles asignadas al género *Paguristes*. Las especies fósiles *Paguristes cecconi* De Angeli y Caporiondo, 2017, y *Paguristes sossanensis* De Angeli y Caporiondo, 2009, muestran una clara afinidad con el género *Clibanarius* (Fig. 19). El género *Paguristes* estaba compuesto por una gran cantidad de taxones morfológicamente diferentes y, actualmente, el género se ha dividido en varios géneros menos variables (ver McLaughlin *et al*., 2010). Debido a estas afinidades, se ha considerado que las especies *P. cecconi* y *P. sossanensis* deben ser asignadas al género *Clibanarius*, aunque muestran ligeras diferencias que permiten mantenerlas como especies separadas de *Clibanarius isabenaensis*.

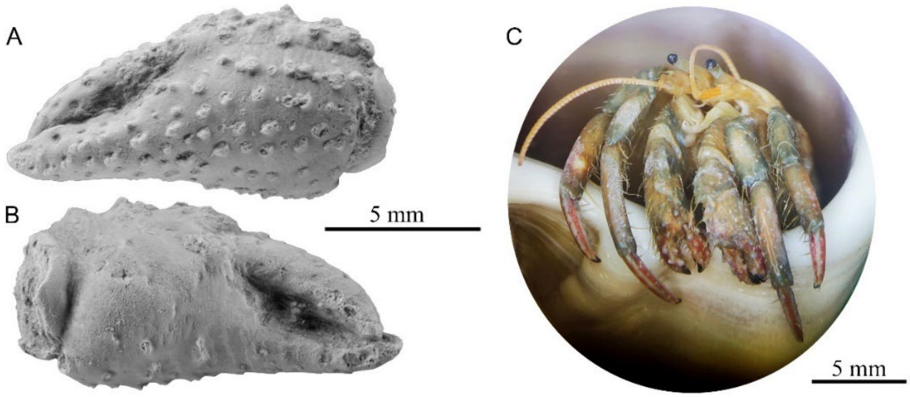

Figura 19: **A-B**: Holotipo de *Clibanarius isabenaensis* Ferratges, Artal, van Bakel y Zamora, 2022 de la Fm Serraduy (Ypresiense) en vista exterior (A) e interna. **C**: *Clibanarius erythropus* actual (Latreille, 1818), del mar Mediterráneo (Ferratges col.).

Figure 19: **A-B**: Holotype of *Clibanarius isabenaensis* Ferratges, Artal, van Bakel & Zamora, 2022 from the Serraduy Fm (Ypresian) in outer (**A**) and inner view. **C**: Modern *Clibanarius erythropus* (Latreille, 1818), from Mediterranean sea (Ferratges col.).

Género *Petrochirus* Stimpson, 1859

El género *Petrochirus* está representado en el registro fósil por numerosas quelas incompletas o mal conservadas que se han asignado tradicionalmente a este género, principalmente en base a su forma subrectangular y la ornamentación escamosa o pavimentada (ver Ferratges *et al*., 2022a y referencias). Debido al escaso e incompleto material, y la dificultad para realizar comparativas con otras especies asignadas a este género, se ha preferido mantener los dos morfotipos encontrados en el Eoceno inferior y el superior asignables a este género (Fig. 20) en nomenclatura abierta.

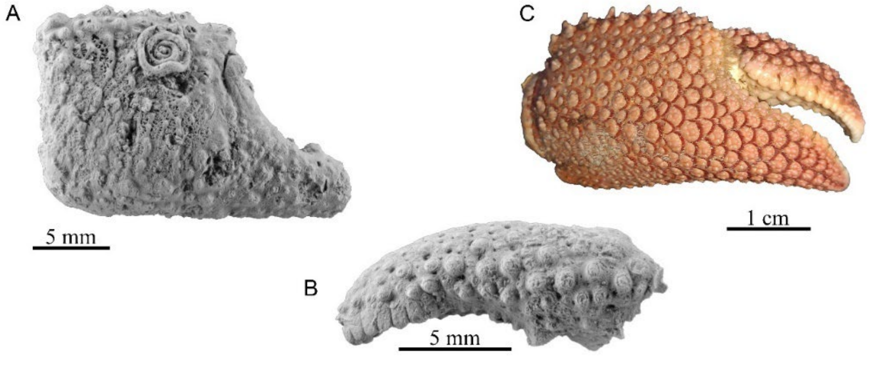

Figura 20: **A**: *Petrochirus* sp. de la Fm Serraduy (Ypresian); **B**: *Petrochirus* sp. de la Formación Arguis (Priaboniense); **C**: Quelípedo derecho de *Petrochirus diogenes* actual (Linnaeus, 1758), de México (Ferratges col.).

Figure 20: **A**: *Petrochirus* sp. from the Serraduy Fm (Ypresian); **B**: *Petrochirus* sp. from the Arguis Formation (Priabonian); **C**: Right cheliped of modern *Petrochirus diogenes* (Linnaeus, 1758), from Mexico (Ferratges col.).

Género *Parapetrochirus* † Ferratges, Artal y Zamora, 2021

Se han descrito otras dos especies nuevas incluidas en la familia Diogenidae. Sin embargo, debido a la ausencia de similitudes con otros géneros, se ha creado un nuevo género para incluir estos taxones: *Parapetrochirus robustus* Ferratges, Artal y Zamora, 2021, y *Parapetrochirus serratus* Ferratges, Artal, van Bakel y Zamora, 2022, ambos del Eoceno inferior de la zona de Isábena (Fig. 21). Su descubrimiento aumenta el conocimiento sobre la diversidad morfológica de este grupo durante el Eoceno.

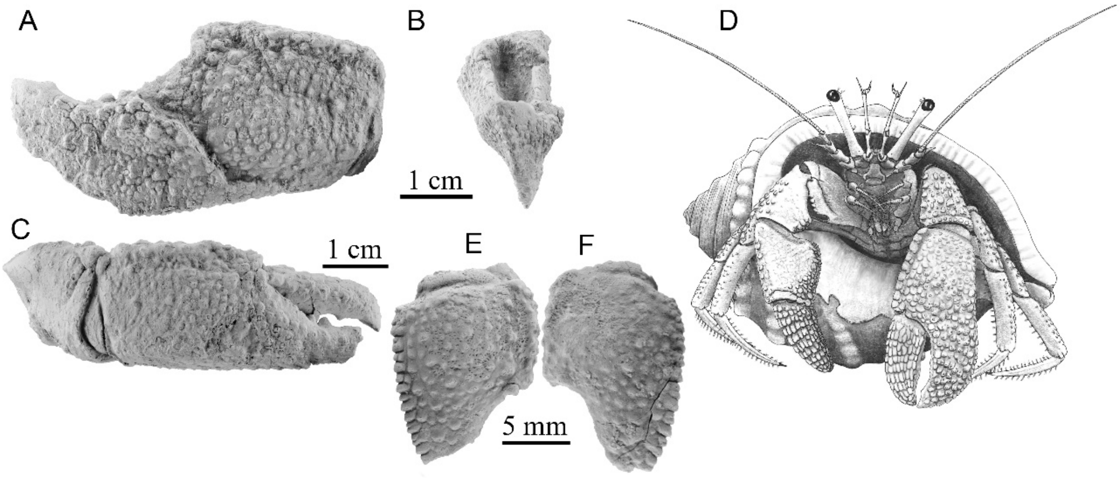

Figura 21: Holotipo de *Parapetrochirus robustus* Ferratges, Artal y Zamora, 2021 (MGSB68569) de la Formación Ypresian Roda (Bacamorta, Huesca, España). **A**: vista lateral del lado exterior de la chela izquierda; **B**: vista frontal de la chela izquierda; **C**: vista lateral del lado exterior de la chela derecha; **D**: reconstrucción idealizada de *Parapetrochirus robustus*. Las partes no conservadas en el material fósil se han inferido tentativamente de taxones modernos estrechamente relacionados. **E**-**F**: P*arapetrochirus serratus* Ferratges, Artal, van Bakel y Zamora, 2022, de la Formación Ypresian Serraduy (Huesca, España), mostrando su simetría.

Figure 21: Holotype of *Parapetrochirus robustus* Ferratges, Artal & Zamora, 2021 (MGSB68569) from the Ypresian Roda Formation (Bacamorta, Huesca, Spain). **A**: lateral view of outer side of left chela; **B**: frontal view of left chela; **C**: lateral view of outer side of right chela; **D**: Idealized reconstruction of P*arapetrochirus robustus.* The parts not preserved in the fossil material have been tentatively inferred from closely related modern taxa. **E**-**F**: *Parapetrochirus serratus* Ferratges, Artal, van Bakel & Zamora, 2022, from the Ypresian Serraduy Formation (Huesca, Spain), showing its symmetry.

Familia *Annuntidiogenidae* Fraaije, 2014

Género *Paguristes* Dana, 1852

El género *Paguristes* Dana, 1852 fue previamente considerado miembro la familia Diogenidae (*sensu lato*), posición que fue revisada por Fraaije (2014) y Fraaije *et al*. (2017). Estos autores propusieron su inclusión en una nueva familia (Annuntidiogenidae Fraaije, 2014). Se ha seguido tentativamente esta ubicación propuesta por Fraaije (2014) y Fraaije *et al*. (2017; 2022) para ubicar la nueva especie *Paguristes perlatus* Ferratges, Artal, van Bakel y Zamora, 2022 (Fig. 22).

Como se ha explicado en el caso del género *Clibanarius*, los representantes modernos del género *Paguristes* originalmente incluían una gran cantidad de taxones morfológicamente diferentes y, actualmente, el género se ha dividido en varios géneros menos variables (ver McLaughlin *et al*., 2010). Desafortunadamente, la mayoría de los criterios diagnósticos utilizados para las especies modernas no se conservan en el registro fósil. El género *Paguristes* es morfológicamente diverso en los ecosistemas modernos (Rahayu, 2006), con más de 120 especies (McLaughlin *et al*., 2010; Komai *et al*., 2015). Debido a que las características de los quelípedos estudiados son similares a las de los miembros de *Paguristes*, el nuevo material se incluye tentativamente dentro de este género. Actualmente este género se distribuye principalmente en áreas de aguas poco profundas de regiones tropicales y templadas (p. ej., Rahayu, 2006; Rahayu y Forest, 2009; Trivedi y Vachhrajani, 2017).

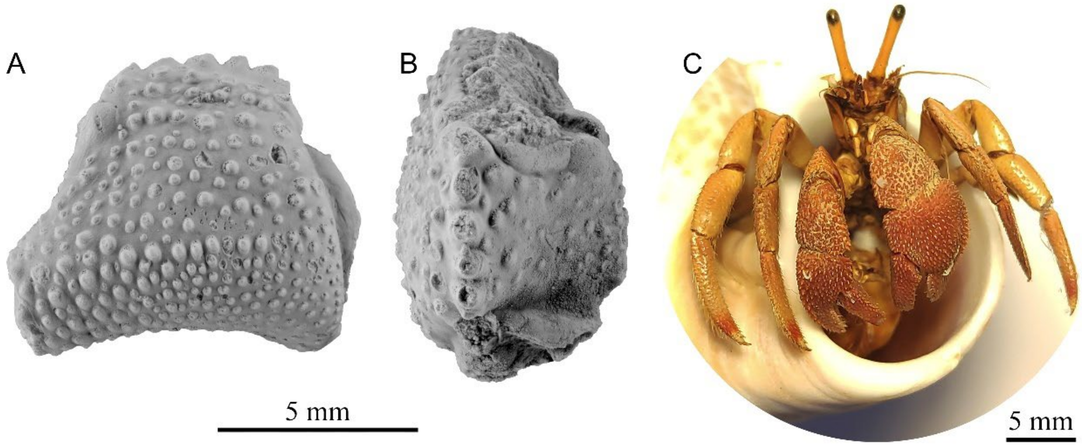

Figura 22: **A-B**: Holotipo de *Paguristes perlatus* Ferratges, Artal, van Bakel y Zamora, 2022 (MPZ 2022/38); **C**: *Paguristes eremita* (Linnaeus, 1767), del mar Mediterráneo (Ferratges col.).

Figure 22: **A-B**: Holotype of *Paguristes perlatus* Ferratges, Artal, van Bakel y Zamora, 2022 (MPZ 2022/38); **C**: *Paguristes eremita* (Linnaeus, 1767), from Mediterranean sea (Ferratges col.).

Familia Calcinidae Fraaije, Van Bakel, and Jagt, 2017

Género *Dardanus* Paul’son, 1875

El género *Dardanus* Paul’son, 1875 fue previamente considerado miembro de la familia Diogenidae (*sensu lato*) y su posición fue revisada por Fraaije *et al*. (2017). Estos autores propusieron su inclusión en Calcinidae, y esto es actualmente un tema de debate (ver Lemaitre y McLaughlin, en World Paguroidea and Lomisoidea Database, y WoRMS). Sin embargo, la filogenia de los paguroideos no está dentro de los objetivos de esta Tesis Doctoral; por consistencia se ha seguido tentativamente a Fraaije *et al*. 2017; 2022 para situar la nueva especie *Dardanus balaitus* Ferratges, Artal, van Bakel y Zamora, 2022 (Fig. 23).

La morfología general de las quelas y los caracteres distintivos de *D. balaitus* concuerdan con el género moderno *Dardanus* Paul'son, 1875 (ver detalles en Ferratges *et al*., 2022a), como por ejemplo la especie *D. arrosor* (Fig. 23), mostrando quelas robustas con crestas oblicuas y poros setales alineados.

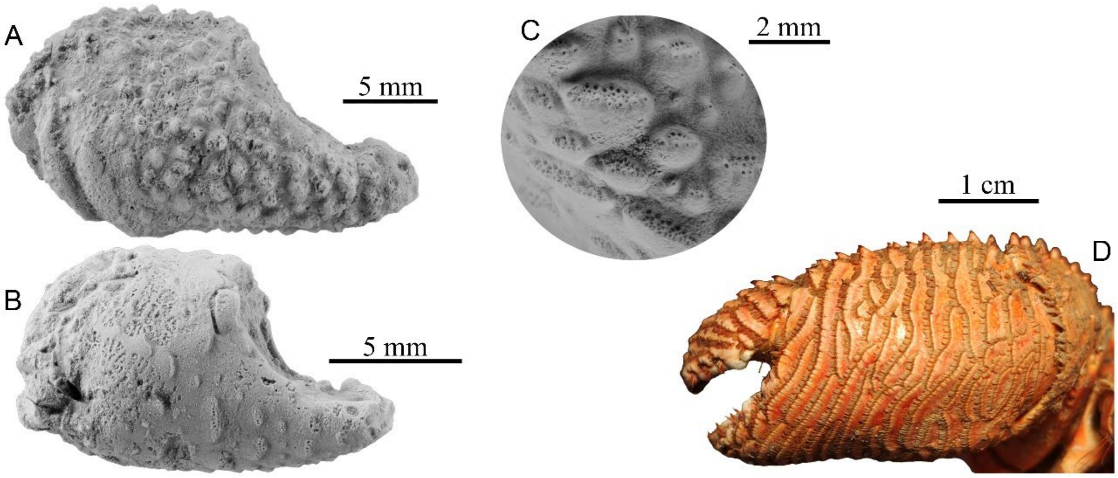

Figura 23: *Dardanus balaitus* Ferratges, Artal, van Bakel y Zamora, 2022; **A**: Holotipo MGSB77622, chela derecha; **B**: Paratipo MGSB77623, chela izquierda; **C**: Detalle de la distribución de los pozos de setal; **D**: *Dardanus arrosor* del mar Mediterráneo (Ferratges col.).

Figure 23: *Dardanus balaitus* Ferratges, Artal, van Bakel y Zamora, 2022; **A**: Holotype MGSB77622, right chela; **B**: Paratype MGSB77623, left chela; **C**: Detail of the distribution of the setal pits; **D**: *Dardanus arrosor* from Mediterranean sea (Ferratges col.).

Género *Eocalcinus* † Via, 1959

Hallazgos recientes de la especie tipo con ambas quelas permitieron la asignación de este género a la familia Calcinidae (Ossó, 2020). Los especímenes estudiados se pueden asignar a *Eocalcinus* a partir de un conjunto de características (ver detalles en Ferratges *et al*., 2021a, 2022a). A lo largo de esta Tesis Doctoral se han descrito dos especies de este género: *Eocalcinus veteris* Ferratges, Artal, van Bakel y Zamora, 2022; y *Eocalcinus gerardbretoni* Ferratges, Artal y Zamora, 2021 (Fig. 24).

Eocalcinus veteris corresponde a la especie estratigráficamente más antigua del género, y a permitido proponer una tendencia general hacia formas más redondeadas (ver Ferratges *et al*., 2022a). Esta tendencia hacia formas más redondeadas, con un margen inferior sinuoso y una sección más plano-convexa podría estar relacionada con la progresiva adaptación de la quela mayor para realizar una función opercular, adaptándose a la forma de la apertura de la concha receptora (Ferratges *et al*., 2021a) (Fig. 24E-F). Por otro lado, la especie *Eocalcinus gerardbretoni* corresponde a la especie estratigráficamente más moderna de este género, y muestra un contorno claramente semicircular (Fig. 24). La comparación con especies modernas con morfología similar como el género *Coenobita* sugiere el uso de la chela izquierda como opérculo que encajaba firmemente con la apertura de la concha ocupada (Fig. 24E).

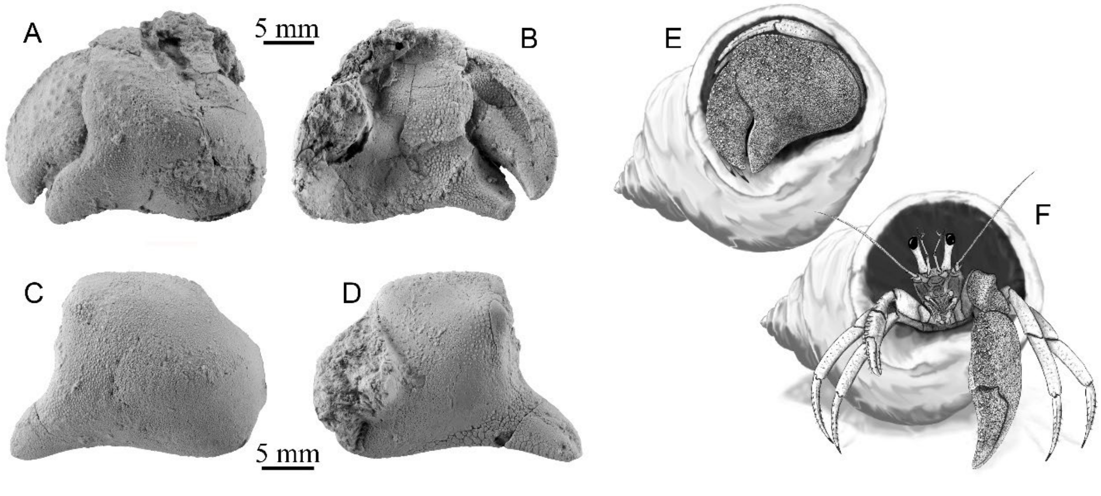

Figura 24: **A**-**B**: Holotipo de *Eocalcinus gerardbretoni* Ferratges, Artal y Zamora, 2021 (MPZ 2020/617) de los niveles priabonianos de la Formación Arguis (Yeste, Huesca, España) **A**: vista lateral del lado exterior de la chela izquierda; **B**: vista lateral del lado interno de la chela izquierda; **C**-**D**: chela izquierda de *Eocalcinus veteris* Ferratges, Artal, van Bakel y Zamora, 2022 (Paratype MPZ 2021/29), vista lateral del lado exterior (**C**) e interior (**D**). **E**-**F**: Reconstrucción idealizada de *Eocalcinus gerardbretoni* en posición defensiva y la función opercular del quelípedo izquierdo (**E**) y reconstrucción de la posición de marcha (**F**).

Figure 24: **A**-**B**: Holotype of *Eocalcinus gerardbretoni* Ferratges, Artal & Zamora, 2021 (MPZ 2020/617) from the Priabonian levels of the Arguis Formation (Yeste, Huesca, Spain) **A**: lateral view of outer side of left chela; **B**: lateral view of inner side of left chela; **C**-**D**: left chela of *Eocalcinus veteris* Ferratges, Artal, van Bakel & Zamora, 2022 (Paratype MPZ 2021/29), lateral view of outer (**C**) and inner (**D**) side. **E**-**F**: Idealized reconstruction of *Eocalcinus gerardbretoni* in defensive position and the opercular function of the left cheliped (**E**) and reconstruction of the walking position (**F**).

Familia Paguridae Latreille, 1802

Género *Pagurus* Fabricius, 1775

Numerosos taxones fósiles han sido asignados al género *Pagurus* (ver Ferratges *et al*., 2022a), y es ampliamente reconocido que probablemente sea un grupo compuesto por diferentes géneros, por lo que es necesaria una revisión profunda (Schweitzer y Feldmann, 2001a). Esto sucede porque la mayoría de las características taxonómicas y diagnósticas para diferenciar los géneros modernos no se conservan en el material fósil (ver Jagt *et al*., 2006; Fraaije, 2014; Fraaije *et al*., 2014). El material recuperado comparte varias características con los miembros modernos del género *Pagurus*, por lo que se ha adoptado un enfoque conservador y se ha asignado a este género pero con nomenclatura abierta.

Género *Anisopagurus* McLaughlin, 1981

La especie *Anisopagurus primigenius* Ferratges, Artal, van Bakel y Zamora, 2022, corresponde a la primera cita de este género en el registro fósil. Se diferencia de otras especies del género por su densidad de la ornamentación y la forma de sus tubérculos fungiformes, cubriendo toda la superficie externa y las dos filas de espinas en el margen superior (ver Ferratges *et al*., 2022a). Este descubrimiento sirve para tener una idea más clara del origen de este género y de la diversificación del grupo.

6.1.1.1. A new hermit crab out of its shell from the Eocene Arguis Formation, Huesca, Spain.

Ferratges, F.A., Zamora, S., Aurell, M. (2020). A new hermit crab out of its shell from the Eocene Arguis Formation, Huesca, Spain. *Acta Palaeontologica Polonica*, 65(4), 787–792. https://doi.org/10.4202/app.00779.2020

Brief report *Acta Palaeontologica Polonica* 65 (4): 787–792, 2020

A new hermit crab out of its shell from the Eocene Arguis Formation, Huesca, Spain

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Semi-articulated paguroids are rare fossils, and there are only few records from Cenozoic strata. Here we present a new and exceptionally preserved hermit crab (Diogenidae) from the Eocene of Huesca (Spain) that preserves the anterior part of the carapace, together with appendages. *Diogenes augustinus* sp. nov. represents one of most completely preserved hermit crabs known to date, providing crucial information to understand the evolution of the family Diogenidae. It is characterized by poorly marked regions of shield, absence of Y-line and markedly unequal and robust chelipeds. The specimen is preserved out of its host shell suggesting rapid burial in siliciclastic strata of a prodeltaic environment.

Introduction

Hermit crabs (superfamily Paguroidea Latreille, 1802) are an iconic group of decapod crustaceans with very specialized characteristics that usually include a poorly mineralized and asymmetric abdomen. This is the result of a life confined to empty gastropod shells (e.g., Walker 1992), or in cavities of sponges, corals and plant remains (e.g., De Forges et al. 2001). Due to the weakly mineralised body and articulations, the fossil record of paguroids is poor and often dominated by isolated chelipeds and other dissociated remains (e.g., Hyžný et al. 2016; Fraaije et al. 2020, and references therein).

Examples of articulated hermit crabs in the fossil record are rare, and only few nearly complete specimens are known; in most cases preserved in situ, inside gastropods or other shells (see Fraaije and Polkowsky 2016 and Pasini et al. 2020, who summarized main records). Because they hide naturally inside shells, hermit crabs usually reveal only a small part of their anatomy (for instance, chelipeds and sectioned pereiopods) or occur as incomplete remains with articulated chelipeds (e.g., Schweitzer and Feldmann 2001; Fraaije et al. 2011). So far, for only seven specimens, the anterior part of the carapace (shield), in association with, chelipeds have been recorded (Jagt et al. 2006; Garassino and Schweigert 2006; Fraaije et al. 2008; Garassino et al. 2009; Schweigert et al. 2013; Fraaije and Polkowsky 2016; Pasini et al. 2020). This information allows a better understanding of how chelipeds are associated with body fossils. Here we describe an extraordinary example of a paguroid from the Eocene Arguis Formation (South Pyrenean Basin, northeast Spain) that is preserved out its host shell and retains a partial carapace, plus chelipeds and walking legs.

Institutional abbreviations.—MPZ, Museo de Ciencias Naturales de la Universidad de Zaragoza, Spain.

Nomenclatural acts.—This published work and the nomenclatural acts it contains, have been registered in Zoobank: urn:lsid:zoobank.org:pub:1B4F2880-02E2-4D94-958F-4E30C973536F

Geological setting

The present material comes from sandstone and marly beds in the lower part of the Arguis Formation (middle–upper Eocene), as exposed along the southern margin of the Jaca-Pamplona Basin, between the villages of Belsué and Lúsera (Huesca) (co-ordinates 42°18’54” N, 0°20’41” W). This basin, located in the south-central Pyrenean zone (Sierras Exteriores), formed in consequence of the propagation of the Pyrenean tectonic structures during the Paleogene (Millán et al. 1994; Huyghe et al. 2009). This propagation during the middle and late Eocene resulted in the formation of reliefs that became part of sediment source areas for deltaic complexes (Dreyer et al. 1999).

The Arguis Formation (latest Lutetian–early Priabonian) consists of four deepening-shallowing third-order sequences, I to IV (Millán et al. 1994). Specifically, the paguroids described come from prodeltaic sandstone found in the lower part of Sequence II as described by Millán et al. (1994). The late Bartonian age of Sequence II is well constrained by magnetostratigraphical and palaeontological data (Pueyo et al. 2002; Silva-Casal et al. 2019). The Arguis Formation includes highly fossiliferous intervals, with benthic foraminifera, decapod crustaceans, echinoderms, and molluscs (e.g., Ferratges et al. 2020).

Systematic palaeontology

Systematic classification follows McLaughlin (2003) and carapace terminology follows Fraaije et al. (2019).

Order Decapoda Latreille, 1802

Infraorder Anomura MacLeay, 1838

Superfamily Paguroidea Latreille, 1802

Family Diogenidae Latreille, 1802

https://doi.org/10.4202/app.00779.2020

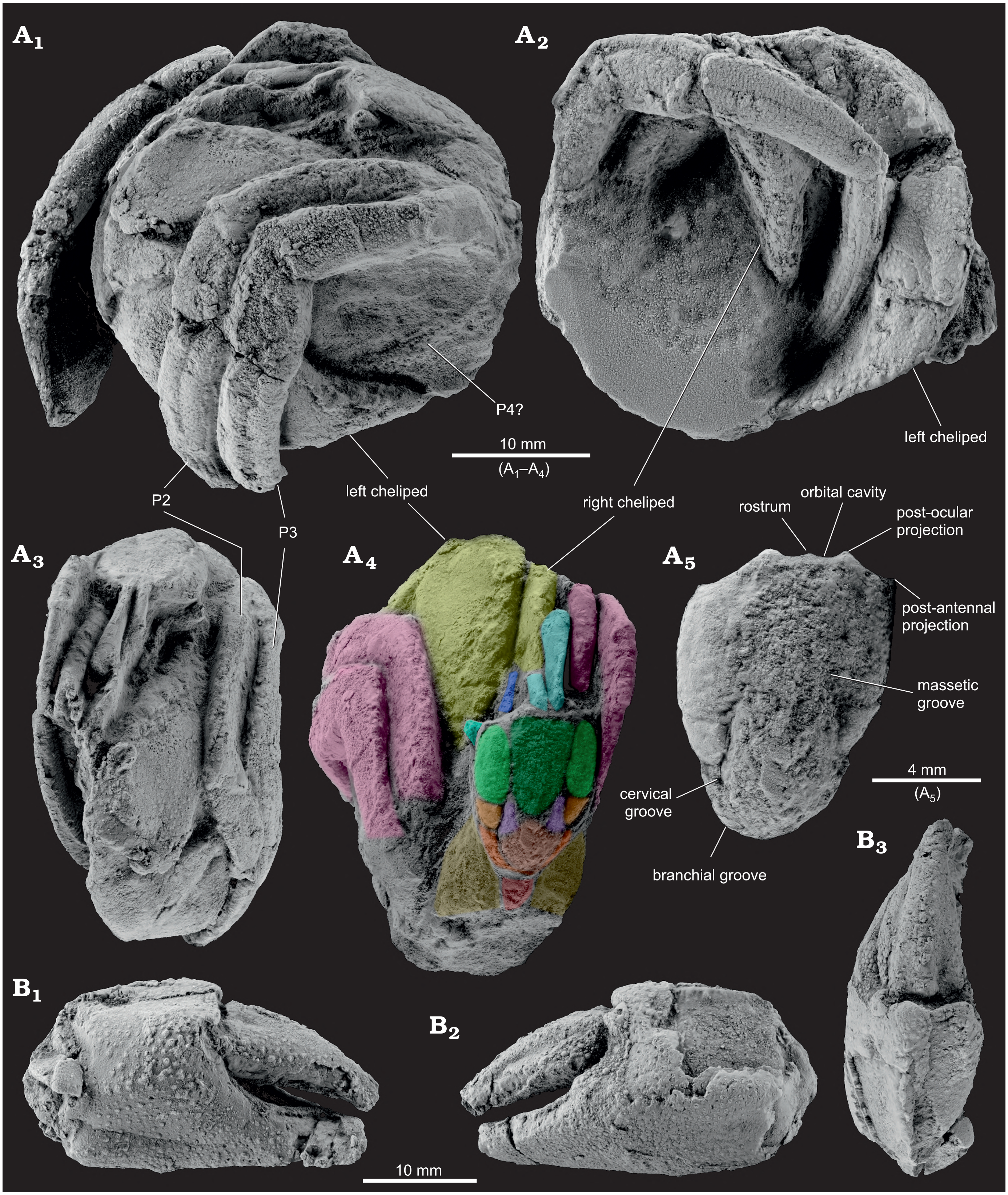

Fig. 1. Paguroid crab *Diogenes augustinus* sp. nov. from the upper Bartonian of Arguís Formation, Eocene, Lúsera, Huesca, Spain. **A**. Holotype (MPZ2020/54), in left lateral (A_1), right lateral (A_2), and frontal (A_3) views. Dorsal region details (A_4): light blue, eyestalk; dark blue, maxilliped?; turquoise, antenna; light green, massetic; dark green, anterior gastric; orange, lateral branchial; purple, keraial; light orange, anterior branchial; dark orange, mesobranchial; dark yellow, metabranchial; red, cardiac. Shield details (A_5). P_2, P_3, P_4?, pereiopods. **B**. MPZ2020/55, paratype, isolated left cheliped in mesial (B_1), outer (B_2), and dorsal (B_3) views. Specimens have been photographed dry and coated with an ammonium chloride sublimated.

Genus *Diogenes* Dana, 1851

Type species: *Pagurus miles* Fabricius, 1787, by subsequent designation of Stimpson (1859); Eocene–Recent.

Diogenes augustinus sp. nov.

Figs. 1, 2.

Zoobank LSID: urn:lsid:zoobank.org:act:FFF586B9-DBC5-455B-A38A-DD3011628FB9

Etymology: In honour of Agustín Gálvez (Zaragoza, Spain) who found and donated the specimen.

Type material: Holotype: MPZ2020/54, articulated specimen, partial carapace, plus chelipeds and walking legs. Paratypes: MPZ2020/55 and MPZ2020/56, isolated chelipeds. From the type locality and horizon.

Type locality: Village of Lúsera, Huesca Province, Spain.

Type horizon: Arguis Formation, upper Bartonian, middle–upper Eocene.

Material.—Type material only.

Diagnosis.—Shield longer than wide, length/width ratio 1.32, slightly convex transversely and longitudinally; rostrum not prominent. Orbital cavity concave, shallow antennal cavities. Regions of shield poorly marked; massetic region elongated, with perpendicular striate. Anterior branchial area globose, subtriangular. Eyestalks smooth, shorter than shield, diameter 1.42 mm. Chelipeds markedly unequal, left largest; palm quadrate, without stridulatory mechanism on mesial face of palm. Carpus triangular; axis of carpal-propodal articulation oblique in relation to sagittal plane. P2 merus depressed on outer side. Dorsolateral faces of propodus covered with small granules. Dactyls of P2 and P3 about same length as propodus, margin smooth.

Measurements (in mm).—MPZ2020/54: shield length 10.74; shield width 8.08; eyestalk length 7.63; left manus length 15.12; left manus height 14.29; right manus length 8.01; right manus height 7.05. MPZ2020/55: major cheliped height 19.35; length 17.74. MPZ2020/56: major cheliped height 17.33.

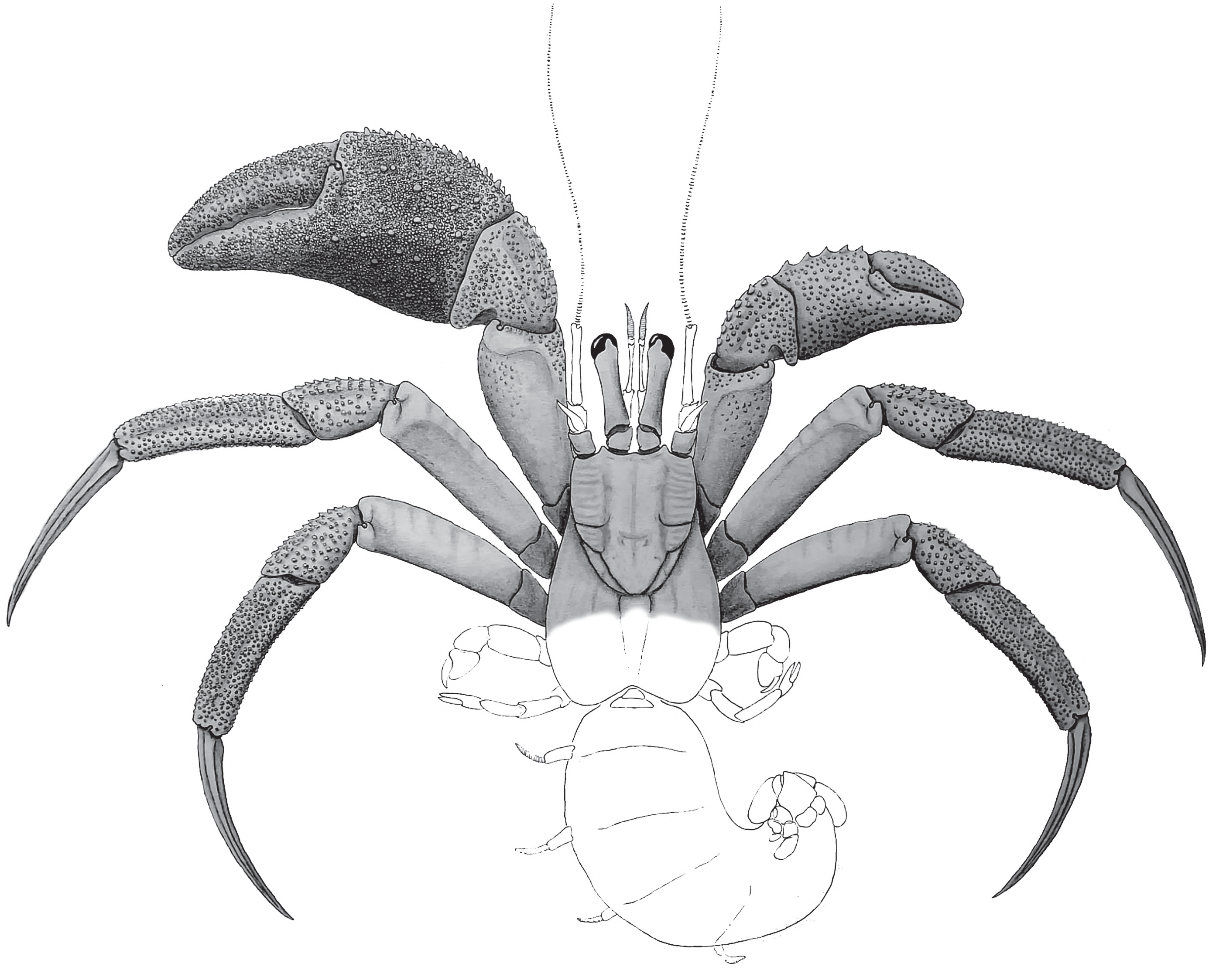

Fig. 2. Reconstruction of *Diogenes augustinus* sp. nov. Parts shown in grey are those preserved in the fossil material available. Other parts have been reconstructed from the most closely related modern taxa.

Description.—Shield longer than wide, slightly domed; surface roughened by shallow grooves, except for most of gastric region which is smooth with a subtle longitudinal ridge; rostrum weakly developed; anterior margin weakly convex; orbital cavity shallow; post-ocular projection acute; post-antenal projection slightly rounded; central gastric furrow present, but weakly developed; massetic groove weakly marked; massetic region elongated, with perpendicular stretch marks; keraial region poorly differentiated; gastric regions flat; U-shaped cervical groove; posterior carapace not well preserved (Fig. 1A). Eyestalks slightly longer than half length of shield. Chelipeds markedly unequal, with the left considerably larger; without stridulatory mechanism developed on the mesial face of the palm. Major cheliped: palm longer than broad, lateral surface of carpus covered with densely small granules; upper margin with pointed conical granules; weakly granulated dorso-ventrally (Fig. 1). Minor cheliped: palm covered by small and conic wide-spaced granules, upper margin with five pointed teeth. Merus and carpus of both chelipeds less granulated than palm; subtriangular fixed finger broad at base, with rounded distal extremity; fingers curved ventromesially; moveable finger longer than mesial margin of palm. Ambulatory legs symmetrical; merus subrectangular and elongate, upper margin convex, less ornamented than carpus and propodus; outer side of P2 merus depressed to accommodate P3; carpus subtriangular; carpus and propodus of P2–P3 with slightly serrated dorsal margins. Dactylus of ambulatory legs as long as propodus, broadly curved (Figs. 1, 2).

Remarks.—Reconciliation of fossils and neontologist classifications are problematic, because most of the taxonomic features to differentiate between modern genera are not preserved in extinct material (e.g., Jagt et al. 2006; Fraaije 2014; Fraaije et al. 2014). This drawback is exacerbated by the fact that the majority of fossil paguroids are found as disarticulated elements or, in the best cases, they are hidden inside gastropod shells; and this hampers our ability to provide a complete description of specimens. This explains why the systematic placement of fossil paguroids is fraught with difficulties (Fraaije and Polkowsky 2016). Fortunately, the material described herein includes both the chelipeds and the carapace and represents one of the few examples in which all of the anterior portion of the animal is available.

Despite these drawbacks, McLaughlin (2003) listed important morphological characters to distinguish between different modern taxa that can also be recognised in fossil species. For instance, Fraaije et al. (2019), among others, included detailed data on shields of extant taxa that can be seen in fossils.

The material studied retains delicate diagnostic characteristics, such as the morphology of the shield, cheliped ornamentation, ocular peduncles and ambulatory legs. This allows its definite assignment to the family Diogenidae. We include the new taxon in *Diogenes* on the basis of similarities in features of chelipeds, pereiopods and distribution of dorsal carapace regions. Our material also shows corrugated and poorly defined massetic regions, a gastric region without Y-line and eyestalks that are long and thin (Fig. 2). Diogenids of Eocene age include nine genera that have been described on the basis of isolated chelae only (Garassino et al. 2009; De Angeli and Caporiondo, 2017), making comparison with our material difficult.

The modern genera *Dardanus* Paul'son, 1875 and *Calcinus* Dana, 1851, show similar characteristics to those observed in the studied specimen. However, *Diogenes augustinus* sp. nov. differs from both genera in having a near-straight frontal area, a less well-developed rostrum, a well-defined anterior branchial region (triangular in shape), much larger ambulatory dactyli; in addition, it lacks a Y-line on the posterior part of the shield. The genus *Petrochirus* Stimpson, 1858 has a characteristic squamose ornamentation; moreover, the anterior branchial region is not clearly defined.

Stratigraphic and geographic range.—Type locality and horizon only.

Concluding remarks

Articulated hermit crabs are rare fossils; mostly only isolated chelipeds are available that offer little information on the overall build of the animals. The depositional setting from which the present articulated specimen was recovered corresponds to a deltaic complex, some few kilometres away of the sediment source area (Millán et al. 1994; Dreyer et al. 1999). The matrix is a fine sandstone, with rare associated molluscs and irregular echinoids. Field observations suggest that bioturbation was rare at these levels except for vertical burrows assigned to *Skolithos.*

Based on taphonomic experiments, Klompmaker et al. (2017) have recently demonstrated that hermit crabs decay and disarticulate rapidly, only a few days after death. Articulated specimens will be preserved only under certain environmental conditions such as anoxic sea floors (e.g., Garassino et al. 2009) or in areas where sedimentation rates are high (e.g., Shives and Dunbar 2010). With this in mind, we consider the present specimens to have been transported and buried rapidly after the animals abandoned their host shells. High sedimentation rates in the study area were probably responsible for keeping at least one specimen intact by avoiding post-mortem interactions with scavengers. The specimen is preserved out of its host shell; there is no trace of shell material around the crab. This agrees with observations on modern representatives that suggest shell abandonment occurs in 46% of hermit crabs that are smothered after sudden episodic sedimentation (Shives and Dunbar 2010). In fact, episodic high-hydrodynamic pulses associated with a deltaic environment increase sedimentation rate and can bury benthic organisms even alive (e.g., Nichols et al. 1978; Hinchey et al. 2006; Shives and Dunbar 2010). In the study area this is also emphasised by the creation of tectonically induced, large spaces open to sedimentation (Millán et al. 1994).

The data provided by the present material reinforces the ideas previously documented that an increase in sedimentation rate, sudden sedimentary events and absence of scavengers favour the preservation of articulated hermit crabs. The fact that the new material is articulated and occurs outside of the host shells supports the fact that sedimentation rates were very high in this area, probably because it was close to the source area and local tectonics were conducive to such events.

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New hermit crabs (Paguroidea, Anomura) from the Eocene of Huesca, Spain

Nuevos cangrejos ermitaños (Paguroidea, Anomura) del Eoceno de Huesca, España

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ABSTRACT

In this study, a new genus and a new species of fossil hermit crabs (Anomura, Paguroidea) are described from the southern Pyrenean basins (Huesca, NE Spain). *Parapetrochirus* nov. with *P. robustus* n. gen., n. sp., as type species, comes from the lower Eocene (Ypresian) Roda Formation. It preserves both chelipeds exhibiting a notable heterochely, a larger left cheliped and a concavity without granulation in the inner upper portions. *Eocalcinus gerardbretoni* n. sp. originates from the highest levels of the Arguis Formation (Priabonian) in Yeste locality. This species is characterized by a hemispherical outline and a sinuous lower margin of the chela, which differs from the type species of the genus. The cheliped morphology of such described species allows inclusion in the families Diogenidae and Calcinidae, respectively. Fossil paguroids are relatively rare in the Eocene of Spain, therefore, the description of these two new taxa increases the known variety of this group. *Parapetrochirus robustus* n. gen., n. sp. inhabited siliciclastic substrates within a prodelta environment and *E. gerardbretoni* n. sp. was collected from the last levels of coral rudstones just below the continental influence of Yeste-Arrés Formation.

Keywords: Crustacea, Decapoda, benthonic, taxonomy, Eocene, Ypresian, Priabonian.

RESUMEN

En este trabajo se describe un nuevo género y especie de cangrejos ermitaños fósiles (Anomura, Paguroidea) correspondientes a las cuencas del sur de los Pirineos en la Huesca, (noreste) España. Como especie tipo, se encuentra Parapetrochirus nov., con P. robustus n. gen., que procede del Eoceno inferior (Ypresiano) de la Formación Roda. Este fósil preserva ambos quelípedos con una notable heteroquelia, un quelípedo izquierdo más grande y una superficie cóncava sin granulaciones en las porciones superiores internas. Eocalcinus gerardbretoni n. sp., procede de los niveles más altos de la Formación Arguis (Priaboniano) en la localidad de Yeste. Éste se caracteriza por su forma hemisférica y un margen inferior sinuoso de la quela, lo cual difiere de la especie tipo del género. La morfología de quelípedo de estas especies permite su inclusión en las familias Diogenidae y Calcinidae, respectivamente. Los paguroideos fósiles son relativamente raros en el Eoceno de España, por tanto, la descripción de estos dos nuevos fósiles taxonómicos incrementa la variedad conocida del grupo. Parapetrochirus robustus n. gen., n. sp. habitaba en los sustratos siliciclásticos de ambiente prodelta y E. gerardbretoni n. sp. fue recolectado en los últimos niveles de los rudstones de coral, justo debajo de la influencia continental de la Formación Yeste-Arrés.

Palabras clave: Crustacea, Decapoda, bentónicos, taxonomía, Eoceno, Ypresiano, Priaboniano.

1. Introduction

Hermit crabs are an interesting group of decapod crustaceans with a scattered and fragmentary fossil record (*i.e.*, Via, 1959; Beschin *et al.*, 2002, 2005, 2010, 2012; De Angeli *et al.*, 2009; Garassino *et al.* 2009a, 2009b; Pasini and Garassino, 2010a, 2010b; Pasini and Garassino, 2011; Fraaije *et al.*, 2011, 2015, 2020; Garassino *et al.*, 2014; Schweigert *et al.*, 2013; Fraaije, 2014; Hyžný *et al.*, 2016; De Angeli and Caporiondo, 2017; Ossó, 2020 Pasini *et al.*, 2020). The vast majority of this group has a very specialized morphology bearing a poorly mineralized and asymmetric abdomen, as a result of a life confined to empty molluscs (*e.g.*, Walker, 1992), or in other cavities like sponges, corals or plant remains (*e.g.*, de 2010; Lemaitre, 1989, 1990). This peculiar morphology favours rapid disarticulation and most fossil remains correspond to isolated propodi (see Klompmaker *et al.*, 2017).

Here we describe two new taxa of paguroids from the Eocene of the south-central Pyrenees Basins (Spain). Previous records of decapod crustaceans from this area are relatively common (*i.e.*, Via, 1969, 1973; Fraaye, 1995; Fraaije and Pennings, 2006; Artal and Castillo, 2005; Van Bakel *et al.*, 2012; Artal *et al.*, 2013a, 2013b; Ossó *et al.*, 2014; Dominguez and Ossó, 2016; López-Horgue and Bodego, 2017; Artal and Van Bakel, 2018a, 2018b, 2020; Ferratges *et al.*, 2019, 2020a, 2020b; Artal and Van Bakel, 2020); but paguroids are rare and fragmentary (*e.g* Via, 1959, 1969; Solé and Via, 1989; Ferratges *et al.*, 2020a), with the exception of the semi-articulated specimen described by Ferratges *et al.* (2020b).

2. Geological setting

The southern Pyrenean basins record one of the most complete Eocene marine sedimentary successions in Europe, with decapod crustaceans previously described from several outcrops (see above). These basins were located in the south-central Pyrenean zone (Figure 1), and paleogeographically, were located in tropical latitudes during the Paleocene-Eocene (*e.g.*, Hay *et al.* 1999; Silva-Casal *et al.* 2017). This area corresponded to an elongated gulf connected to the west by the Bay of Biscay, on the southern limit of the axial zone of the Pyrenees (Hay *et al.*, 1999).

The material described herein comes from two outcrops (Figure 1A); one corresponding to lower Eocene (middle Ypresian) sandstones and marly beds, in the lower part of the Roda Formation (Cuevas-Gozalo *et al.*, 1985) (Figure 1C); and the other one corresponding to upper Eocene (Priabonian) sandstones and marly beds, in the upper part of the Arguis Formation (Millán *et al.* 1994; Silva-Casal *et al.*, 2017) (Figure 1B).

The lower Eocene material was collected from the "Barranco de Bacamorta" in the neighbourhood of the village of Bacamorta, in northeaster Huesca province, Aragón, Spain (co-ordinates 42º21'48"N, 0º24'56"E). The Roda Formation includes highly fossiliferous intervals, which have provided an important assemblage of decapods; *Zanthopsis dufuorii* (H. Milne Edwards *in* d'Archiac, 1850), *Periacanthus ramosus* Artal and Castillo, 2005, *Eosymethis aragonensis* Van Bakel, Guinot, Artal, Fraaije and Jagt, 2012, *Collinscarcinus obliquesulcatus* Artal and Van Bakel, 2020, *Archaeoportunus isabenensis* Artal, Ossó and Domínguez, 2013, *Gaudipluma bacamortensis* Artal, Van Bakel, Fraaije and Jagt, 2013, have been previously documented. The material was collected from the upper portion of the beds bearing *Gaudipluma bacamortensis* in limestones of the Roda Formation, near to Bacamorta.

The upper Eocene material comes from Yeste, a small village in north Huesca province, Aragón, Spain (co-ordinates 42º23'09"N, 0º40'42"W). The Arguis Formation includes highly fossiliferous intervals, which have provided an important assemblage of decapods (see Ferratges *et al.*, 2020a). The material was collected from the last carbonatic levels of sequence IV in the rail cut of the train going from Huesca to Canfranc. This corresponds approximately with the last levels of coral rudstones just below the Yeste-Arrés Formation, represented in section 11 of Morsilli *et al.* (2012).

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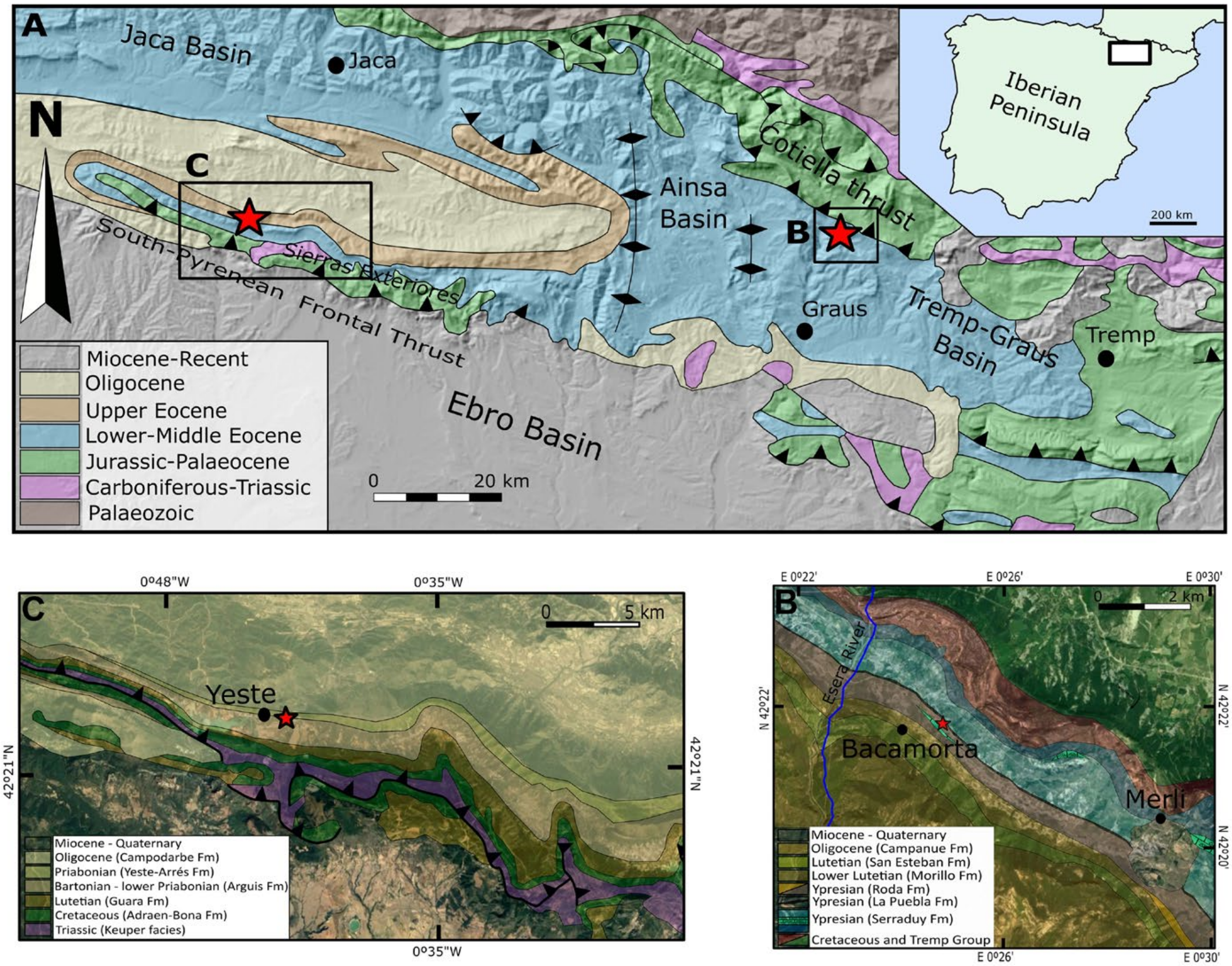

Figure 1 Geological and stratigraphic setting of the studied material. A: Location of the Tremp-Graus and Jaca-Pamplona Basins in the South-Central Pyrenean zone (modified from Dreyer *et al*., 1999). The red stars show the location of the studied outcrops (B, C).

From an environmental point of view, the Roda Formation represents a prodelta environment and the last intervals of the Arguis Formation are the last episodes of reef influence within the mesophotic ecological zone.

3. Material and methodology

Parapetrochirus robustus n. gen., n. sp. was collected from a single block of limestone that after preparation contained two chelipeds which that probably correspond to the same individual. Evidence supporting that both chelipeds correspond to the same individual include 1) close proximity of both chelipeds within the same rock and 2) morphological features of both chelipeds including a concavity without ornamentation in the upper inner portions and similar granulation pattern 3) there are a left and right cheliped, its sizes fit one specimen. *E. gerardbretoni* n. sp. was instead recovered from a carbonate block, with no other remains of crustaceans.

The specimens were prepared using a Micro Jack 2 air scribe (Paleotools) and binocular magnifying, and later photographed dry and coated with ammonium chloride sublimate. Detailed photography of the cheliped surfaces was made using a Nikon d7100 camera (Nikon, Tokyo, Japan) with a macro 60-mm-lens.

The specimens are deposited in the Museo Geológico del Seminario de Barcelona (MGSB) and the Museo de Ciencias Naturales de la Universidad de Zaragoza (Spain) (MPZ). *Eocalcinus gerardbretoni* n. sp. was collected under permit EXP: 032/2018 from the Servicio de Prevención, Protección e Investigación del Patrimonio Cultural (Gobierno de Aragón). *Parapetrochirus robustus* n. gen., n. sp. was collected in the early 80s and is housed within the historic collection of the Seminario de Barcelona.

4. Systematic Paleontology

Order Decapoda Latreille, 1802
Infraorder Anomura MacLeay, 1838
Superfamily Paguroidea Latreille, 1802
Family Diogenidae Ortmann, 1892
Genus *Parapetrochirus* n. gen.
Zoobank ID code: urn:lsid:zoobank.org:pub:92F-D0E58-ED01-438B-8417-85F13C7819B6
Figures 2 and 3

Type species: *Parapetrochirus robustus* n. gen., n. sp., by monotypy.
Diagnosis: Heterochelid chelipeds strongly robust, left largest. Left propodus large, palm subtrapezoidal, margins inclined; fixed finger notably large, fairly strong; dorsolateral surface of propodus covered with scale-shaped tubercles; lower margin laterally compressed, keel-shaped. Right palm subrectangular, triangular in cross-section; carpus subtriangular; axis of carpal-propodal articulation oblique in relation to sagittal plane. Except for the upper mesial portions, all segments are densely covered with a characteristic squamose ornamentation.
Etymology: The name refers to the similarity of the new genus to *Petrochirus* Stimpson, 1858 due to its characteristic squamose ornamentation on the outer surface of the palms and dactylus.
Material: Two chelipeds of large size, with four articulated segments, merus, carpus, propodus (propodus comprises palm plus fixed finger) and dactylus. The number of the only specimen known and holotype is MSGB68569. Measurements: left propodus length: 51.93 mm; left manus length: 28.75 mm; left manus height: 26.58 mm; right manus length: 29.84 mm; right manus height: 20.04 mm.
Type locality: Bacamorta, Huesca Province, Spain.
Type horizon: Roda Formation, lower Eocene (middle Ypresian).

Parapetrochirus robustus n. sp.
Zoobank ID code: urn:lsid:zoobank.org:act:EB43F1F0-76DD-4B9F-AB0D-7837682A5462

Diagnosis: As for the genus, by monotypy.
Etymology: From the Latin word "robustus", meaning robust.
Description: Paguroid of large size with markedly heterochely. Left propodus largest and conspicuously robust, palm subtrapezoidal, with oblique margins, converging towards the carpus; palm longer than high, higher distally, at the movable finger junction. Upper margin straight, fairly inclined, lower margin straight, also inclined. Both margins with dentiform tubercles. Inner and outer surface of palm densely tuberculated, covered with closely spaced squamose granules. Fixed finger extremely robust, distal tip of finger directed upwards; lower margin arched in the first portion; extremely keeled in the distal portion; occlusal edge bearing some few large denticles. Dactylus unknown.

Right cheliped large. Palm subrectangular, fairly longer than high, with the upper and lower margins straight, parallel, bearing small denticles. Carpo-propodial articulation sinuous. The ornamentation of the inner and outer surfaces consists of squamose closely spaced tubercles. Fixed finger long, straight, incomplete; the occlusal edge bearing some few strong teeth. Dactylus long, with semi-circular section, distal tip of finger curved,

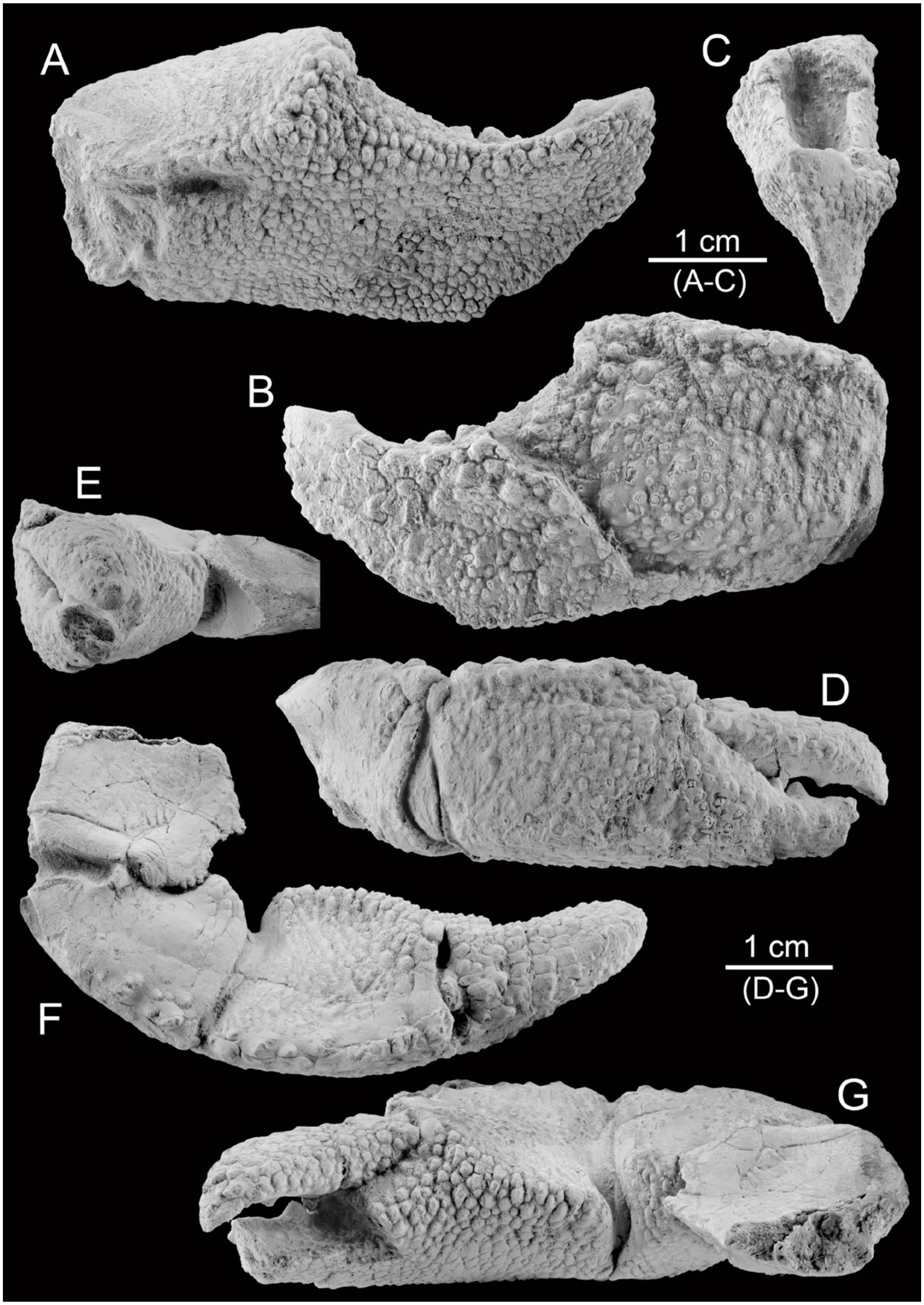

Figure 2 *Parapetrochirus robustus* n. gen., n. sp. (MGSB68569) from the Ypresian Roda Formation (Bacamorta, Huesca, Spain). A: lateral view of inner side of left chela; B: lateral view of outer side of left chela; C: frontal view of left chela; D: lateral view of outer side of right chela; E: frontal view of right cheliped; F: upper view of right cheliped; G: lateral view of inner side of right cheliped. Specimen whitened with ammonium chloride sublimated.

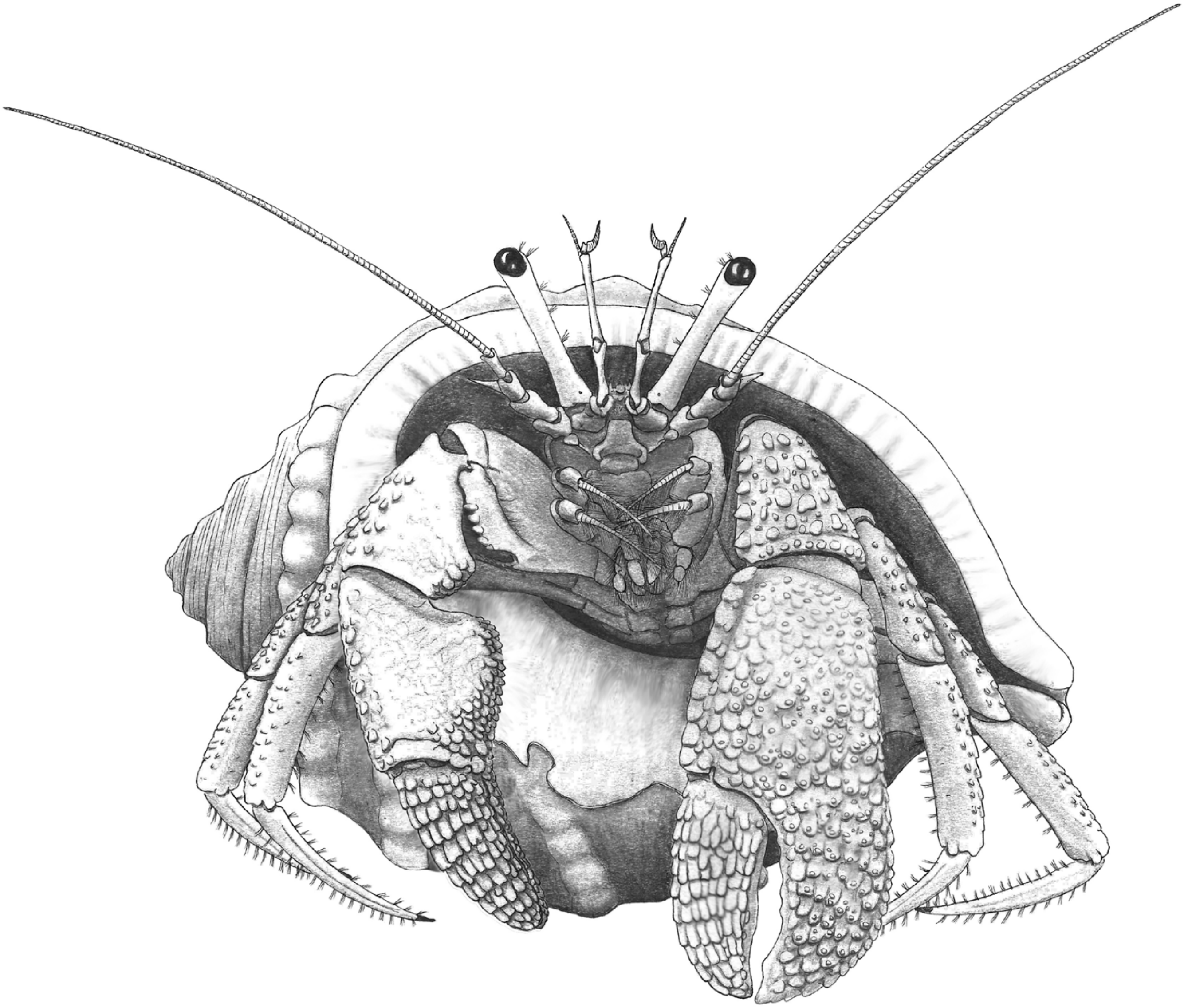

Figure 3 **Idealized reconstruction of *Parapetrochirus robustus* n. gen., n. sp. The parts not preserved in the fossil material have been tentatively inferred from closely related modern taxa.**

directed downwards; occlusal edge bearing few teeth. Both fingers covered with dense squamose granules. Inner and outer surfaces bearing scarce, small, setal pits. Carpus stout, subtriangular, with a strong extension for the articulation with the merus; mesial portion without ornamentation; upper margin with denticles; outer surface densely granulated. Merus subtrapezoidal, stout, with a large rounded extension and a notable concavity for the articulation with the carpus. Mesial portion nearly flat, somewhat concave, without ornamentation, lower margin strongly ridged. All segments in both chelipeds exhibit a notable concavity, without ornamentation, and a strong ridge, in the upper portion of the mesial view.

Remarks: The main characters of the new taxon fit the general diagnosis of the extant and extinct Diogenidae (McLaughlin, 2003; McLaughlin *et al.*, 2007; De Angeli and Caporiondo, 2017). The general morphology of chelipeds, like shape and size of the propodus, the ornamentation, and the notable heterochely confirms affinities with differ-

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ent genera within the family. Thus, we can assign with confidence *Parapetrochirus* n. gen. to Diogenidae (see also McLaughlin *et al.*, 2010).

Nevertheless, diagnostic characters of the studied specimen justify the description of a new genus. The combination of a robust subtrapezoidal palm, the extraordinarily large size and stout aspect of the fixed finger in the left propodus; with appreciable concavities in the upper mesial portions of the left and right chelipeds constitute an important difference with all other extinct and extant genera assigned to the Paguroidea (McLaughlin *et al.*, 2010; De Angeli and Caporiondo, 2017; Schweitzer and Feldmann, 2001).

Diogenes Dana, 1851, seems a close genus to *Parapetrochirus* n. gen. due to the notable differences in shape and size between the two chelipeds, being the left one the larger. The right cheliped presents important similarities, such as the general shape and the dense ornamentation (McLaughlin, 2003; Ferratges *et al.*, 2020b). However, the new taxon exhibits important differences in the left cheliped including a robust propodus, with an especially large and broad fixed finger, extremely keeled lower margin and a concave upper margin.

Some Italian fossil records appear to be superficially close to the new genus, as *Calcinus agnoensis* Beschin, De Angeli, Checchi and Zarantonello, 2005 or *Petrochirus savii* Beschin, De Angeli, Checchi and Zarantonello, 2012 (De Angeli and Caporiondo, 2017). The former exhibits a subcircular left chela, with arched margins, whereas *Parapetrochirus* n. gen. has a subtrapezoidal palm, with the margins inclined. The latter, is surprisingly assigned to the genus *Petrochirus*, indicating that has subequal chelipeds, while *Petrochirus* is diagnosed by having unequal chelipeds.

Other Italian representatives recovered from Eocene levels, as *Pagurus valdagnensis* Beschin, De Angeli, Checchi and Zarantonello, 2012 or *Eocalcinus cavus* Beschin, Busulini, De Angeli and Tessier, 2002 (Beschin *et al.*, 2012). These fossils look superficially similar because of the shape of the propodus, with a robust fixed finger. Nevertheless, the large concavities in both chelipeds, and the peculiar left propodus provide important morphological differences. *Petrochirus mezi* Lörenthey, 1909 (Beschin *et al.*, 2006, p. 99, fig. 9a, b) is larger and more robust than *Parapetrochirus* n. gen. In addition, it has a very different outline and the lower and upper margins do not have keels.

We can exclude the belonging of the new genus to *Petrochirus* Stimpson, 1858 having the right cheliped bigger than the left (McLaughlin, 2003). The right chela seems similar. However, the fossil species of *Petrochirus* need to be revised (Bermúdez *et al.*, 2017; De Angeli and Caporiondo, 2017; Vega *et al.*, 2008) since most of them were erected based upon very fragmentary material or just because a superficial appearance due to the dense and characteristic squamose ornamentation.

North American representatives of the superfamily, with very complete chelipeds also look superficially similar, as *Paguristes hokoensis* Schweitzer and Feldmann, 2001 or *Pagurus malloryi* Schweitzer and Feldmann, 2001. The former can be easily distinguished due to the subequal chelipeds, with thin and elongated fixed fingers; the latter exhibits a right cheliped larger than the left, as diagnostic in the genus *Pagurus* Fabricius, 1775.

Other families as Coenobitidae with terrestrial habitats, and peculiar left chelae or Xylopaguridae, which presents a notable asymmetry in the chelipeds and an especial habitat, are easily distinguished despite the common shared characters within the superfamily.

Family Calcinidae Fraaije, Van Bakel and Jagt, 2017

Genus *Eocalcinus* Via, 1959

Type species: *Eocalcinus eocenicus* Via, 1959, by original designation.

Species: *Eocalcinus albus* Beschin, Busulini and Tessier, 2010; *E. gerardbretoni* n. sp. (herein); *E. cavus* Beschin, Busulini, De Angeli and Tessier, 2002; *E. eocenicus* Via, 1959.

Eocalcinus gerardbretoni n. sp.

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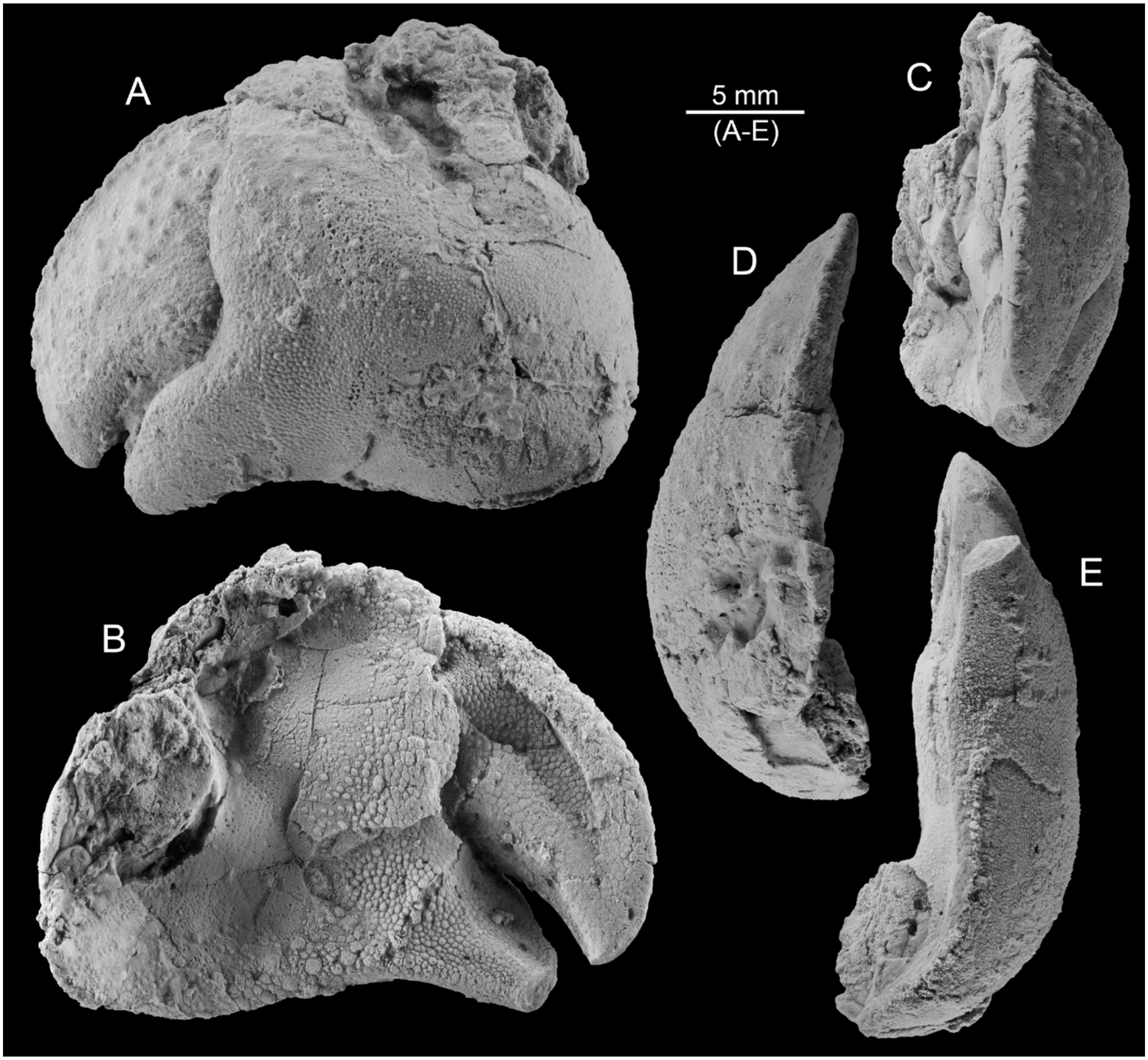

Figure 4 *Eocalcinus gerardbretoni* n. sp. (MPZ 2020/617) from the Priabonian levels of the Arguis Formation (Yeste, Huesca, Spain) A: lateral view of outer side of left chela; B: lateral view of inner side of left chela; C: frontal view of left chela; D: upper view of left chela; E: inferior view of left chela. Specimen whitened with ammonium chloride sublimated.

Diagnosis: Left propodus hemicircular, stout. Palm higher than long; lower margin sinuous both in lateral and lower view. Fixed finger with occlusal edge sinuous, obliquely oriented.

Etymology: The species is dedicated to the French paleocarcinologist Gérard Breton, for a lifetime dedicated to the study of geology and paleontology and special interest in decapod crustaceans.

Material: Single specimen corresponding to the left chelae. Holotype MPZ 2020/617. Propodus length 23.30 mm; manus length: 20.76 mm; manus height: 20.02 mm.

Type locality: Yeste, Huesca, Spain.

Type horizon: Last carbonate level of the Arguis Formation in section 11 of Morsilli *et al.* (2012).

Description: Stout left propodus planoconvex and subcircular. Lower margin sharp, strongly

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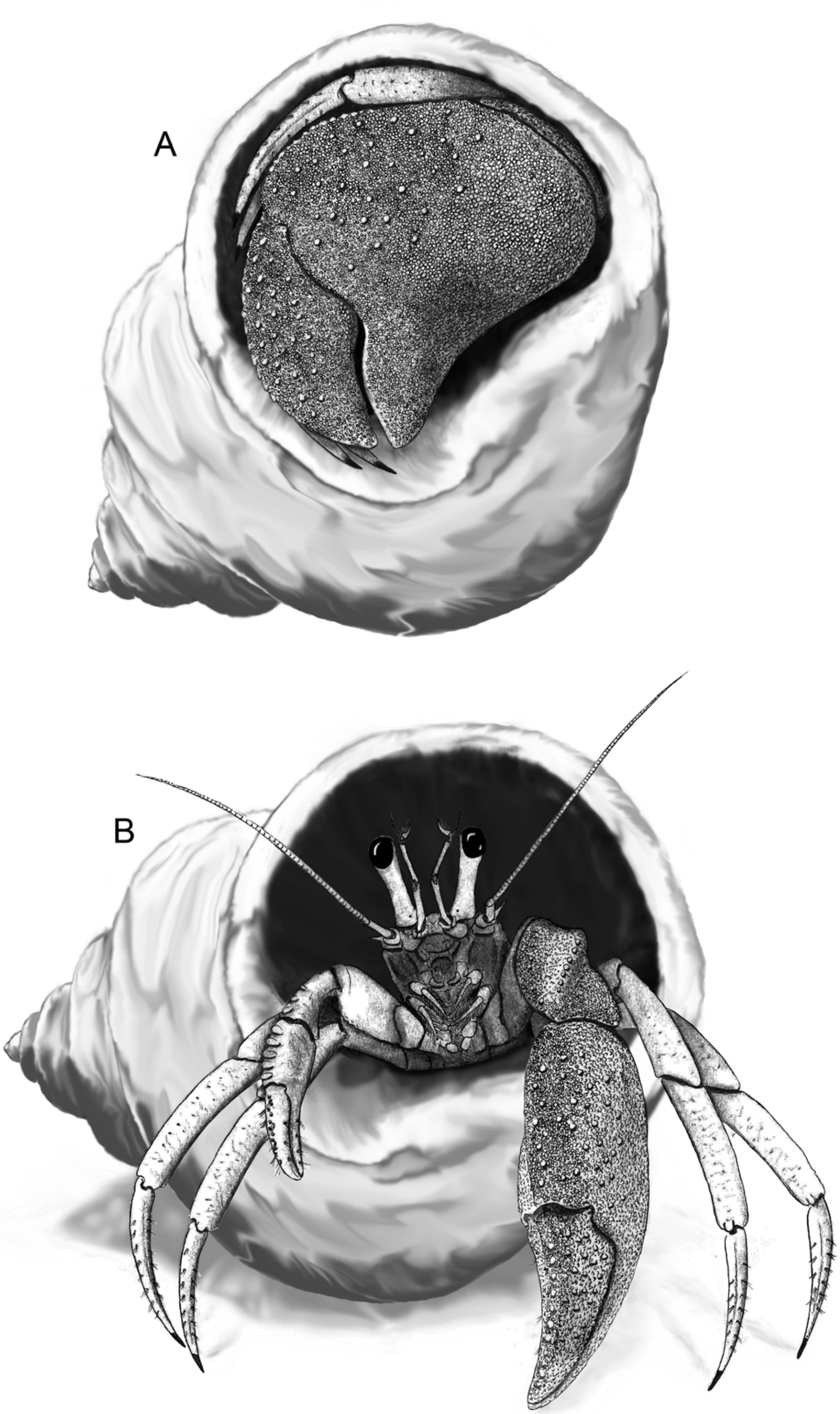

Figure 5 Idealized reconstruction of *Eocalcinus gerardbretoni* n. sp. A: reconstruction of the defensive position and the opercular function of the left cheliped; B: reconstruction of the walking position. The right cheliped has been based on *Eocalcinus eocenicus* Via, 1959, recently described by Ossó (2020). The parts not preserved in the fossil material have been tentatively inferred from closely related modern taxa.

sinuous, in lateral and lower, inferior view; outer surface strongly convex; inner surface concave. Palm slightly higher than long, with a strong concavity at the base of the fixed finger. Fixed finger short, robust, with the first portion of the occlusal edge concave, and after strongly arched (strongly convex). Dactylus very robust, triangular in cross-section, with the occlusal edge concave, obliquely oriented, smooth. Ornamentation, on the fixed finger and lower portion of the palm, is densely covered with small granules, very close together (pavement-like) and very uniform. Upper portion of palm and dactylus is covered with circular, small granules of similar size alternated with some larger granules.

Remarks: The studied specimen can be assigned to *Eocalcinus* based upon the general outline of the left chela, being hemicircular in shape; the lower margin of the propodus that is concave in the middle portion; the upper margin of the palm which is broadly arched; the fixed robust finger, without teeth in the occlusal edge, joining tightly the movable finger; the dactylus, that exhibits a broadly arched upper margin; and the whole chela is densely ornamented with small granules.

We justify the description of the new species *E. gerardbretoni* based upon a more subcircular general outline; the palm is somewhat higher than long; a lower margin convex in the proximal portion and concave in the middle; an occlusal margin of the fingers sinuous; a fixed finger notably short, stout, a lower margin with a strong concavity in the first portion and a strong convexity in the median portion; and granulation in the lower portion of the palm with elongated small granules, obliquely oriented.

The type species, *E. eocenicus*, shows some differences with *E. gerardbretoni* n. sp. with a chela more hemielliptical in shape; propodus longer than high, the palm being elongated; the lower margin of the propodus is nearly straight, only slightly concave in the middle portion; the fixed finger has straight margins; the dactylus is nearly straight in the occlusal edge, and exhibits notable small teeth in the upper margin; the ornamentation in the lower portion of the palm consists of very small circular granules, very uniformly distributed (Via, 1959).

Eocalcinus cavus Beschin, Busulini, De Angeli and Tessier, 2002 has a more elongated chela; the palm longer than high; the lower margin of the propodus is nearly straight, only weakly concave; the fixed finger is much more elongated, and the occlusal margin is only somewhat arched; the lower portion of the palm bears larger granules (Beschin *et al.*, 2002; De Angeli and Caporiondo, 2017). Comparison with *E. albus*, Beschin, Busulini and Tessier, 2010, is almost impossible because this species was described based upon only a single dactylus. However, this dactylus has a totally straight occlusal margin, and the upper margin is gently denticulated (Beschin, *et al.*, 2010).

All other species of *Eocalcinus* with the exception of the type species are represented by the left chelae (or a single dactylus of the left chelae in the case of *E. albus*). Recent finds of the right chelae of *E. eocenicus* allowed the assignment of this genus to the family Calcinidae (Ossó, 2020). The strong heterochely of *Eocalcinus* and its comparison with similar morphology in modern taxa (*i.e. Coenobita*), suggests the use of the left chela as an operculum that fitted tightly with the aperture of the host shell (Figure 5A).

5. Final remarks and conclusions

The record of Eocene paguroids in Spain is poor and often fragmentary. Via (1959) described *Pagurus marceti*, *Pagurus marini* and *Eocalcinus eocenicus* based on very fragmentary material. Ferratges *et al.* (2020b) recently described a new and very complete specimen of *Diogenes augustinus* comprising both chelae, locomotory legs and the cephalic shield which clearly provide important morphological information. The description of *Parapetrochirus robustus* n. gen., n. sp. and *Eocalcinus gerardbretoni* n. sp. increases our knowledge and known number of paguroids in the Spanish Eocene. The former represents an interesting find in prodelta marls of the Roda Formation. The latter appears in the last levels of reef influence of the Arguis Formation and increases the spatial and temporal distribution of *Eocalcinus* to the western Pyrenees.

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6.1.1.3. Filling the early Eocene gap of paguroids (Decapoda, Anomura): A new highly diversified fauna from the Spanish Pyrenees (Serraduy Formation, Graus-Tremp Basin)

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Filling the early Eocene gap of paguroids (Decapoda, Anomura): a new highly diversified fauna from the Spanish Pyrenees (Serraduy Formation, Graus-Tremp Basin)

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Abstract.—A highly diversified fauna of hermit crabs associated with reef environments from the Serraduy Formation (lower Eocene) in the southern Pyrenees (Huesca, Spain) is described. Other European Eocene outcrops have yielded paguroids associated with a single environment; however, the studied association represents one of the highest paguroid diversities in a single Eocene outcrop worldwide. The new material increases the diversity of known fossil paguroids, including eight species from which six are new: *Clibanarius isabenaensis* n. sp., *Parapetrochirus serratus* n. sp., *Dardanus balaitus* n. sp., ?*Petrochirus* sp., *Eocalcinus veteris* n. sp., ?*Pagurus* sp., *Paguristes perlatus* n. sp., and *Anisopagurus primigenius* n. sp. We erected a new combination for *Paguristes sossanensis* De Angeli and Caporiondo, 2009 and *Paguristes cecconi* De Angeli and Caporiondo, 2017 and transfer them to the genus *Clibanarius*. This association contains the oldest record of the genera *Eocalcinus* and *Anisopagurus*. Our data demonstrate that paguroids were diverse by the early Eocene in coral-reef environments and fill an important gap between the poorly known Paleocene assemblages and the more diverse mid- to late Eocene ones.

UUID: http://zoobank.org/091f7a79-946c-4cd9-bdad-f727695e8503

Introduction

Hermit crabs (superfamily Paguroidea Latreille, 1802) are an interesting and diverse group of decapod crustaceans with a widely distributed but fragmentary fossil record (i.e., Via, 1959; Beschin et al., 2002, 2005, 2010, 2012; De Angeli et al., 2009; Garassino et al., 2009a, b; Pasini and Garassino, 2010a, b, 2011; Fraaije et al., 2011, 2015, 2020; Schweigert et al., 2013; Fraaije, 2014; Garassino et al., 2014; Hyžný et al., 2016; De Angeli and Caporiondo, 2017; Ferratges et al., 2020, 2021a; Mironenko, 2020; Ossó, 2020; Pasini et al., 2020) that extends back to the Jurassic (see Fraaije et al., 2022). This is due in part to their highly specialized morphology with poorly mineralized pleon adapted to life inside empty shells or other cavities (e.g., Lemaitre, 1989, 1990; Walker, 1992; de Forges et al., 2001). After death, disarticulation occurs rapidly, and the fossil record of this group is represented mostly by isolated propodi and chelae, which are the harder and more resistant parts (see Klompmaker et al., 2017).

Eocene outcrops in Europe have provided a rich diversity of hermit crabs, especially in the middle and late Eocene, concentrated in reef environments from Italy (Beschin et al., 2007, 2015, 2018, 2019; Tessier et al., 2011) and Hungary (Müller and Collins, 1991) and siliciclastic prodelta environments from Italy (De Angeli and Caporiondo, 2017). By contrast, early Eocene material is rarer and concentrated in only a few localities (see Fraaije et al., 2011; Beschin et al., 2016; Fraaije and Polkowsky, 2016; Ferratges et al., 2021b). However, Paleocene records of paguroids are scarce, and hermit crab assemblages of this age remain largely understudied (see Jakobsen et al., 2020 and references therein).

During the Paleocene–Eocene, the southern Pyrenean basin corresponded to an elongated gulf located in tropical latitudes (Hay et al., 1999), resulting in a biodiversity hotspot of several marine invertebrates, including decapod crustaceans, and the development of coral-reef environments (Ferratges et al., 2021b). In this sense, the early Eocene seems to be an important period of diversification of hermit crabs, with the appearance of several modern families. Here we describe eight taxa of paguroids from the middle Ypresian (lower Eocene) associated with reef environments from the Ramals outcrop in the Pyrenees of Huesca, Spain. This locality has provided a great diversity of other decapod crustaceans (Artal and Via, 1989; Artal and Castillo, 2005; Artal and van Bakel, 2018a, b; Ferratges et al., 2019, 2021b; Artal et al., 2022), but paguroids remained undescribed until the present study.

The aim of the present study includes the description of new paguroids discovered in the Serraduy Formation (Ypresian,

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lower Eocene) from the southern Pyrenees (Spain). This important association shows diverse paguroids associated with a reef environment. The presence of complete chelae allows comparison with both modern and fossil representatives of the group and enlarges the general knowledge of the European fossil record of Paguridae.

Locality, materials, and methods

Locality.—The material described herein was collected from the lower Eocene (middle Ypresian) Serraduy Formation of the Tremp-Graus Basin. All specimens were collected from the same levels described by Ferratges et al. (2021b) and Artal et al. (2022).

Materials.—The studied material comprises 130 specimens represented by isolated left and right propodi belonging to eight genera and eight species, from which six are formally named. The material included in the present study was collected from the outcrop that exposes the transition between the reef limestones and the overlying Riguala Marls at a locality known as "Barranco de Ramals" (see Ferratges et al., 2021b for further information).

Some of this material (50 isolated propodi, 5.49% of the total decapod crustacean assemblage) was recovered during a paleoecological study of the area (see Ferratges et al., 2021b). The remaining specimens (80 isolated propodi and chelae) were studied in historical museum collections (MGSB). The studied chelae are well preserved, usually with their cuticle and without deformation.

Left and right chelae showing apparent homochely, as in the new species included in *Clibanarius*, *Parapetrochirus*, and *Dardanus*, have been considered to belong to the same taxon. In the case of taxa with probably asymmetric chelae (heterochely), assignment to the same taxon has been discarded due to very different ornamentations between different genera and to the fact that none of the known representatives of these genera fit with the other chelae collected in the same area. This is the case of the genera *Petrochirus* Stimpson, 1859, *Eocalcinus* Via, 1959, *Pagurus* Fabricius, 1775, *Paguristes* Dana, 1852, and *Anisopagurus* McLaughlin, 1981.

Methods

The specimens were prepared using a Micro Jack 2 air scribe (Paleotools) and binocular magnifying. They were later photographed dry and coated with ammonium chloride sublimate. Detailed photography of the cheliped surfaces was made using a Nikon d7100 camera (Nikon, Tokyo, Japan) with a 60 mm macro lens.

Repositories and institutional abbreviations.—The specimens are deposited in the Museo Geológico del Seminario de Barcelona (MGSB) and the Museo de Ciencias Naturales de la Universidad de Zaragoza (Spain) (MPZ). The material deposited in MPZ was collected under permit EXP: 032/2018 from the Servicio de Prevención, Protección e Investigación del Patrimonio Cultural (Gobierno de Aragón). The material deposited in MGSB was collected in the early 1980s and is housed within the historical collection of the Seminario Conciliar de Barcelona.

Systematic paleontology

Systematic classification follows McLaughlin (2003), McLaughlin et al. (2007; 2010), and Fraaije et al. (2022). For the morphological terminology of chelipeds, see Figure 1.

Order Decapoda Latreille, 1802
Infraorder Anomura MacLeay, 1838
Superfamily Paguroidea Latreille, 1802
Family Diogenidae Ortmann, 1892
Genus *Clibanarius* Dana, 1852

Type species.—*Cancer clibanarius* Herbst, 1791 (Herbst, 1791–1796).

Fossil species included.—*C. sossanensis* (De Angeli and Caporiondo, 2009); *C. cecconi* (De Angeli and Caporiondo, 2017); *C. isabenaensis* n. sp.

Clibanarius isabenaensis new species
Figure 2

Type material.—The holotype is MGSB77625, a near-complete, well-preserved left chela retaining cuticle. There are three paratypes (MGSB85955, MPZ 2021/30, MPZ 2022/1), which lack the dactylus.

Diagnosis.—Small left and right chela. Right and left propodus with slightly tilted carpo-propodus articulation, oriented at angle over 50°. Palm anteriorly convergent. Both propodi of similar size and shape (homochely). Two rows of conical spines on upper margin. Four rows of spiny granules on outer surface of palm. Inner surface of palm smooth. Fingers slender, rounded, elongated, bearing granules and setal pits of large size. Occlusal margin with acute outer sides.

Description.—Small left and right chelae of presumably similar shape and size. Palm subrectangular, somewhat longer than high. Complete propodus about 13.0 mm long, 7.0 mm palm length, and 6 mm palm height. Oval cross section. Inner surface fairly convex, nearly smooth. Outer surface densely granular, bearing four principal rows of spinose tubercles with setal pits near the base, directed upward. Upper margin with two rows of conical spines. Lower margin straight, rounded, with small conical granules directed forward. Posterior part of palm with prominent groove on both inner and outer surfaces, probably related to the articulation with the carpus. Fingers long, circular in cross section, slender, curved, with broad space between their occlusal margins. Large setal pits on fixed finger, of similar size and randomly distributed (Fig. 2).

Etymology.—The specific name comes from Isábena, the municipality of the province of Huesca where the material was collected.

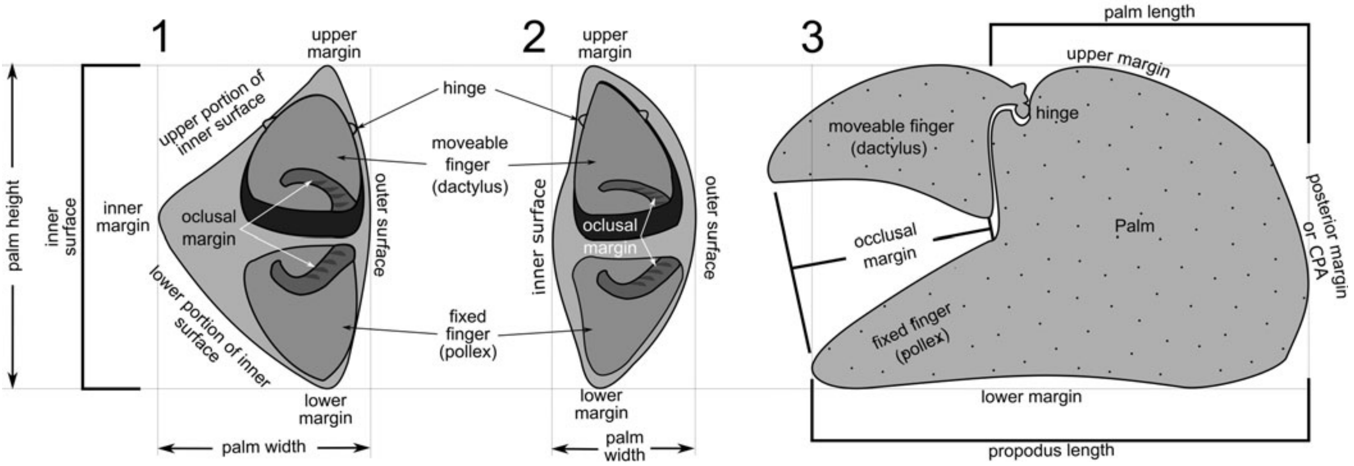

Figure 1. Simplified anatomical scheme of cheliped morphotypes of paguroids. (**1**, **2**) Frontal view of two different morphotypes. (**3**) Lateral view. CPA = carpopropodus articulation.

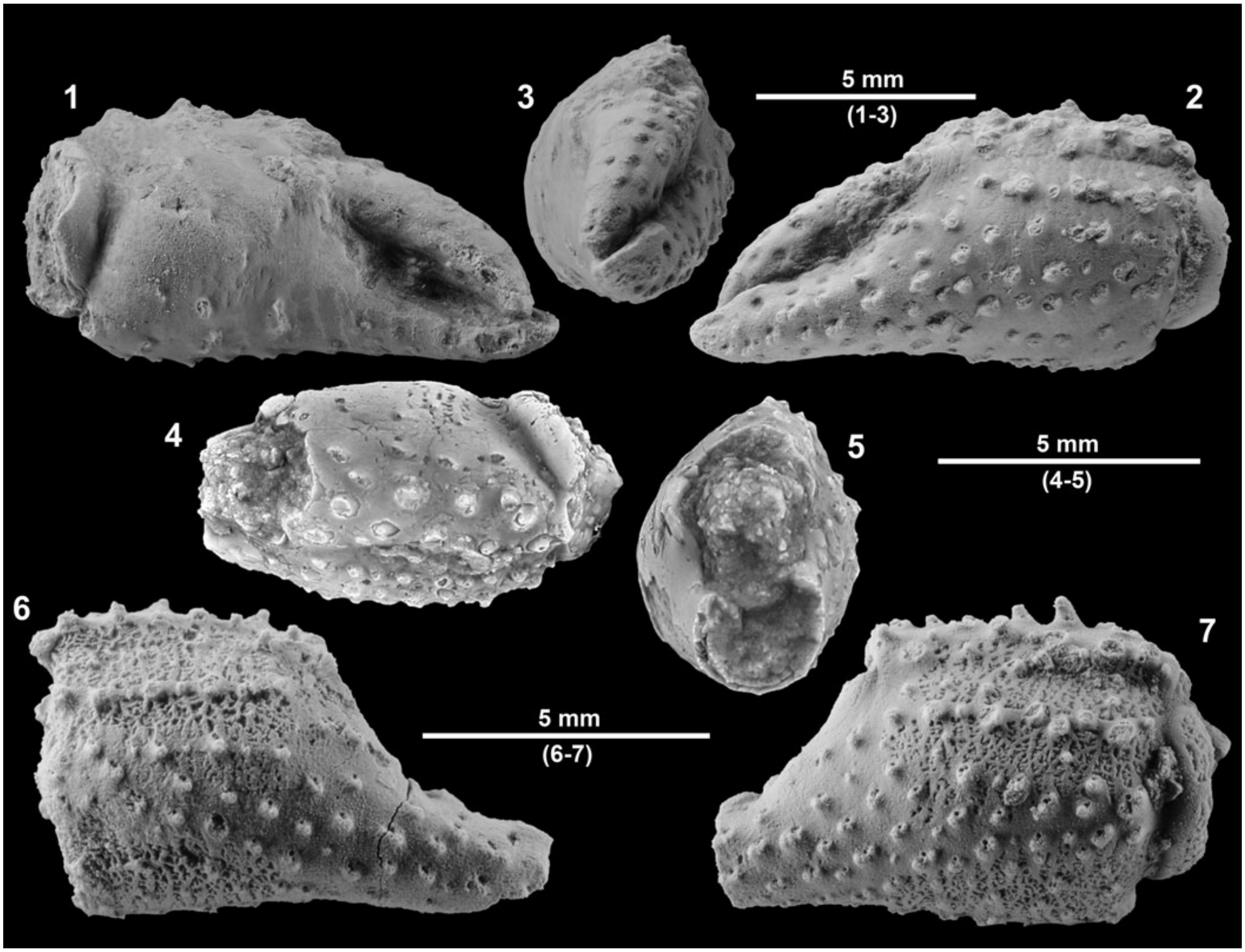

Figure 2. *Clibanarius isabenaensis* n. sp. (**1–3**) Holotype MGSB77625: (**1**) lateral view of inner side of left chela; (**2**) frontal view; (**3**) outer side lateral view of left chela. (**4, 5**) Paratype (MGSB85955), left chela: (**4**) upper view (**5**) frontal view. (**6**) Paratype MPZ 2021/30, lateral view of outer side of right chela. (**7**) Paratype MPZ 2022/1, lateral view of outer side of left chela.

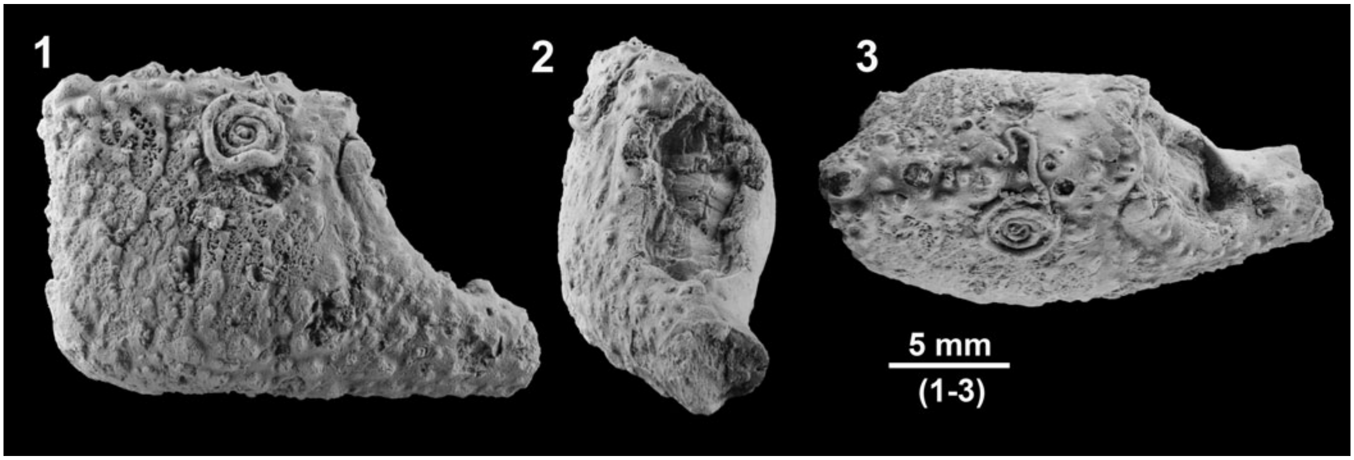

Figure 3. ?*Petrochirus* sp. (**1–3**) Right cheliped (specimen MPZ 2022/10): (**1**) lateral view of outer side; (**2**) frontal view; (**3**) upper view.

Other material examined.—Ten additional specimens MGSB85956a–j and five additional specimens at MPZ 2022/2–6. All the examined materials have a similar size.

Remarks.—The new species shows characteristics of the palm typical of the genus *Clibanarius*, as well as the presumed homochely, the small and similar size of both chelae, and the outer surface covered by small spines. Nevertheless, some taxonomic doubts exist with respect to species of the genus *Clibanarius* that are closely related to each other, and in some cases, this strong morphological similarity has raised questions about their status as separate species (McLaughlin et al., 2010). In most extant species, the fingers present a robust, stout shape, being strongly thick and clearly short (Sánchez and Campos, 1978; McLaughlin, 2003; McLaughlin et al., 2007, 2010; Negri et al., 2014). In almost all modern species included in the genus *Clibanarius*, the occlusal margins of the fingers are straight, with no gap between them (with some exceptions such as *C. antillensis* Stimpson, 1859 and *C. ambonensis* Rahayu and Forest, 1992). *Clibanarius isabenaensis* n. sp. exhibits longer and thinner fingers than the most modern representatives of the genus *Clibanarius*, with a curved dactylus and pollex, occlusal margin curved, with a wide gap between the fingers. However, we consider that the similarities presented by the new species justify inclusion in this genus.

Some species included in the genus *Paguristes* are similar to the new species, including several modern and fossil species (i.e., Müller and Collins, 1991; Blow and Manning, 1996; Beschin et al., 2005, 2007, 2018; De Angeli and Caporiondo, 2009, 2017; Garassino et al., 2009b). However, modern representatives of the genus *Paguristes* originally included a large number of morphologically different taxa, and currently, the genus has been split into several less-variable genera (see McLaughlin et al., 2010). Unfortunately, most diagnostic criteria used for modern species are not preserved in the fossil record. In any case, extant species assigned to *Paguristes* show certain differences from the new species: (1) heterochely; (2) shorter and more robust fingers; (3) setal pits tend to show a different distribution from that of the material assigned to *Clibanarius isabenaensis* n. sp. (grouping of several setal pits in front of the tubercles, oriented distally, instead of a large setal pit oriented obliquely upward). Furthermore, the extant species of *Paguristes* do not present tubercle alignment as in the new species (i.e., Rahayu and McLaughlin, 2006; Rahayu, 2007; Komai, 2010; McLaughlin et al., 2010). The fossil species *Paguristes cecconi* De Angeli and Caporiondo, 2017 shows a clear affinity with the material studied here. Nevertheless, *P. cecconi* differs from *C. isabenaensis* n. sp. by having a less elongate shape and fewer and more robust spiny tubercles on the upper margin (see De Angeli and Caporiondo, 2017, p. 15–16, fig. 7, t. 3). Furthermore, *C. isabenaensis* n. sp. has slightly less convergent upper and lower margins than *P. cecconi*. The species *Paguristes sossanensis* De Angeli and Caporiondo, 2009 also shows similarities with *C. isabenaensis* n. sp. in the general shape of the chela and distribution of the tubercles (see De Angeli and Caporiondo, 2009, p. 24–25, figs. 2, 3). However, *P. sossanensis* shows a more globose morphology, smaller tubercles on the outer surface, reduced spines on the upper margin, and a shorter and more robust fixed finger. For these reasons, we consider that the species *P. cecconi* and *P. sossanensis* should be assigned to the genus *Clibanarius*.

Genus *Petrochirus* Stimpson, 1859

Type species.—*Pagurus granulatus* Olivier, 1811 (= *Cancer bahamensis* Herbst, 1796 (for 1791 in Herbst, 1782–1804]), by original designation.

Fossil species included.—*Petrochirus bahamensis* (Herbst, 1791); *P. bouvieri* Rathbun, 1919a; *P. diogenes* (Linnaeus, 1758); *P. inequalis* Rathbun, 1919b; *P. mezi* (Lőrenthey, 1909); *P. minutus* Beschin et al., 2016; *P. poscolensis* Beschin et al., 2006; *P. priscus* (Brocchi, 1883); *P. sanctilazzari* Baldanza et al., 2014; *P. savii* Beschin et al., 2012; *P. taylori* Rathbun, 1935.

?*Petrochirus* sp.

Figure 3

Description.—Propodus length: 22.0 mm; palm length: 14.7 mm; palm height: 14.0 mm. Palm subrectangular, outer surface of palm densely coarsely granulate; inner surface less ornamented with granules. On the outer surface, more dense and coarse tubercles; on the inner surface, more numerous in the upper portion; lower portion nearly smooth. Both surfaces convex. Palm sigmoidal in cross section. Upper margin with four prominent spines surrounded by other smaller spines, irregularly distributed. Upper and lower margins of propodus straight (Fig. 3). Incomplete remains of fixed finger exhibit a robust construction and strong occlusal molariform teeth.

Material examined.—Four specimens corresponding to one isolated propodus (MPZ 2022/10) and three movable fingers (MPZ 2022/11–12, MPZ 2022/59).

Remarks.—This taxon is characterized by a subquadrate palm, with fairly convex inner and outer surfaces and densely covered by unevenly spaced granules. The fixed finger is not complete, but the first portion suggests it is robust, rounded, and elongated. Numerous incomplete or badly preserved chelae (Portell and Agnew, 2004; Vega et al., 2008; Collins et al., 2009a, b; Bermudez et al., 2017; Luque et al., 2020) have been traditionally assigned to *Petrochirus* mainly on the basis of a subrectangular shape and the squamous or pavement-like ornamentation (see Beschin et al., 2002; Todd and Collins, 2005; Vega et al., 2009; De Angeli and Caporiondo, 2017; Luque et al., 2017). The most similar fossil remains are from *P. savii* from Italy. Major differences are the coarser, larger granules on the outer surface and the bigger, more numerous granules on the inner surface of the palm in the Spanish form. The Italian form is characterized by a more elongate, subrectangular palm; an outer surface with smaller granules; an inner surface of the palm smooth, reticulate, with very few granules (De Angeli and Caporiondo, 2017).

Genus *Parapetrochirus* Ferratges, Artal, and Zamora, 2021a

Type species.—*Parapetrochirus robustus* Ferratges, Artal, and Zamora, 2021 (Ferratges et al., 2021a).

Fossil species included.—*P. robustus* Ferratges, Artal, and Zamora, 2021; *P. serratus* n. sp.

Parapetrochirus serratus new species
Figure 4

Type material.—The holotype is MPZ 2022/7, a well-preserved left propodus, with cuticle preserved; there are also three paratypes (two right propodi and one isolated dactylus): MGSB77621a–c.

Diagnosis.—Upper and lower margins of the palm notably ridged; oblique strong ridge on the medial portion of the inner surface of the palm; occlusal margin of the fixed finger bearing three molariform teeth, various small setal pits, and two relatively large elliptical depressions with numerous setal pits. The propodi are of similar size and shape (homochely).

Description.—Propodus length: 19.5 mm; palm length: 12.8 mm; palm height: 13.9 mm of holotype. Upper and lower margins of the palm strongly ridged, angular, developed as a strong oblique ridge in the inner margin. Upper margin straight, becoming higher proximally; lower margin straight, also higher proximally. Both margins with dentiform tubercles. Inner and outer surface of palm densely tuberculated, covered with closely spaced squamose granules. Palm with convex upper and lower margins, triangular in cross section, longer than high, with the upper and lower margins straight, subparallel, somewhat inclined, outer portion only somewhat convex, nearly flat; both margins angular, keeled, with notable conical denticles directed forward. Propodi are of similar size and shape (homochely), forming a circular shield when joined (Fig. 4.1, 4.5). The ornamentation of the inner and outer surfaces consists of squamose closely spaced tubercles. Fixed finger robust, triangular in cross section, straight. Dactylus robust; the occlusal edge is concave, smooth, bearing up to three molariform teeth, about four small setal pits, and two large depressions near the tip that exhibit multiple, numerous small setal pits (Fig. 4.10, 4.11).

Etymology.—From the Latin *serratus,* referring to its serrated margins.

Other material examined.—Eleven additional specimens at MGSB85957a–k, and three specimens at MPZ (one left dactylus: MPZ 2021/37; two fragments: MPZ 2022/8–9. All the examined material has similar size to the type material.

Remarks.—Incomplete remains of fossil paguroids with squamous ornamentation have usually been assigned to the genus *Petrochirus* (i.e., Portell and Agnew, 2004; Todd and Collins, 2005; Vega et al., 2008; Bermúdez et al., 2017; Luque et al., 2017, 2020). Some are recorded as extant species (i.e., Todd and Collins, 2005; Collins et al., 2009a, b; Luque et al., 2017). *Petrochirus* Stimpson, 1859 is characterized by globular chelipeds with elongate and subrectangular palms covered by numerous granules on the inner and outer surfaces. However, the genus *Parapetrochirus* is characterized by angular, strongly ridged upper and lower margins of the palm and a strong oblique ridge situated in the medial portion of the inner surface and margins bearing strong conical teeth. Some rather complete chelae from Italy identified as *Petrochirus savii* (De Angeli and Caporiondo, 2017) and *Petrochirus sanctilazzari* Baldanza et al., 2014 appear morphologically similar to the Spanish genus *Parapetrochirus*. *Petrochirus savii* presents striking similarities, mainly in the occlusal margins. The lower occlusal margin of *Petrochirus savii* presents some characters that are nearly identical to *Parapetrochirus serratus* n. sp., such as molariform teeth and deep elliptical depressions (De Angeli and Caporiondo, 2017). Differences in *Petrochirus savii* from *Parapetrochirus serratus* are palm more elongate; subrectangular; upper and lower margin of palm rounded, not crested; different ornamentation; near absence of granules on the inner portion; smaller granules, not pavement-like, on the outer portion. Main differences in *Petrochirus sanctilazzari* from *Parapetrochirus serratus* are a

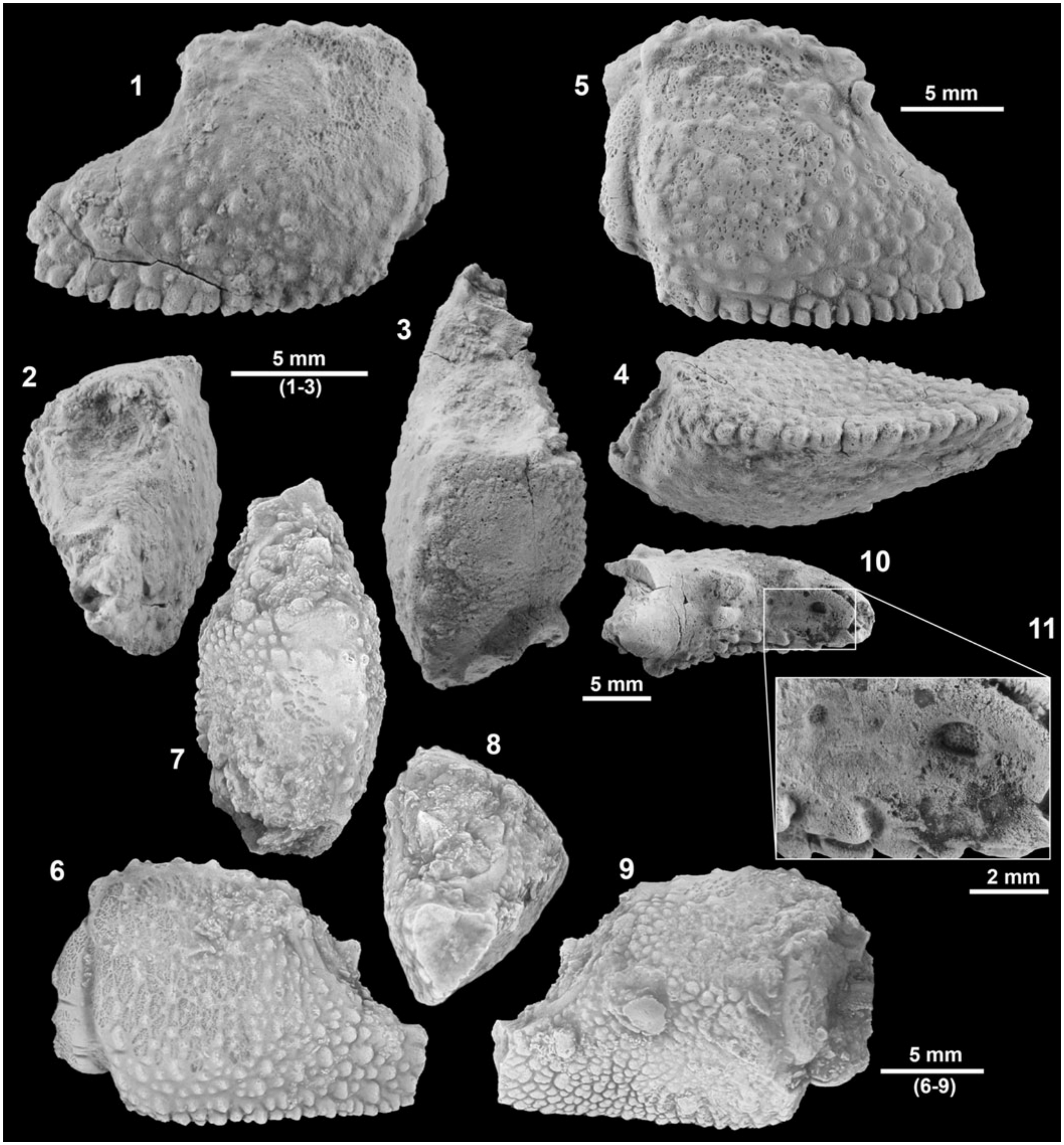

Figure 4. *Parapetrochirus serratus* n. sp. (**1–4**) Holotype MPZ 2022/7, left chela: (**1**) lateral view of outer side; (**2**) frontal view; (**3**) upper view; (**4**) lower view. (**5**) Paratype MGSB77621a, lateral view of outer side of right cheliped. (**6–9**) Paratype MGSB77621b, right chela: (**6**) lateral view of outer side; (**7**) upper view; (**8**) frontal view; (**9**) inner side lateral view. (**10**) Occlusal margin of isolated dactylus (paratype MGSB77621c). (**11**) Detail of the capsulated setal pits of the occlusal margin of dactylus.

more elongated palm and more rounded lower and upper margins in the former.

The Mexican *Petrochirus* sp. from the lower Eocene (Vega et al., 2008) shows some similarities to *Parapetrochirus serratus* n. sp. such as upper and lower margins bearing conical teeth, dense ornamentation, and a subrectangular propodus. The main differences in the Mexican specimen are: (1) absence of a strong oblique ridge on the inner surface; (2) lower margin strongly arched; (3) outer surface of the palm scarcely granulated (see Vega et al., 2008).

Parapetrochirus serratus n. sp. shows similarities to *Calcinus agonensis* Beschin et al., 2005 in the general outline and ornamentation of the chela. However, the new species presents more weakly developed tubercles on the upper margin and a more serrated lower margin. In addition, modern representatives of the genus *Calcinus* show a great diversity of shapes and need deep systematic review. In any case, the modern forms assigned to the genus *Calcinus* present clear differences from *P. serratus* n. sp. such as: (1) evident heterochely and (2) globose chelae, not rounded or opercular as is the case with fossil material (i.e., Forest, 1958, p. 4–7, 9–12, figs. 6–12; Haig and McLaughlin, 1984, p. 109–110, 112, 117, figs. 1, 2; Poupin, 1997, figs. 4–7; Asakura and Tachikawa, 2000, p. 270, 275, figs. 2, 6; Asakura, 2002, p. 29, 32, 34–35, 37, 41, 47, 51–52, 56–57, 59, 64–65, figs. 2–6, 8, 10, 13–16, 18–21; Poupin and Lemaitre, 2003, p. 5, 7, figs. 1–3, 5).

The species *Parapetrochirus robustus* from the upper Ypresian of Huesca (Spain) also shows similarities with the new species in the ornamentation; inner and outer surface of the palm densely tuberculated, covered with squamose granules; robust fixed finger; lower margin arched proximally, and keeled in the distal portion (see Ferratges et al., 2021a). However, *P. serratus* n. sp. has a much more compact shape, with an oval outline, less compressed in the lower zone, convergent upper and lower margins, not divergent as in *P. robustus*, and less dense ornamentation. In addition, the new species presents both chelipeds with very similar morphology.

Family Annuntidiogenidae Fraaije, 2014
Genus *Paguristes* Dana, 1852

Type species.—*Paguristes hirtus* Dana, 1852 by subsequent designation of Stimpson, 1859.

Fossil species included.—*Paguristes baldoensis* Garassino, De Angeli, and Pasini, 2009 (Garassino et al., 2009b); *P. cecconi* De Angeli and Caporiondo, 2017; *P. chipolensis* Rathbun, 1935; *P. clampensis* De Angeli and Caporiondo, 2017; *P. cserhatensis* Müller, 1984; *P. florae* Collins, Fraaye, and Jagt, 1995; *P. hokoensis* Schweitzer and Feldmann, 2001; *P. johnsoni* Rathbun, 1935; *P. lineatuberculatus* Beschin et al., 2006; *P. liwinskii* Fraaije, Van Bakel, and Jagt, 2015; *P. mexicanus* (Vega et al., 2001); *P. michikoae* Karasawa and Fudouji, 2018; *P. oligotuberculatus* Müller and Collins, 1991; *P. ouachitensis* Rathbun, 1935; *P. paucituberculatus* Beschin, Busulini, and Tessier in Beschin et al., 2016; *P. prealpinus* Beschin et al., 2005; *P. santamartaensis* Feldmann, Tshudy, and Thomson, 1993; *P. sossanensis* De Angeli and Caporiondo, 2009; *P. subaequalis* (Rathbun, 1926); *P. teruakii* Karasawa and Fudouji, 2018; *P. wheeleri* Blow and Manning, 1996; *P. whitteni* Bishop, 1983 (modified from Schweitzer et al., 2010 and Fraaije et al., 2015).

Remarks.—The genus *Paguristes* Dana, 1852 was previously considered in the family Diogenidae (sensu lato), a position that was revised by Fraaije (2014) and Fraaije et al. (2017). These authors proposed its inclusion in a new family (Annuntidiogenidae Fraaije, 2014). Paguroid phylogeny is not in the scope of this paper, and we follow at this moment placement of the genus *Paguristes* in the Annuntidiogenidae as proposed by Fraaije (2014) and Fraaije et al (2017, 2022).

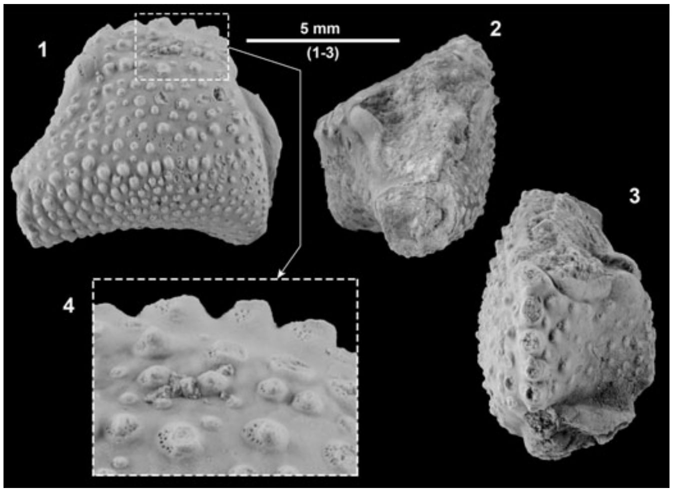

Figure 5. *Paguristes perlatus* n. sp. (**1–4**) Holotype (MPZ 2022/38), left chela: (**1**) lateral view of outer side; (**2**) frontal view; (**3**) upper view. (**4**) Detail of the distribution of the setal pits. Specimens whitened with ammonium chloride sublimate.

Paguristes perlatus new species
Figure 5

Type material.—The holotype, MPZ 2022/38, is a left propodus (propodus length without fixed finger: 8.0 mm; palm length: 7.2 mm; palm height: 7.0 mm).

Diagnosis.—Palm subquadrate; upper margin short, with strong conical teeth; lower margin fairly concave. Outer surface convex, densely granular. Inner surface with strong ridge. Upper portion of the inner surface concave; lower portion concave. Carpo-propodus articulation oblique. Fingers curving inward laterally when seen from dorsal view.

Description.—Chela of small size, palm subquadrate, slightly higher than long; outer surface concave, densely covered by evenly spaced perliform granules; inner surface bearing a strong medial ridge (inner margin), the lower portion densely granular. Inner margin rounded, strongly concave. Propodus with concavity on the upper portion of inner surface when seen from frontal view, fingers curving laterally. Lower portion of the inner surface concave. Upper margin short, bearing strong conical teeth. Lower margin longer, notably concave. Carpo-propodus articulation fairly oblique, short (Fig. 5).

Etymology.—The name refers to the characteristic perlated tubercles on the outer surface of the palm.

Remarks.—The genus *Paguristes* is morphologically diverse in modern ecosystems (Rahayu, 2006). Members of *Paguristes* in the fossil record are diagnosed by various characteristics (i.e., Beschin et al., 2012, 2016): carpus short, highest distally, with concave, arcuate lower margin and ornamented with spines and nodes; palm short, shortest along the upper margin, ornamented with numerous tubercles and spines; fixed finger stout and very high proximally. Because the features of the chelipeds of the fossil material are similar to members of *Paguristes*, the new material is placed tentatively within this genus.

Paguristes perlatus n. sp. exhibits a short upper margin of the palm bearing strongly marked conical teeth. The lower margin is fairly concave with a marked convexity in the proximal portion. Palm robust, globular, somewhat higher than long. Both surfaces are convex, the outer surface densely covered by pearled granules, the inner surface with an oblique ridge, the lower portion with numerous granules. Carpo-propodus articulation oblique. All the characters fit with the general morphological characteristics of the genus *Paguristes*. Major differences from the extant species are the ornamentation of the palm, which exhibits conical spines and the usually less concave lower margin of palm (Provenzano, 1965; Campos and Sanchez, 1995; Manjón et al., 2002; Lima and Santana, 2017). The morphologically closest fossil form is *Paguristes prealpinus*, which shares the main morphological characteristics described here. Major differences from the new species are the more subrectangular shape of the palm, the upper margin with less marked conical teeth; the concavity in the lower margin distally situated; granulation in the outer surface less marked and more irregularly distributed (Beschin et al., 2012; De Angeli and Caporiondo, 2017). *Paguristes cecconi* is assigned in this study to *Clibanarius*, as indicated in the preceding.

The fossil species *Paguristes hokoensis*, *P. liwinskii*, and *P. teruakii* exhibit the characteristic lateral curvature of the fingers from dorsal view, the conical teeth in the upper margin, and the granulated outer surface. However, *P. hokoensis* and *P. teruakii* have different ornamentation, a more elongated outline, strongly convergent upper and lower margins, and more rounded proximal lower margin (see Schweitzer and Feldmann, 2001, p. 193–195, fig. 13; Karasawa and Fudouji, 2018, p. 26, fig. 2). Major differences in *P. liwinskii* are the coarse granulation of the palm, the oval outline with markedly convex lower margin, and the smoother inner surface (Fraaije et al., 2015, p. 590, fig. 1C).

Extant *Paguristes* consists of over 120 species (McLaughlin et al., 2010; Komai et al., 2015). Several authors suggested extant *Paguristes* are mainly distributed in shallow-water areas of the temperate–tropical waters (i.e., Rahayu, 2006; Rahayu and Forest, 2009; Trivedi and Vachhrajani, 2017).

Family Calcinidae Fraaije, Van Bakel, and Jagt, 2017

Genus *Dardanus* Paul'son, 1875

Type species.—*Dardanus hellerii* Paul'son, 1875 by monotypy.

Fossil species included.—*D. arnoldi* Rathbun, 1926; *D. arrosor* (Herbst, 1796) (Herbst, 1782–1804); *D. balaitus* n. sp.; *D. bayani* Beschin et al., 2016; *D. biordines* Collins in Todd and Collins, 2005; *D. braggensis* Beschin, Busulini, and Tessier, 2015; *D. curtimanus* Müller and Collins, 1991; *D. gemmatus* (Milne Edwards, 1848); *D. hungaricus* (Lörenthey in Lörenthey and Beurlen, 1929); *D. impressus* (De Haan, 1833–1850); *D. lauensis* Rathbun, 1945; *D. mediterraneus* (Lörenthey, 1909); *D. mexicanus* Vega et al., 2001; *D. muelleri* Karasawa and Inoue, 1992; *D. squamatus* Collins in Collins et al., 2009 (Collins et al., 2009b); *D. substriatiformis* (Lörenthey in Lörenthey and Beurlen, 1929).

Remarks.—The genus *Dardanus* Paul'son, 1875 was previously considered in the family Diogenidae (sensu lato), and its position was revised by Fraaije et al. (2017). However, paguroid phylogeny is not in the scope of this paper; for consistency, we here follow Fraaije et al. (2017, 2022).

Dardanus balaitus new species

Figure 6

Type material.—The holotype, MGSB77622, is a near-complete, well-preserved right propodus, retaining cuticle. There are two paratypes, one left propodus without dactylus, MGSB77623, and one isolated finger, MPZ 2021/36.

Diagnosis.—Elongated propodus; palm globular. Inner surface convex, lower portion with notable arched lobes, upper portion nearly smooth; lower portion with notable arched lobes bearing numerous setal pits. Outer surface convex, densely granulated, with spaced granules and tubercles, all of them bearing numerous setal pits on tips and in anterior portion.

Description.—Propodus length: 20.0 mm; palm length: 12.0 mm; palm height: 13.0 mm of the holotype. Elongated propodus; palm globular, with rounded sides and margins. The inner surface bears an oblique inflation in the medial portion. Outer surface of the palm convex, ornamented with obliquely situated tubercles and oblique short or elongated raised lobes. The tubercles in the upper portion bearing one, two, three, or four setal pits, with several small setal pits in the anterior side. The lower portion of the outer surface with raised oblique lobes, the larger ones bearing about seven or eight setal pits on the tip and numerous, irregular, smaller setal pits on the anterior side. The setal pits on the anterior side are numerous and of irregular size; in the larger lobes, up to 18 smaller pits and up to eight larger pits. Inner surface smoother, less ornamented, but with large oblique rows of setal pits in the lower portion; the larger ones up to 20 irregular setal pits. Upper margin of palm with two rows of small conical teeth. Fixed finger with depressed, smooth occlusal margin; outer side of the finger with one strong, molariform tooth (Fig. 6).

Etymology.—The specific name refers to the pre-Roman mythological character "*Balaitús*," who lived in the Pyrenees and was dedicated to causing storms in the mountains.

Other material examined.—Nineteen additional specimens (isolated propodi) in MGSB85958a–s and one isolated dactylus at MPZ 2021/36.

Remarks.—The general morphology of chelae in the new taxon conforms with modern genus *Dardanus* Paul'son, 1875 because the chelipeds are globular, with rounded margins and sides, with inner and outer surface fairly convex (i.e., Collins and Donovan, 2010; Garassino et al., 2014) and because of the notable raised tubercles and lobes bearing numerous setal pits on the tips, and still more numerous setal pits in the anterior portion of each tubercle or elongated lobe. All of them appear obliquely situated, with the appearance of striations. This characteristic

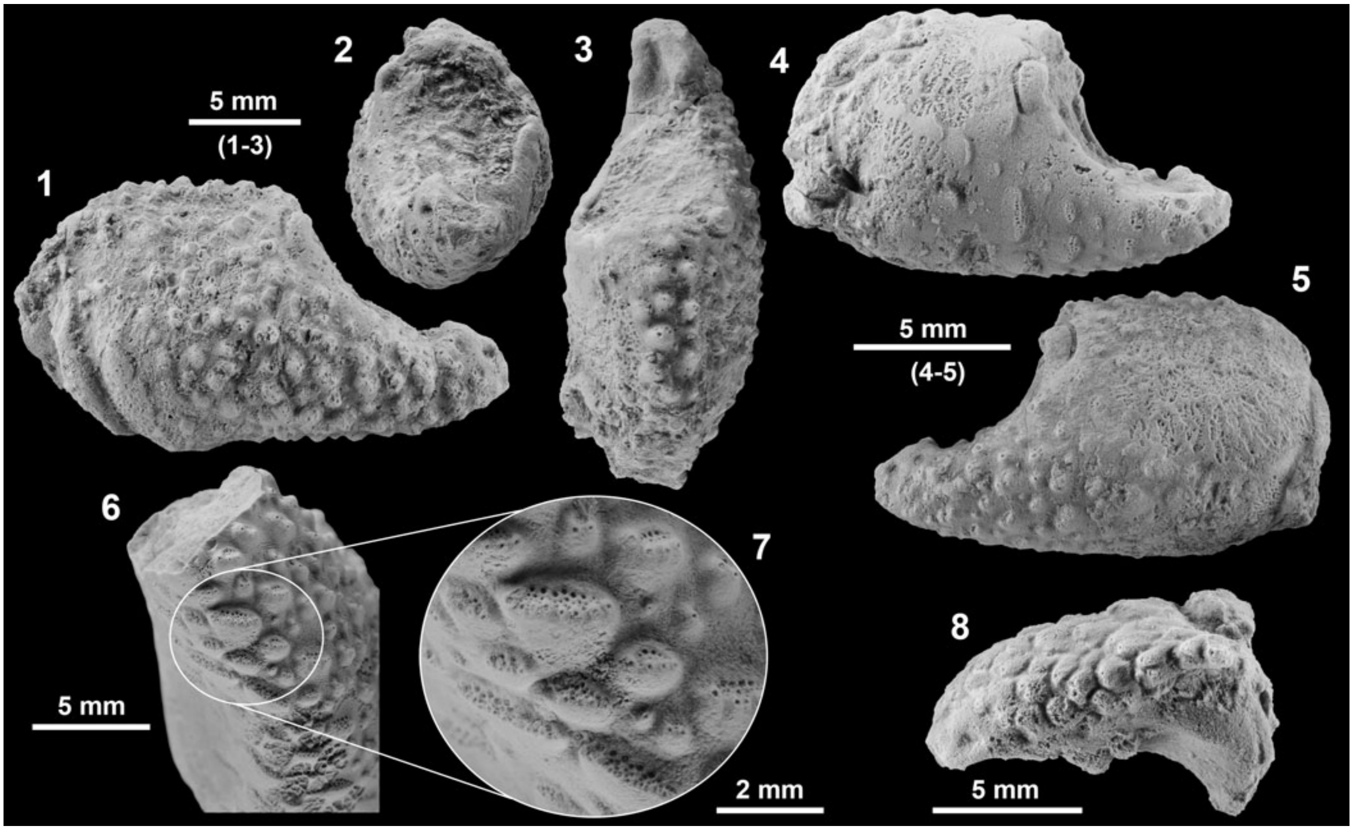

Figure 6. *Dardanus balaitus* n. sp. (**1–3**) Holotype MGSB77622, right chela: (**1**) lateral view of outer side; (**2**) frontal view; (**3**) upper view. (**4, 5**) Paratype MGSB77623, left chela: (**4**) lateral view of inner side; (**5**) lateral view of outer side. (**6**) Oblique interior view of the paratype MGSB77623. (**7**) Detail of the distribution of the setal pits. (**8**) Isolated dactylus (MPZ 2021/36).

can be observed in both extant (Sánchez and Campos, 1978; McLaughlin, 2003; McLaughlin et al., 2007, 2010) and fossil taxa (Collins and Donovan, 2010; Fraaije et al., 2011; Beschin et al., 2012; Garassino et al., 2014). In addition, the fossil species assigned to *Dardanus* usually present long oblique or vertical ridges (i.e., Garassino et al., 2014; Beschin et al., 2021), with some exceptions such as *D. colosseus* Fraaije and Polkowsky, 2016 and *D. vandeneeckhauti* Fraaije et al., 2011. Some of the distinctive characters of *D. balaitus* n. sp. are shared with the species *D. arrosor*, with robust chelae and oblique tuberculate ridges (McLaughlin et al., 2007, fig. 76). Nevertheless, the new species presents notable differences in the general shape of the chelipeds, being more rounded, and is distinct in having a peculiar distribution of tubercles and arched raised lobes, as it is the peculiar distribution of setal pits. The tubercles with one, two, three, or four setal pits on the tip; oblique arched lobes with up to eight setal pits on the tip: all tubercles and arched lobes with numerous and irregular setal pits in the anterior side (Fig. 6). The main difference with *D. substriatus* Garassino et al., 2014 from the Pleistocene of Italy is the complete vertical striae on the outer surface of the propodus, which is absent in the new species (Garassino et al., 2014).

Genus *Eocalcinus* Via, 1959

Type species.—Eocalcinus eocenicus Via, 1959, by original designation.

Fossil species included.—Eocalcinus albus Beschin, Busulini, and Tessier, 2010; *E. cavus* Beschin et al., 2002; *E. eocenicus* Via, 1959; *E. gerardbretoni* Ferratges, Artal, and Zamora, 2021 (Ferratges et al., 2021a); *E. veteris* n. sp.

Eocalcinus veteris new species
Figures 7, 8

Type material.—The holotype, MGSB77593, is a complete left propodus (length: 31.0 mm; palm length: 24.0 mm; palm height: 19.0 mm) with well-preserved cuticle. There are two paratypes, MPZ 2021/29 and MPZ 2022/13, complete left propodi.

Diagnosis.—Left propodus semicircular, stout. Palm longer than high; lower margin sinuous in both lateral and lower views. Fixed finger with occlusal edge sinuous, obliquely oriented.

Description.—The complete propodus of the holotype is 32.0 by 20.0 mm. Palm only somewhat longer than high. Lower margin slightly sinuous, nearly straight in proximal portion, fixed finger curving downward. Lower margin less ridged, more rounded. Dense tiny granulation on outer surface and fingers. Granules close together, pavement-like. Spaced bigger granules in upper portion. Clear setal pits, mainly on fingers. Inner portion of palm smooth, with scarce granules (Fig. 7).

Stout left propodus planoconvex and subcircular. Lower margin sinuous in lateral and lower inferior views; outer surface

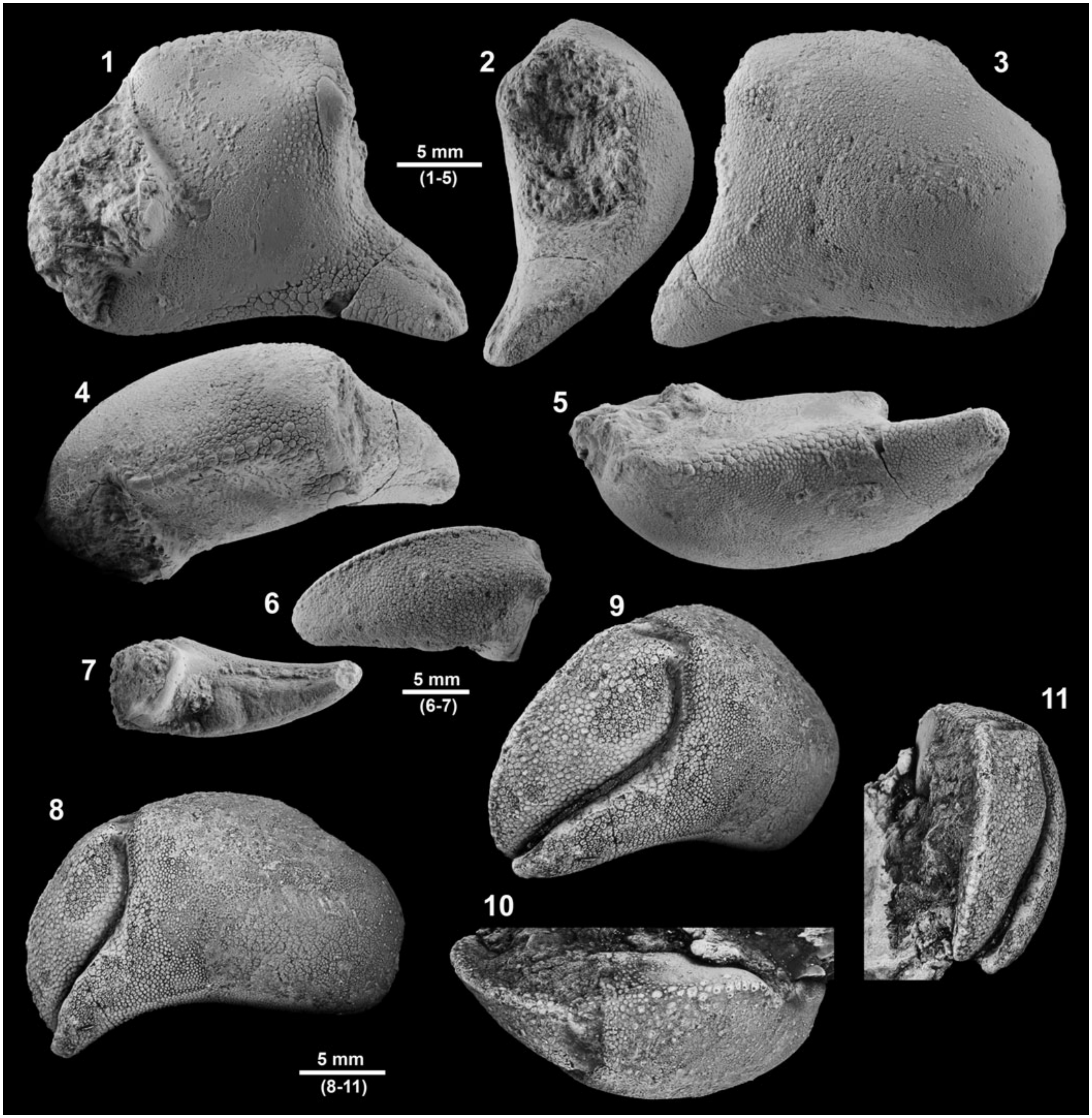

Figure 7. *Eocalcinus veteris* n. sp. (**1–5**) Paratype MPZ 2021/29), left chela: (**1**) lateral view of inner side; (**2**) frontal view; (**3**) lateral view of outer side; (**4**) upper view; (**5**) inferior view. (**6, 7**) Isolated dactylus (MPZ 2022/13) in lateral and occlusal margin (inferior view). (**8–11**) Holotype (MGSB77593), left chela: (**8**) oblique lateral view of outer side; (**9**) oblique frontal view; (**10**) upper view; (**11**) frontal view.

convex; inner surface weakly convex, nearly flat. Palm slightly longer than high. Fixed finger short, robust, arched (strongly convex). Dactylus very robust, triangular in cross section, with the occlusal edge concave, smooth. Ornamentation on the fixed finger and palm is densely covered with small granules, very close together (pavement-like), and very uniform.

Etymology.—The specific name *veteris* comes from Latin and means "old," "ancient," referring to the fact that it is the oldest member of the genus.

Other material examined.—Thirty-six additional specimens numbered MGSB77594a–z and MGSB85959a–j and 24 additional specimens numbered MPZ 2022/14–37.

Remarks.—The studied specimens can be assigned to *Eocalcinus* because of the general outline of the left chela, being hemicircular in shape; the lower margin of the propodus that is concave in the middle portion; the upper margin of the palm, which is broadly arched; the robust fixed finger, without

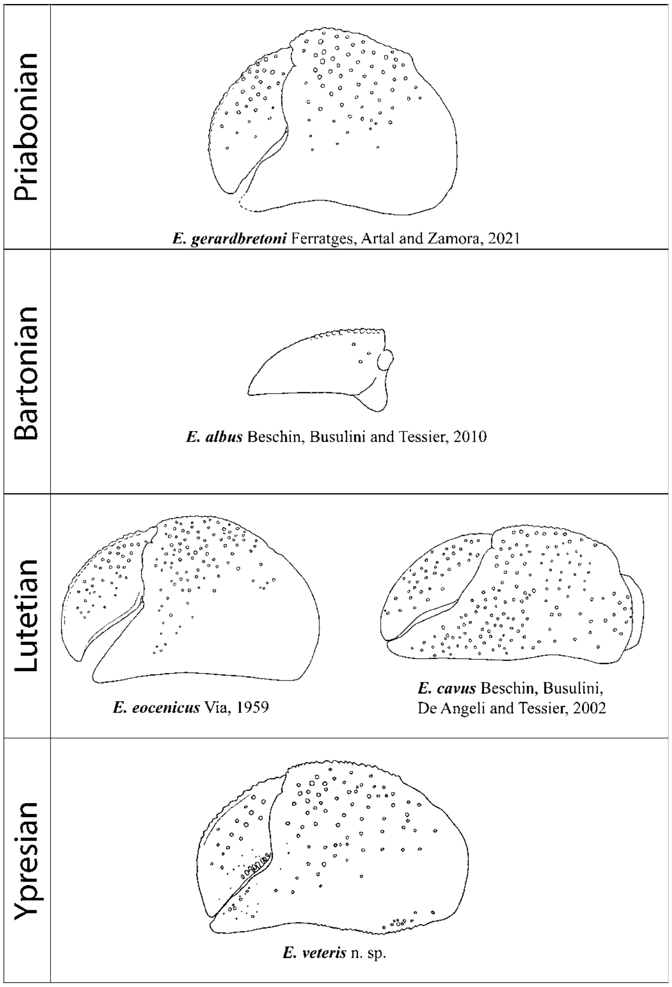

Figure 8. Shape change of the left chelas of *Eocalcinus* during the Eocene.

teeth on the occlusal edge, joining tightly the movable finger; the dactylus, which exhibits a broadly arched upper margin; and because the whole chela is densely ornamented with small granules. The new species, *E. veteris*, is clearly distinguishable from other species of the genus in having a less subcircular general outline; the distinction is also based on a palm somewhat longer than high and a lower margin convex in the proximal portion and concave in the middle portion.

The type species, *E. eocenicus*, shows some differences from *E. veteris* n. sp. In *E. eocenicus*, the major chela is more semielliptical; the propodus longer than high, the palm longer than high; the lower margin of the propodus is nearly straight, only slightly concave in the middle portion; the fixed finger has straight margins; the dactylus is nearly straight in the occlusal edge and exhibits notable small teeth in the upper margin. The lower margin is only slightly sinuous from lateral view (slightly concave in median portion), strongly sinuous when seen from the lower view. The lower margin is strongly ridged and raised in the proximal portion (adaptation for gastropod apertures). There are spaced large granules, mainly in the upper portion; the ornamentation in the lower portion of the palm consists of very small circular granules, very uniformly distributed (Via, 1959), while granules are smaller in the new species. Granules are larger in *E. eocenicus* than in *E. veteris* n. sp. Inner portion of palm smooth, with scarce granules in *E. veteris*.

Eocalcinus cavus has a more elongated left chela; the palm is longer than high; the lower margin of the propodus is nearly straight and only weakly concave; the fixed finger is much more elongated, and the occlusal margin is only somewhat arched; the lower portion of the palm bears larger granules (Beschin et al., 2002; De Angeli and Caporiondo, 2017). Comparison of the new species with *E. albus* is almost impossible because the latter was described on the basis of a single dactylus only. However, this dactylus has a totally straight occlusal margin, and the upper margin is gently denticulated (Beschin et al., 2010).

All other species of *Eocalcinus*, with the exception of the type species, are represented by the left chelae (or a single dactylus of the left chelae in the case of *E. albus*). Recent finds of the right chelae of *E. eocenicus* allowed the assignment of this genus to the family Calcinidae (Ossó, 2020).

Eocalcinus veteris n. sp. corresponds to the stratigraphically oldest species of the genus (see Fig. 8) and allows us to trace a general trend toward more rounded shapes (Fig. 8). This oldest species presents a more elongated outline, a straighter lower margin, and a less marked plano-convex section (O-shaped section) than in more recent species (D-shaped section). This trend toward more rounded shapes, with a sinuous lower margin and a more plano-convex section, could be related to the progressive adaptation of the major chela to perform an opercular function, adapting to the shape of the aperture of the host shell (as proposed by Ferratges et al., 2021a, p. 9, figs. 4, 5).

Family Paguridae Latreille, 1802
Genus *Pagurus* Fabricius, 1775

Type species.—*Cancer bernhardus* Linnaeus, 1758 by original designation.

Fossil species included.—*Pagurus alabamensis* Rathbun, 1935; *P. alatoides* Philippe and Secrétan, 1971*; P. albus* Müller, 1979 (=*P. tuberculosus* Harvey, 1998); *P. avellanedai* Via, 1951; *P. banderensis* Rathbun, 1935; *p.* aff. *P. bernhardus* (Linnaeus, 1758); *P. concavus* Müller, 1979; *P. convexus* Whetstone and Collins, 1982; *P. granosipalm* (Stimpson, 1859); *P. langei* Collins and Jakobsen, 2003; *P. latidactylus* Müller and Collins, 1991; *P. malloryi* Schweitzer and Feldmann, 2001; *P. manzonii* (Ristori, 1888); *P. marceti* Via, 1959; *P. marini* Via, 1959; *P. mezi* Lörenthey, 1909; *P. rakosensis* Müller, 1979; *P. squamosus* Ristori, 1886; *P. texensis* Franţescu, 2014; *P. travisensis* Stenzel, 1945; *P. turcus* Müller, 1984, and *P. valdagnensis* Beschin et al., 2012.

?*Pagurus* sp.
Figure 9

Description.—Right cheliped moderately stout, short (Fig. 9). Palm subquadrate in shape, densely covered by subconical granules on the outer surface; inner surface smooth; gently convex dorsal surface, with numerous closely spaced small conical tubercles; inner surface gently convex, with scattered small, low tubercles. Lower margin slightly concave. The preserved portion of dactylus robust, with the same ornamentation as the palm.

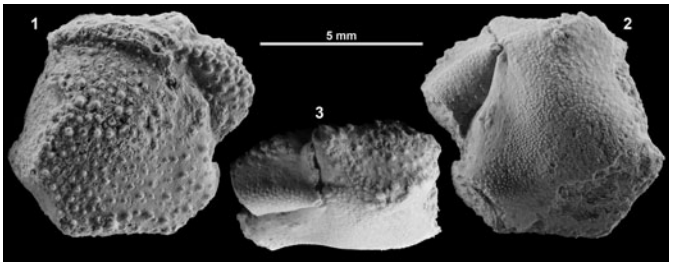

Figure 9. ?*Pagurus* sp. (**1–3**) Right cheliped (specimen MPZ 2021/32): (**1**) lateral view of outer side; (**2**) lateral view of inner side of right chela; (**3**) oblique upper view. Specimen whitened with ammonium chloride sublimate.

Material.—MPZ 2021/32 is a partial right chela (length 6.2 mm and width 6.5 mm) with well-preserved cuticle, and MPZ 2022/60 is a partial right propodus.

Remarks.—Numerous fossil taxa have been assigned to the genus *Pagurus* (see the preceding), and it is widely acknowledged to most likely be a cluster of different genera, so a revision is necessary (Schweitzer and Feldmann, 2001). This happens because most of the taxonomic and diagnostic features to differentiate between modern genera are not preserved in fossil material (i.e., Jagt et al., 2006; Fraaije, 2014; Fraaije et al., 2014).

The recovered material consists of a very incomplete single right chela, but it shares several features with extant members of *Pagurus*. According to the general shape of the chela (a well-developed palm that maintains its height along its entire length) and dense tuberculate ornamentation, appears to be most similar to the genus *Pagurus*. For this reason, we have taken the most conservative approach and placed the material within *Pagurus*.

The extant species of the genus present a robust right chela, globular, with outer and inner surface of the palm strongly convex, and the outer surface of propodus covered by dense granules (Sánchez and Campos, 1978; McLaughlin et al., 2010; Lima and Lemaitre, 2016). Fossil species are also characterized by globular, convex surfaces with the outer surface of the propodus densely granulated (Via, 1959; Schweitzer and Feldmann, 2001; De Angeli and Caporiondo, 2017). Some recent species (i.e., *P. spinossior* Komai, Reshmi, and Kumar, 2013) bear similarities with the scarce material recovered, so we tentatively assign the new material to this genus.

Genus *Anisopagurus* McLaughlin, 1981

Type species.—*Pylopagurus bartletti* Milne Edwards and Bouvier, 1893 by subsequent designation of McLaughlin, 1981.

Species included.—*Anisopagurus actinophorus* Lemaitre and McLaughlin, 1996; *A. asteriscus* Lemaitre, 2020; *A. bartletti* (Milne Edwards and Bouvier, 1893); *A. hopkinsi* Lemaitre and McLaughlin, 1996; *A. pygmaeus* (Bouvier, 1918); *A. vossi* Lemaitre and McLaughlin, 1996.

Remarks.—The genus *Paguritta* Melin, 1939 shows similarities with *Anisopagurus* due to the general shape of the chela and the row of spines on the upper and lower margins of the palm. *Anisopagurus* is distinguishable from *Paguritta* in having the outer surface of the palm densely covered by hemispherical, pearled granules closely spaced (while all species of *Paguritta* bear small conical spines); the fingers are characterized by strong longitudinal ridges, while in all species of *Paguritta* the fingers are flattened (see Komai and Nishi, 1996, p. 463–464, 472, figs. 4, 5; Komai and Okuno, 2001, p. 299, figs. 3, 4; McLaughlin and Lemaitre, 1993, p. 5, figs. 1, 3, 5, 7, 9, 11).

The modern genus *Rhodochirus* McLaughlin, 1981 also shows similarities with *Anisopagurus* in the general shape of the chela. However, *Rhodochirus* presents some differences, such as the more pointed fingers, coalescent granules on fixed finger, outer surface of the palm covered with large spiny tubercles with basal rosettes (see McLaughlin, 2003, p. 117, 127, fig. 6; Parente and Hendrickx, 2005, fig. 1; Komai, 2013, p. 29).

Anisopagurus primigenius new species
Figure 10

Type material.—The holotype, MPZ 2021/31, is a complete right propodus (propodus length: 9.9 mm; palm length: 5.2 mm; palm height: 5.6 mm) with well-preserved cuticle but without movable finger. There are two incomplete right propodi (paratypes), MPZ 2022/39 and MGSB77624.

Diagnosis.—Right cheliped suboperculate, D-shaped in cross section; posterior margin slightly offset toward the inner surface; outer surface of palm tuberculated, surrounded by spines directed vertically; inner surface with squamous tubercles.

Description.—Right cheliped suboperculate (Fig. 10), ovate, approximately twice as long as high, flattened dorsoventrally, D-shaped in cross section; angle of articulation propodus/carpus 15° from perpendicular; upper margin broadly arched, bearing small conical teeth directed forward; lower margin slightly arched. Palm semicircular, as long as high, with median region moderately elevated in the outer surface, surrounded by a more or less flat surface. Outer surface covered with numerous fungiform tubercles and surrounded by strong spines directed nearly vertically forming crown-like shape (Fig. 10). Inner surface convex, with small squamous tubercles. Fingers slender and elongated, dactylus and fixed finger with a longitudinal ridge. Fixed finger with blunt termination, about as long as the palm. Occlusal margin with two aligned molariform teeth. Left cheliped unknown.

Etymology.—From the Latin adjective *primigenius* (the oldest) to emphasize the geological seniority of this paguroid.

Other material examined.—Two partial right propodi (MPZ 2022/39 and MPZ 2022/61) and one isolated right dactylus (MPZ 2022/40).

Remarks.—Ferratges et al. (2021b) tentatively suggested that this taxon could be assigned to either *Paguritta* Melin, 1939 or *Rhodochirus* McLaughlin, 1981. However, a more detailed study of the material suggests that this species fits better in *Anisopagurus*. *Anisopagurus primigenius* n. sp. can be differentiated from other species of the genus on the basis of

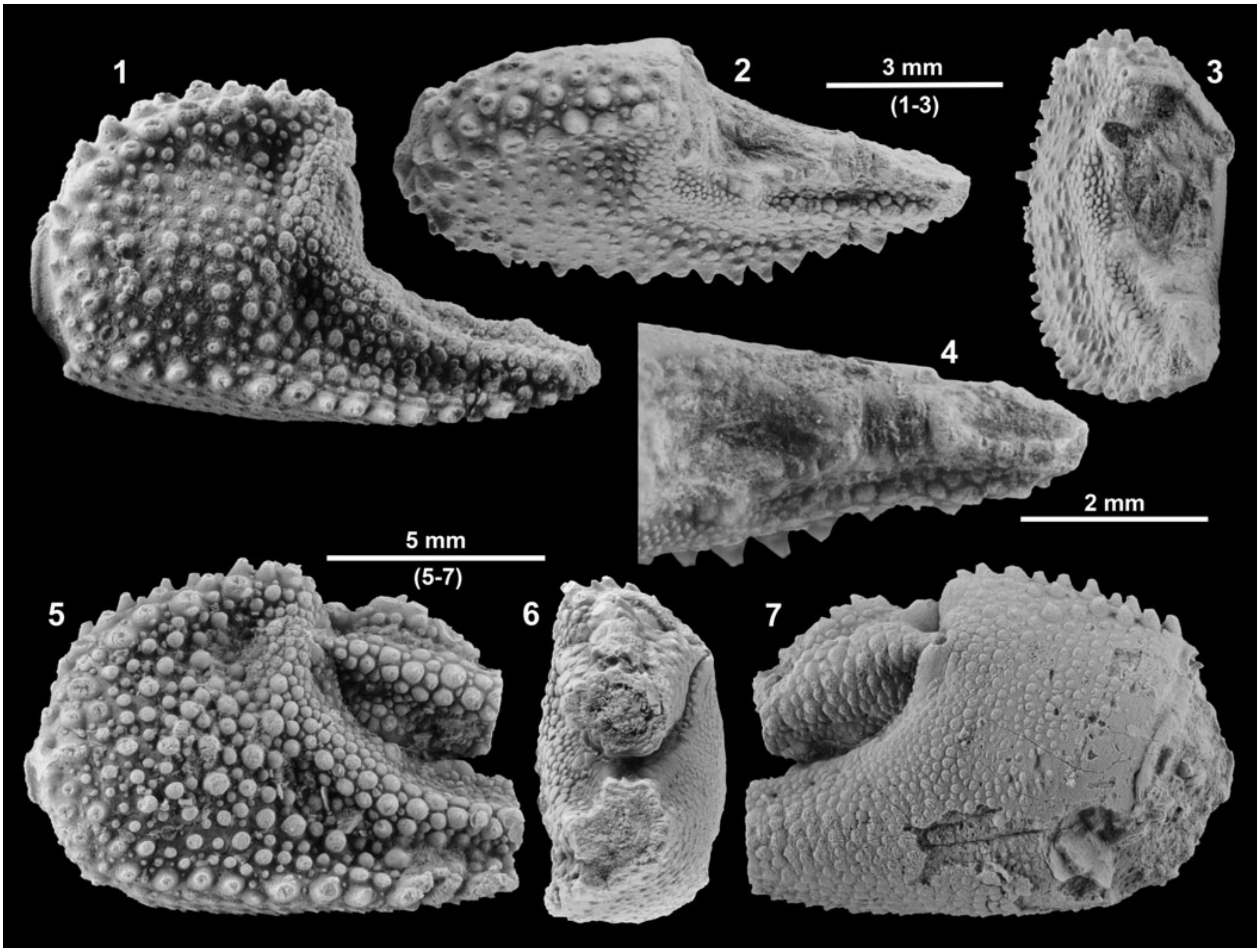

Figure 10. *Anisopagurus primigenius* n. sp. (**1–4**) Holotype (MPZ 2021/31), right chela: (**1**) lateral view of outer side; (**2**) oblique upper view; (**3**) frontal view. (**4**) Detail of the occlusal margin with two teeth. (**5–7**) Paratype (MGSB77624), right chela: (**5**) lateral view of outer side; (**6**) frontal view; (**7**) lateral view of inner side. Specimens whitened with ammonium chloride sublimate.

its density of ornamentation and shape of its fungiform tubercles, covering the entire outer surface, very tight on both fingers, almost coalescing, and the two rows of spines on the upper margin.

A. primigenius n. sp. is morphologically close to species of *Paguritta* due to the general shape of the chela and the row of spines in the upper and lower margins of the palm. Nevertheless, *A. primigenius* n. sp. is easily distinguishable from *Paguritta* sp. by having the outer surface of the palm densely covered by closely spaced hemispherical, pearled granules (while all species of *Paguritta* bear small conical spines); the fingers are characterized by strong longitudinal ridges in *A. primigenius* n. sp. while in all species of *Paguritta* the fingers are flattened (see Mclaughlin and Lemaitre, 1993, p. 5, figs. 1, 3, 5, 7, 9, 11; Komai and Nishi, 1996, p. 463–464, 472, figs. 4, 5; Komai and Okuno, 2001, p. 299, figs. 3, 4).

The modern species assigned to *Rhodochirus* also show similarities with *Anisopagurus primigenius* n. sp. in the general shape of the chela. However, differences include the more pointed fingers, coalescent granules on the fixed finger, and outer surface of the palm covered with large spiny tubercles with basal rosettes (see McLaughlin, 2003, p. 117, 127, fig. 6; Parente and Hendrickx, 2005, fig. 1; Komai, 2013, p. 29).

Regarding the fossil record, *Anisopagurus primigenius* n. sp. seems to share some characteristics with *Lessinipagurus granulatus* and *L. planus*, such as the general ornamentation and the fixed and movable fingers with elongated longitudinal ridges. Nevertheless, *A. primigenius* n. sp. presents differences in the general shape, with a more elongated propodus and fingers. In *Lessinipagurus*, the complete chela is subcircular, not elongated, and the upper margin is extremely salient, visor-shaped (see Beschin et al., 2012, p. 29, fig. 22; De Angeli and Caporiondo, 2017, p. 20–22, figs. 14, 15).

Final remarks and conclusions

The global record of Paleogene paguroids is poor and often fragmentary. Specifically, in the Iberian Peninsula, only six species have previously been described from the Eocene. Via (1959) first described *Pagurus marceti*, *Pagurus marini*, and *Eocalcinus eocenicus* on the basis of fragmentary material. Ferratges et al. (2020) described a nearly complete specimen of *Diogenes* *augustinus*, and Ferratges et al. (2021b) recently described two new species (*Parapetrochirus robustus* and *Eocalcinus gerardbretoni*) from the lower and upper Eocene, respectively.

This new contribution includes representatives of four families (Annuntidiogenidae, Diogenidae, Calcinidae, and Paguridae) and increases our knowledge of known taxa (six new species) of paguroids from the early Eocene associated with reef environments. Specifically, the studied assemblage of paguroids inhabited shallow reef complexes of the Serraduy Formation within the euphotic to mesophotic zone (see Ferratges et al., 2021b).

Some of the taxa studied in the present work show close relationships with several modern genera (*Anisopagurus*, *Clibanarius*, *Dardanus*, *Paguristes*, *Pagurus*, *Petrochirus*). In general, these modern hermit crabs are common in intertidal and shallow-water areas of tropical and temperate seas (i.e., Forest and Saint-Laurent, 1968; Hazlett, 1981; Leite et al., 1998; Melo, 1999; Rahayu, 2006; Rahayu and Forest, 2009; Mantelatto et al., 2010; McLaughlin et al., 2010; Trivedi and Vachhrajani, 2017).

This study contributes to the understanding of paguroid diversity during the Eocene in the southern Pyrenean basins. In addition, the data provided increase the knowledge of European fossil paguroids, providing several new taxa, some of which correspond to the oldest representatives of their respective genera. Our study also increases the temporal distribution of the genus *Eocalcinus* with the oldest record of the genus. In addition, the new materials assigned to this genus suggest an evolutionary trend toward more rounded shapes. The oldest species of *Eocalcinus* had a more elongated outline, a straighter lower margin, and a less marked plano-convex section of the palm. This trend toward more rounded shapes could be related to the progressive adaptation of the major chela to perform an opercular function (Ferratges et al., 2021a).

Gastropod shells are vital for most hermit crab species, being essential for their survival (see Tricarico and Gherardi, 2006 and references therein). The great abundance and diversity of gastropods observed in the studied outcrop (see Ferratges et al., 2021b) probably contributed to the diversity of hermit crabs. In modern ecosystems, the availability of gastropod shells plays an important role in limiting the abundance of hermit crabs (Vance, 1972; Bach et al., 1976; Kellogg, 1976), and their diversity reduces competition between different genera. In fact, some modern species show a marked preference for certain empty shells over others (i.e., Vance, 1972; Conover, 1978; Bertness, 1980). Thus, the mechanism allowing coexistence of several taxa in the same environment involves both resource and habitat partitioning (Vance, 1972).

The data provided here show a great diversity of paguriods at the beginning of the Eocene, which is richer than Paleocene records (see Jakobsen et al., 2020 and references therein), and show that the reefs of the lower Eocene were important hotspots of pagurid diversities comparable to modern ecosystems.

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6.1.2. BRACHYURA

Los cangrejos verdaderos o braquiuros se encuentran entre los habitantes más diversos de las comunidades bentónicas actuales, estando presentes en gran cantidad de nichos, especialmente en sistemas arrecifales (Plaisance *et al*., 2011, Hurley *et al*., 2016). El conjunto de nichos ecológicos y los factores ecológicos que ofrecen los arrecifes probablemente afectaron a la diversificación de los braquiuros durante el Eoceno, y como consecuencia muchas familias modernas aparecen en el Eoceno (p. ej., Brösing, 2008; Tsang *et al*., 2014; Schweitzer y Feldmann, 2015; Ferratges *et al*., en revisión). El grupo en general muestra una gran diversificación en el Eoceno (p. ej., Fraaije, 2003; Feldmann y Schweitzer, 2006; Brösing, 2008; Hartzell, 2022). Se ha propuesto que su éxito evolutivo puede estar relacionado con sus hábitos y su morfología compacta (Števčić, 1971) (Figs. 3, 25A-B).

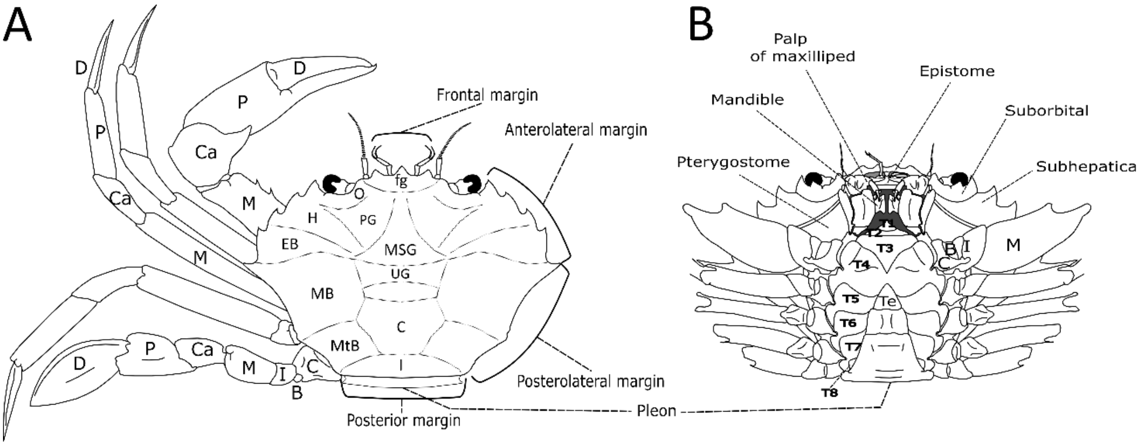

Figura 25: Anatomía dorsal (**A**) y ventral (**B**) de un braquiuro: C-D: Regiones del caparazón y terminología utilizada en el texto. PG = región protogástrica; MSG = región mesogastrica; H = región hepática; UG = región urogástrica; C = región cardíaca; EB = región epibranquial; PB = región posbranquial (regiones meso y metabranquial); I = región intestinal; fg = surco frontal; bcg = surco branquiocárdico.

Figura 25: Dorsal (**A**) and ventral (**B**) anatomy of a brachyuran: C-D: Carapace regions and terminology used in the text. PG = protogastric region; MSG = mesogastric region; H = hepatic region; UG = urogastric region; C = cardiac region; EB = epibranchoial region; PB = postbranchial region (meso- and metabranchial regions); I = intestinal region; fg = frontal groove; bcg = branchiocardiac groove.

En gran medida, el material recolectado durante esta Tesis Doctoral es fragmentario y se compone de caparazones aislados. Sin embargo, estos restos presentan importantes características morfológicas que permiten no solo relacionarlos con otros taxones, sino que aportan datos acerca del origen de diferentes grupos y permiten proporcionar descripciones formales de los nuevos taxones (Fig. 26).

Para la estructuración de este subapartado se ha organizado el orden de los artículos de manera que en primer lugar se abordan los cangrejos más primitivos (hasta hace poco agrupados como "podotremas") y posteriormente los más derivados (Eubraquiuros). Después se hace un estudio filogenético centrado en los parthenopidos un grupo con representantes actuales y fósiles, y que era especialmente problemático desde un punto de vista filogenético (Parthenopoidea MacLeay, 1838).

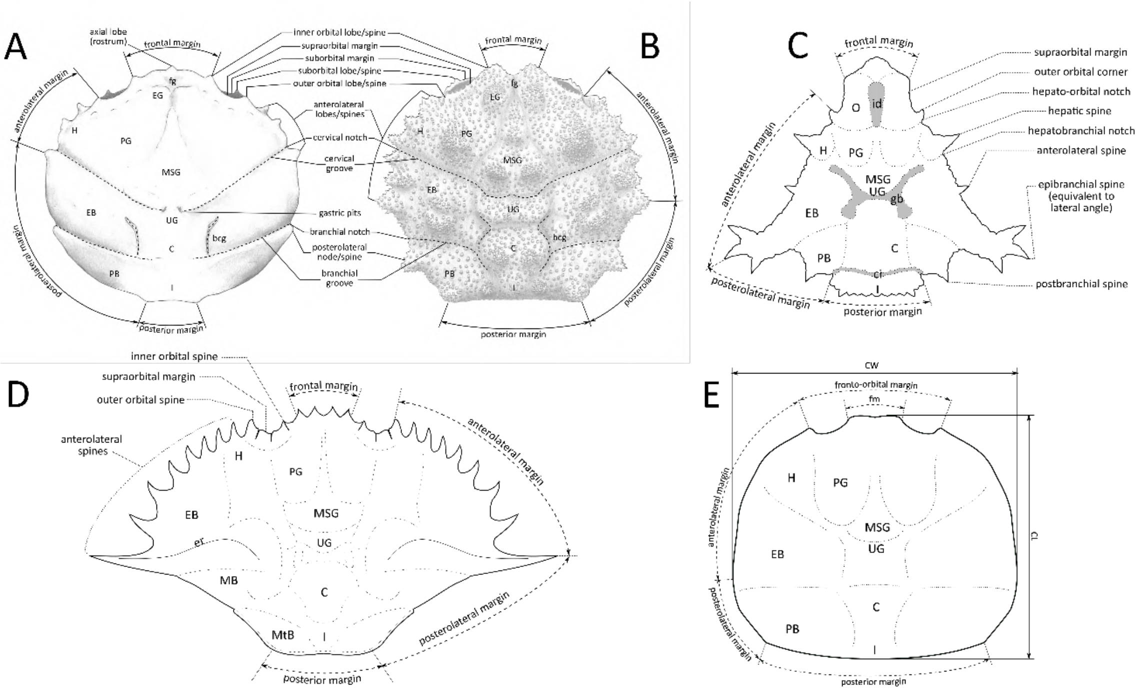

Figura 26: Ejemplos de diferentes esquemas de planos corporales estudiados durante la tesis. **A**-**B**: Regiones del caparazón y terminología dromioideos (s. lat.) utilizado en el texto (basado en McLay, 1999); **C**: *Phrynolambrus*; **D**: *Portunus*; **E**: *Asthenognathus*; C: región cardíaca; EB: región epibranquial; EG: región epigástrica; H: región hepática; I: región intestinal; MSG: región mesogastrica; MtB: región metabranquial; PG: región protogástrica; UG: región urogástrica; PB: región posbranquial (regiones meso y metabranquial); bcg: surco branquiocárdico; ci: surco cardio-intestinal; fg: surco frontal; gb: surco gastro-branquial; id: depresión inter-orbital.

Figure 26: Examples of different body plan schemes studied during the PhD. **A**-**B**: Carapace regions and terminology in a dromiid (s. lat.) crab used in the text (based on McLay, 1999); **C**: *Phrynolambrus*; **D**: *Portunus*; **E**: *Asthenognathus*; C: cardiac region; EB: epibranchial region; EG: epigastric region; H: hepatic region; I: intestinal region; MSG: mesogastric region; MtB: metabranchial region; PG: protogastric region; UG: urogastric region; PB: postbranchial region (meso- and metabranchial regions); bcg: branchiocardial groove; ci: cardio-intestinal groove; fg: frontal groove; gb: gastro-branchial groove; id: inter-orbital depression.

Infraorden Brachyura Linnaeus, 1758

Superfamilia Dromioidea De Haan, 1833

Los dromioideos modernos son constituyentes importantes en latitudes tropicales o subtropicales y están representados por más de 140 especies (p. ej., Guinot y Tavares, 2003; De Grave *et al*., 2009). Por lo general, están asociados con ambientes arrecifes o fragmentos de corales que van desde la zona intermareal hasta aguas más profundas (1-450 m; p. ej., McLay, 1993, 2001; Takeda y Manuel-Santos, 2006). Los dromioideos suelen transportar fragmentos de esponjas u otros objetos con la ayuda de los pereiópodos P4-P5 (Dromiidae) o se esconden en grietas de coral y otros sustratos duros (Dynomenidae) (McLay, 2001).

A lo largo de la presente Tesis Doctoral se han estudiado diversos representantes de este grupo. Entre ellos, destaca la agrupación del Eoceno inferior de Ramals que corresponde a taxones asociados a ambientes arrecifales. Otras localidades con afloramientos del Paleoceno y Eoceno en toda Europa han proporcionado drómidos y dinoménidos similares (ver detalles en Artal *et al*., 2022). Sin embargo, todos esos conjuntos se caracterizan por una baja diversidad.

El registro de dromioideos del Eoceno incluye 58 especies descritas hasta la fecha (ver detalles en Artal *et al*., 2022). Muchos de estos se conocen en cuencas del área mediterránea y están relacionados principalmente con ambientes coralinos (ver Artal *et al*., 2022). Con base a datos sedimentológicos, parece probable una preferencia por los ambientes de arrecifes para el Ypresiense. Esto puede estar relacionado con el desarrollo de complejos de arrecifes "modernos", como resultado de las condiciones climáticas y ambientales de la época (ver Pomar *et al*., 2017), que permitieron que los dromioides habitaran tales entornos. Sin embargo, durante el Eoceno medio, esta tendencia parece haberse invertido y las mayores diversidades aparecen en ambientes siliciclásticos o no arrecifales sobre plataformas poco profundas. Esto podría estar relacionado con un cambio en las preferencias ambientales de los drómidos en ese momento y su expansión en ambientes siliciclásticos, pero también podría estar relacionado con el pobre registro de facies arrecifales en este intervalo de tiempo. Finalmente, durante el Eoceno tardío se observa un nuevo incremento en la diversidad en los ambientes arrecifales.

Familia Dromiidae De Haan, 1833

Subfamilia Basinotopinae Karasawa, Schweitzer, and Feldmann, 2011

Género *Mclaynotopus* † Artal, Ferratges, van Bakel y Zamora, 2022

Se ha descrito este nuevo género para incluir la nueva especie *Mclaynotopus longispinosus* Artal, Ferratges, van Bakel y Zamora, 2022 y la especie *Mclaynotopus alpina* (Glaessner, 1929) antes incluida en el género *Dromilites*, ya que sus características diferían del resto de dromioideos (Fig. 27E-F).

Subfamilia Dromiinae De Haan, 1833

Género *Torodromia* † Artal, Ferratges, van Bakel y Zamora, 2022

Se ha descrito este nuevo género para incluir la nueva especie *Torodromia elongata* Artal, Ferratges, van Bakel y Zamora, 2022, ya que sus características diferían del resto de dromioideos (Fig. 27C-D). Los caracteres principales de *Torodromia* permiten su inclusión en la subfamilia Dromiinae.

Subfamily Sphaerodromiinae Guinot and Tavares, 2003

Género *Basidromilites* † Artal, Ferratges, van Bakel y Zamora, 2022

Se ha descrito este nuevo género para incluir a la nueva especie *Basidromilites glaessneri* Artal, Ferratges, van Bakel y Zamora, 2022 (Fig. 27A-B), y la especie *Basidromilites pastoris* (Via, 1959) antes incluida en el género *Dromilites*. También se ha recuperado un espécimen cuyas características eran similares a ambas especies pero con ligeras diferencias, por lo que se ha dejado en nomenclatura abierta (*Basidromilites* sp.).

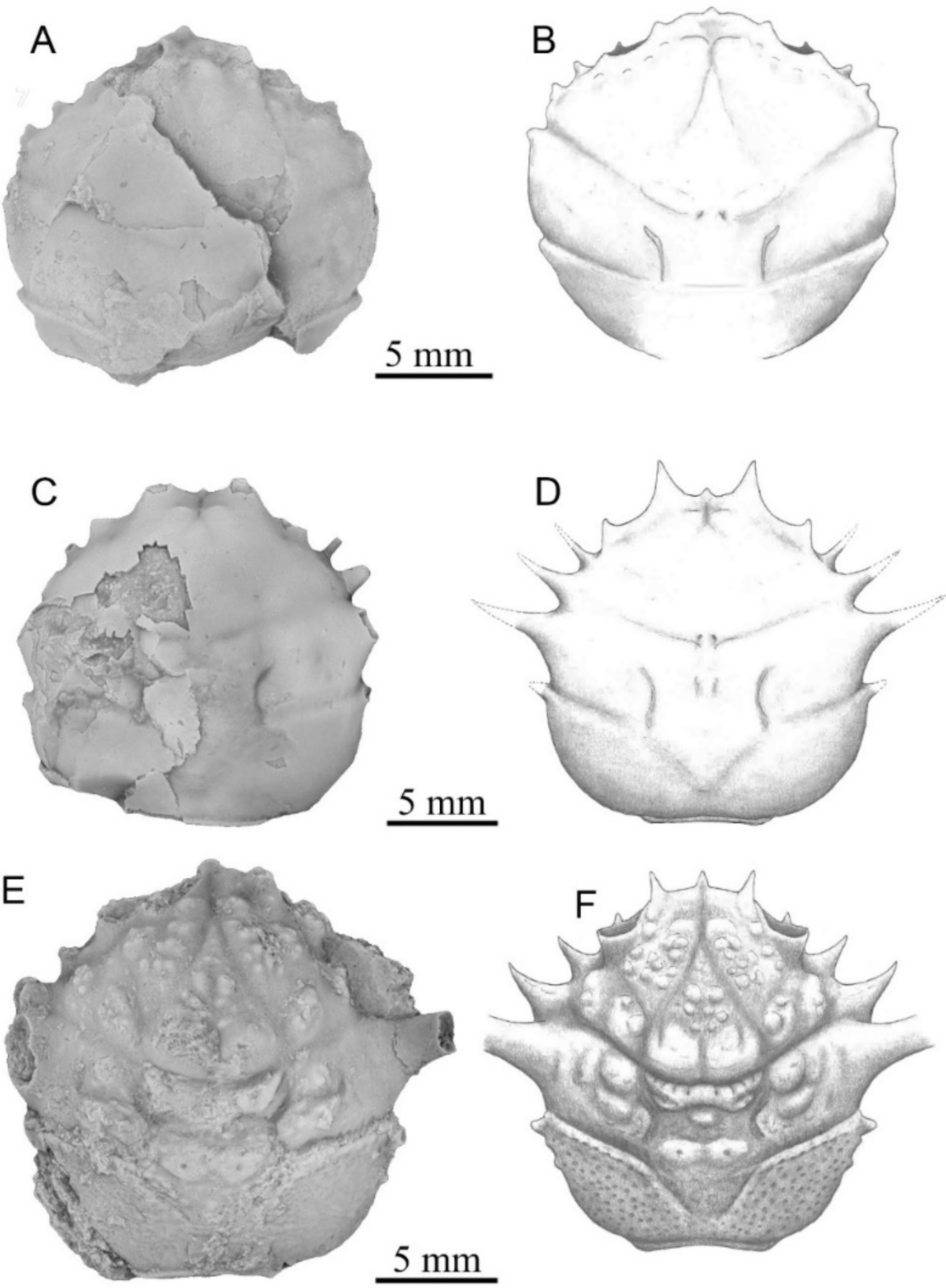

Figura 27: Representantes de la Familia Dromiidae De Haan, 1833 del Eoceno inferior de Ramals y sus respectivas reconstrucciones: **A**-**B**: *Basidromilites glaessneri* Artal, Ferratges, van Bakel y Zamora, 2022 (paratipo MGSB77600); **C**-**D**: *Torodromia elongata* Artal, Ferratges, van Bakel y Zamora, 2022 (holotipo MGSB77595); **E**-**F**: *Mclaynotopus longispinosus* Artal, Ferratges, van Bakel y Zamora, 2022 (MGSB77597).

Figure 27: Representatives of the Family Dromiidae De Haan, 1833 from the early Eocene of Ramals and their respective reconstructions: **A**-**B**: *Basidromilites glaessneri* Artal, Ferratges, van Bakel & Zamora, 2022 (paratype MGSB77600); **C**-**D**: *Torodromia elongata* Artal, Ferratges, van Bakel & Zamora, 2022 (holotype MGSB77595); **E**-**F**: *Mclaynotopus longispinosus* Artal, Ferratges, van Bakel & Zamora, 2022 (MGSB77597).

Familia Dynomenidae Ortmann, 1892

Subfamilia Dynomeninae Ortmann, 1892

Género *Dynomene* † Desmarest, 1823

La descripción de los géneros y especies incluidas en Dynomenidae, se realiza generalmente en base a un conjunto de caracteres que no se preservan habitualmente en el registro fósil (ver detalles en Ossó *et al*., 2020a), por lo que la descripción del material fósil se limita a las características dorsales. En este caso, las características morfológicas dorsales coinciden con las principales características diagnósticas de Dynomenidae más que de Dromiidae (ver detalles en Ossó *et al*., 2020a), y en particular con el género *Dynomene*, pero difieren lo suficiente para considerarla como una especie diferente: *Dynomene collinsi* Ossó, Domíngues, De Angeli y Ferratges, 2020.

La presencia de *Dynomene collinsi* en los afloramientos del Priaboniense inferior del sector central de las cuencas Surpirenaicas representa el primer registro del género en el Cenozoico de la Península Ibérica, y rellena la brecha temporal entre las especies de este género durante el Ypresiense y el Oligoceno presentes en el norte de Italia (Ossó *et al*., 2020a).

Subfamilia Paradynomeninae Guinot, 2008

Género *Kromtitis* † Müller, 1984

El género *Kromtitis* se ha relacionado previamente con ciertos dinoménidos modernos, como *Paradynomene* Sakai 1963 (ver Beschin *et al*., 2007; Guinot, 2008). En la nueva especie *Kromtitis isabenensis* Artal, Ferratges, van Bakel y Zamora, 2022 (Fig. 28A-B) así como en sus congéneres, todas las características son las que también se ven en los representantes modernos de la subfamilia Paradynomeninae (ver McLay y Ng, 2005), por lo que se incluye en este grupo.

Género *Sierradromia* † Artal, Ferratges, van Bakel y Zamora, 2022

Se ha descrito este nuevo género para incluir a la nueva especie *Sierradromia gladiator* Artal, Ferratges, van Bakel y Zamora, 2022 (Fig. 28C-D). Este nuevo género y especie es diferente al resto de dromioideos (actuales y fósiles), sin embargo, la mayoría de las características son las que también se ven en los representantes de la subfamilia Paradynomeninae, por lo que se incluye en este grupo, ampliando su diversidad conocida.

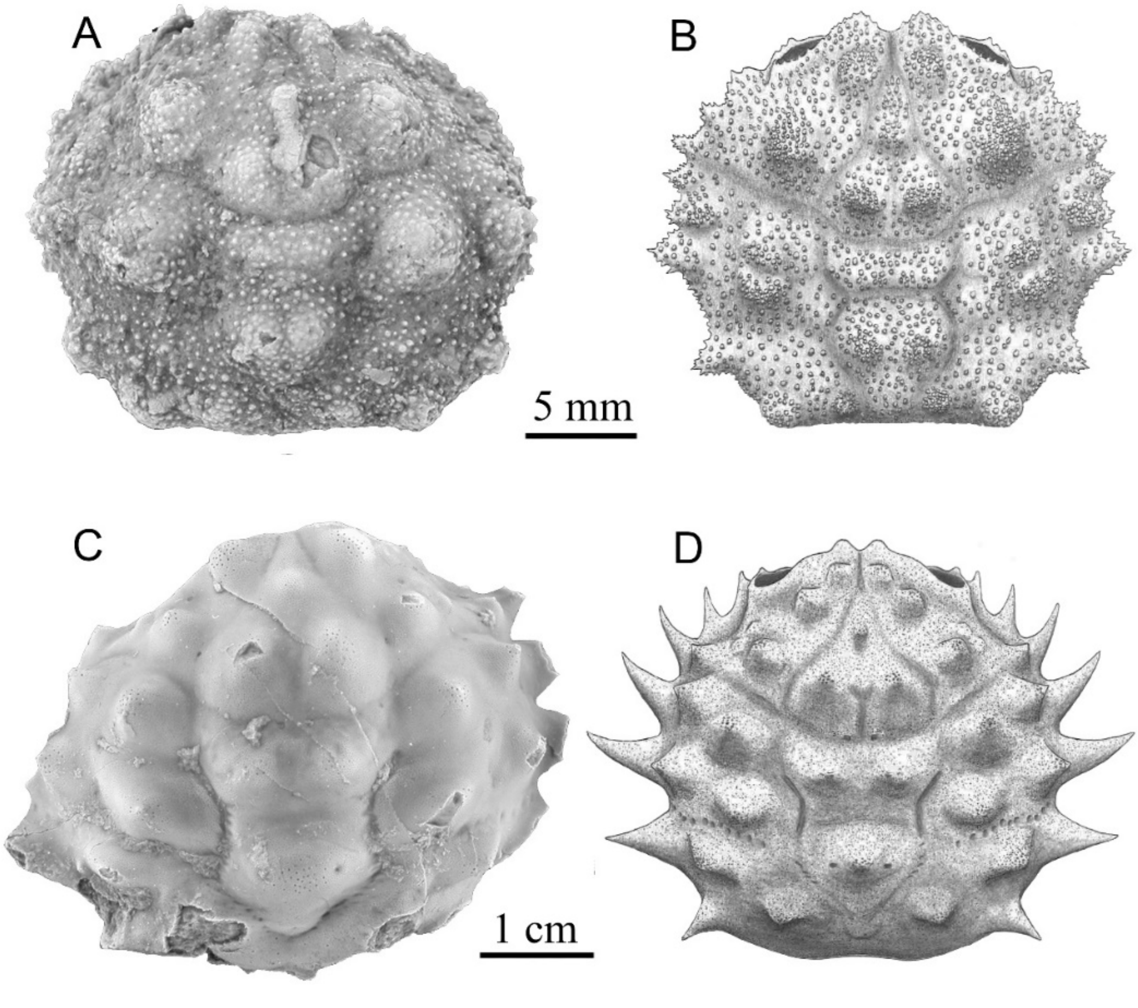

Figura 28: Representantes de la Familia Dynomenidae Ortmann, 1892 del Eoceno inferior de Ramals: **A**-**B**: *Kromtitis isabenensis* Artal, Ferratges, van Bakel y Zamora, 2022 (Holotipo MGSB75450) y su reconstrucción; **C**-**D**: *Sierradromia gladiator* Artal, Ferratges, van Bakel y Zamora, 2022 (Holotipo MGSB75454) y su reconstrucción.

Figure 28: Representatives of the Family Dynomenidae Ortmann, 1892 from the early Eocene of Ramals: **A**-**B**: *Kromtitis isabenensis* Artal, Ferratges, van Bakel & Zamora, 2022 (Holotype MGSB75450) and its reconstruction; **C**-**D**: *Sierradromia gladiator* Artal, Ferratges, van Bakel & Zamora, 2022 (Holotype MGSB75454) and its reconstruction.

Familia *incertae sedis*

Género *Basinotopus* † M'Coy, 1849

El Eoceno inferior de Ramals ha proporcionado restos de una especie de *Basinotopus* no asignable a una especie concreta. Sin embargo, este nuevo descubrimiento extiende la presencia del género al Eoceno inferior de la Península Ibérica (ver Artal *et al*., 2022).

Género *Gemmellarocarcinus* † Checchia-Rispoli, 1905

El Eoceno superior de La Peña ha proporcionado una nueva especie de un drómido problemático: *Gemmellarocarcinus riglosensis* Ferratges, Zamora y Aurell, 2020 (Fig. 29); que muestra similitudes con otras especies de este género (ver detalles Ferratges *et al*., 2020a). Esta nueva cita extiende la presencia del género al Eoceno superior de la Península Ibérica. La ubicación de *Gemmellarocarcinus* a nivel de familia es problemática (Karasawa *et al*., 2011) debido a la ausencia de elementos esternales y pleonales (igual que en la mayoría de los representantes de este grupo), por lo que se consideró a *G. riglosensis* como *incertae sedis* dentro de la superfamilia Dromioidea.

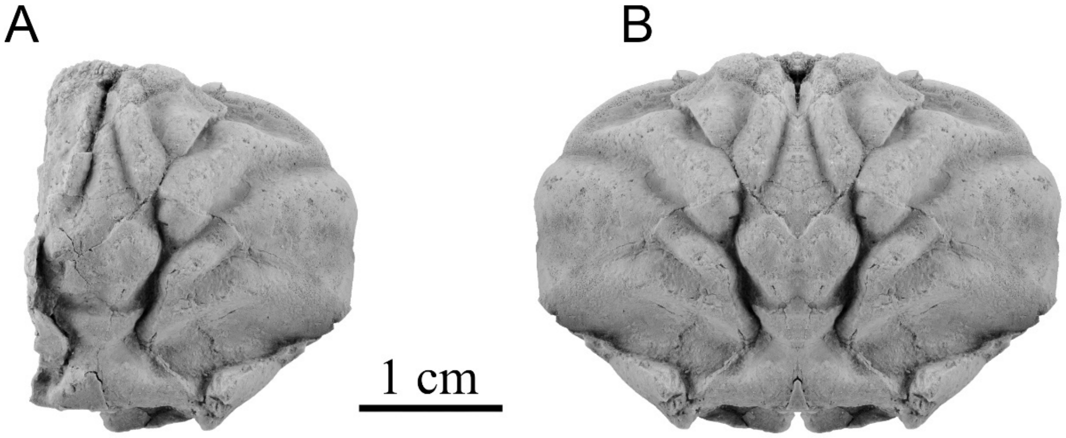

Figura 29: *Gemmellarocarcinus riglosensis* Ferratges Zamora y Aurell, 2020a, A: holotipo (MPZ 2019/1722), en vista dorsal. B. reconstrucción en espejo.

Figure 29: *Gemmellarocarcinus riglosensis* Ferratges Zamora & Aurell, 2020a, A: holotype (MPZ 2019/1722), in dorsal view. B. mirrored reconstruction.

Superfamilia Homoloidea De Haan, 1839

Familia Homolidae De Haan, 1839

Género *Paromola* Wood-Mason en Wood-Mason y Alcock, 1891

Se ha descrito una nueva especie de cangrejo homólido de la Formación Roda (Eoceno inferior, Ypresiense). A pesar de que el único ejemplar se halla parcialmente fragmentado (Fig. 30), la similitud morfológica con especies actuales de los elementos conservados, permite su ubicación en el género *Paromola* Wood-Mason and Alcock, 1891. Además, *Paromola bretoni* corresponde al primer homólido encontrado en el Cenozoico de la Península Ibérica y uno de los más antiguos de este género (ver detalles en Ferratges *et al*., 2021b).

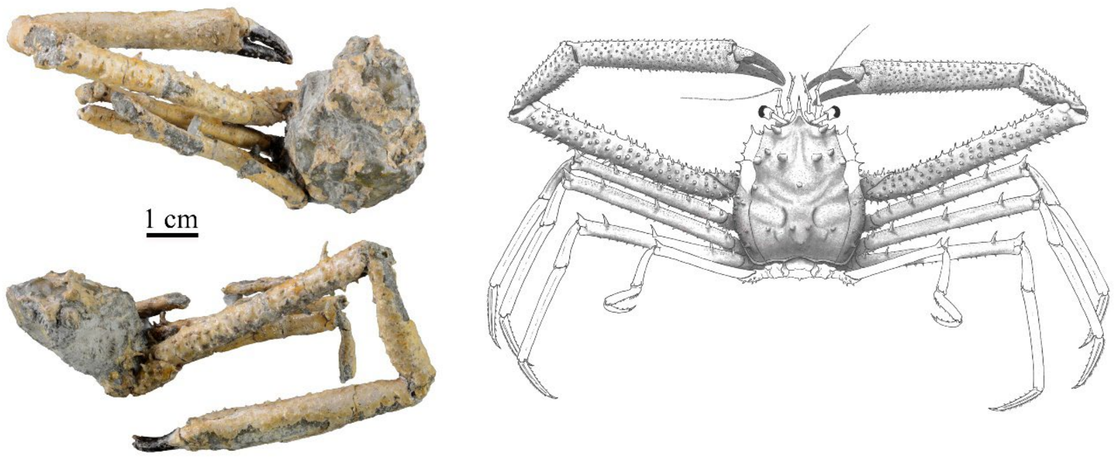

Figura 30: Holotipo de *Paromola bretoni* Ferratges, Domínguez y Ossó, 2021 (MPZ 2020/615). **A**: vista dorsal; **B**: vista frontal; **C**: Reconstrucción idealizada de *Paromola bretoni*, las partes sombreadas tomadas del espécimen y las partes claras tomadas de Paromola spp.

Figure 30: Holotype of *Paromola bretoni* Ferratges, Domínguez & Ossó, 2021 (MPZ 2020/615). **A**: dorsal view; **B**: frontal view; **C**: Idealized reconstruction of *Paromola bretoni*, the shaded parts taken from the specimen, and light parts taken from extant Paromola spp.

Superfamilia Raninoidea De Haan, 1839

Se han recogido algunos taxones pertenecientes a la Superfamilia Raninoidea en diferentes áreas muestreadas. Destacan los del Eoceno inferior, de los cuales se han asignado a géneros concretos dos de estos taxones (ver abajo). El resto se encuentra actualmente en estudio.

Los análisis estadísticos llevados a cabo en Ferratges *et al*. (2021c) indican que este conjunto es característico del frente arrecifal (*inner fore-reef*). Sin embargo, el estudio de los parientes modernos indica que están adaptados a sustratos blandos (ver detalles en Ferratges *et al*., 2021c), por lo que probablemente ocupaban áreas de fondos blandos cercanas al arrecife. Esto parece sugerir que no fueron sólo los eubraquiuros los que utilizaron la periferia de los ambientes arrecifales como refugio en el Eoceno temprano.

Familia Raninidae De Haan, 1839

Subfamilia Raninoidinae† Lőrenthey in Lőrenthey and Beurlen, 1929

Género *Quasilaeviranina* † Tucker, 1998

Uno de los taxones que se ha podido asignar a un género concreto es *Quasilaeviranina* sp. (ver Ferratges *et al*., 2021c y Fig. 31D-E), que corresponde a la primera cita de este género en la Península Ibérica.

Subfamilia Ranininae De Haan, 1839

Género *Ranina* Lamarck, 1801

El otro ranínido que se puede asignar a un género concreto es *Ranina* sp. (ver Ferratges *et al*., 2021c y Fig. 31A-B). Según Nyborg *et al*. (2003), el género *Ranina* estaba bien establecido en el Océano Pacífico nororiental desde al menos el Eoceno temprano. Este nuevo taxón representa la primera cita del género *Ranina* en la Península Ibérica, e indica que este género se estableció en la periferia de ambientes circundantes a los arrecifales del Eoceno inferior de la Cuenca de Tremp-Graus, también en el Eoceno inferior.

Recientemente, Pasini y Garassino (2017) hicieron una revisión de las especies fósiles pertenecientes al género *Ranina* Lamarck, 1801 (Fig. 31C). Estos autores concluyen que la sistemática de este género es problemática, y la asignación específica de esta especie está actualmente en estudio. Sin embargo, las características del nuevo material se ajustan a la diagnosis general de *Ranina* (actual y fósil) recientemente revisada por Karasawa *et al*. (2014).

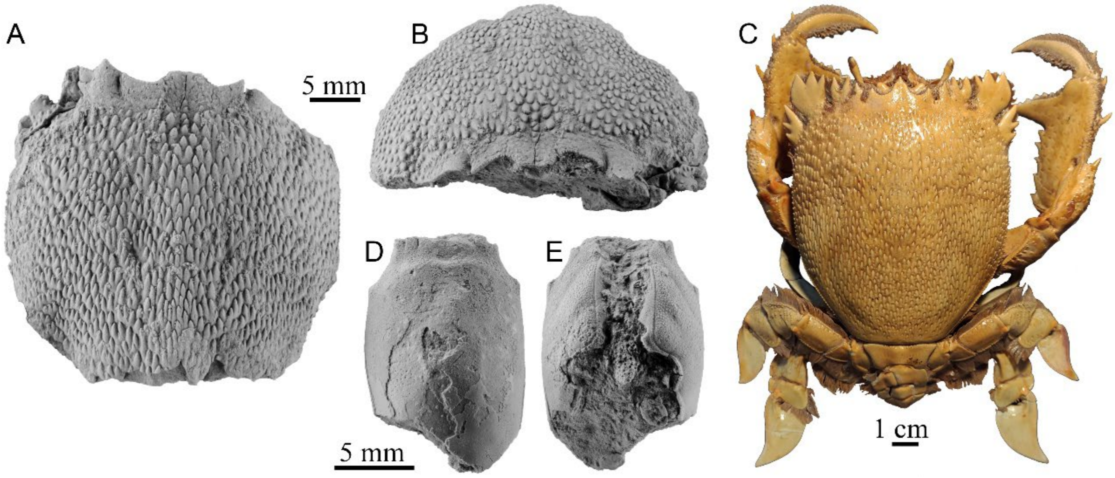

Figura 31: Raninoides del Eoceno temprano de Ramals: **A**-**B**: *Ranina* sp.; **D**-**E**: *Quasilaeviranina* sp.; **C**: *Ranina ranina* actual de Filipinas (Ferratges col.).

Figure 31: Raninoids from early Eocene of Ramals: **A**-**B**: *Ranina* sp.; **D**-**E**: *Quasilaeviranina* sp.; **C**: modern *Ranina ranina* from Philippines (Ferratges col.).

Sección Eubrachyura De Saint Laurent, 1980

Superfamilia Carpilioidea Ortmann, 1893

Los carpiliidos (Superfamilia Carpilioidea) son un grupo actualmente poco diverso, típico de ambientes arrecifales, pero durante el Eoceno muestran una gran diversidad (p. ej., Schweitzer *et al*., 2018). En el área de estudio se han reconocido diferentes taxones, la mayoría de los cuales estan aun por estudiar o en estudio.

Familia Carpiliidae Ortmann, 1893

Género *Liopsalis* † Von Meyer, 1862

Por el momento únicamente se ha asignado un carpílido a nivel de género y especie: *Liopsalis* cf. *anodon* (ver detalles en Ferratges *et al*., 2020a y Fig. 32). El material tipo de *Liopsalis anodon* proviene del Eoceno medio de Italia. Se han asignado otras dos especies a este género, a saber, *L. klipsteini* del Eoceno medio de Alemania y *L. simplex* (Stoliczka, 1871) del Eoceno medio (Luteciense) de la India. Este hallazgo extiende la distribución del género al Eoceno superior de la Península Ibérica.

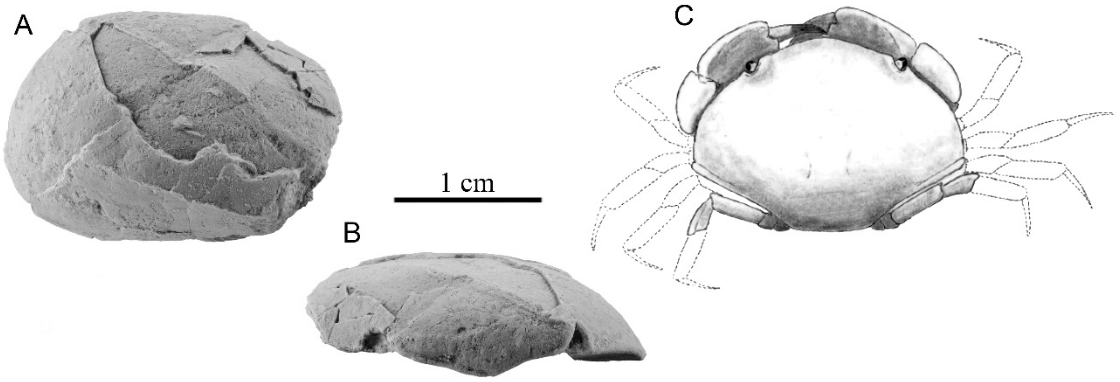

Figura 32: **A**-**B**: *Liopsalis* cf. *anodon* del Eoceno superior de la Fm Arguis; **C**: reconstrucción idealizada de *Liopsalis* sp.

Figure 32: **A**-**B**: *Liopsalis* cf. *anodon* from the upper Eocene of the Arguis Fm; **C**: Idealized reconstruction of *Liopsalis* sp.

Superfamilia Parthenopoidea MacLeay, 1838

Entre los diferentes grupos estudiados destaca el caso de los parthenopoideos con uno de sus representantes más antiguos: *Aragolambrus* Ferratges, Zamora y Aurell, 2019, del Eoceno inferior de Huesca y descrito en el transcurso de esta investigación. Los representantes modernos de este grupo tienen una distribución principalmente tropical o subtropical y generalmente están asociados con sustratos siliciclásticos móviles desde la zona intermareal hasta las aguas profundas (ver detalles en Ferratges *et al*., 2019). Muchas de estas especies modernas muestran caracteres derivados, con quelípedos muy desarrollados (como por ejemplo *Spinolambrus macrochelos*).

El registro fósil indica que durante el Eoceno este grupo estaba representado por al menos 19 especies, muchas de ellas de cuencas situadas en el área mediterránea, y están relacionadas con ambientes arrecifales o coralinos-algales (ver detalles en Ferratges *et al*., 2019). Los representantes de los parthenopoideos del Eoceno ocuparon sustratos siliciclásticos (58%) y carbonatados (42%). Estos datos sugieren que el amplio rango de tolerancia ambiental observado en los parthenopoideos modernos ya se estableció durante el Eoceno. Durante el Ypresiense (Eoceno inferior) los parthenopoideos tenían preferencia por ambientes arrecifales. Esto probablemente esté relacionado con la aparición y desarrollo de complejos arrecifales modernos, debido a las condiciones climáticas y ambientales de esa época (ver 3.2.2. Contexto paleoclimático). Desde el Luteciense en adelante, los representantes de este grupo ocuparon principalmente ambientes siliciclásticos en plataformas poco profundas.

Sin embargo, es necesario mencionar que los estudios filogenéticos realizados en esta tesis indican que varias de las especies asignadas a este grupo por criterios morfológicos superficiales quedan fuera de Parthenopoidea, por lo que deberán ser revisadas en el futuro (ver Ferratges *et al*., en preparación).

Familia Parthenopidae MacLeay, 1838

Género *Aragolambrus* † Ferratges, Zamora y Aurell, 2019

La especie *Aragolambrus collinsi* Ferratges, Zamora y Aurell, 2019 (Fig. 33A-B) muestra similitudes con varios géneros modernos que presentan un tamaño reducido de los quelípedos (en comparación a otros parthenópidos). Las especies que comparten estas características suelen ser habitantes de arrecifes o frentes arrecifales y zonas con fragmentos/escombros de coral a profundidades de unos 20–30 m.

Familia Dairodidae Števčić, 2005

Género *Phrynolambrus* † Bittner, 1893

Se han recuperado varios especímenes del género *Phrynolambrus* (Fig. 33C-D) excepcionalmente bien preservados (ver Ferratges *et al*., en preparación). Este nuevo material ha permitido analizar varias características diagnósticas de la anatomía de este género útiles para fines comparativos taxonómicos y filogenéticos. Los datos obtenidos muestran una clara afinidad por el moderno género *Dairoides*, cuya posición sistemática ha sido controvertida y discutida en los últimos años (ver Ferratges *et al*., en revisión).

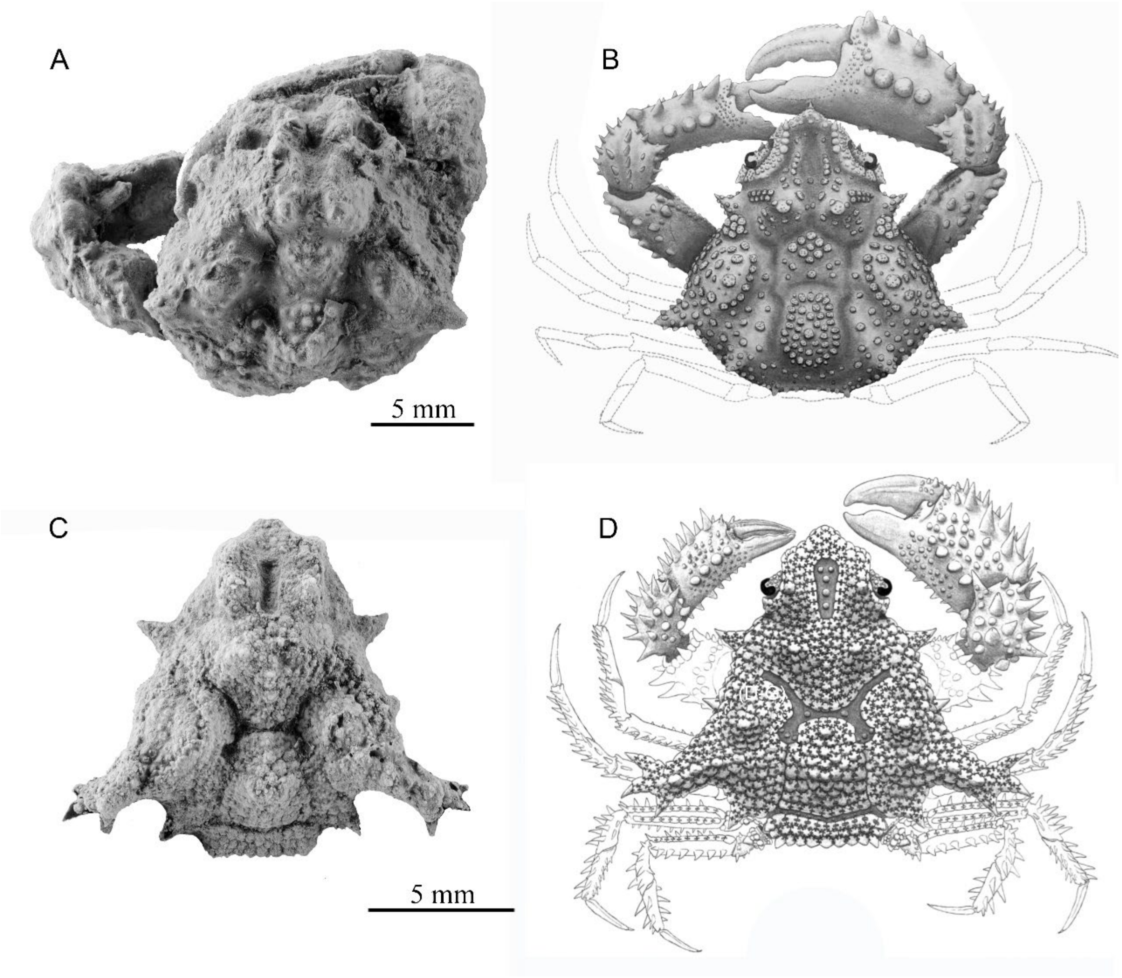

Figura 33: Partenopoideos estudiados durante la tesis doctoral: **A**: *Aragolambrus collinsi* Ferratges, Zamora y Aurell, 2019 (holotipo MPZ-2019/210) del Eoceno inferior y su reconstrucción (**B**) a partir del holotipo y nuevo material examinado; **C**: Paratipo de *Phrynolambrus sagittalis* Ferratges, Luque, Domínguez, Ossó, Aurell y Zamora, en prensa; y su reconstrucción (**D**) a partir del holotipo.

Figure 33: Parthenopoids studied during the PhD: **A**: *Aragolambrus collinsi* Ferratges, Zamora & Aurell, 2019 (holotype MPZ-2019/210) from the lower Eocene and its reconstruction based on the holotype and new examined material; **C**: Paratype of *Phrynolambrus sagittalis* Ferratges, Luque, Domínguez, Ossó, Aurell & Zamora, in press; and its reconstruction (**D**) based on the holotype.

Superfamilia Pilumnoidea Samouelle, 1819

Familia Pilumnidae Samouelle, 1819

Género *Galenopsis* † A. Milne-Edwards, 1865

El material tipo de *G. crassifrons* procede del Eoceno superior de Vicenza (Italia) (A. Milne-Edwards 1865); posteriormente, también se ha registrado desde el Eoceno medio de Alicante (España; véase Via, 1991). Su hallazgo en el yacimiento de La Peña (Huesca) amplía el área de distribución de la especie hasta el Eoceno superior del norte de la Península Ibérica. Además, el examen de los diferentes elementos anatómicos recuperados, juntamente con el material tipo y de otras localidades de Europa, ha permitido crear una reconstrucción idealizada de la especie (Fig. 34B).

Género *Lobogalenopsis* † Müller y Collins, 1991

Hasta esta investigavión solo se había asignado a este género la especie tipo, *L. quadrilobata*, con registros del Eoceno inferior del norte de Italia (Tessier *et al*., 2011; Beschin *et al*., 2015, 2016, 2018) y el Eoceno superior del norte de Italia, Hungría (Müller y Collins 1991) y Sicilia (Italia) (Di Salvo 1933). Con *Lobogalenopsis joei* Ferratges, Zamora y Aurell, 2020 la distribución del género se extiende al Eoceno superior de la Península Ibérica (ver detalles en Ferratges *et al*., 2020a).

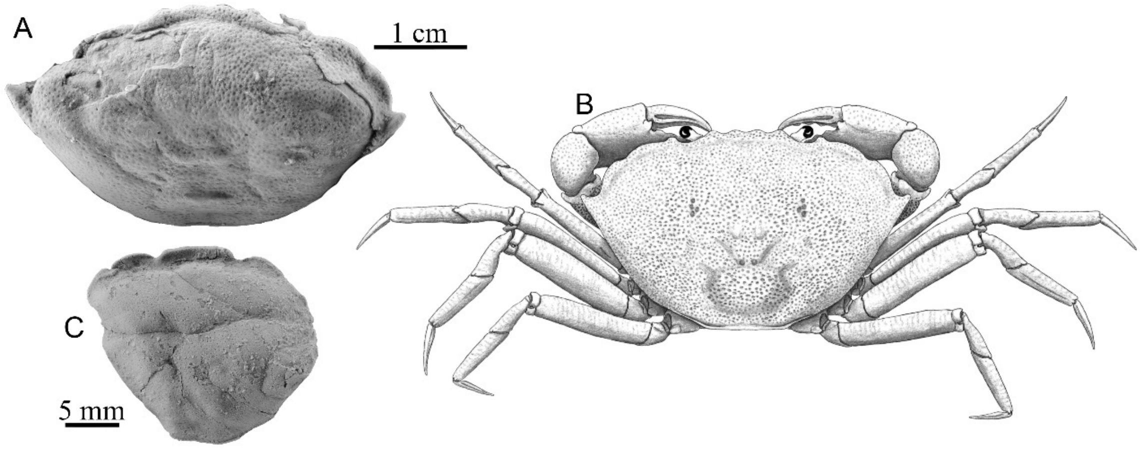

Figura 34: **A**: *Galenopsis crassifrons* A. Milne-Edwards, 1865 (MPZ 2019/1736) del Eoceno superior de la Fm Arguis y su reconstrucción (**B**). **C**: *Lobogalenopsis joei* Ferratges, Zamora y Aurell, 2020

Figure 34: **A**: *Galenopsis crassifrons* A. Milne-Edwards, 1865 (MPZ 2019/1736) from the upper Eocene of the Arguis Fm and its reconstruction (**B**). **C**: *Lobogalenopsis joei* Ferratges, Zamora & Aurell, 2020

Superfamilia Dairoidea Serène, 1965

Familia Dairidae Serène, 1965

Género *Daira* De Haan, 1833

El género *Daira* comprende solo dos especies actuales, *D. perlata* de entornos coralinos en el Indo-Pacífico, y *D. americana*, que normalmente se encuentra en hábitats rocosos o coralinos a lo largo de las costas del Pacífico de Centroamérica, desde el sur de

California hasta Ecuador (Rathbun, 1930). Además de las dos especies actuales existen 11 especies en el registro fósil. Todas ellas tienen caparazones completamente cubiertos por tubérculos en forma de hongo, cuyos "sombreros petaloides" están en contacto entre sí y forman un mosaico de polígonos. Con frecuencia, su presencia es indicativa de un conjunto diverso de crustáceos decápodos (ver Ferratges *et al*., 2020a y referencias). La especie *Daira corallina* Ferratges, Zamora y Aurell, 2020 (Fig. 35), corresponde a la primera cita de este género en el Eoceno de la Península Ibérica.

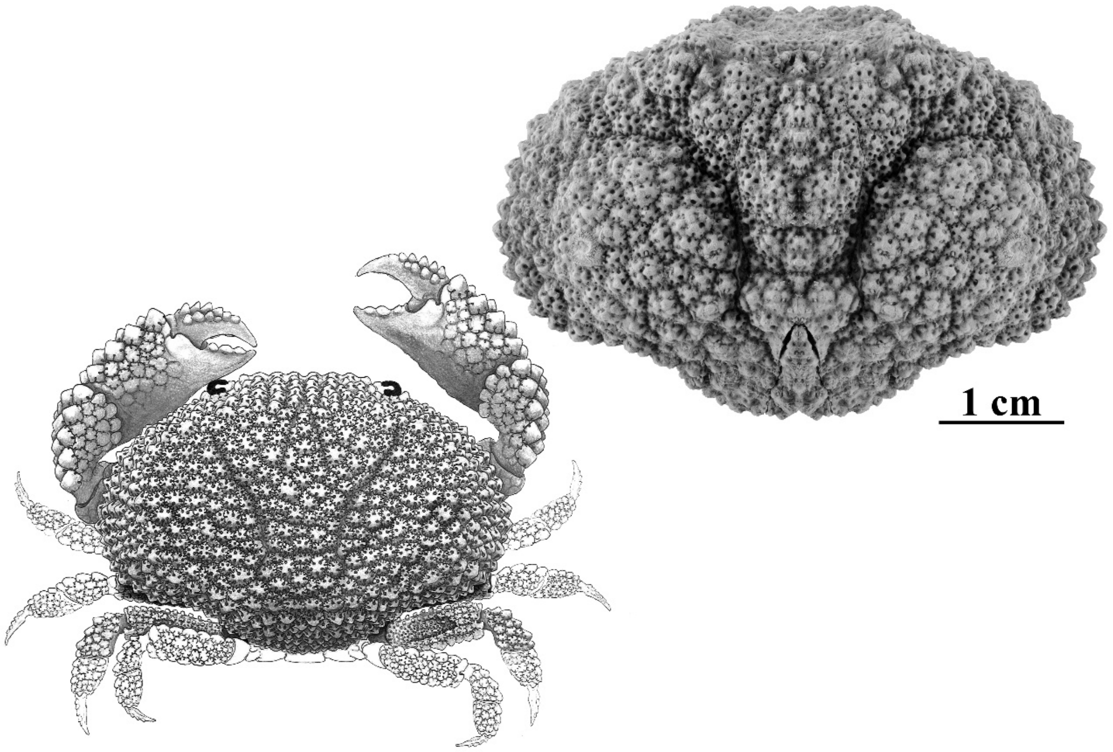

Figura 35: Reconstrucción en espejo del holotipo de *Daira corallina* Ferratges, Zamora y Aurell, 2020 (MPZ 2019/1691), y su reconstrucción.

Figure 35: Mirrored reconstruction of the holotype of *Daira corallina* Ferratges, Zamora & Aurell, 2020 (MPZ 2019/1691), and its reconstruction.

Superfamilia Xanthoidea MacLay, 1838

Familia Panopeidae Ortmann, 1893

Género *Scultoplax* Müller y Collins, 1991

Se realizó una revisión de la especie *Eoacantholobulus oscensis* (Ossó y Domínguez, 2017) del Priaboniense de Huesca, y se comparó con el material priaboniense italiano asignado a *Sculptoplax rigida* Müller y Collins, 1991. El examen detallado de estas dos especies sugiere que pertenecen al mismo género por lo que la especie *E. oscensis* se transfirió al género *Sculptoplax* como *S. oscensis* (Ossó y Domínguez, 2017). Sin embargo, a pesar de las fuertes similitudes dorsales entre ambos taxones, algunas diferencias son evidentes (ver detalles en Ossó *et al*., 2020a), por lo que se han mantenido en especies diferentes.

Superfamilia Grapsoidea MacLeay, 1838

Familia Varunidae H. Milne-Edwards, 1853

Subfamilia Asthenognathinae Stimpson, 1858

Género *Asthenognathus* Stimpson, 1858

El género *Asthenognathus* se encuentra en ecosistemas modernos de aguas poco profundas en mares templados y tropicales, y las especies se distribuyen en el Pacífico Indo-Occidental (Japón, China y Corea), el Mediterráneo occidental y el Mar del Norte (Francia) y el Atlántico oriental (África noroccidental) (ver Monod, 1956; Sakai, 1976; Manning y Holthuis, 1981; Falciai y Minervini, 1992; Lee *et al*., 2010; Jourde *et al*., 2012). El género incluye solo tres especies vivas: *A. inaequipes*, *A. atlanticus* y *A. hexagonum* (ver Ng *et al*., 2008). Estas especies viven comúnmente como comensales de moluscos, cnidarios y equinodermos, dentro de tubos de poliquetos o en las madrigueras de calianassidos (Woodward y Barrett, 1858; Schmitt *et al*., 1973; Glémarec y Hily, 1979; Jourde *et al*., 2012). Algunos ejemplares, sin embargo, tienen vida libre, y la mayoría de las especies pasan una parte de sus vidas independientes de sus huéspedes (Jourde *et al*., 2012). Hay registros de individuos asociados a sustratos siliciclásticos móviles y fondos fangosos (Falciai y Minervini, 1992; Lee *et al*., 2010; Jourde *et al*., 2012).

La especie *Asthenognathus fernandezi* Ferratges, Zamora y Aurell, 2022c (Fig. 36), del Ypresiense superior, representa el registro más antiguo de este género y el primer registro en el Eoceno. Schweitzer y Feldmann (2001b) sugirieron una alta latitud sur para el origen de la subfamilia Asthenognathinae, dispersándose hacia el Pacífico y el Atlántico Norte. El hallazgo de esta especie indica la presencia de este género en latitudes templadas del hemisferio norte y en estratos más antiguos, y en base a la forma de su cuerpo y extremidades sugiere una adaptación temprana a vivir dentro de cavidades cilíndricas (ver detalles en Ferratges *et al*., 2022c).

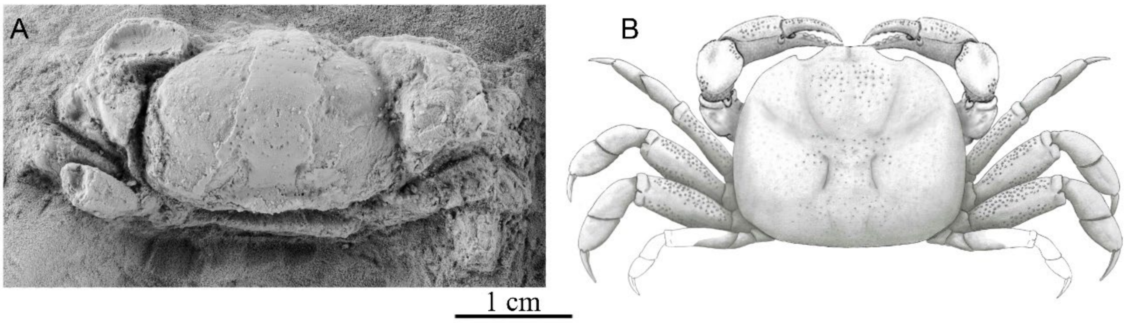

Figura 36: **A**: *Asthenognathus fernandezi* Ferratges, Zamora y Aurell, 2022 en vista dorsal (paratipo MPZ 2022/42); y su reconstrucción (**B**) a partir de holotipos y paratipos.

Figure 36: **A**: *Asthenognathus fernandezi* Ferratges, Zamora & Aurell, 2022 in dorsal view (paratype MPZ 2022/42) and its reconstruction (**B**) based on holotype and paratypes.

6.1.2.1. A highly diverse dromioid crab assemblage (Decapoda, Brachyura) associated with pinnacle reefs in the lower Eocene of Spain

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A highly diverse dromioid crab assemblage (Decapoda, Brachyura) associated with pinnacle reefs in the lower Eocene of Spain

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Abstract.—A highly diverse fauna of dromioid brachyurans from the Serraduy Formation (lower Eocene) in the western Pyrenees (Huesca, Spain) is described and illustrated. Recorded taxa are *Mclaynotopus longispinosus* new genus new species, *Torodromia elongata* n. gen. n. sp., *Basidromilites glaessneri* n. gen. n. sp., ?*Basidromilites* sp., *Sierradromia gladiator* n. gen. n. sp., *Kromtitis isabenensis* n. sp., and ?*Basinotopus* sp. Other European outcrops have yielded dromioids in association with specific environments, likely coral and sponge reef and siliciclastic soft bottoms; but the present material constitutes the most diverse dromioid assemblage from the lower Eocene worldwide. These dromioids co-occurred with a rich invertebrate fauna and lived near coral–algal reef mounds. Sedimentological data suggest that most of the fauna accumulated in fore reef settings as a result of storm activity. The present material greatly increases the diversity of known dromioid crabs associated with Eocene reef environments.

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Introduction

The superfamily Dromioidea De Haan, 1833 comprises notable representatives in modern ecosystems from rocky shores to deep sea (McLay, 1993, 1999, 2001; McLay and Ng, 2005). The fossil record of dromioids extends back to the Jurassic (see Jagt et al., 2015 and Luque et al., 2019 and references therein), and the group attained maximum diversity during the lower Eocene (Ypresian; see Table 1) in reef environments of northern Italy (Beschin et al., 2002, 2005, 2007, 2012, 2016a, b, 2018) and Spain (herein). Detailed systematic reviews of dromioids during recent years have resulted in new classificatory schemes (Karasawa et al., 2011; Schweitzer et al., 2012; Guinot et al., 2013; Jagt et al., 2015; Guinot, 2019; Van Bakel et al., 2020) based mainly on new discoveries and considering their importance in decapod crustacean phylogeny.

The Eocene record of dromioid crabs is comparatively rich, but material is often fragmentary. To date, 53 extinct species of dromioids are known from the Eocene, with the highest diversities associated with reef environments in the Atlantic–Tethyan Realm (Desmarest, 1822; Bittner, 1893; Checchia-Rispoli, 1905; Via, 1959; Quayle and Collins, 1981; Solé and Via, 1989; Müller and Collins, 1991; Blow and Manning, 1996; Beschin et al., 2002, 2007, 2009b, 2012, 2015, 2016a, 2016b, 2017, 2018, 2019; Collins and Jakobsen, 2004; Jakobsen and Feldmann, 2004; Van Bakel et al., 2009; Franţescu et al., 2010; De Angeli and Ceccon, 2014; Artal et al., 2016; Ossó, 2019; Ferratges et al., 2020) (see Table 1).

Here we describe new dromioid taxa from a decapod crustacean assemblage associated with reef facies of an early Eocene age in the Pyrenees (Huesca, Spain). This specific locality corresponds to a reef environment that has already yielded a wide range of decapod crustaceans (Artal and Via, 1989; Artal and Castillo, 2005a; Artal and Van Bakel, 2018a, b; Ferratges et al., 2019). Among the material recognized at this outcrop, dromioids represent only a small portion (3.1%) of the total assemblage (see Ferratges et al., 2021), yet surprisingly, they are unusually highly diverse compared with other Eocene assemblages. This new discovery has prompted a revision of all Eocene dromioid faunules to compare these in terms of diversity and environment with the present material.

Geological setting

The southern Pyrenean basins were located at tropical latitudes during the Paleogene (e.g., Hay et al., 1999; Silva-Casal et al., 2019) and, in the Eocene, formed part of an elongated gulf that connected in the west to the Bay of Biscay and was limited in the north to the axial zone of the Pyrenees (see Plaziat, 1981; Garcés et al., 2020). These basins rank among the most complete records of Eocene marine sedimentary successions in Europe, with decapod crustacean taxa described from several outcrops (e.g., Via, 1969, 1973; Artal and Castillo, 2005b; Artal et al.,

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*Corresponding author.

‡These authors have contributed equally.

Table 1. Eocene representatives of genera placed in the superfamily Dromioidea De Haan 1833. New representatives of genera within the superfamily Dromioidea from the "Barranco de Ramals" outcrop and described herein indicated in bold.

Family	Subfamily	Genus	Species	Locality	Age	Lithology	Environment
Dromiidae De Haan, 1833	Basinotopinae Karasawa, Schweitzer, and Feldmann, 2011	*Basinotopus* M'Coy, 1849	*lamarckii* (Desmarest, 1822)	UK, Italy	Lutetian	siliciclastic	shallow platform
			lothi (Förster and Mundlos, 1982)	Germany	Priabonian/ Oligocene	siliciclastic	shallow platform?
			tricornis Collins and Jakobsen, 2004	Denmark	Ypresian–Lutetian	siliciclastic	shallow platform
			sp.	Spain	Ypresian	limestone	reef
		***Mclaynotopus* n. gen.**	*alpina* (Glaessner, 1929)	Austria	Lutetian	siliciclastic	shallow platform?
			***longispinosus* n. sp.**	Spain	Ypresian	limestone	reef
		Noetlingocarcinus Karasawa, Schweitzer, and Feldmann, 2011	*claudiopolitana* (Bittner, 1893)	Italy	Lutetian	siliciclastic	shallow platform
			messinai Beschin et al., 2012	Italy	Bartonian	siliciclastic	shallow platform
			veronensis (Bittner, 1886)	Italy	Priabonian	siliciclastic	shallow platform
	Dromiinae De Haan, 1833	*Acanthodromia* Milne-Edwards, 1880	*zannatoi* Beschin et al., 2016a	Italy	Ypresian	limestone	reef
		Ameridromia Blow and Manning, 1996	*hyneorum* Blow and Manning, 1996	South Carolina (USA)	Lutetian–Bartonian	limestone	shallow platform?
		Basadromia Artal et al., 2016	*longifrons* Artal et al., 2016	Spain	Priabonian	siliciclastic	shallow platform
		Dromia Weber, 1795	*fossata* (Müller and Collins, 1991)	Hungary	Priabonian	limestone	reef
			subglobosa (Müller and Collins, 1991)	Hungary	Priabonian	limestone	reef
		Dromidia Stimpson, 1858	*bedetteae* Blow and Manning, 1996	South Carolina (USA)	Lutetian–Bartonian	limestone	shallow platform
		Pseudodromilites Beurlen, 1928	*hilarionis* (Bittner, 1883)	Spain, Italy	Lutetian	siliciclastic-carbonate	shallow platform
		Quinquerugatus Franţescu, Feldmann, and Schweitzer, 2010	*holthuisi* Franţescu, Feldmann, and Schweitzer, 2010	South Carolina (USA)	Bartonian	limestone	shallow platform
		***Torodromia* n. gen.**	***elongata* n. sp.**	Spain	Ypresian	limestone	reef
	Goniodromitinae Beurlen, 1932	*Biohermia* Beschin et al., 2016a	*chalmasi* Beschin et al., 2016a	Italy	Ypresian	limestone	reef
		Paradistefania Beschin, Busulini, and Tessier, 2015	*denticulata* Beschin et al., 2016a	Italy	Ypresian	limestone	reef
			piccolii Beschin, Busulini, and Tessier, 2015	Italy	Ypresian	limestone	reef
		Trechmannius Collins and Donovan, 2006	*circularis* Collins and Donovan, 2006	Jamaica	Lutetian–Bartonian	siliciclastic	shallow platform
	Sphaerodromiinae Guinot and Tavares, 2003	***Basidromilites* n. gen.**	***glaessneri* n. sp.**	Spain	Ypresian	limestone	reef
			pastoris (Via, 1959)	Spain, Italy	Lutetian	siliciclastic	shallow platform
			sp.	Spain	Ypresian	limestone	reef
		Dromilites Milne Edwards, 1837	*belli* Van Bakel et al., 2017	UK	Ypresian	siliciclastic (phosphatic nodules)	shallow platform
			bucklandii Milne Edwards, 1837	UK	Ypresian	clay	shallow platform
			vicensis Barnolas, 1973	Spain, Italy	Lutetian	siliciclastic	shallow platform
		Cracchidynomene Beschin et al., 2016a	*areolata* Beschin et al., 2016a	Italy	Ypresian	limestone	reef

Dynomenidae Ortmann, 1892	Dynomeninae Ortmann, 1892	*Dynomene* Desmarest, 1822	*vetusta* Beschin et al., 2016a	Italy	Ypresian	limestone	reef
			lessinea Beschin, De Angeli, and Checchi, 2001	Italy	?Priabonian–Oligocene	limestone	reef
		Eotrachynotocarcinus Beschin et al., 2007	*airaghii* Beschin et al., 2007	Italy	Ypresian	limestone	reef
		Ovamene Müller and Collins, 1991	*franciae* Müller and Collins, 1991	Hungary	Priabonian	limestone	reef
	Graptocarcininae Van Bakel, Guinot, Corral and Artal, 2012	*Graptocarcinus* Roemer, 1887	*eocenicus* Beschin et al., 2016b	Italy	Lutetian	siliciclastic	shallow platform
	Metadynomeninae Guinot 2008	*Dromiopsis* Reuss, 1858	*ceratoi* Beschin et al., 2016a	Italy	Ypresian	limestone	reef
			longitudovata Beschin et al., 2016a	Italy	Ypresian	limestone	reef
			marginospinosa Beschin, Busulini, and Tessier in Beschin et al., 2019	Italy	Priabonian	limestone	reef
			paleogenica De Angeli and Ceccon, 2014	Italy	Ypresian	siliciclastic	reef
			parvula Beschin et al., 2016a	Italy	Ypresian	limestone	reef
			paucigranosa Beschin et al., 2007	Italy	Ypresian	limestone	reef
			rocchettii Beschin, Busulini, and Tessier in Beschin et al., 2019	Italy	Priabonian	limestone	reef
			vicetinus Beschin et al., 2016a	Italy	Lutetian	siliciclastic	shallow platform
		Metadynomene McLay, 1999	*veronensis* Beschin, Busulini, and Tessier, 2015	Italy	Ypresian	limestone	reef
	Paradynomeninae Guinot, 2008	*Kromtitis* Müller, 1984	*bicuspidatus* Beschin, Busulini, and Tessier, 2009a	Italy	Priabonian	siliciclastic	shallow platform
			***isabenensis* n. sp.**	Spain	Ypresian	limestone	reef
			koberiformis Beschin et al., 2007	Italy	Ypresian	limestone	reef
			levigatus Beschin et al., 2007	Italy	Ypresian	limestone	reef
			lluisprietoi Ossó, 2019	Spain	Lutetian	?siliciclastic	shallow platform
			pseudolothi Beschin et al., 2016b	Italy	Lutetian	siliciclastic	shallow platform
			subovatus Beschin et al., 2007	Italy	Ypresian–Priabonian	limestone	reef
			tergospinosus Beschin, Busulini, and Tessier in Beschin et al., 2018	Italy	Priabonian	limestone	reef
			tetratuberculatus Beschin et al., 2002	Italy	Lutetian	siliciclastic	shallow platform
		Paradynomene Sakai, 1963	*antiqua* Beschin et al., 2016a	Italy	Ypresian	limestone	reef
			pentagonalis (Müller and Collins, 1991)	Hungary-Italy	Priabonian	limestone	reef
		***Sierradromia* n. gen.**	***gladiator* n. sp.**	Spain	Ypresian	limestone	reef
	Insertae sedis	*Cyamocarcinus* Bittner, 1883	*angustifrons* Bittner, 1883	Italy	Ypresian–Priabonian	limestone	reef
			budensis Oppenheim, 1899	Italy	Ypresian	limestone	reef
		Gemmellarocarcinus Checchia-Rispoli, 1905	*disalvoi* Beschin, Busulini, and Tessier in Beschin et al., 2018	Italy	Priabonian	limestone	reef
			loerentheyi Checchia-Rispoli, 1905	Italy	Lutetian–Priabonian	limestone	reef
			riglosensis Ferratges, Zamora, and Aurell, 2020	Spain	Priabonian	limestone	reef

2006, 2013; Ossó et al., 2014; Dominguez and Ossó, 2016; López-Horgue and Bodego, 2017; Artal and Van Bakel, 2018a, b, 2020; Ferratges et al., 2019, 2020). These successions document a wide range of depositional settings, from proximal alluvial to shallow marine in the east to slope and deep-marine and abyssal plains in the west (e.g., Garcés et al., 2020).

The material described herein was collected from the lower Eocene (middle Ypresian) Serraduy Formation of the Tremp-Graus Basin, and more specifically from the classic outcrop of "Barranco de Ramals" near the villages of La Puebla de Roda and Serraduy in the northeast of the province of Huesca (Aragón, Spain; Fig. 1). This locality has yielded an important assemblage of decapod crustaceans in association with pinnacle coral reefs (Via, 1973; Artal and Via, 1989; Artal and Castillo, 2005a; Fraaije and Pennings, 2006; Artal and Van Bakel, 2018a, b; Ferratges et al., 2019, 2021) as well as diverse invertebrate faunas (see Zamora et al., 2018; Ferratges et al., 2021). However, dromioid crabs remained undescribed until now.

Low depositional rates and optimum climatic conditions favored the development of a set of pinnacle reefs on top of the *Alveolina* limestones, which suggests a setting of intermediate depth and wave action (Gaemers, 1978). The Riguala Marls Member, which overlies the reefal unit, has been dated as early to middle Ilerdian (Serra-Kiel et al., 1994), which corresponds to the global Ypresian Stage (Pujalte et al., 2009). This unit formed as a forereef facies in which most of the material was derived from the reef as a result of storm activity, inclusive of the crab specimens described herein (see Ferratges et al., 2021 for more details). Thus, the dromioids, as well as other decapod crustaceans recovered from the same outcrop, lived near these reef pinnacles (Ferratges et al., 2021).

Materials and methods

Specimens were collected from the outcrop that exposes the transition between the reef limestones and the overlying Riguala Marls at a locality known as "Barranco de Ramals." A total of 162 specimens of dromioids have been studied from this outcrop. Some of this material (18 carapaces and 17 isolated propodi; 3.1% of total assemblage) was recovered during a detailed paleoecological study of the area in years 2018–2019 (see Ferratges et al., 2021 for more details). The remaining specimens (95 carapaces and 33 isolated propodus) were taken from historical museum collections. All material was prepared using a Micro Jack 2 air scribe (Paleotools; Brigham, Utah, USA), and fine, marly matrix was removed chemically using potassium hydroxide (KOH). Next, specimens were photographed dry and coated with ammonium chloride sublimate. Detailed photographs of carapace surfaces were taken using a Nikon D7100 camera (Nikon, Tokyo, Japan) with a macro 60 mm lens.

Repositories and institutional abbreviations.—Part of the material was collected during the early 1980s (see Artal and Via, 1989); this is housed in the collections of the Geological Museum of the Barcelona Seminary (MGSB). More recent collections in the area were made to quantify the abundance and distribution of taxa (see Ferratges et al., 2021); this material was recovered under permit EXP: 032/2018 from the "Servicio de Prevención, Protección e Investigación del Patrimonio Cultural (Gobierno de Aragón)" and is currently deposited in the paleontological collections of the Museo de Ciencias Naturales de la Universidad de Zaragoza (MPZ). The terminology used in the text is summarized in Figure 2.

Systematic paleontology

Classification and terminology used herein follow Guinot (2008, 2019), Guinot et al. (2013), and Jagt et al. (2015), but see alternative hypothesis of classification in Karasawa et al. (2011) and Luque et al. (2019).

Superfamily Dromioidea De Haan, 1833
Family Dromiidae De Haan, 1833
Subfamily Basinotopinae Karasawa, Schweitzer, and Feldmann, 2011

Diagnosis.—"Carapace slightly longer than wide, broadly triangular; rostrum broadly triangular, axially sulcate, with well developed median rostral spine; orbits deep, oblique, directed anterolaterally, suborbital margin with large spine; short segment between outer-orbital angle and first anterolateral spine, placing them at same level; lateral margin with three spines anterior to intersection of cervical groove and one very long, posterolaterally directed spine posterior to intersection of cervical groove; cervical, postcervical, and branchiocardiac grooves deep, cervical and branchiocardiac grooves intersecting carapace margin and extending onto flank; carapace with large nodes on regions" (Karasawa et al., 2011, p. 539).

Genus *Mclaynotopus* new genus

Type species.—*Mclaynotopus longispinosus* n. sp. by present designation.

Other species.—*Mclaynotopus alpina* (Glaessner, 1929).

Diagnosis.—Carapace subpentagonal, about as long as wide. Frontal margin trilobed, all spines of nearly equal size. Maximum width in anterior portion, at level of epibranchial region. Orbits directed anterolaterally, with blunt spine on suborbital margin. Anterolateral margins with three long spines, excluding outer orbital spine; last hepatic and large epibranchial nearly fused at base. Posterolateral margins with small spine, followed by small tubercle. Dorsal regions well defined by swellings and grooves. Dorsal surface with small granules in anterior portion, pitted posteriorly.

Etymology.—Named in honor of Colin McLay (University of Canterbury, New Zealand), who has contributed greatly to our general knowledge of dynomeniform crabs, plus the suffix "notopus."

Remarks.—The morphologically most closely similar genus, *Basinotopus* (see the following), is characterized by a broadly triangular carapace outline (see Karasawa et al., 2011, p. 539); the maximum width is in the posterior portion, at the level of the metabranchial region. The front is prominent, with a long

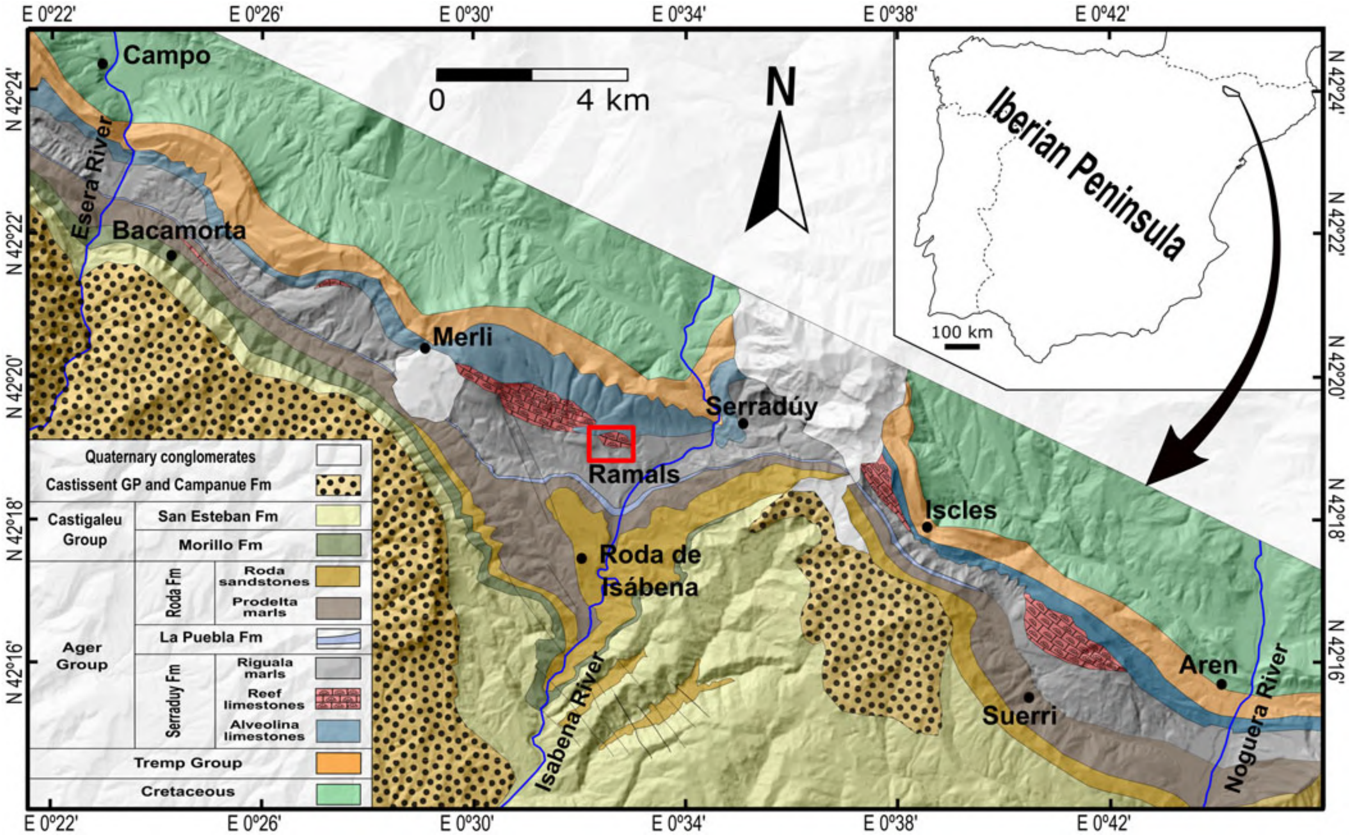

Figure 1. Geological map of the western sector of the Tremp-Graus Basin (modified after Serra-Kiel et al., 1994). The boxed area between Merli and Serraduy marks the location of the study area.

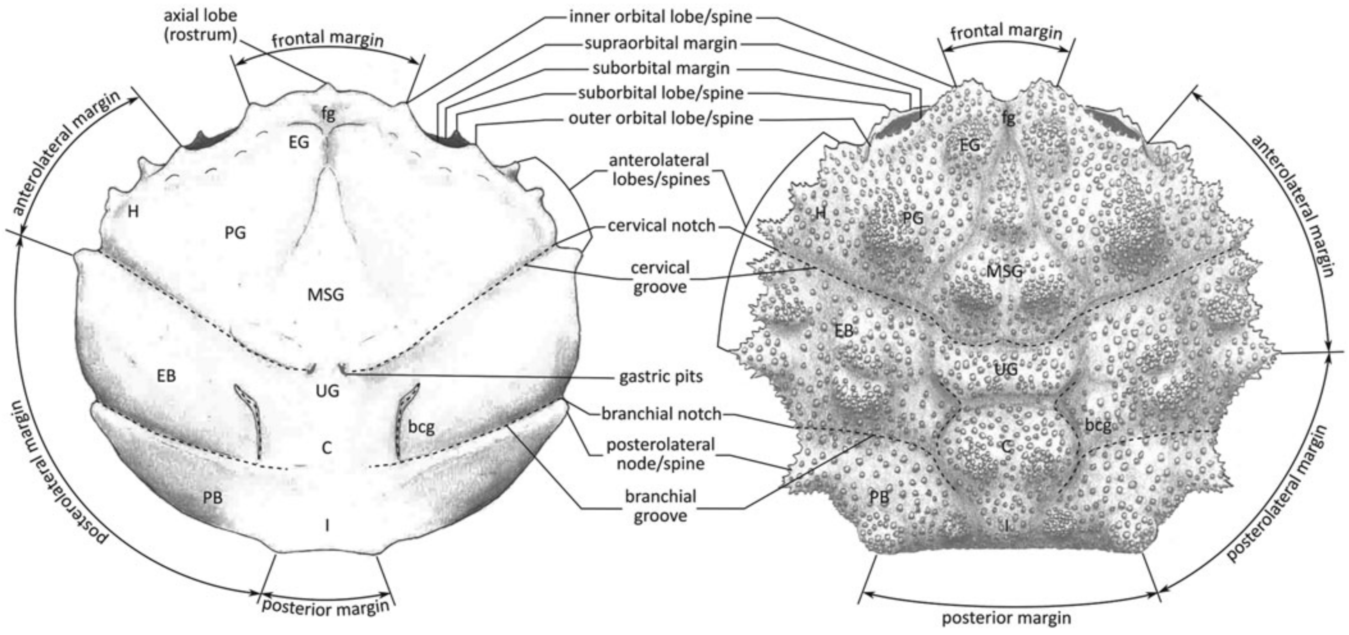

Figure 2. Carapace regions and terminology in a dromiid (s. lat.) crab used in the text (based on McLay, 1999). EG = epigastric region; PG = protogastric region; MSG = mesogastric region; H = hepatic region; UG = urogastric region; C = cardiac region; EB = epibranchoial region; PB = postbranchial region (meso- and metabranchial regions); I = intestinal region; fg = frontal groove; bcg = branchiocardiac groove.

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axial spine; the orbits are larger, with oblique supraorbital margin; the epibranchial spine is invariably weak, short, and thin; a more-projected lateral spine is situated posterior to the branchial notch, being posterolaterally directed. The lateral spines in *Basinotopus* are always weak, thin, and moderately long (see Busulini et al., 1983; Collins and Jakobsen, 2004; Beschin et al., 2005; Van Bakel et al., 2009).

The new genus shows a number of clearly distinct characters, such as a subpentagonal carapace, with the maximum width in the epibranchial region; the frontal margin is nearly straight, with a weakly projected axial spine, two longer and thin inner orbital spines; the outer portion of the supraorbital margin is nearly horizontal; the epibranchial spine is extremely large and long, with a very broad base; the second anterolateral spine is fairly strong, nearly fused to the epibranchial spine, both are in close approximation. On the basis of these features, we consider the erection of a new genus warranted. We transfer *Dromilites alpina* Glaessner, 1929 to the new genus because of similar outline of carapace and similar distribution of dorsal regions.

Mclaynotopus longispinosus new species
Figures 3, 4.

Type material.—The holotype is MGSB77597, a well-preserved carapace, with cuticle preserved; there are five paratypes: MGSB77598a–e.

Diagnosis.—Subpentagonal carapace. Trilobed front, lateral spines of similar size, axial spine somewhat smaller. Anterolateral margins with three long spines; second hepatic and the epibranchial nearly fused, close together. Epibranchial spine large, stout; base occupying entire epibranchial area. Tips of dorsal regions and dorsal granules blunt, clearly rounded.

Description.—Carapace subpentagonal, nearly as long as wide (length/width ratio about 0.95), broadly convex in both directions. Maximum width at level of epibranchial region, just posterior to extremely pronounced epibranchial spine. Dorsal surface strongly convex. Front broad, deflexed axially, broadly triangular or V-shaped in frontal view, with shallow axial depression, trilobed in dorsal view, with two robust inner orbital spines; the two inner orbital spines strong, stout, upwardly directed, not very projected, ventral side flattened, dorsal side rounded; axial spine situated in lower plane, short and robust subtriangular base, spinous tip, directed forward, visible in dorsal view. Orbits large, anterolaterally directed, slightly raised in lateral portion; outer orbital corner with deep incision, bounded by projected outer orbital and suborbital spines; subelliptical in frontal view, suborbital margin with strongly projected spine, with broadly triangular base and irregular lobe in distal portion.

Entire lateral margin with four spines, one small posterior tubercle, and two weak notches. Anterolateral margin nearly straight, only slightly convex, bearing two acute hepatic spines and one larger epibranchial spine, with broad triangular base; portion behind orbit, short, nearly vertical. Second hepatic spine larger than first spine, close to extremely projected epibranchial spine and almost fused to it. Epibranchial projection large, projected, laterally and upwardly directed, with broadly triangular base occupying entire distal portion of epibranchial region. Anterolateral and posterolateral margins nearly equal in length, posterolateral nearly straight in first portion, broadly convex posteriorly, with thin, long postbranchial, conical spine, and small posterior tubercle. Lateral margins with two slight indentations, corresponding to intersection of cervical and branchial grooves. Posterior margin nearly straight, slightly concave axially, rimmed, slightly less wide than orbitofrontal margin.

Dorsal regions defined by swollen lobes, divided into portions by grooves. Cervical groove well defined, reaching ventral portion of carapace. Branchial groove straight, nearly horizontal, bounded posteriorly by strong rim, axially interrupted by broad cardiac swelling. Branchiocardiac grooves sinuous, deep, short. Mesogastric region subtriangular, with arched base, bounded by deep cervical groove; posterior portion divided into two gently swollen lobes, separated by shallow axial groove; anterior extension swollen, bearing notable scattered tubercles. Protogastric region large; posterior portion defined by subelliptical swelling; anterior portion elongated, bearing tubercles. Hepatic region small, slightly inflated, with scarce tubercles. Suborbital region with small inflation. Urogastric region broad, arched, bounded by deep grooves, surface covered by large irregular pits and vertical depressions. Epibranchial region large, bearing two transverse swellings. Meso- and metabranchial regions undifferentiated, large, gently swollen, densely covered by small pits. Cardiac region large, subpentagonal, strongly swollen, bounded by numerous tubercles, bearing three notable tubercles; two anterior ones with large central pit and posterior one, situated apically, with some granules. Intestinal region small, depressed. Ventral portion of carapace with deep extensions of cervical and branchial grooves and with suborbital and subhepatic swellings. Chelipeds elongated; merus subtriangular in cross section, smooth; carpus slightly longer than tall; surface with some widely spaced smooth tubercles. Manus longer than tall, slightly divergent distally, elliptical in cross section; upper margin with three small, aligned tubercles; lower margin slightly concave at the base of the fixed finger, surface smooth (Fig. 3.6, 3.7).

Etymology.—The specific name refers to the elongated spines on the lateral carapace margins.

Other material examined.—Fifty-four incomplete carapaces (MGSB77630a–j; MGSB77632a–q; MGSB77634a–q; MPZ-2021/46; MPZ-2021/153–2021/161) and 15 isolated chelipeds (MGSB77620; MPZ-2021/148–2021/152).

Remarks.—*Dromilites alpina*, which was subsequently listed as *Basinotopus alpina* (see Collins and Jakobsen, 2004; Van Bakel et al., 2009), is a species that can be reassigned to *Mclaynotopus* n. gen. with confidence. Its carapace features match the generic diagnosis (see the preceding), e.g., the subpentagonal outline, the similarly distributed dorsal regions, and an extremely elongate epibranchial spine. However, the epibranchial projection in that species is much thinner, with the base not totally occupying the epibranchial margin. Moreover, the contiguous hepatic spine, which is nearly fused to it in the new species, is clearly separated in *M. alpina*. *Mclaynotopus alpina* also shows distinct dorsal

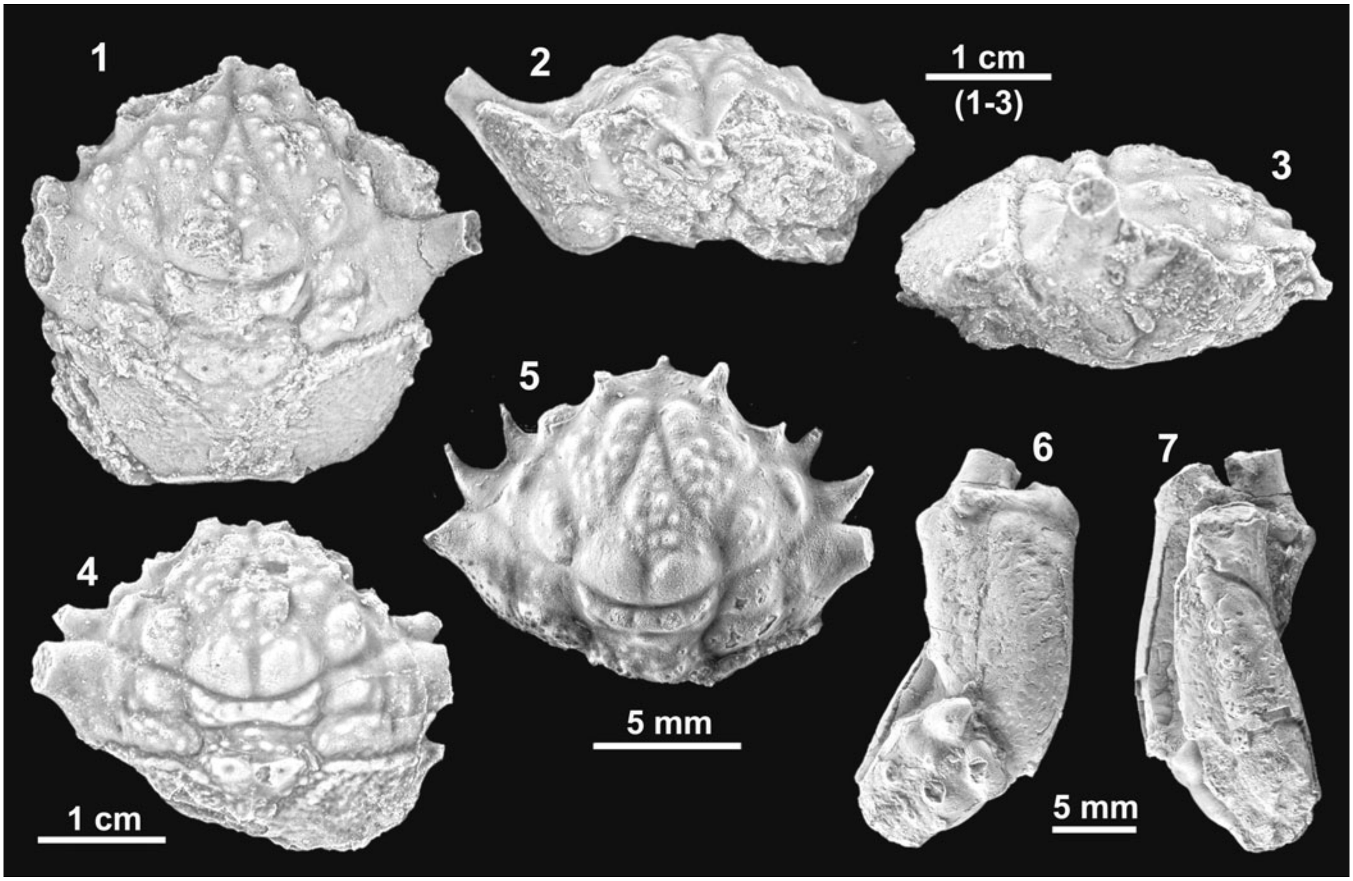

Figure 3. *Mclaynotopus longispinosus* n. gen. n. sp. from the Serraduy Formation (Huesca, North Spain). (**1–3**) Holotype MGSB77597 in dorsal, frontal, and right lateral views, respectively. (**4**) Paratype MGSB77598 in dorsal view. (**5**) Paratype MPZ-2021/153 in dorsal view. (**6**, **7**) Isolated cheliped (MPZ-2021/148), presumably of *Mclaynotopus longispinosus*, in outer and inner views, respectively. Specimens whitened with ammonium chloride sublimate before photography.

regions: the protogastric and the anterior extension of the mesogastric are much more ridged. Regions in general have more acute conical tips, such as the mesogastric and epibranchial, and the urogastric has longer lateral portions (see Glaessner, 1929, pl. 8).

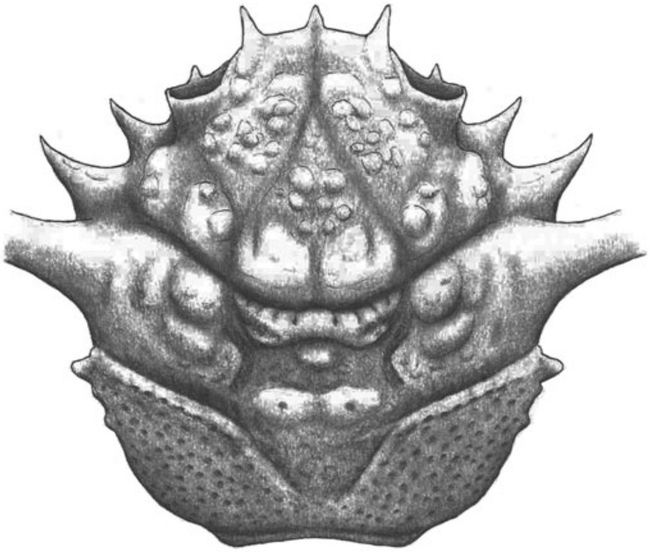

Figure 4. Reconstruction of *Mclaynotopus longispinosus* n. gen., n. sp.

Subfamily Dromiinae De Haan, 1833

Diagnosis.—"Carapace longer than wide to wider than long; rostrum typically bilobed; orbits without augenrest, deep, circular; orbital margin often with protuberance or rim, subouterorbital spine often visible in dorsal view; cervical groove weak; postcervical groove sometimes present; branchiocardiac groove present" (Karasawa et al., 2011, p. 541).

Genus *Torodromia* new genus

Type species.—*Torodromia elongata* n. sp. by present designation.

Diagnosis.—Carapace longitudinally elongate, slightly wider than long; frontal margin bilobed, with two thin, long inner orbital spines and barely visible axial spine; orbits large, concave, directed forward. Anterolateral margins with three conspicuously long spines; two posterior ones rather robust and with broad base. Posterolateral margin with single thin spine. Dorsal regions nearly smooth, with only gentle swellings and weak grooves. Small oblique depressions in gastric area.

Etymology.—The generic name combines *toro*, Spanish for bull, in reference to the horned rostrum, and *dromia*.

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Remarks.—The main characters of *Torodromia* n. gen. allow placement in the Dromiinae. These include a carapace of equal length and width, a typically bilobed rostrum, a suborbital spine that is visible in dorsal view, weak cervical and branchial grooves, and marked branchiocardiac groove (Schweitzer et al., 2012; Feldmann and Schweitzer, 2019). Diagnostic features of the new genus include large and long spines on lateral carapace margins, barely defined dorsal regions, and a deep, short groove in the frontal margin. Fossil representatives of the Dromiinae can be easily distinguished from *Torodromia*, as indicated in the following.

Basadromia Artal et al., 2016, has a frontal margin with four spines, while lateral margins lack prominent spines, having merely small denticles. Dorsal regions in *Basadromia* are swollen; there are numerous grooves and a dense granulation. Artal et al. (2016) and Feldmann and Schweitzer (2019) placed this genus in the Dromiinae.

Pseudodromilites Beurlen, 1928 also possesses two strongly projected triangular spines on the frontal margin, and dorsal regions have pronounced grooves and are distinctly swollen. Lateral margins in *Pseudodromilites* have small lobes or small subtriangular spines while the dorsal surface is strongly granulated (De Angeli and Alberti, 2018, p. 158).

Quinquerugatus Franţescu, Feldmann, and Schweitzer, 2010 exhibits a nearly straight frontal margin when seen in dorsal view. It has larger supraorbital margins than in *Torodromia* and lateral margins bear small, short, and conical spines while the cervical groove is well defined, deep in the axial portion, bearing two small pits; the branchial groove is deep and well marked (Franţescu et al., 2010, p. 260).

The new genus can be differentiated from the extant *Cryptodromia* (Schweitzer et al., 2012) by possessing larger and longer spines on the lateral margins, a slightly developed axial spine in the frontal margin, a deep axial frontal groove, and deep branchiocardiac grooves.

Torodromia elongata new species
Figures 5.1–5.3, 6.

Type material.—The holotype is MGSB77595, a near-complete, well-preserved carapace, retaining cuticle. There is one paratype, MGSB77596, which lacks a portion of the posterior margin of the carapace.

Diagnosis.—As for genus (monotypy).

Description.—Carapace suboval, slightly wider than long (length/width ratio 0.93). Maximum width posterior to epibranchial spine. Dorsal surface convex in both directions. Front deflexed, relatively narrow, bilobed in dorsal view, strongly V-shaped in frontal view, margin slightly rimmed, with a short but deep axial groove; the two inner orbital spines strong, robust, directed forward, with broadly triangular base, the axial spine situated in lower plane, thin, short, inclined forward, poorly visible in dorsal view. Orbits large, arched in appearance in dorsal view, anterolaterally directed, slightly raised in lateral portion; large, subelliptical in frontal view, bearing small, thin suborbital spine. The whole lateral margins broadly arched, with four projected spines and two faint notches. Anterolateral margin arched, bearing two thin, long hepatic projections (first one thinner, acute, second one larger) and strong epibranchial spine with broadly triangular base. Posterolateral margin equaling width of anterolateral, arched, bearing notable notch and posterior thin, projected, branchial spine. Lateral margins with two marked indentations corresponding to cervical and branchial grooves. Posterior margin nearly straight, slightly rimmed, slightly wider than frontal margin. Dorsal regions relatively well defined by gently swollen lobes and shallow grooves. Cervical groove weakly marked, more evident in central portion, interrupted by two small gastric pits. Branchial groove well defined, posteriorly bounded by a thin ridge. Branchiocardiac grooves deep, short, and axially concave. Epigastric regions small, well marked, swollen, separated by short but deep groove. Mesogastric and protogastric regions scarcely differentiated. Hepatic region large and gently swollen. Urogastric region subtrapezoidal and slightly inflated. Epibranchial and postbranchial regions large, gently swollen, separated by thin ridge. Cardiac region broad, swollen, subpentagonal. Intestinal region small, depressed. Anterior dorsal surface covered with diminutive pits.

Etymology.—From the Latin *elongatus*, in reference to its elongated carapace shape.

Other material examined.—Two additional specimens, MGSB77631a, b.

Remarks.—Torodromia elongata n. gen. n. sp. is morphologically close to the extant *Cryptodromia tuberculata* Stimpson 1858, which has an elongated carapace outline, the frontal margin characterized by a thin axial spine and two projected lateral spines, and the lateral margins arched, bearing thin and relatively elongated spines (McLay and Ng, 2005, p. 8). However, the new fossil species differs in having larger and longer spines on the lateral margins while the axial spine on the frontal margin is slightly developed, the axial frontal groove is deep, and branchiocardiac grooves are also deep.

Quinquerugatus holthuisi Franţescu, Feldmann, and Schweitzer, 2010, differs in several features (see the preceding); the familial level placement of this taxon should be revised. It would appear better accommodated in the subfamily Sphaerodromiinae (see the following).

Subfamily Sphaerodromiinae Guinot and Tavares, 2003

Diagnosis.—“Carapace longer than wide or about as long as wide; rostrum projecting beyond orbits; orbital area composed of two contiguous circular depressions, outer depression deeper, essentially continuous with orbit, poorly separated from orbit; lateral rim merging with or separated only by short distance from outerorbital angle; subhepatic region inflated; cervical groove weak, postcervical and branchiocardiac grooves well defined” (Schweitzer et al., 2012, p. 33).

Genus *Basidromilites* new genus

Type species.—Basidromilites glaessneri n. gen. n. sp. by the present designation.

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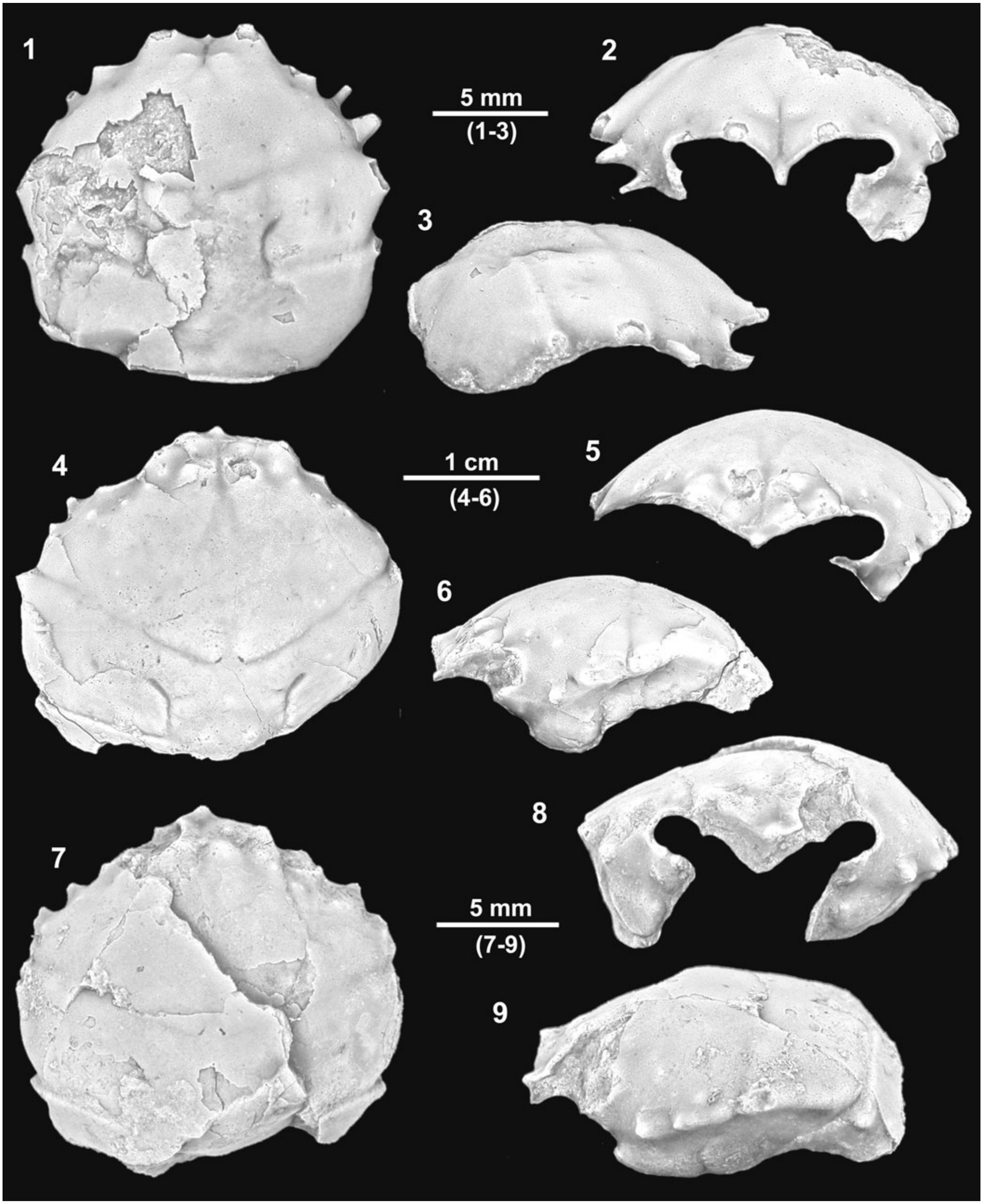

Figure 5. Dromioids from the Serraduy Formation (Huesca, North Spain). (**1–3**) *Torodromia elongata* n. gen. n. sp. holotype MGSB77595 in dorsal, frontal, and right lateral views, respectively. (**4–9**) *Basidromilites glaessneri* n. gen. n. sp.: (**4–6**) holotype MGSB77599 in dorsal, frontal, and left lateral views, respectively; (**7–9**) paratype MGSB77600 in dorsal, frontal, and left lateral views, respectively.

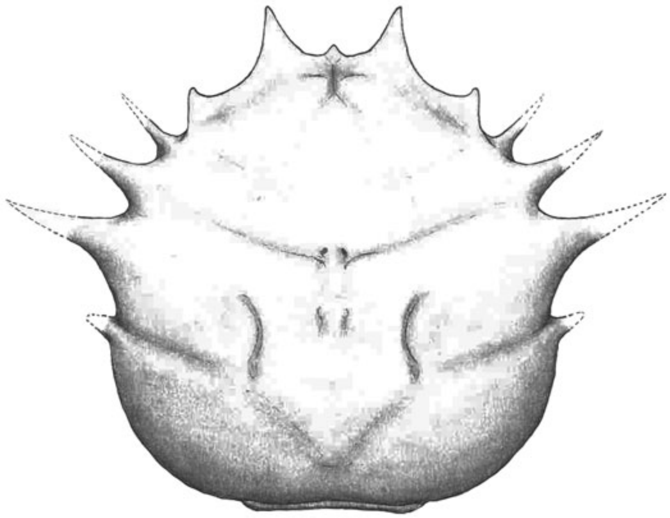

Figure 6. Reconstruction of *Torodromia elongata* n. gen. n. sp.

Other species.—*Basidromilites pastoris* (Via, 1959).

Diagnosis.—Carapace subcircular, length nearly equaling width. Maximum width at level of epibranchial region. Front subtriangular, trilobed in dorsal view, axial lobe slightly projected. Entire lateral margin convex, angular. Anterolateral margins broadly arched, bearing small spine and angular, crested, complex node. Small epibranchial spine behind cervical notch. Posterolateral margin broadly convex, bearing a small node behind branchial groove. Cervical groove slightly developed, branchial groove bounded by a ridge, branchiocardiac grooves short, arched, deep. Dorsal regions smooth except for small epibranchial swellings.

Etymology.—The generic name combines the root *Basi*, to match *Basinotopus*, and *dromilites*, a common generic name among dromioids.

Remarks.—The main characters of *Basidromilites* n. gen. match the diagnosis of the subfamily Sphaerodromiinae. These include a subglobose carapace of nearly equal width and length, the front projected beyond orbits, the dorsal surface with regions poorly defined, and weakly marked dorsal grooves (Guinot and Tavares, 2003; Schweitzer and Feldmann, 2010) as indicated in the preceding. *Basidromilites* n. gen. can be differentiated from *Dromidia bedetteae* Blow and Manning, 1996 in that the latter exhibits a narrow, U-shaped frontal margin with the lateral spines very projected, a suboval, transversely elongate carapace outline, and a marked suborbital spine that is clearly visible in dorsal view (Blow and Manning, 1996, pl. 1). *Quinquerugatus* shows peculiar characters, such as a near-straight front in dorsal view, a subpentagonal carapace outline, a very projected suborbital spine that is visible in dorsal view, and urogastric and cardiac regions that are swollen (Franţescu et al., 2010, p. 260, fig. 3).

Basidromilites glaessneri new species
Figures 5.4–5.9, 7.

Type material.—The holotype, an almost complete carapace, is MGSB77599. There is one paratype, MGSB77600, in comparable preservation.

Diagnosis.—Species of *Basidromilites* characterized by three clear lobes on frontal margin, with axial one more projected, dorsal surface rather smooth, dorsal grooves weak.

Description.—Carapace subcircular. Length nearly equaling the width (length/width ratio about 0.95). Maximum width at level of epibranchial region, about carapace mid-length. Dorsal surface strongly convex in both directions. Front broad, V-shaped in frontal view, short, shallow axial groove, strongly deflexed axially, broadly triangular, trilobed in dorsal view, with two robust lateral lobes; the two inner orbital lobes robust, not very projected; axial lobe situated in a lower plane, short and robust, subtriangular, directed forward, visible in dorsal view. Orbits large, anterolaterally directed, slightly raised in lateral portion, with suborbital spine visible dorsally; subelliptical in frontal view, bearing two small spines on suborbital margin.

Entire lateral margins markedly ridged, angular in cross section, bearing four projected nodes and two notable notches (Figs. 5, 7). Anterolateral margin broadly arched, bearing two strong lateral hepatic spines and strong epibranchial spine, with broadly triangular base; portion behind orbit short, arched. First lateral spine short yet robust, with blunt tip, not very projected, second node complex, composed of three ridged lobes, first two more pronounced. Posterolateral margins of equal size, broadly arched, bearing a strong branchial indentation and blunt yet robust branchial node. Entire lateral margin with two notable indentations, corresponding to cervical and branchial grooves. Posterior margin not well preserved.

Dorsal regions barely differentiated. Epibranchial regions well defined by two small subcircular swellings. Hepatic and suborbital regions bearing small tubercle. Mesogastric and urogastric regions undifferentiated, large, smooth. Epibranchial region large. Cardiac region defined only by branchiocardiac grooves. Ventral portions of carapace broadly swollen, suborbital region small, inflated; subhepatic region large, strongly swollen. Cervical groove shallow, V-shaped, weakly marked from side to side of carapace, interrupted by two oblique axial slits, present in ventral portion. Branchial groove well defined, oblique, relatively deep in outer portions, bounded by marked ridge, interrupted by broad cardiac area, deep in ventral portion. Branchiocardiac grooves arched, short.

Etymology.—The specific name honors Martin Fritz Glaessner (1906–1989) for his contributions to our knowledge of fossil dromiacean crabs.

Other material examined.—Five incomplete carapaces (MGSB77619a–d, MPZ-2021/162).

Remarks.—The new genus differs from species of *Dromilites* (e.g., *D. bucklandii* Milne Edwards, 1837; *D. belli* Van Bakel et al., 2017; *D. montenati* Robin et al., 2017; *D. vicensis*

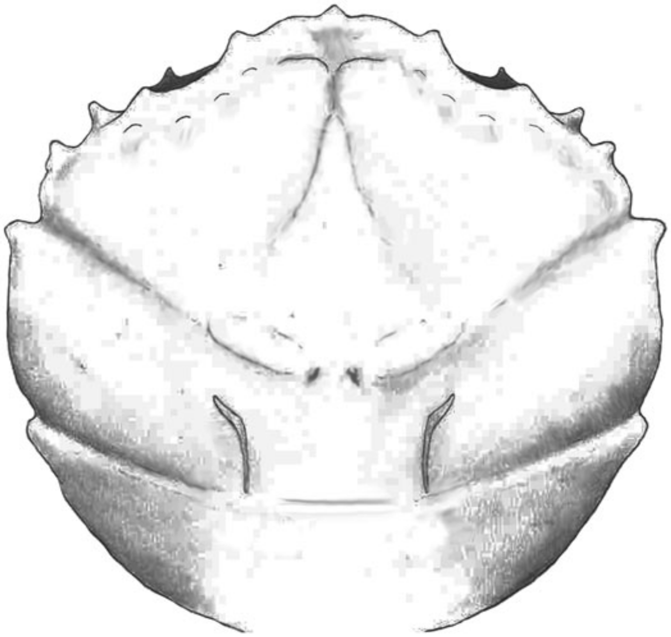

Figure 7. Reconstruction of *Basidromilites glaessneri* n. gen. n. sp.

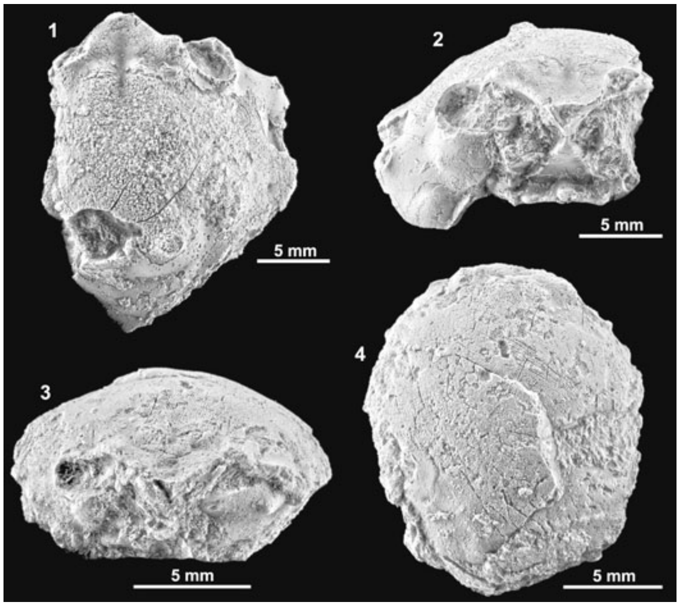

Figure 8. Specifically indeterminate dromiids from the Serraduy Formation (Huesca, North Spain). (**1**, **2**) ?*Basinotopus* sp. (MGSB77912) in dorsal and frontal views, respectively. (**3**, **4**) *Basidromilites* sp. (MGSB77628) in frontal and dorsal views, respectively.

Barnolas, 1973), which all have a frontal margin with two prominent lateral nodes, an axial node that is barely visible in dorsal view (see Milne Edwards, 1837; Via, 1959; Barnolas, 1973; Robin et al., 2017; Van Bakel et al., 2017) while usually the dorsal grooves are more clearly marked (see Barnolas, 1973), and a trend to have dorsal swellings (see Van Bakel et al., 2017).

However, the frontal margin in *Dromilites pastoris* Via, 1959 is similar to that of the present species, with a slightly projected axial lobe and similar cervical and branchial grooves. *Dromilites pastoris* does differ in having three small, lobe-like hepatic nodes anterior to the cervical groove and two small lateral nodes behind the cervical groove, two clear cardiac pits, and a prominent ridge behind the branchial groove. On this evidence, *D. pastoris* is reassigned to the new genus.

Basidromilites sp.
Figures 8.3, 8.4

Description.—Carapace suboval, longer than wide (length/width ratio about 1.14). Maximum width probably at level of epibranchial region, about carapace mid-length. Dorsal surface strongly convex in both directions. Front broad, conspicuously deflexed axially, broadly triangular, trilobed in dorsal view, with two robust lateral nodes; the two outer orbital lobes strong, robust, not very projected; axial lobe situated in lower plane, directed forward, barely visible in dorsal view. Front V-shaped in frontal view, shallow axial depression. Orbits large, anterolaterally directed, margins markedly raised; subelliptical in frontal view, with outer orbital corner pointed. The whole lateral margins not well preserved, appearing to have been angular in cross section. Anterolateral margin with one small hepatic node and larger posterior node anterior to cervical notch and one larger lobe posterior to cervical notch. Posterolateral margin somewhat longer, bearing angular lobe in front of branchial notch. Posterior margin not preserved. Gastric regions undifferentiated except for two small epigastric inflations. Branchial regions large, broadly swollen, separated by weak branchial groove. Hepatic region small, barely differentiated. Cervical and branchial grooves weakly developed, more visible in distal portion. Branchiocardiac grooves not well preserved. Dorsal surface densely covered by diminutive pits.

Material.—A single, near-complete carapace, MGSB77628.

Remarks.—The slightly projected frontal margin, with three discrete nodes, and the lobes on the lateral margins (mainly the angular hepatic lobe) are similar to *Basidromilites* n. gen. The smooth carapace with weak cervical and branchial grooves also matches the diagnosis of that new genus. *Basidromilites* sp. bears a more elongated carapace outline and more weakly marked dorsal carapace grooves than *Basidromilites glaessneri*.

Family incertae sedis
Genus *Basinotopus* M'Coy, 1849

Type species.—*Dromilites lamarckii* Desmarest, 1822 by monotypy.

?*Basinotopus* sp.
Figure 8.1, 8.2

Material.—A single incomplete carapace, MGSB77912.

Description.—Carapace of probable elongate outline. Maximum width probably at level of epibranchial region, about carapace mid-length. Dorsal surface strongly convex in both directions. Front broad, deflexed axially, broadly triangular, trilobed in dorsal view, with two robust lateral spines; the two inner orbital spines strong, robust, not very projected, with blunt tip, upwardly directed; axial spine situated in lower plane, very robust, broadly subtriangular, directed forward, entirely visible in dorsal view. Front V-shaped in frontal view, shallow axial depression. Orbits large, anterolaterally directed, margins markedly raised, with suborbital spine and suborbital margin, clearly visible dorsally; subelliptical in frontal view, bearing strong spine, with broadly triangular base on suborbital margin. Lateral margins not well preserved. Epigastric regions with small yet distinct swellings. Mesogastric regions well defined by large, projected, subcircular lobes. Hepatic region small, bearing small subcircular swelling. Suborbital and subhepatic regions large, broadly swollen. Cervical groove marked only in axial portion. Epistome robust, large, subtriangular.

Remarks.—This dromioid is of robust appearance, with thick cuticle and stout marginal nodes. The projected front, and particularly the robust axial spine, plus the two lateral spines recall *Basinotopus tricornis* Collins and Jakobsen, 2004. As seen in the genus *Basinotopus* are also the closed and obliquely directed orbit, with the suborbital margin and suborbital spine well visible in dorsal view. The main diference is the smooth or pitted carapace surface, which is also characteristic of *Lucanthonisia* Van Bakel et al., 2009. Features preserved in MGSB77912 match those of genera assigned to the Basinotopinae (Karasawa et al., 2011; Schweitzer et al., 2012).

Family Dynomenidae Ortmann, 1892
Subfamily Paradynomeninae Guinot, 2008

Diagnosis.—“Body thick, uniformly covered with tubercles, granules and/or spines. Carapace longer than wide or as long as wide, sometimes slightly wider than long, subquadrangular, may be suboval; dorsal surface convex, distinctly areolated, often with swellings or bosses, usually densely ornamented. Cervical groove entire, not reaching lateral carapace margin; frontal, cervical, branchial, branchiocardiac grooves pronounced. Anterolateral margins subparallel or slightly convex, distinctly joining corners of buccal cavity, armed with 4–6 irregular salient teeth or prominences. Posterolateral margin with produced and elongated subdistal tooth; a tooth present posteriorly, variously salient. Posterior region of carapace recessed; posterior margin strongly concave. Frontal margin usually distinctly projecting, tridentate, rarely bidentate; supraorbital margin with small tubercles, notch; infraorbital margin with granules, teeth, notches. Orbits oblique, clearly visible from dorsal view” (Guinot, 2008, p. 11–13).

Genus *Kromtitis* Müller, 1984

Type species.—*Dromilites koberi* Bachmayer and Tollmann, 1953, by monotypy.

Other species included.—*K. bicuspidatus* Beschin, De Angeli, and Zorzin, 2009b; *K. daniensis* Collins, 2010; *K. koberiformis* Beschin et al., 2007; *K. levigatus* Beschin et al., 2007; *K. lluisprietoi* Ossó, 2019; *K. pentagonalis* Müller and Collins, 1991; *K. pseudolothi* Beschin et al., 2016b; *K. spinulata* Portell and Collins, 2004; *K. subovatus* Beschin et al., 2007; *K. tergospinosus* Beschin, Busulini, and Tessier in Beschin et al., 2018; *K. tetratuberculatus* Beschin et al., 2002.

Kromtitis isabenensis new species
Figures 9, 10

Type material.—The holotype, MGSB75450, is a complete carapace (16 mm long and 15 mm wide) with well-preserved cuticle. There are two paratypes, MGSB75451a, b.

Diagnosis.—Carapace subquadrate, slightly wider than long, lateral margins arched; frontal margin projected, with two inner orbital nodes and deep axial notch; orbits inclined, with oblique supraorbital and suborbital margins; anterolateral margins broadly arched, bearing six robust, subtriangular spines; posterolateral margin converging posterorly, bearing a strong spine and notable concavity behind epibranchial spine; posterior margin straight; dorsal regions well defined by numerous raised swellings with rounded sides; metabranchial region with horizontal row of four swellings; dorsal surface uniformly and densely granulate.

Description.—Carapace subquadrate, lateral margins arched, slightly wider than long (length/width ratio about 0.85). Maximum width at level of epibranchial region, about carapace mid-length. Dorsal surface convex in both directions. Front V-shaped in frontal view, narrow, granulated, strongly deflexed axially, broadly triangular, with deep axial groove; bilobed in dorsal view, with two robust lateral nodes and V-shaped axial incision; the two inner orbital nodes strong, robust, markedly projected. Orbits large, anterolaterally directed, granulated, slightly raised in lateral portion; margin strongly angular in outer corner, with two suborbital nodes visible dorsally; subelliptical in frontal view, bearing acute outer spine and stout inner lobe on suborbital margin. Entire lateral margins broadly arched, bearing numerous projected spines and small posterior concavity; postbranchial spine is the largest. Anterolateral margin broadly arched, bearing at least three projected irregular spines anterior to cervical notch, and two posterior ones; projected spines covered with numerous tubercles and intermediate space bearing acute granules; portion behind orbit short, arched. Posterolateral margins of similar length, slightly sinuous, bearing a very small epibranchial spine, slight concavity, relatively long and acute projection, and blunt posterior node. Posterior margin concave, equaling orbitofrontal margin in length. Dorsal regions defined by swollen lobes and shallow depressions. Dorsal grooves shallow, weakly marked. Cervical groove weakly defined, deeper in ventral portion of carapace. Branchial groove weakly marked in marginal portion, deeper in ventral portion of carapace. Branchiocardiac grooves arched. Mesogastric region subtriangular, with arched base, bounded by shallow cervical groove; posterior portion defined by two strong protuberances separated by shallow depression; narrow anterior extension bearing small swelling. Protogastric region large, posterior portion defined by strongly projected

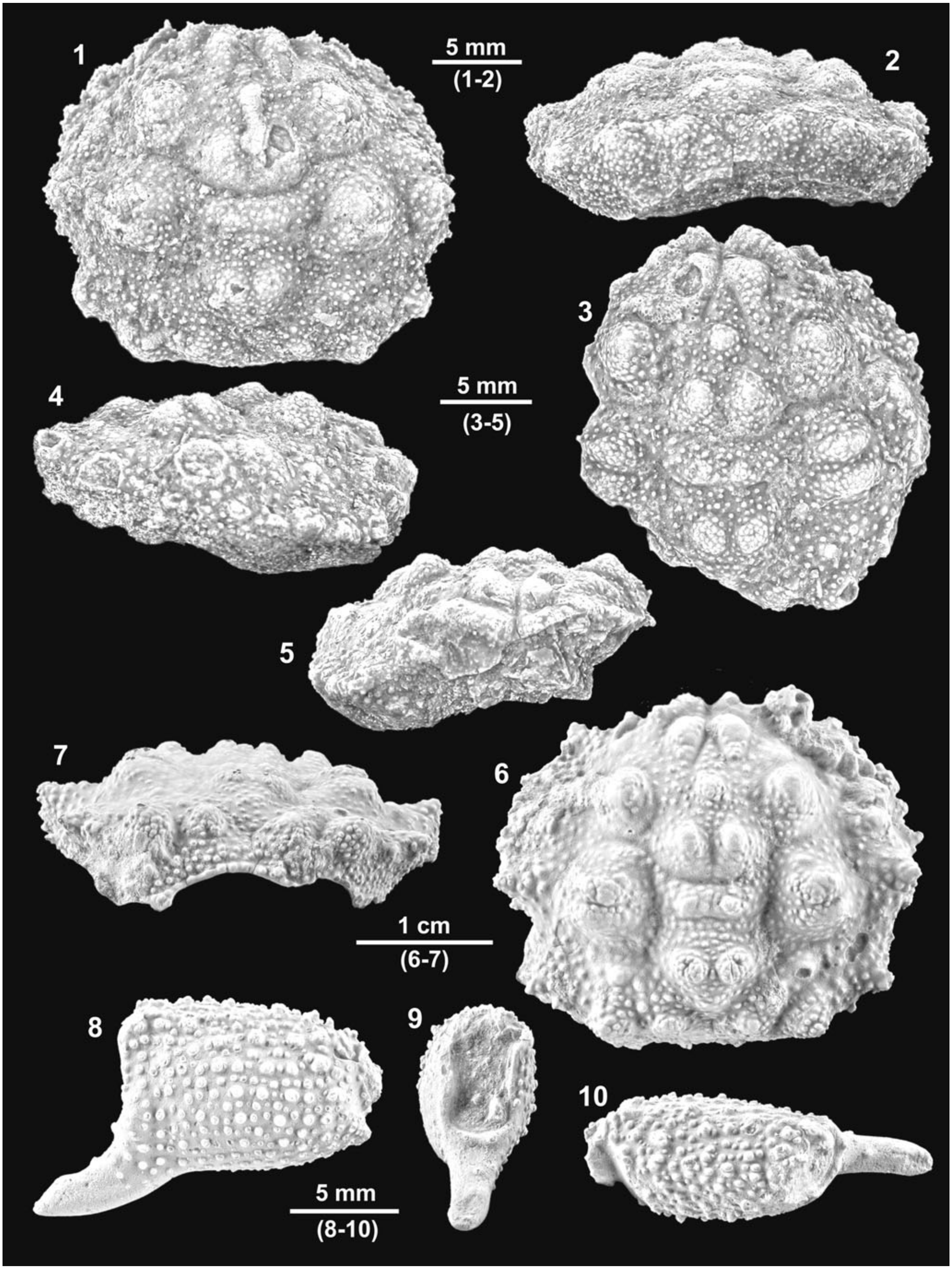

Figure 9. *Kromtitis isabenensis* n. sp. from the Serraduy Formation (Huesca, Spain). (**1**, **2**) Holotype (MGSB75450) in dorsal and posterior views, respectively. (**3–5**) Paratype (MGSB75451a) in dorsal, left lateral, and frontal views, respectively. (**6, 7**) MGSB77633 from Carrasquero, near Ramals, in dorsal and posterior views, respectively. (**8–10**) Isolated propodus, presumably of *Kromtitis isabenensis* n. sp., in left lateral, frontal, and dorsal views, respectively (MPZ-2021/163).

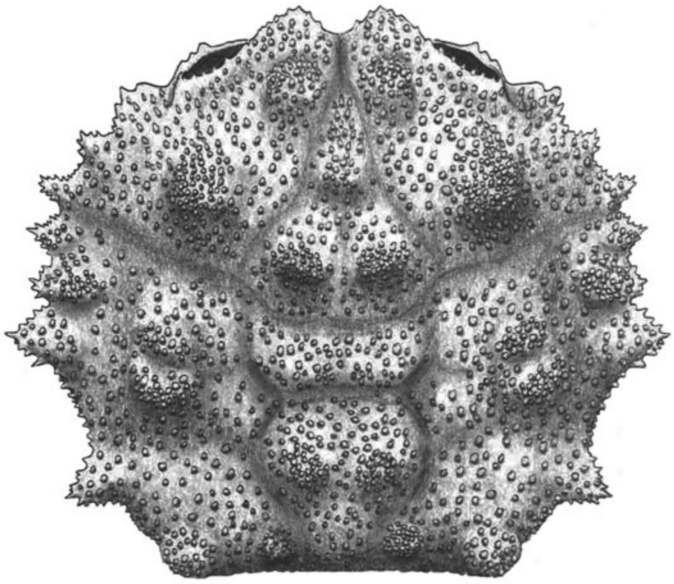

Figure 10. Reconstruction of *Kromtitis isabenensis* n. sp.

swelling, anterior portion elongated, joining epigastric swellings. Hepatic region small, bearing small tubercle. Urogastric region low, narrow, with two lateral tubercles. Epibranchial region large, inner portion defined by strong subcircular elevation, usually barely divided by a median sulcus; outer portion bearing two smaller elevations, anterior rounded, small, posterior stronger, with acute tip. Mesobranchial region depressed. Metabranchial regions large, with two strong protuberances, outer portion larger, reaching posterolateral carapace corner. Cardiac region large, raised, subpentagonal inverted in shape, anterior portion bearing strong elevations, apex barely marked. Intestinal region small, depressed. Dorsal surface densely covered by tiny granules.

Etymology.—The specific name refers to the municipality of Isabena, located a few kilometers to the south of the study area.

Other material examined.—MGSB77635a, b, two incomplete carapaces from Barranco de Ramals. Another well-preserved carapace, MGSB77633, originates from the neighboring locality of Carrasquero (Huesca). In addition, there are 30 isolated propodi (MGSB85952; MPZ-2021/163–2021/171).

Remarks.—*Kromtitis isabenensis* n. sp. can be differentiated from congeners on the basis of its projected front, with a deep V-shaped notch; oblique supraorbital margins, inclined at about 45°; a lateral margin with stout and subtriangular spines; a different distribution of dorsal regions, with broadly rounded tips; and a dorsal surface that is densely and uniformly covered by tiny granules.

The genus *Kromtitis* has previously been linked to certain extant dynomenids, such as *Paradynomene* Sakai, 1963 (see Beschin et al., 2007, p. 27; Guinot, 2008, p. 21). In *K. isabenensis*, as well as in its congeners, all features are those also seen in modern representatives of the subfamily Paradynomeninae (see McLay and Ng, 2005). The four tubercles in the posterior carapace portion (metabranchial area) in *K. isabenensis* are a diagnostic feature of the genus *Paradynomene* (see McLay and Ng, 2005). This conservative character has often not been mentioned in previous papers. The concavities in the posterolateral margins are also remarkable. Finally, the orbitofrontal construction is similar, in dorsal view, in both *K. isabenensis* and *P. tuberculata* Sakai, 1963 (McLay and Ng, 2004, p. 5).

Kromtitis isabenensis is morphologically close to *K. lluispietroi* Ossó, 2019 (both have a subquadrate outline, granular nodes on the lateral margins, and similarly distributed dorsal regions). However, the latter is easily distinguished in having clearly deeper cervical groove, an inner epibranchial swelling that is clearly separated into two differentiated portions, one below the other, and a dorsal surface that is covered by non-uniform and irregular granules ("surface sparsely granulate with coarse granules," according to Ossó, 2019, p. 3). In addition, the dorsal regions are covered by numerous tubercles of different sizes, the spines on the lateral margins are composed of numerous tubercles of different sizes, and the concavity in the posterolateral margin is more clearly marked.

The new species is also close to *K. koberiformis*, but that species differs in having a straighter front with projected inner orbital spines. In addition, the posterior margin is straighter and broader and dorsal regions clearly differentiated, smaller, and more raised, like large tubercles. The dorsal granulation is also dense, but with larger and more irregular granules. *Kromtitis koberi*, type species of the genus, is easily distinguished by its more clearly ridged dorsal regions and irregular granules that are seen only on the highest portions of carapace regions. *Kromtitis tetratuberculatus* has an arched frontal margin, larger, more rounded swellings in dorsal regions, and larger dorsal granules, while *K. subovatus* exhibits a projected frontal margin with a less clearly developed median notch, and dorsal regions are more strongly tuberculated with less-evident dorsal granulation. *Kromtitis levigatus* differs even more, with a straight frontal margin, dorsal regions with fewer divisions, and a lack of small granules on the dorsal surface.

The sole American species, *K. spinulata*, is characterized by a nearly subelliptical outline, being wider than long, a projected axial portion of the frontal margin, long and acute spines on the lateral margins, and a lack of surface granulation. *Kromtitis pentagonalis* is clearly distinct in having larger, close-set dorsal swellings on dorsal regions, with limited space between them, and a smooth dorsal surface, without granules (Müller and Collins, 1991, pl. 3).

Genus *Sierradromia* new genus

Type species.—*Sierradromia gladiator* n. sp. by present designation.

Diagnosis.—Carapace transversely subelliptical, slightly wider than long; frontal margin projected, with two strong inner orbital spines and a deep axial notch; entire lateral margins broadly arched, bearing seven long, robust, and dorsoventrally flattened spines; posterior margin narrow, nearly straight; dorsal regions conspicuously subdivided, with numerous

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strongly raised, conical swellings; two longitudinal axial grooves bounding mesogastric, urogastric, and cardiac regions; tips of dorsal regions with perforations.

Etymology.—The generic name derives from its resemblance to a mountain range, *sierra* in Spanish, and the suffix *dromia*.

Remarks.—The placement of extinct genera within the Dromiacea has always been controversial (Guinot, 2008, 2019; Guinot et al., 2013). Ventral characters are rarely preserved in fossil brachyurans, which explains why genera have been assigned to different families or subfamilies on the basis of few characters, in most cases only those of dorsal carapace (Schweitzer and Feldmann, 2010; Schweitzer et al., 2010, 2012; Karasawa et al., 2011). On the basis of particular dorsal carapace features, such as arched lateral margins, a projected frontal margin with two intraorbital nodes and a deep axial notch, inclined orbits with oblique supraorbital and suborbital margins, broadly arched anterolateral margins with some spines, a backward-converging posterolateral margin, well-defined dorsal regions by raised swellings, and a metabranchial region with a horizontal row of four swellings (in this case conical spines), we tentatively place *Sierradromia* n. gen. in the subfamily Paradynomeninae.

Sierradromia gladiator new species

Figures 11, 12

Type material.—Holotype, a near-complete carapace, is MGSB75454. There are two paratypes, both of which are slightly compressed: MGSB75455a, b.

Diagnosis.—As for genus (monotypy).

Description.—Carapace subelliptical, slightly wider than long (length/width ratio about 0.91). Maximum width at level of epibranchial region, just posterior to second epibranchial spine. Dorsal surface strongly convex in both directions, flanks of carapace oblique. Front V-shaped in frontal view, narrow, deflexed axially, fairly bilobed in dorsal view, with two notable lateral spines and deep axial indentation, deep axial groove; the two inner orbital spines robust, short; axial node situated in lower plane, not visible in dorsal view.

Orbits large, anterolaterally directed, slightly raised in lateral portion, with strong suborbital spine visible dorsally; subelliptical in frontal view; bearing a strongly projected, robust subtriangular spine on ventral orbital region. The whole lateral margins with seven robust spines and three notably deep notches. Anterolateral margin broadly arched, with two strong hepatic spines and two projected epibranchial spines, portion posterior to outer orbital corner strongly concave. All projections robust, dorsoventrally flattened, laterally and upwardly directed; two epibranchial largest, with broad subtriangular base, separated by short yet deep indentation. Posterolateral margins of similar length, broadly arched, bearing two strong spines in meso- and metabranchial marginal sides, strongly projected, dorsoventrally flattened, and upwardly directed. Posterior margin nearly straight, weakly concave, slightly narrower than orbitofrontal margin.

Dorsal regions well defined by shallow grooves and projected protuberances; axial swellings with rounded tip, upwardly directed, marginal swellings more conical, laterally directed. Mesobranchial region subtriangular with rounded sides; defined by two strong posterior protuberances and a smaller axial protuberance in anterior extension. Protogastric region defined by two protuberances of similar size, situated obliquely. Epigastric regions small, two transverse inflations separated by shallow groove. Hepatic region small, bearing weak conical swelling. Urogastric region inverted subtrapezoidal in shape, large, broad, and long, bearing two strong swellings with rounded tips. Cardiac region large, subpentagonal, transversely inflated, anterior portion with large pits. Epibranchial region large, bearing four conical protuberances. Meso- and metabranchial regions undifferentiated, bearing two transverse inflations. Intestinal region small, depressed. Ventral portion of carapace with conical suborbital spines and subhepatic and subbranchial inflations. Cervical groove shallow but well defined, well marked on ventral side and notching lateral margins. Branchial groove barely marked, bearing irregular small inflations and pits, reaching and notching lateral margins. Branchiocardiac groove sinuous, relatively deep. Dorsal surface densely covered by diminutive pits, bearing small perforations, mainly on highest part of the swollen regions.

Etymology.—The specific name "gladiator" refers to the fictitious Roman legionary, Maximus Decimus Meridius, in view of the resemblance of the carapace to the helmet that he wears in the film *The Gladiator*.

Other material examined.—MGSB77629a–q; MGSB77913a–e; MPZ-2021/50; MPZ-2021/172; MPZ-2021/173.

Remarks.—The new taxon is clearly distinct from *Kierionopsis nodosa* Davidson, 1966 (see also Armstrong et al., 2009, p. 749), which was assigned to the Dromiinae (Schweitzer et al., 2010) and subsequently transferred to the Dynomenidae (Schweitzer et al., 2012). The genus *Kierionopsis* Davidson, 1966 differs in having a much more elongated outline and in the number and shape of the spines on the lateral margins, the deeper cervical and branchial grooves, and the differently situated dorsal regions that are also distinct in shape and number, mainly the cardiac region, which is extremely raised and directed backward.

Sierradromia gladiator n. gen. n. sp. is superficially close to *Dromilites montenati*; however, the latter can be distinguished by the different number, shape, and length of the projections on the lateral margin. In addition, the dorsal regions exhibit important differences in shape, size, and distribution, being defined by small tubercles rather than raised conical swellings, and the dorsal grooves are clearly distinct in shape, course, and depths. The orbits are distinct, and the segment behind the outer corner is utterly different while the posterior margin is extremely concave (weakly concave or nearly straight in the new genus and species), and the carapace outline appears to be more subcircular.

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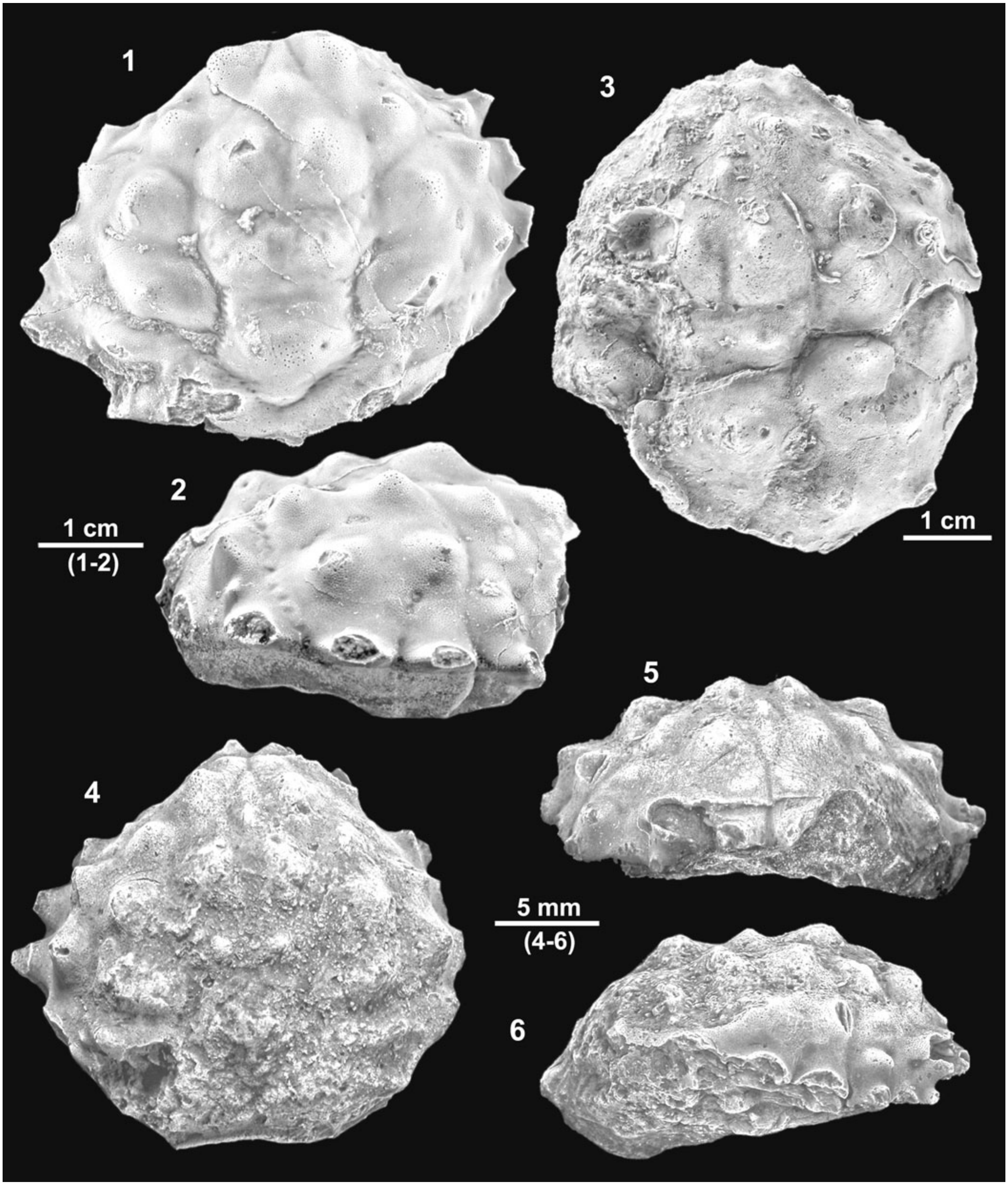

Figure 11. *Sierradromia gladiator* n. gen. n. sp. from the Serraduy Formation (Huesca, Spain). (**1**, **2**) Holotype (MGSB75454) in dorsal and right lateral views, respectively. (**3**) Dorsal view of paratype (MGSB75455a) with some epibionts (serpulids and oysters). (**4–6**) Paratype (MGSB75455b) in dorsal, frontal, and right lateral views, respectively.

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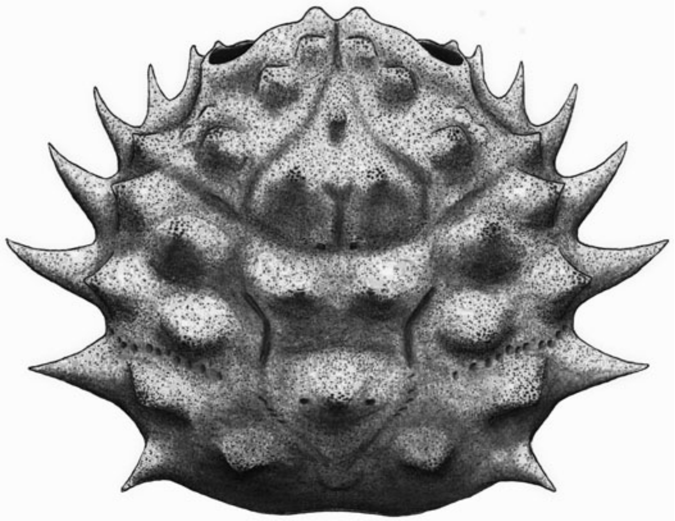

Figure 12. Reconstruction of *Sierradromia gladiator* n. gen. n. sp.

Eocene dromioid crabs in time and space

Modern dromioids are important constituents at tropical and subtropical latitudes and are represented by more than 140 species (e.g., Guinot and Tavares, 2003; De Grave et al., 2009). Usually, they are associated with coral- and sponge-rich environments and hard substrates (reefs, forereefs, or coral rubble) ranging from the intertidal to deep waters (1–450 m; e.g., McLay, 1993, 2001; Takeda and Manuel-Santos, 2006). Dromioids usually carry fragments of sponges or other objects with the help of P4–P5 (Dromiidae) or hide in crevices of coral and other hard substrates (Dynomenidae) (cf. McLay, 2001).

The Eocene dromioid assemblage from Ramals corresponds to taxa associated with reef environments. Other localities exposing Paleocene and Eocene rocks across Europe have similar dromiids and dynomenids (e.g., Beschin et al., 2007, 2015, 2016a, b, 2018, 2019; Tessier et al., 2011). However, all those assemblages are characterized by a low diversity. Decapod crustacean faunules from the middle Danian (lower Paleocene) at Fakse (eastern Denmark) comprise a wide array of dromioids in a coral-rich setting (e.g., Woodward, 1901; Wienberg Rasmussen, 1973; Collins and Jakobsen, 1994; Jakobsen and Collins, 1997; Collins, 2010). However, species and genera are different from those studied in the present work; dynomeniform crabs, in particular, are clearly distinct, with four species of *Dromiopsis* Reuss, 1859 (Jakobsen and Collins, 1997). The present faunule resembles the dromioid fauna from the Danian of the Paris Basin (France), with merely a single dynomenid and sphaerodromiid taxon each (Robin et al., 2017). The early Eocene faunas in northern Italy document an intermediate diversity, with at least four species of *Dromiopsis* and other paradynomenid forms. The only taxon in the Spanish assemblage in common with the Ypresian of Italy is the genus *Kromtitis*, with three recorded Italian species (Beschin et al., 2016a, b). Only three species of dromioids have been recorded from the Ypresian of the United Kingdom: two sphaerodromiids and one basinotopid (Collins, 2003; Van Bakel et al., 2017). Deposits of Ypresian/Lutetian age in Denmark share only a single basinotopid (Collins and Jakobsen, 2004) with the Huesca assemblage. Thus, the Ramals faunule includes novel forms of dromioids that appear for the first time at such latitudes during the Eocene. Morphologically more modern dromioids are known mainly from Lutetian strata in Italy (Busulini et al., 1983; Beschin et al., 2005) and Catalonia (Via, 1969; Solé and Via, 1989).

Table 2. Summary of environmental distribution patterns, as listed in Table 1.

Eocene stage	Number of species in coral-rich settings	Number of species in setting lacking corals
Ypresian	26	3
Lutetian	1	15
Bartonian	0	4
Priabonian	12	4

The Eocene record of dromioids includes 58 species described to date (Table 1). Many of these are known from basins in the Mediterranean area and are related mainly to coral-rich settings (56%) (see Tables 1, 2). On the basis of sedimentological data, a preference for reef environments appears likely for the Ypresian (lower Eocene); almost all published occurrences stem from such depositional settings. This can be related to the development of "modern" reef complexes because of climatic and environmental conditions at the time (see Pomar et al., 2017), which enabled dromioids to inhabit such settings. However, during the middle Eocene, this trend appears to have reversed, and higher diversities then occur in siliciclastic or non-reef environments over shallow platforms. This could be related to a switch in environmental preferences of dromioids at that time and their expansion into siliciclastic environments, but it might also be linked to the poor record of reef facies in this time interval. Finally, during the late Eocene, a new increase in diversity is observed in reef settings.

The abundance and diversity of dromioids at Ramals suggest this group was diversified and specialized for inhabiting this type of coral-rich environment during the early Eocene. It was probably related earlier with the Cretaceous Crab Revolution (see Schweitzer and Feldmann, 2015; Luque et al., 2019), documenting several species that are closely similar to extant forms. Our present data support the widely accepted view that past reefs were biodiversity hotspots (e.g., Förster, 1985; Müller et al., 2000; Krobicki and Zatoń, 2008; Klompmaker, 2013; Klompmaker et al., 2013). The great diversity within a single group of decapod crustaceans (i.e., dromioids) is probably related to the location of the study area within reef mounds and associated coral rubble under mesophotic conditions, as well as to abundant crevices that this environment provided for refuge, feeding, and other interactions.

Although the present work discusses only a single reef mound environment of middle Ypresian (early Eocene) age, similar studies in other areas could potentially provide important ecological data on the distribution of dromioid crabs in ancient marine settings.

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6.1.2.2. First record of Dynomene (Brachyura, Dromioidea) from the Eocene of the Iberian Peninsula and remarks on the generic placement of Eoacantholobulus oscensis (Brachyura, Xanthoidea).

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Article

First record of *Dynomene* (Brachyura, Dromioidea) from the Eocene of the Iberian Peninsula and remarks on the generic placement of *Eoacantholobulus oscensis* (Brachyura, Xanthoidea)

Àlex Ossó, José Luis Domínguez, Antonio De Angeli, and Fernando A. Ferratges

With 2 figures

Abstract: A new species of *Dynomene* from the Priabonian (Upper Eocene) of the central Pyrenees in Aragón (Spain) is described as the first record of the genus from the Iberian Peninsula. The new species reveals close similarities to other dromioid species described from the Priabonian of Hungary. The panopeid *Eoacantholobulus oscensis* Ossó & Domínguez, 2017, from the same locality, is reviewed and transferred to the genus *Sculptoplax*, after comparisons with specimens of *Sculptoplax rigida* Müller & Collins, 1991 from the Priabonian of Italy. The present note again provides evidence of the close relationship between the Late Eocene decapod crustacean faunas of the westernmost Tethys and the Pyrenean basins.

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Key words: Dynomenidae, Panopeidae, Priabonian, Pyrenees, Hungary, Italy, new taxon.

1. Introduction

A new dynomenid, *Dynomene collinsi*, is described from lower Priabonian strata of the central Pyrenees in Aragón (Spain). This record adds to the number of species of fossil decapod crustaceans already known from the Yebra de Basa outcrops (Artal et al. 2013; Ossó et al. 2014; Domínguez & Ossó 2016a; Domínguez & Ossó 2016b; Ossó & Domínguez 2017). Dynomenids have a fossil record that extends back into the Late Jurassic of Europe (Van Bakel et al. 2012); modern representatives inhabit tropical and warm parts of the Atlantic, Indian and Pacific oceans (see McLay 1999). The systematic placement of the family Dynomenidae Ortmann, 1892, and of some dynomenid genera in particular, has often been discussed in recent years (e.g., McLay 1999; Guinot 2008; Schweitzer & Feldmann 2009; Van Bakel et al. 2012) and has been summarised by Guinot et al. (2013: 153–154). Based on our present knowledge, the genus *Dynomene* Desmarest, 1823 first appeared during the Ypresian (Early Eocene), with records from northeastern Italy (Beschin et al. 2016), where it ranges into the Oligocene (Beschin et al. 2001). The presence of *Dynomene collinsi* n. sp. in the neighbouring Pyrenean basins during the Priabonian strongly suggests a westerly Tethyan origin of the genus, where it appeared to be confined during the Paleogene. In contrast, the genus is widely distributed in the Neogene of the central Paratethys, Caribbean and Pacific Ocean, being typical coral-associated crabs in shallow waters (Rathbun 1945; Müller 1979; Karasawa 1993; Portell & Collins 2004), similar to some extant dynomenid species. However, other modern species of dynomenid inhabit deeper waters of the continental shelf (McLay 1999). The discovery of *Dynomene collinsi* n. sp. in the cen-

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tral Pyrenees of Aragón constitutes the first record of the genus from the Iberian Peninsula.

In addition, a recent study of specimens of *Sculptoplax rigida* Müller & Collins, 1991 from the Priabonian of northern Italy, had led us to re-examine the type series of *Eoacantholobulus oscensis* Ossó & Domínguez, 2017 from the Priabonian of the central Pyrenees of Aragón. As a result, we here transfer the species *E. oscensis* to *Sculptoplax*.

2. Geological setting

The decapod crustacean material studied was recovered from the Margas de Pamplona Marls Formation (Puigdefàbregas 1975), which forms part of the sedimentary infill of the Jaca Basin (west-central Pyrenees), one of the subbasins of the South Pyrenean Foreland Basin. Specifically, our material was collected near the village of Fanlillo, in the municipality of Yebra de Basa (province of Huesca, Aragón).

The biostratigraphy (Canudo & Molina 1988; Canudo et al. 1988) and magnetostratigraphy (Hogan 1991) indicates a Bartonian–Priabonian age for the Margas de Pamplona Formation. In addition, the calibration published by Pueyo-Morer et al. (2002) has dated the lower and upper boundaries of this unit at 40.32 and 37.17 Ma, which corresponds to a Bartonian–early Priabonian age (International Commission on Stratigraphy; http://www.stratigraphy.org/index.php/ics-chart-timescale).

This formation consists of grey and blue marly deposits that correspond to a distal offshore environment that graded into sandstone delta-mouth bars with abundant vegetative remains in the uppermost levels. According to Montes Santiago (2009), faunal distribution within this unit, with records of bryozoans, nummulitid foraminifera, bivalves, siliceous sponges and decapod crustaceans in the lower levels, and corals, algae, gastropods and decapod crustaceans in the upper (outcrop levels), indicates a decrease of water depth.

The specimens studied were recovered from the uppermost levels of the Margas de Pamplona Formation of early Priabonian age, which consist of marls interbedded with thin sandstone deposits, with plant remains consisting of leaves, stems and mangrove-palm fruits, as well as other indeterminate remains, suggesting that the area was a delta under tidal and/or storm influence (Oms & Remacha 1992), representing a transition from deep- to shallower-marine deposition.

Institutional abbreviations: MPZ – Museo de Ciencias Naturales de la Universidad de Zaragoza (Spain); MCV – Museo Civico "D. Dal Lago" of Valdagno (Vicenza, Italy).

3. Systematic palaeontology

The higher-level classification used here follows Guinot et al. (2013).

Section Podotremata Guinot, 1977
Subsection Dynomeniformia Guinot, Tavares & Castro, 2013
Superfamily Dromioidea De Haan, 1833
Family Dynomenidae Ortmann, 1892
Subfamily Dynomeninae Ortmann, 1892
Genus *Dynomene* Desmarest, 1823

Type species: *Dynomene hispida* (Latreille, *in* Milbert 1812).

Dynomene collinsi n. sp.
Fig. 1

Etymology: Dedicated to Joe S.H. Collins, whose works enlightened us.

Type material: One partially preserved dorsal carapace, MPZ 2019/1469 (holotype), measuring 13.3 mm in length and 17.2 mm in width; the fronto-orbital width is 12.2 mm.

Type locality and horizon: Yebra de Basa, province of Huesca, Aragón (Spain) from the Margas de Pamplona Formation (lower Priabonian).

Diagnosis: Carapace relatively small, rounded in outline; wider than long; moderately convex longitudinally, faintly convex transversely; surface smooth, finely punctate; regions faintly defined. Fronto-orbital margin wide, almost continuous with supraorbital margin, diverging from longitudinal midline under angle of about 70º; front triangular, downturned, sulcate by medial groove that widens posteriorly. Orbits enlarged, oblique. Anterolateral margin with at least two triangular teeth. Posterior margin concave. Gastric process faintly marked; epigastric lobes prominent; protogastric lobes divided distally by frontal groove. Cardiac region pentagonal, faintly marked, with two contiguous acute tubercles. Cervical groove opened V-shaped, medially interrupted, weakly defined laterally. Branchiocardiac grooves marked, with muscle scars.

Description: Carapace relatively small, rounded in outline; wider than long; moderately convex longitudinally, faintly convex transversely; smooth, finely punctate; regions weakly marked. Fronto-orbital margin wide, about two-thirds of maximum width, almost continuous with supraorbital mar-

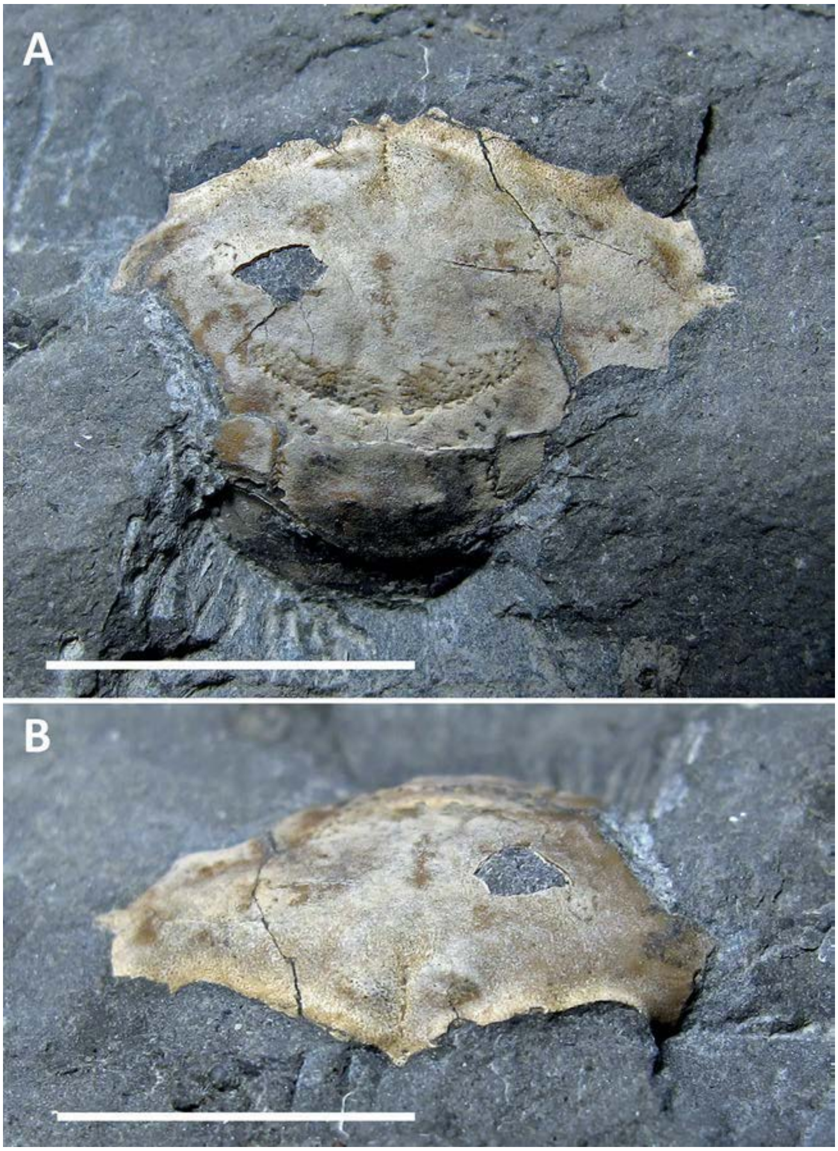

Fig. 1. *Dynomene collinsi* n. sp., MPZ 2019/1469 (holotype), Priabonian, Yebra de Basa (Huesca, Spain), in dorsal (A) and frontal (B) views. Scale bar equal 10 mm.

gin, faintly rimmed; diverging from longitudinal midline under an angle of about 70º. Front triangular, downturned, weakly projected, with a well-marked medial narrow gutter that posteriorly separates the epigastric lobes. Orbits enlarged, oblique; supraorbital margin entire; inner orbital corner marked as a slightly raised fold; outer orbital corner rounded, raised. Anterolateral margin with at least two triangular teeth; first anterolateral tooth well separated from the outer orbital corner, wide, blunt; second anterolateral tooth laterally projected, acute triangular. Posterolateral margins not preserved. Posterior margin concave, rimmed. Gastric process faintly marked; epigastric lobes prominent, stepped frontally, separated by the medial frontal groove, which widens posteriorly between the anterior portion of protogastric lobes; protogastric lobes divided distally by the enlarged portion of the medial frontal groove; meso- and mesogastric regions indistinct, separated from urogastric region by cervical groove. Cardiac region pentagonal, faintly marked, with two contiguous acute tubercles. Intestinal region not well preserved. Hepatic region slightly swollen. Cervical groove broadly V-shaped (halfmoon-shaped), medially interrupted between the two gastric pits, weakly defined laterally, not reaching the lateral margin. Branchial groove not observable. Branchiocardiac grooves marked, with marked muscle scars. Transverse ranges of muscle scars along the median part of cervical groove, paralleling above and obliquely below in the gastric area. Set of muscle scars along the shallow gastro-hepatic groove.

Remarks: Descriptions of genera and species of the Dynomenidae usually is based on a set of characters and features such as, among others, setae, gills, uropods and the nature of the fifth pereiopod (McLay 1999), or on sterno-abdominal features (Guinot 2008). However, such features are related to soft parts that are usually not preserved during the fossilisation process, or concern hard parts not retained in our specimen, which is only partially preserved and thus our description covers merely dorsal carapace features.

However, preservation, although partial, of the sole specimen of *Dynomene collinsi* n. sp. available to date, allows observation of the main characters such as the rounded outline, convex carapace, triangular front continuous with enlarged orbits, absence of pseudo-rostral teeth, presence of a broad V-shaped cervical groove and toothed anterolateral margins. These features match the main diagnostic features of dorsal carapaces of the Dynomenidae well (e.g., the clearly triangular front), rather than those of dromiids (McLay 1999; Guinot & Tavares 2003; Guinot 2008).

According to Guinot (2008), extant dynomenids can be divided into four subfamilies: Acanthodromiinae Guinot, 2008, Dynomeninae Ortmann, 1892, Metadynomeninae Guinot, 2008 and Paradynomeninae Guinot, 2008. Added to these is an extinct family, Graptocarcininae Van Bakel, Guinot, Carmelo Corral & Artal, 2012. Assignment of the new species to the Dynomenidae and the genus *Dynomene* is supported by its possession of a rounded carapace that is wider than long, a smooth surface and an incomplete cervical groove. Members of the Acanthodromiinae are defined by having a longer-than-wide, oblong and spinose carapace, which rules out any subfamily relationship with *Dynomene collinsi* n. sp. Although appearing morphologically similar to *Metadynomene* McLay, 1999, the sole genus of the Metadynomeninae, which usually has a carapace of equal width and length and a complete cervical groove that crosses the entire carapace, the new species has a carapace that is wider than long and the cervical groove is incomplete. Species of *Paradynomene* Sakai, 1963 and of extinct genera included in the Paradynomeninae, such as *Kieronopsis* Davidson, 1966 and *Kromtitis* Müller, 1984, clearly differ from *Dynomene collinsi* n. sp. in usually having a longer-than-wide carapace, strongly covered with tubercles, granules and spines. In addition, the placement of the new species in the genus *Dynomene* appears appropriate in view of those features that the only specimen available presents (see McLay 1999; Guinot 2008).

Discussion: Based on the proposed generic placement of *Dynomene collinsi* n. sp., we have compared it with all exclusively extinct species of *Dynomene* (e.g., Schweitzer et al. 2010; Beschin et al. 2016), as follows. *Dynomene acutispinis* (Rathbun, 1945), from the Pliocene of Fiji, differs from *D. collinsi* n. sp. in having a wider and larger carapace, a more acute outer orbital angle and a less prominent cardiac region, and it lacks the characteristic muscle scars which the new species possesses. In addition, the temporal and geographical differences justify the separation of both species (see Rathbun 1945; Smithsonian Museum Collections: https://www.si.edu/sisearch/collection-images?edan_q=decapoda, last visit: November 11, 2017, as *Xantho acutispinis*). *Dynomene emiliae* Müller, 1979 from the Miocene of Bulgaria, Hungary and Poland, appears to be very similar to *D. collinsi* n. sp., but differs in having a shorter fronto-orbital margin (slightly more than 50 per cent, while in the new species this is about two thirds) and by absence of the two well-marked cardiac tubercles which *D. collinsi* n. sp. has (see Müller 1979: 65, pl. 33, figs. 1–6). *Dynomene lessinea* Beschin, De Angeli & Checchi, 2001, from the Oligocene of northern Italy, differs from *D. collinsi* n. sp. in having much more defined regions, a more accentuated fronto-orbital rim and two large rounded inflations in the epibranchial region, absent in the new species (see Beschin et al. 2001: 17–18, text-fig. 4; pl. 1, figs. 5, 8). *Dynomene shinobui* Karasawa, 1993, from the Miocene of southwest Japan, shows subtle differences with *D. collinsi* n. sp. such as a bilobed front, more curved anterolateral margins and absence of the two well-marked cardiac tubercles and muscle scars seen in *D. collinsi* n. sp.; moreover, the temporal and geographical difference justify their differentiation (Karasawa 1993: 41, figs. 12, 14–16). *Dynomene variabilis* Portell & Collins, 2004, from the Miocene of Jamaica, differs from the new species in having a notched, more rimmed front and more clearly marked gastric regions (Portell & Collins 2004: 113–115, fig. 1.1). *Dynomene vetusta* Beschin, Busulini, Tessier & Zorzin, 2016, from the Lower Eocene of northeastern Italy, differs from *D. collinsi* n. sp. in having a relatively longer carapace and in the presence of rounded inflations scattered in the branchial regions, which are absent in *D. collinsi* n. sp. (Beschin et al. 2016: 66–68, text-fig. 37; pl. 8, figs. 2, 3a, b).

Extant species of *Dynomene* that also have a fossil record according Schweitzer et al. (2010: 66), including *D. hispida* Latreille *in* Milbert, 1812 and *D. praedator* A. Milne-Edwards, 1879, have also been compared to *D. collinsi* n. sp. *Dynomene hispida* differs from the new species in having a faintly notched front, a supraorbital margin with small spines near the postorbital corner and scattered granules over the branchial regions (e.g., McLay 1999: 473–481, fig. 18a). *Dynomene praedator* differs from *D. collinsi* n. sp. by a supraorbital margin that is clearly rimmed and spiny near the outer orbital corner; moreover, the anterolateral margins are not clearly toothed as in *D. collinsi* n. sp. and the dorsal surface is covered by coarse granules that are scattered along the branchial and hepatic regions. In the new species, these regions are smooth (e.g., McLay 1999: 481–488, fig. 19a).

Dromilites subglobosa Müller & Collins, 1991, from the Priabonian of Hungary (Müller & Collins 1991: 64–65, pl. 3, figs. 1–3; text-fig. 3c), presents striking similarities to *D. collinsi* n. sp., such as a rounded and smooth carapace and a triangular front. The Hungarian species is here transferred to *Dynomene*. However, it differs from the new species in having the angle between the fronto-orbital margin and the longitudinal midline of about 50º, whereas in the new species that angle is about 70º. In addition, *Dromilites fossata* Müller & Collins, 1991, of the family Dromiidae De Haan, 1833, should be re-examined, in particular the front and orbits, to establish its family assignment (Müller & Collins 1991: 64–65, pl. 3, figs. 1–3; text-fig. 3c; Schweitzer et al. 2012: 28, 31; Jagt et al. 2015: 867).

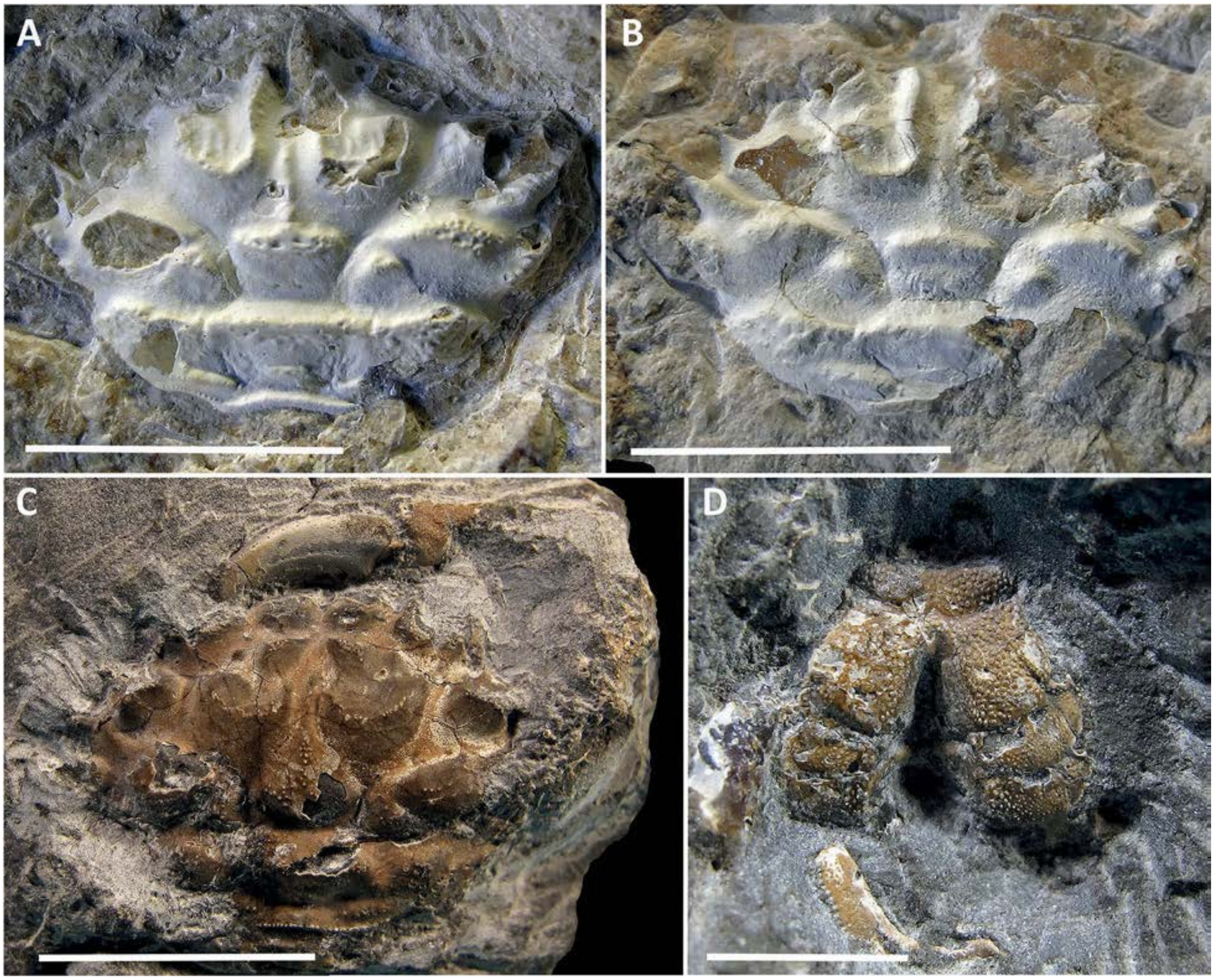

Fig. 2. A, B – *Sculptoplax rigida* Müller & Collins, 1991, Priabonian, Orgiano (Italy). A: MCV 19/06, in dorsal view. B: MCV 19/07, in dorsal view. **C, D** – *Sculptoplax oscensis* (Ossó & Domínguez, 2017), MPZ-2017/542 (holotype), Priabonian, Yebra de Basa (Huesca, Spain) in dorsal (C) and ventral (D) views. Scale bars equal 10 mm (A–C) and 5 mm (D).

4. Remarks on the generic placement of *Eoacantholobulus oscensis* Ossó & Domínguez, 2017 and the systematic position of the genus *Sculptoplax* Müller & Collins, 1991

During a visit to Italy in 2018, we were able to examine two complete specimens of *Sculptoplax rigida* (Fig. 2A, B) from Priabonian levels at the San Feliciano quarry (Orgiano, Vicenza, northeastern Italy), which led us to consider a possible relationship between this species and *Eoacantholobulus oscensis* (Fig. 2C, D) from the Priabonian of Aragón (Spain).

Indeed, the poor illustration of the fragmentary holotype and its diagrammatic interpretation (Müller & Collins 1991: 90, pl. 8, fig. 13; text-fig. 5G), are the reason why we did not consider *Sculptoplax rigida* in our comparisons when describing *Eoacantholobulus oscensis* (see also Beschin et al. 2018: 195, fig. 127). However, the examination of two complete Italian specimens of *Sculptoplax rigida* contained in the collections of the Civic Museum "D. Dal Lago" of Valdagno (MCV19/06 and MCV19/07; Fig. 2A, B), another incomplete carapace (MCV19/08) and the original pictures of Müller & Collins (1991) have allowed us to state that, indeed, those Italian specimens are, at least, congeneric with *Eoacantholobulus oscensis* from Spain.

Nevertheless, in spite of the strong dorsal similarities between both taxa, such as the general outline and, in particular, the pattern of the acute transverse dorsal ridges and curved protogastric ridges, some differences are evident. For instance, in *Eoacantholobulus oscensis*, the epigastric region has two short, weakly marked granular transverse ridges; in contrast, in *Sculptoplax rigida*, this region is defined as a distal continuation of the internal branch of the J-shaped protogastric ridges. The protogastric lobes present two marked raised granular ridges, the first short, anteriorly placed, the second arcuate at the median portion of the protogastric lobe in *E. oscensis*, whereas in *S. rigida* they are clearly continuous, opposed J-shaped ridges. The posterior mesogastric lobe is swollen and granular in *E. oscensis*, while in *S. rigida* it is transversely ridged. Furthermore, the mesobranchial ridges and the cardiac ridge form a continuous line in *S. rigida*, whereas in *E. oscensis* this line appears interrupted and less continuous (Fig. 2; Müller & Collins 1991; Ossó & Domínguez 2017).

The above-mentioned dorsal characters are constant in all specimens of the type series of *Eoacantholobus oscensis* (see Ossó & Domínguez 2017, figs. 1, 2) and these differences allow to treat these taxa as separate species. Although the great similarities among Eocene faunas of the western Tethys and the Pyrenean basins (Domínguez & Ossó 2016a), the continental separation between both marine areas that already existed during the Priabonian, could have favoured allopatric speciation, as in this case.

Consequently, *Eoacantholobulus oscensis* is transferred herein to the genus *Sculptoplax*, as *S. oscensis*. In addition, the systematic placement of *Sculptoplax* within the Panopeidae Ortmann, 1893 is considered valid, as based on evidence provided by the dorsal and sterno-pleonal features preserved in the Aragonese specimens (Ossó & Domínguez 2017: 603–604), rather than within the Xanthidae (Karasawa & Kato 2001: 272).

5. Conclusions

The presence of *Dynomene collinsi* n. sp. in lower Priabonian levels of the central Pyrenees constitutes the first record of the genus from the Cenozoic of the Iberian Peninsula, and fills the gap between Ypresian and Oligocene species of *Dynomene* that have been recorded from the westernmost Tethyan Realm (Beschin et al. 2001; Beschin et al. 2016).

As previously suggested by Vía (1969, 1991) and Domínguez & Ossó (2016a), the present study corroborates the similarity, either at generic or even specific level, between the decapod crustacean faunas from the western Tethys (Hungary and northern Italy) and those from the central Pyrenees of Spain during the Priabonian. The progressive closure between the Tethys and North Atlantic, through the South Pyrenean basins during the Late Eocene (e.g., Puigdefàbregas et al. 1986) could have promoted allopatric speciation.

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6.1.2.3. First record of a homolid crab (Crustacea: Decapoda: Homoloidea) from the early Eocene of the Iberian Peninsula

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First record of a homolid crab (Crustacea: Decapoda: Homoloidea) from the early Eocene of the Iberian Peninsula

Primer registro de un cangrejo homólido (Crustacea: Decapoda: Homoloidea) del Eoceno temprano de la Península Ibérica

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ABSTRACT

We describe a new species of homolid crab from the Ypresian (early Eocene) Roda Formation of Huesca province (Aragon, Spain). In spite of the fragmentary condition of the sole specimen, some preserved frontal elements, and in particular the complete left cheliped, allow inclusion it within the genus *Paromola* Wood-Mason in Wood-Mason and Alcock, 1891, based on morphological similarities with the extant species of this genus. Direct comparison with specimens of the extant *Paromola cuvieri* (Risso, 1815) confirms this systematic assignment. *Paromola bretoni* n. sp. is the first homolid reported in the Cenozoic of the Iberian Peninsula, and expands the rich decapod fossil record of the Eocene basins of southern Pyrenees.

Keywords:Systematics, Brachyura, Homolidae, Ypresian, Pyrenees.

RESUMEN

Se describe una nueva especie de cangrejo homólido, de la Formación Roda, Ypresiano (Eoceno temprano) de la provincia de Huesca (Aragón, España). A pesar de que el único ejemplar se halla parcialmente fragmentado, la similitud morfológica con especies actuales de los elementos conservados de la región frontal y en especial el completo quelípedo izquierdo, permite ubicarlo en el género Paromola Wood-Mason Wood-Mason and Alcock, 1891. Comparaciones con ejemplares actuales de Paromola cuvieri (Risso, 1815) confirmarían la validez de esta ubicación sistemática. Paromola bretoni n. sp. es el primer homólido reportado en el Cenozoico de la Península Ibérica y amplia la riqueza de registros sobre decápodos fósiles del Eoceno en las cuencas Surpirenaicas.

Palabras clave: Sistemática, Braquiura, Homolidae, Ypresiano, Pirineos

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1. Introduction

Records of fossil homolids in the Eocene of Europe are not uncommon, for instance in northern Italy, where several genera and species of Homolidae De Haan, 1839 have been described (De Angeli *et al.*, 2019, p. 20), as well as in the British Isles (Collins *et al.*, 2020, p. 32) and Denmark (Collins *et al.*, 2005, p. 19–20). Records of the Homolidae have never been reported to date from the Eocene of the Iberian Peninsula. Therefore, this is the first report for the family in the Eocene of the Iberian Peninsula. Here we report the first occurrence fossil homolid crabs in the Eocene of the Iberian Peninsula. The material is represented by a crab carapace fragmentarily preserved, decorticated, and preserving some cuticle remains and pereopods, recovered from early Eocene strata near the village of Roda de Isábena (Huesca province, Aragon, Spain). A proper mechanical preparation of the holotype, partially destroyed by a previous inadequate attempt of preparation, allowed us to reveal important elements, such as the complete left cheliped and partial ambulatory legs. The remains of the intralineal carapace and of the left extralineal flank, with partially preserved cuticle, and the peculiar morphology of the left cheliped, as well as the presence of the *linea homolica*, indicate a clear affinity with Homolidae.

Here we describe *Paromola bretoni* n. sp., a new fossil species of the extant genus *Paromola*, with only two other fossil species known: *P. rosenburgensis* Nyborg and Garassino, 2017, and *P. vetula* Crawford, 2008 (see Nyborg and Garassino, 2017).

Extant species of *Paromola* are spread worldwide (Guinot and Richer de Forges, 1995, fig. 70), usually inhabiting the upper bathyal zone common among homolids, albeit they can also inhabit shallower depths (*ibid*, p. 489–491, fig. 76), similar to the palaeoenvironment where the fossil specimen dwelt. Explanation on the former and current systematics of Homoloidea De Haan, 1839 are summarized by Guinot (2019, p. 753).

2. Geological setting

The Tremp-Graus Basin (southern Pyrenees) records marine sediments from the Thanetian–lower Cuisian (lower Ypresian, lower Eocene). Paleogeographically, during the Paleocene–Eocene, these basins corresponded to an elongated gulf connected to the west by the Bay of Biscay, located on the southern limit of the axial zone of the Pyrenees, in tropical latitudes (Hay *et al.*, 1999). The Upper Palaeocene to Lower Eocene in this area consists in the following formations: Serraduy, Puebla Limestone, Roda, Morillo and San Esteban (Figure 1); and it is bounded by unconformities related to tectonic activity (Leren *et al.*, 2010).

The studied material comes from the exposed outcrop of prodelta marls corresponding to the Roda Formation (Figure 1), located near to Roda de Isábena (northeast of Huesca, Spain). This formation exposes a thick succession of marls and sandstones and has provided an interesting decapod assemblage (e.g. Vía Boada, 1959; Vía, 1969, 1973; Artal and Castillo, 2004; Artal *et al.*, 2005, 2013a, b; Schweitzer *et al.*, 2007; Van Bakel *et al.*, 2012).

The Roda Formation, is coarsening and shallowing upwards (Molenaar and Martinius, 1990), and show a general progradational pattern to the S and SW (Puigdefàbregas *et al.*, 1985; Molenaar *et al.*, 1988; Lopez-Blanco *et al.*, 1991, 2003; Nio and Yang, 1991; Lopez-Blanco, 1996; Molenaar and Martinius, 1996; Leren *et al.*, 2010).

This formation has been biostratigraphically dated as lower Ypresian in age (Samsó *et al.*, 1990; Tosquella *et al.*, 1990) and consists of a succession of up to 200 m thick formed of shallow-marine, mixed siliciclastic-carbonate deposits (Martinius and Molenaar, 1991).

Abbreviations. MPZ: Museo de Ciencias Naturales de la Universidad de Zaragoza (Spain). ICMD: Institut de Ciències del Mar (ICM-CSIC), Barcelona (Spain).

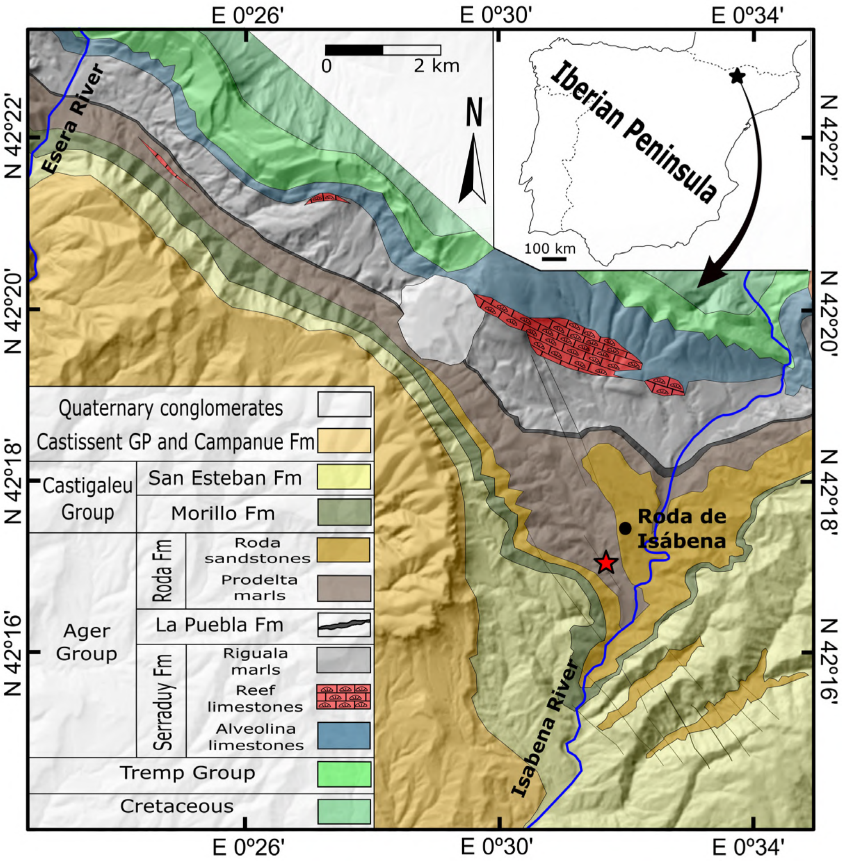

Figure 1 Map location and explanation of formations. Red star indicates outcrop where *Paromola bretoni* n. sp. was recovered.

3. Systematic palaeontology

Infraorder Brachyura Linnaeus, 1758
Section Homoloida Karasawa, Schweitzer and
2011
Feldmann, 2011
Superfamily Homoloidea De Haan, 1839
Family Homolidae De Haan, 1839
Genus *Paromola* Wood-Mason in Wood-Mason
and Alcock, 1891

Type species. *Dorippe cuvieri* Risso, 1815, by original designation.

Species. *Paromola bathyalis* Guinot and Richer de Forges, 1995 (extant); *P. crosnieri* Guinot and Richer de Forges, 1995 (extant); *P. cuvieri* (Risso, 1815) (extant); *P. japonica* Parisi, 1915 (extant); *P. macrochira* Sakai, 1961 (extant); *P. rathbunae* Porter, 1908 (extant); *P. roseburgensis* Nyborg and Garassino, 2017 (fossil); *P. vetula* Crawford, 2008 (fossil).

Paromola bretoni n. sp
urn:lsid:zoobank.org:act:D020CE6C-4633-4712-9C38-6237E281CA04
(Figures 2 and 3)

Diagnosis. Dorsal carapace longitudinally subrectangular; regions fairly defined, marked by shallow incised grooves, some culminated by upward directed spines at anterior third of carapace; widest at level of the mesobranchial region, narrowing in anterior third. Long, pointed, and moderately upturned rostrum; pseudorostral spines directed upwards, originating just above upper margin orbits. Posterior margin concave axially with two lateral reentrants. Cheliped extremely long, subcircular in section, spiny; carpus very elongated; ambulatory legs long, spiny, subcircular in section.

Etymology. Honoring the late Gérard Breton, French palaeocarcinologist.

Material. Holotype MPZ 2020/615, decorti-

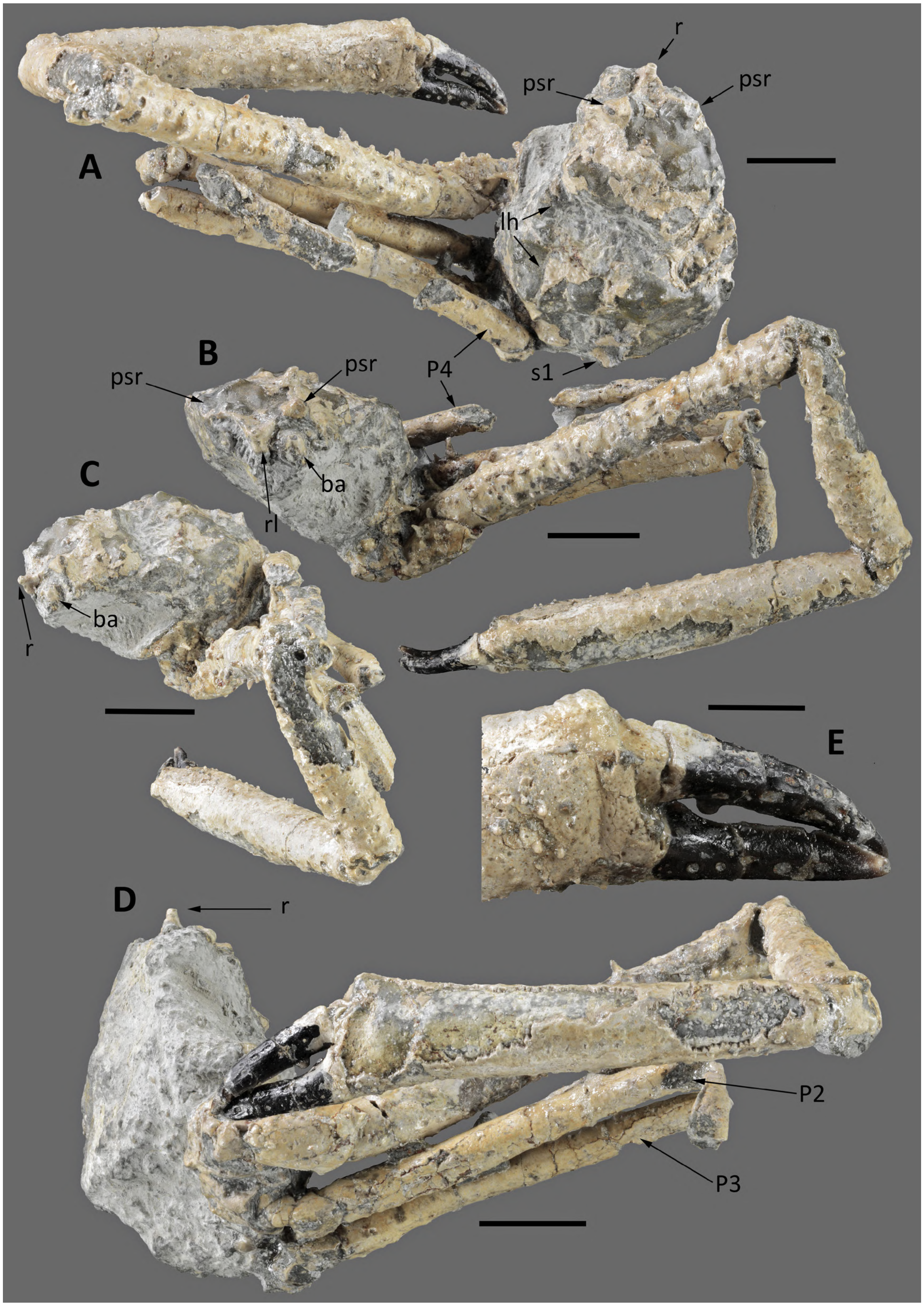

Figure 2 *Paromola bretoni* n. sp., holotype MPZ 2020/615. A: dorsal view; B: frontal view; C: left lateral view; D; ventral view; E: close-up of dactyli. Abbreviations: ba = possibly antennular basal article; lh = *linea homolica*; psr = pseudorostral spines; P2-P4 = ambulatory legs; r = rostrum; rl = rostral lobe; s1 = pleonal somite 1. Photographs by Isabel Pérez Urresti. Scale bar A, B, C, D, equal to 10 mm; E, equal to 5 mm. (Photographs by Isabel Pérez Urresti).

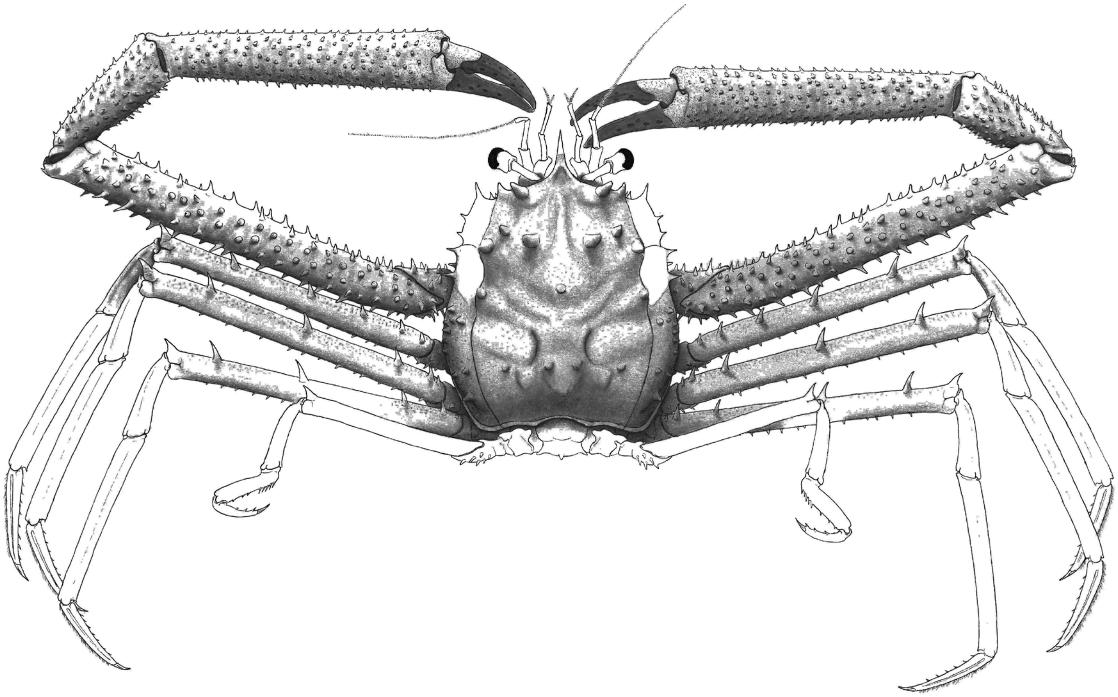

Figure 3 Idealized reconstruction of *Paromola bretoni* n. sp., the shaded parts taken from the specimen, and light parts taken from extant *Paromola* spp. (without scale).

cated crab carapace preserving few remains of cuticle, and complete left cheliped and remains of left ambulatory legs.

Extant comparative examined material. Fourteen samples of *Paromola cuvieri* from the Biological Reference Collections (CBR) at the Institut de Ciències del Mar (ICM-CSIC, Barcelona, Spain) (see Guerrero *et al*., 2020), under the catalog/accession number: ICMD002504, female, juvenile, Namibia; ICMD002505, male, Namibia; ICMD002502, male, juvenile, Barcelona; ICMD002023, female, Catalonia; ICMD119/1998, female, Namibia; ICMD002499, female, Namibia; ICMD002498, male, juvenile, Namibia; ICMD002501, male, juvenile, Namibia; ICMD002500, male, juvenile, Namibia; ICMD002503-1, male, juvenile, Namibia; ICMD002503-2, female, juvenile, Namibia; ICMD120/1998, male, juvenile, Catalonia; ICMD121/1998, male, juvenile, Catalonia; ICMD122/1998, male, juvenile, Catalonia.

Locality Type. Roda de Isábena, Huesca, Spain. *Stratigraphic position and age*. Roda Formation, late Ypresian, early Eocene.

Measurements. Holotype MPZ 2020/615. Carapace length = 36.05 mm: carapace width: 35.44 mm (without lateral spines; half carapace 17.72 mm x 2). Left cheliped (P1): merus = 52.39mm x 6.17mm; carpus = 27.72 mm x 6.7mm; chela = 59.52 x 10.16mm (propodus + dactyli).

Description. Carapace longer than wide, subrectangular, longitudinally ovate in outline; widest at metabranchial region, narrowing in anterior third; fairly defined carapace regions; remains of cuticle of dorsal surface thin, appears gently granulate smooth, bearing presumably large upward directed acute spines (scars). Convex lateral margins of dorsal carapace, weakly vaulted longitudinally and weakly vaulted transversely in intralineal areas. Rostrum simple, pointed, rounded in section, presumably well developed and moderately upturned, rostral lobe axially sulcate; pseudorostral spines present on anterior margin, directed upward. Orbital cavity rounded, upper margin rimmed.

Anterolateral margin not preserved. Posterolateral margin convex, with at least two laterally-projecting spines. Posterior margin rimmed, consisting of three concave arcs, almost equal in length: one axial, and two lateral. Gastric regions not well defined, Epigastric region with two anterior swellings. Protogastric region with four transversely aligned spines (broken). Urogastric region poorly defined, weakly depressed. Cardiac region sub-triangular, with three swellings, two anterior separated by a shallow depression, and one posterior. Intestinal region poorly defined, depressed. Mesobranchial regions positioned on either side of urogastric region, weakly inflated, with at least one small spine (broken); metabranchial regions weakly inflated, with at least two small spines (broken).

Cervical groove pronounced, directed to the flanks of the carapace. Branchiocardiac groove shallow, interrupted medially. *Linea homolica* sinuous. Left cheliped extremely long, subcircular in section; merus strongly spinose; carpus very elongated, both, carpus and propodus, covered with small spines. Dactyli subequal, dark colored, with several setal pits; dactylus with one proximal tooth in occlusal margin; polex edentulous. Meri of P2 to P4, very elongated, with three to six large spines in the upper margin, and small spines in evenly spaced linear arrangement along the whole length of the lower margin.

4. Discussion

Although the studied specimen is partially preserved, some diagnostic characters, such as the well-preserved and extremely long left cheliped, the pointed simple rostrum, the pseudorostral spines, and the *linea homolica*, allow to assign it within the Homolidae with confidence.

The combination of these characters is similar to that of *Paromola*, and fits perfectly with the diagnosis for the genus provided by Guinot and Richer de Forges (1995, p. 358–359), in particular the acute simple rostrum, developed pseudorostral spines, and the long carpus of an extremely long cheliped. Although some other homolids also possess a simple rostrum and long chelipeds, they differ substantially from the studied specimen. For instance, some species of *Homola* Leach, 1816, possess acute rostrum, and long chelipeds, but they are shorter than in the new species (see Guinot and Richer de Forges, 1995, p. 335-338, fig. 11a-b). As well, species of *Moloha* Barnard, 1947, possess long pseudorostral spines, and dorsal carapace with long and sharp spines, which are absent or not preserved in the studied specimen (see Guinot and Richer de Forges, 1995, p. 376–391, figs. 28–33). *Dagnaunus pritchardi* (Jenkins, 1977), from the early Oligocene of South Australia, formerly described as *Paromola pritchardi*, and subsequently transferred to the former genus by Schweitzer *et al.* (2004, p. 134), has longer pseudorostral spines than *P. bretoni* n. sp. (see Jenkins, 1977).

Based upon the above-mentioned characters, and the relatively large size, the placement of that specimen within *Paromola*, seems appropriate until new material confirms the systematic position.

The state of preservation of the carapace of *Paromola bretoni* n. sp., precludes us to compare it further with the fossil species above indicated. Extant species of *Paromola* possess a thin carapace (P. Abelló, pers. comm.), so it can be inferred that the fossil species had the same fragile cuticle, as the studied specimen, which does not help to preserve the entire carapace. However, *P. bretoni* n. sp. differs from *P. roseburgensis* from the early Eocene of Oregon (USA) in having larger size, apparently shorter pseudorostral spines, and different shape of cheliped, which is shorter in *P. roseburgensis* (see Nyborg and Garassino, 2017, p. 140–142, figs. 3, 4). Moreover, *Paromola bretoni* n. sp. differs from *P. vetula*, from the Oligocene of Río Negro (Argentina) by its larger size, and its remains of dorsal carapace preserved are less granulated than in *P. vetula* (see Crawford, 2008). *Londinimola williamsi* Collins and Saward, 2006, from the lower Eocene of Essex (UK), draws attention by its size, and rostral and pseudorostral features, both similar to those of *Paromola bretoni* n. sp. Apparently, *Londinimola william*si is the closest fossil species to our species, by sharing a simple rostrum, pseudorostral spines above upper orbital margin, dorsal regions fairly defined, some culminated by upward directed spines, and linea homolica well defined, but it differs from *Paromola bretoni* n. sp. in having a downturned rostrum instead of upturned; as well, the preserved cheliped and remains of ambulatory legs of *P. bretoni* n. sp. are clearly longer and robust than in *L. williamsi*. In any case, the poor preservation of the new species, does not permit a more detailed comparison (see Collins and Saward, 2006, p. 69–70, pl. 1, figs. 1a-c, 2a, b).

Similarly, comparing *P. bretoni* n. sp. with the extant species of the genus *Paromola* is difficult. However, despite the crushed carapace of *Paromola bretoni* n. sp. could disguise the true length of it, none of those extant species seem to have such left cheliped span with respect to the carapace length. In this sense, examination and measurements of the extant specimens of *P. cuvieri* above listed, show different ratios than *P. bretoni* n. sp., for instance the carapace length/merus P1 length ratio is 0.600, whereas in *P. bretoni* n. sp. that ratio is 0.688, which means that the new species has longer left cheliped with respect to the carapace size than extant *P. cuvieri*, which would favour the specific differentiation between them. Other comparative measurements regarding the carpus of *P. bretoni* n. sp., such as carpus length/merus and length/ratio, do not show substantial differences: 0.505 in *P. cuvieri* vs. 0.529 in P. *bretoni* n. sp. In any case, the temporal span separating *P. bretoni* n. sp. from the extant species, justify the erection of a new species for the Aragonese specimen.

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6.1.2.4. A new genus and species of Parthenopidae MacLeay, 1838 (Decapoda: Brachyura) from the lower Eocene of Spain

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A new genus and species of Parthenopidae MacLeay, 1838 (Decapoda: Brachyura) from the lower Eocene of Spain

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ABSTRACT

We describe *Aragolambrus collinsi* **n. gen., n. sp.** from the Eocene (Ypresian) of Huesca, Aragón, northern Spain, which represents the second report of a fossil Parthenopidae from Spain and the first from the Eocene. *Aragolambrus collinsi* **n. gen. n. sp.** is considered one of the oldest parthenopid crabs, and important morphological features include the shape and size of tubercles of the proto- and mesogastric lobes and the morphology and ornamentation of the chelipeds. The shape of the carapace and orbits of the new species are similar to other Parthenopidae and the distribution and number of the tubercles of the inner margin of the manus suggest inclusion in the subfamily Daldorfiinae. *Aragolambrus collinsi* **n. gen., n. sp.** occurred in coral-algae reefs associated with a rich benthic biota of corals, red algae, echinoderms, molluscs, crustaceans, and fishes within the mesophotic zone. A review of all parthenopid Eocene occurrences suggests that the group originated in reef environments and later occupied more open marine conditions with siliciclastic substrates.

Key Words: Aragón, fossil crabs, paleoecology, Pyrenees, Ypresian

INTRODUCTION

The family Parthenopidae MacLeay, 1838 has received important systematic treatments in the last twenty years (i.e., Tan, 2004; Tan & Ng, 2007a, b). It is currently divided into two subfamilies: Daldorfiinae Ng & Rodríguez, 1986 and Parthenopinae MacLeay, 1838 (Tan & Ng, 2007a, b; De Grave *et al.*, 2009). These works have increased our understanding of the morphology and ecology of the group but the phylogenetic relationships between members of Parthenopidae is still lacking (Tan & Ng, 2007a). Current phylogenetic analyses of major groups of decapod crustaceans suggest Parthenopidae are sister group of Calappidae (Brösing *et al.*, 2007; Tsang *et al.*, 2014).

The fossil record of parthenopid crabs is relatively rich but material is often fragmentary, hampering our ability to reconstruct the origin of such group. There are 51 fossil species of parthenopids currently described (Müller, 1993; Beschin *et al.*, 2001, 2009; Garassino & De Angeli, 2004; De Angeli & Beschin, 2008, 2010; De Grave *et al.*, 2009 and references therein; De Angeli, *et al.*, 2010; Beschin, *et al.*, 2012, 2013, 2015, 2016a, b; Busulini, *et al.*, 2012; Garassino *et al.*, 2012; Varela, 2013; De Angeli & Caporiondo, 2016; Baldanza *et al.*, 2017), with many occurrences in the Eocene (Table 1). Fossil material from the Eocene assigned to this group usually consists of only carapaces, and preservation of the chelipeds in connection with the main body are rare (but see exception in De Angeli & Beschin, 2010). This limits the comparison with the modern representatives of the group in which the margins of the manus, including its shape, and the number and position of the tubercles are taxonomically useful details (Tan & Ng, 2007b).

Although most of the characters used to distinguish modern forms are not preserved in the fossil record (i.e., antennal articles, ambulatory legs.), Tan and Ng (2007a, b) listed important morphological characters to distinguish between different forms, including the shape and ornamentation of the carapace, dorsal regions, rostrum, orbits, and the morphology of the appendages and chelipeds. The features included in hard mineralized parts. like those from the carapace and chelipeds, are likely preserved in fossils allowing assignation of fossil species to some modern genera (i.e., Bittner, 1875, 1893; Quayle & Collins, 1981; Schweitzer *et al.*, 2006; Beschin *et al.*, 2007, 2012, 2013, 2016b; Busulini *et al.*, 2012).

We describe herein new parthenopid crab discovered in the Serraduy Formation (Ypresian, lower Eocene) from the southern Pyrenees (Spain). The presence of relatively complete material, including carapaces with articulated chelipeds, allow comparison with both modern and fossil representatives of the group. Based

Table 1. Representatives of the family Parthenopidae in the Eocene.

Genus	Species	Locality	Age	Type of substrate	Environment
Acantholambrus Blow & Manning, 1996	*A. baumi* Blow & Manning, 1996	North Carolina, USA	Lutetian	siliciclastic	shallow platform
Aragolambrus n. gen.	*A.collinsi* **n. sp**	Huesca, Spain	Ypresian	carbonate	coral-algal reef
Braggilambrus De Angeli & Caporiondo, 2016	*B. tani* De Angeli & Caporiondo, 2016	Verona, Italy	Ypresian	carbonate	coral-algal reef
Eogarthambrus De Angeli, Garassino & Alberti, 2010	*E. guinotae* De Angeli, Garassino & Alberti, 2010	Vicenza, Italy	Ypresian	carbonate	reef
Eurolambrus De Angeli & Beschin, 2010	*E. mainensis* De Angeli & Beschin, 2010	Vicenza, Italy	Lutetian	siliciclastic	shallow platform
Leiolambrus A. Milne-Edwards, 1878	*L. longifrons* Quayle & Collins, 1981	Christchurch Bay, UK	Bartonian	siliciclastic	shallow platform
Lessinilambrus Beschin, De Angeli & Zarantonello, 2013	*L. paleogenicus* Beschin, De Angeli & Zarantonello, 2013	Vicenza, Italy	Lutetian	sSiliciclastic	shallow platform
Mesolambrus Müller & Collins, 1991	*M. declinatus* Müller & Collins, 1991	Vicenza, Italy	Ypresian	carbonate	coral-algal reef
	M. ypresianus Beschin, De Angeli, Checchi & Zarantonello, 2016b	Vicenza, Italy	Ypresian	carbonate	coral-algal reef
Ochtholambrus Tan & Ng, 2007 (Tan & Ng, 2007a)	*O. gambillarai* Busulini, Beschin & Tessier, 2012	Possagno(Treviso), Italy	Priabonian	siliciclastic/ carbonate	shallow platform
Parthenope Weber, 1795	*P. nummulitica* (Bittner, 1875)	Vicenza, Italy	Lutetian-Priabonian	siliciclastic	shallow platform
	P. menini Beschin, De Angeli, Checchi & Zarantonello, 2016b	Vicenza, Italy	Lutetian	siliciclastic	shallow platform
	P. pentagonus Quayle & Collins, 1981	Christchurch Bay, UK	Bartonian	siliciclastic	shallow platform
	P. chiampiensis Beschin, De Angeli & Zarantonello, 2013	Vicenza, Italy	Lutetian	siliciclastic	shallow platform
Phrynolambrus Bittner, 1893	*P. corallinus* (Bittner, 1893)	Verona (Italy)	Priabonian	carbonate	reef
Pseudolambrus Paullson, 1875	*P. antiquus* Beschin, de Angeli, Checchi & Zarantonello, 2016b	Vicenza, Italy	Lutetian	siliciclastic	shallow platform
Rhinolambrus A. Milne-Edwards, 1878	*R. elongatus* Beschin, De Angeli, Checchi & Zarantonello, 2012	Vicenza, Italy	Lutetian	siliciclastic	shallow platform
Daldorfia Rathbun, 1904	*D. salina* Schweitzer, Feldmann, González-Barba & Cosovic, 2006	Baja California, Mexico	Bartonian	siliciclastic	shallow platform
	D. eocenica Beschin, Busulini, De Angeli, & Tessier, 2007	Vicenza, Italy	Ypresian	carbonate	reef

on a review of previous occurrences of parthenopids in the fossil record, we include paleoecological information that can be compared with the ecology of modern forms.

GEOLOGICAL SETTING

The southern Pyrenean basins record one of the most complete Eocene marine sedimentary successions from Europe, with fossil decapods described in several outcrops (i.e., Vía, 1969, 1973; Artal *et al.*, 2013; Ossó *et al.*, 2014; Dominguez & Ossó, 2016; López-Horgue & Bodego, 2017; Artal & Van Bakel, 2018a, b). Paleogeographically, the southern Pyrenean basin was located in tropical latitudes during the Paleocene-Eocene, and corresponded to an elongated gulf connected to the west by the Bay of Biscay, located on the southern limit of the axial zone of the Pyrenees (Hay *et al.*, 1999).

The material described herein was collected from the lower Eocene (middle Ypresian) Serraduy Formation of the Tremp-Graus Basin (Fig. 1). It comes from the classic outcrop known as Barranco de Ramals in the neighborhoods of the villages of La Puebla de Roda and Serraduy, in northeastern Huesca province, Aragón, Spain. This locality has provided an important assemblage of decapods associated with pinnacle coral reefs (Vía, 1973; Artal & Vía, 1988; Artal & Castillo, 2005; Fraaije & Pennings, 2006; Artal & Van Bakel, 2018a, b).

The Serraduy Formation consists of three lithostratigraphic intervals. The lower corresponds to the shallow marine platform, Alveolina limestones. This unit is overlain by a discontinuity surface formed after a widespread flooding event. Low sedimentary rates favoured the development of a set of pinnacle-reefs and associated facies (the Reef limestones interval) on this surface, including a great diversity of invertebrates that suggests an environment with intermediate depths and wave action (Gaemers, 1978). This reefal unit is in turn overlain by the Riguala marls, deposited in a relatively deep, open marine platform, in transition to the most external of slope-basin environments, supporting a lower concentration of benthic communities (Serra-Kiel *et al.*, 1994). The Riguala marls were dated as lower to middle Ilerdian (Serra-Kiel *et al.*, 1994), which corresponds to the global Ypresian Stage (Pujalte *et al.*, 2009).

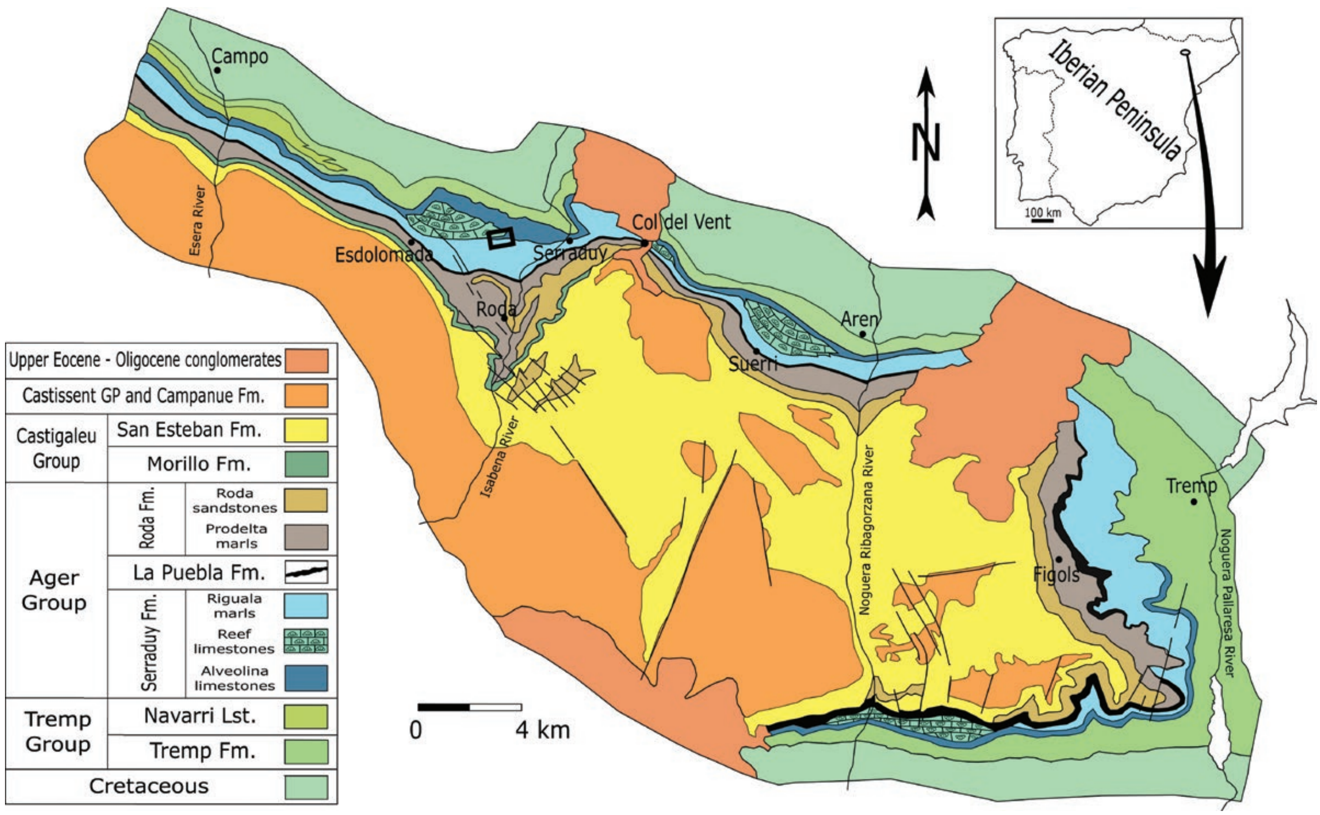

Figure 1. Simplified geological map of the Tremp-Graus Basin, Spain (modified after Serra-Kiel *et al.* 1994). The box between Serraduy and Esdolomada indicates the location of the outcrop that was studied. With permission. This figure is available in colour at *Journal of Crustacean Biology* online.

MATERIALS AND METHODS

Specimens were collected directly from the outcrops exposing the transition between the Reef limestones and Riguala marls. This material includes a series of tempestitic beds that transported detrital material from the reef to the fore-reef facies, including a diverse invertebrate fauna (see Zamora *et al.*, 2018) and coral fragments. Parthenopid crabs are extremely rare in the decapod assemblage from this area. From more than 600 remains of decapods only two carapaces (one of them with chelipeds) and ten isolated right propodi (manus) were identified, all corresponding to the new taxa described herein.

Morphological terminology of Parthenopidae follows Tan & Ng (2007a, b). Carapace measurements are given as carapace width (CW) and carapace length (CL) in millimetres. The carapace width was measured between the tips of the lateral teeth, and carapace length along the mid-line. The propodus of the cheliped is referred to as the manus.

The specimens were prepared using a Micro Jack air scribe (Paleotools; Brigham, UT, USA). The specimens were then photographed dry and coated with ammonium chloride sublimate. Detailed photography of the carapace surfaces was made using a Nikon d7100 camera (Nikon, Tokyo, Japan) with a macro 60 mm lens. Extant material of *Parthenope macrochelos* (Herbst, 1790) (Fig. 2)) was examined for comparisons.

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

SYSTEMATICS

Infraorder Brachyura Linnaeus, 1758

Section Eubrachyura de Saint Laurent, 1980

Subsection Heterotremata Guinot, 1977

Superfamily Parthenopoidea MacLeay, 1838

Family Parthenopidae MacLeay, 1838

Subfamily Daldorfiinae Ng & Rodríguez, 1986

Distinction between the subfamilies Daldorfiinae and Parthenopinae is difficult due to the great variety of shape and ornamentation that they exhibit (Schweitzer *et al.*, 2006). Most of the characters suggested by Tan & Ng (2007a, b) to differentiate between the two subfamilies are not preserved in the fossil material (i.e., antennal articles, ambulatory legs). Nonetheless, Tan and Ng (2007a, b) listed important morphological characters to distinguish between different forms that can be recognized in fossil species. These include: 1) carapace shape, 2) carapace ornamentation, 3) shape and distribution of the dorsal regions, 4) shape of the rostrum and orbits, and 5) cross-section shape and ornamentation of the chelipeds.

Aragolambrus **n. gen.** is characterized by the subtriangular carapace and complete orbits typical of Parthenopinae. The combination of the large epibranchial spines; inflated regions; relatively deeply incised grooves; downturned, sulcate front; the distribution and number of the tubercles on the inner margin of the manus; and the non-triangular shape in cross section, suggest inclusion in Daldorfiinae. The sister group of Parthenopidae is Calappidae

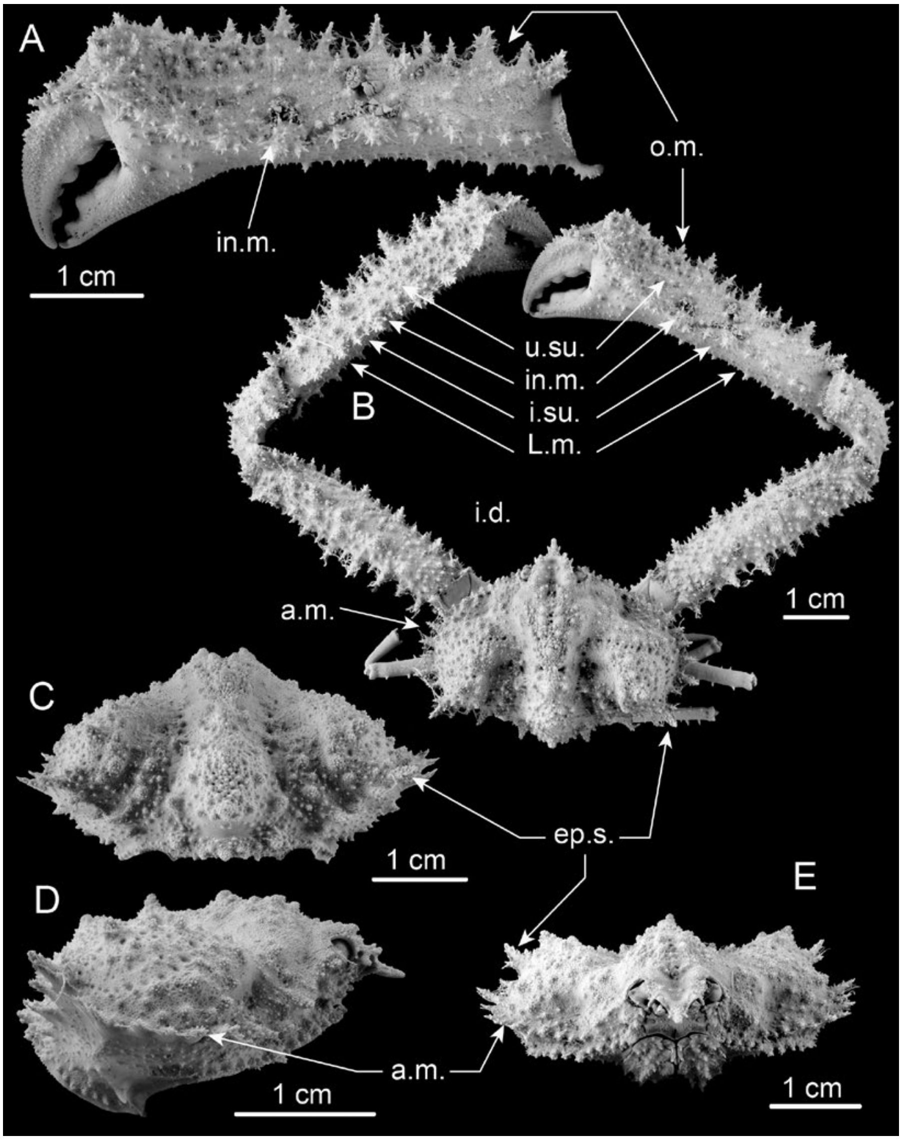

Figure 2. Modern representative of Parthenopidae, *Parthenope macrochelos* (Herbst, 1790) (MPZ 2019/222) showing some of the homologous structures observed in the fossil *Argolambrus collinsi* **n. gen., n. sp.** Inner side of right manus (**A**); dorsal view (**B**); oblique posterior view (**C**); right lateral view (**D**); frontal view (**E**). Abbreviations: in.m., inner margin; o.m.; outer margin; a.m., anterolateral margin; ep.s., epibranchial spine (equivalent to lateral angle); u.su., upper surface; i.su., inner surface. Specimen whitened with ammonium chloride sublimated for photography.

(Brösing *et al.*, 2007; Brösing, 2008; Tsang *et al.*, 2014) of which some members (i.e., *Calappilia* A. Milne Edwards in Bouillé, 1873 and *Bittnerilia* De Angeli & Garassino, 2003; see De Angeli & Garassino, 2003; Beschin & De Angeli, 2008; Busulini *et al.*, 2014) have chelipeds similar those of *Aragolambrus* **n. gen.**, suggesting that such morphology is probably plesiomorphic within parthenopids.

Genus ***Aragolambrus*** **n. gen.**

Diagnosis: Carapace subtriangular, broader than long; regions inflated; dorsal surface tuberculate; epibranchial margin slightly expanded, without crest or row of prominent tubercles; not produced beyond base of pleon. Rostrum downturned, sulcate. Exorbital angle acute. Gastro-orbital notch present. Hepatic margin distinct, not continuous with epibranchial region. Hepatobranchial notch present, distinct. Epibranchial margin convex, angled at last epibranchial spine; spines broadly triangular, closely spaced; last epibranchial spine anterior to posterior margin. Proto-, meso-, and metagastric regions differentiated, without ridge; protogastric region is most developed. Hepatic region inflated, slightly lower than epibranchial, gastric regions. Epibranchial region without continuous diagonal ridge. Pterygostomial ridge present, but not well developed. Subepibranchial region narrow, tuberculate. Epimeral line (or moult line) bordered by numerous small tubercles. Cheliped manus outer margin with three to five teeth, triangular in shape and widely spaced; inner margin composed by only three ornamented tubercles; outer side covered with tubercles of variable size.

Type species: Aragolambrus collinsi Ferratges, Zamora & Aurell, by original designation.

Etymology: The generic name derives from the Autonomous Community of Aragón, Spain in arbitrary combination with the parthenopid generic name *Lambrus*, a common suffix for many parthenopid genera. Gender masculine.

Remarks: The good preservation of the main dorsal characters in the specimens described herein, allow detailed comparison with fossil and extant genera. Based on the diagnostic features provided by Tan & Ng (2007a, b), *Aragolambrus* **n. gen.** can be distinguished from other genera of modern Parthenopidae because of its dorsal tubercles, the shape of the carapace regions, the posterior and lateral margin, and the shape and ornamentation of the chelipeds.

The features that allow inclusion of the new material to new genus are: 1) subtriangular shape of the carapace, which is broader than long; 2) epibranchial region inflated, without a continuous diagonal ridge, with a large spine on the lateral angle, and last epibranchial spine anterior to the posterior margin; 3) hepatic margin distinct, not continuous with the epibranchial region; 4) hepatic region inflated, slightly lower than epibranchial and gastric regions; 5) proto-,meso-, and metagastric regions differentiated, without ridge; 6) protogastric region more developed than meso- and metagastric regions; 7) exorbital angle acute; 8) suborbital region without a diagonal ridge, slightly depressed; and 9) manus not triangular in cross section, with a row of teeth on its inner surface that gives rise to the inner margin.

Many of the species included in the genera of Daldorfiinae (i.e., *Daldorfia* Ng & Rodríguez, 1986, *Niobafia* Tan & Ng, 2007b, and *Thyrolambrus* Rathbun, 1894) show similarities with *Aragolambrus* **n. gen.**, like a protogastric region that is more developed than the meso- and metagastric regions, and a metagastric region that is generally the most depressed region (Tan & Ng, 2007b). The cardiac region in *Daldorfia* is also usually more inflated than the metagastric region, the intestinal region is depressed, and the epibranchial region is the most developed of the three branchial regions. The relatively small size of the chelipeds in relation to the carapace, the cross section of the manus, which is not triangular, and the ornamentation of the chelipeds supports assignment of *Aragolambrus* **n. gen.** to Daldorfiinae.

Aragolambrus **n. gen.** also shows similarities with some genera included in Parthenopinae (i.e., *Aulacolambrus* Paulson, 1875, *Certolambrus* Tan & Ng, 2003, *Rhinolambrus* A. Milne-Edwards, 1878, *Phrynolambrus* Bittner, 1893, and *Neikolambrus* Tan & Ng, 2003), such as the subtriangular shape of the carapace, well-developed dorsal regions, hepatic and epibranchial margins that are not in a straight line; posterolateral regions of the carapace not expanded to cover ambulatory legs, presence of a spine at the lateral angle that separates the anterior margin from the posterior margin; and a carapace that is covered with tubercles. Species assigned to these genera, however, show highly developed chelipeds triangular in cross section, a clear row of tubercles on the inner margin of the manus, and an anterolateral margin of the carapace with a row of spines or tubercles above the epimeral line. Tan & Ng (2007a) created the new genus *Ochtholambrus* to accommodate several species of *Pseudolambrus*. As Tan & Ng (2007a) pointed out "*Ochtholambrus* superficially resembles *Pseudolambrus* and *Parthenopoides*, but can be easily differentiated from the latter two genera in that the two median protogastric tubercles are usually higher than the mesogastric median tubercle. In *Pseudolambrus* and *Parthenopoides* the mesogastric median tubercle is typically higher than the protogastric tubercles." Specimens described herein share with *Ochtholambrus* the typical condition of two median protogastric tubercles higher than the mesogastric median tubercle (see for example *O. stimpsoni* (Garth, 1958)), but *Aragolambrus* **n. gen.** lacks an accused anterolateral margin with a row of aligned teeth (Figs. 3; 4C, D). The new genus also differs in the shape of chelipeds. These are shorter in *Aragolambrus* **n. gen.** and the manus presents a rudimentary row of tubercles on the inner margin (see Fig. 4I), which does not form a ridge as in *Ochtholambrus*.

Nomenclatural statement: A life science identifier (LSID) number was obtained for the new genus and species: urn:lsid:zoobank.org:pub:4EA0FD09-478D-4C94-AD36-A2E87DB01B6A.

Aragolambrus collinsi n. sp.

(Figs. 3, 4)

Type material: The holotype is an almost complete carapace preserving chelipeds (MPZ-2019/211). Paratype material include an isolated carapace (MPZ-2019/210) and ten isolated right propodi

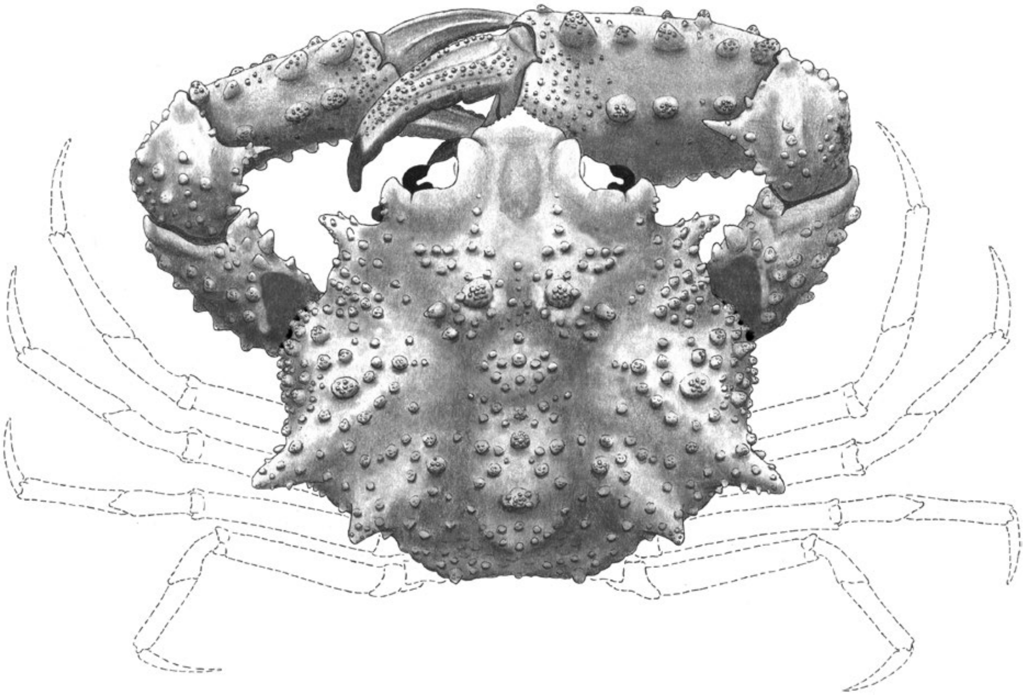

Figure 3. Reconstruction of *Aragolambrus collinsi* **n. gen., n. sp.** based on the holotype and paratype specimens.

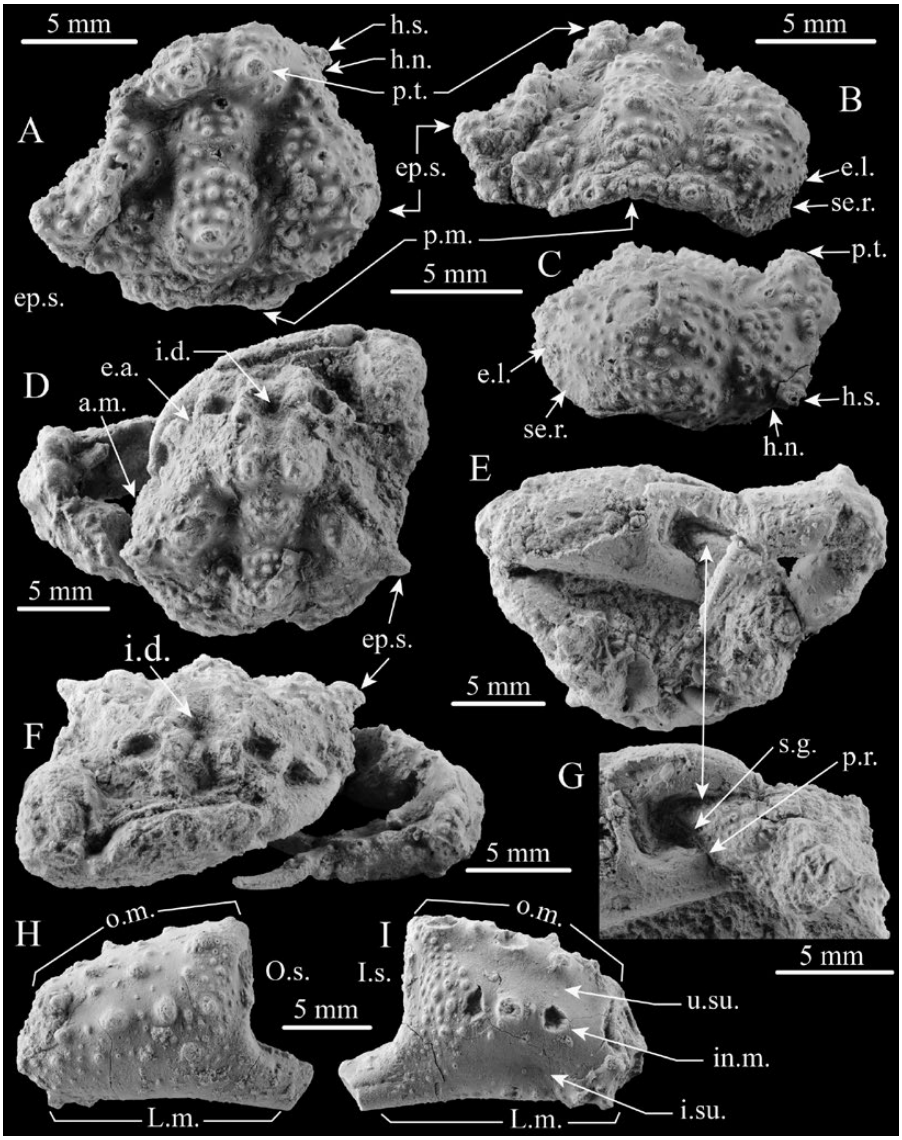

Figure 4. *Aragolambrus collinsi* **n. gen., n. sp.** from the lower Eocene (Serraduy Formation) of Huesca, Spain. Dorsal (**A**), oblique posterior (**B**), and right lateral (**C**) views of the paratype (MPZ-2019/211); dorsal (**I**), ventral (**E**), and frontal (**F**) views of the holotype (MPZ-2019/210); detail of ventral view of the carapace (**G**); outer (**H**) and inner (**I**) surfaces of an isolated manus (MPZ-2019/212). Abbreviations: a.m., anterolateral margin; h.s., hepatic spine; h.n., hepatiobranchial notch; s.g., subhepatic groove; p.r., pterygostomial ridge; se.r., subepibranchial region; p.t., protogastric tubercles; e.l., epimeral line; e.a., extraorbital angle; L.m., lower margin; o.m., outer margin; I.s., inner surface; in.m., inner margin; u.su., upper surface; i.su., inner surface; ep.s., epibranchial spine (equivalent to lateral angle); O.s., outer surface; p.m., posterolateral margin; i.d., interorbital depression. Specimens whitened with ammonium chloride sublimated for photography.

(MPZ-2019/212–221). Holotype: CW 15.91 mm CL 16.21 mm; paratype: CW 15.95 mm, CL 13.66 mm.

Type locality: Barranco de Ramals, Puebla de Roda, Huesca province, Spain.

Type horizon: Serraduy Formation, middle Ypresian, lower Eocene.

Diagnosis: As for genus.

Description: Carapace subtriangular, slightly broader than long (Figs. 3, 4A, D); rostrum downturned; orbits separated by interorbital depression (Fig. 4D). Regions inflated; dorsal surface tuberculate (Figs. 3, 4A, D); epibranchial margin slightly expanded, without crest or row of prominent tubercles. Exorbital angle acute (Fig. 4D). Gastro-orbital groove deep. Wide fronto-orbital margin, 53.5% of total width; anterolateral margin longer than posterolateral margin, tuberculate, with numerous small granular tubercles; lateral angle rounded (Fig. 4A, D). Hepatic margin distinct, not continuous with epibranchial region, with prominent spine bearing smaller tubercles. Hepatobranchial notch present (Fig. 4A, C). Epibranchial margin convex, angled at last epibranchial spine; last epibranchial spine anterior to posterior margin, directed laterally, oblique to axis (Fig. 4D); margins of spine bearing smaller tubercles; posterolateral margins convex, with several small blunt tubercles (Fig. 4A); posterior margin slightly concave, granulate (Fig. 4B). Proto-, meso-, metagastric regions differentiated. Hepatic region narrow, inflated, slightly lower than epibranchial, gastric regions. Epibranchial region without continuous diagonal ridge, but with 2 granulate, oblique reliefs; surface with irregular tubercles. Supraorbital region raised; lateral portion with suture. Suborbital region without diagonal ridge, slightly depressed; protogastric region inflated, with 2 large tubercles, more inflated than mesogastric region; mesogastric region separated from protogastric region by short, narrow groove; metagastric region not inflated, groove separating metagastric from mesogastric region conspicuously shallow. Mesobranchial region inflated, higher than metabranchial with large nodose tubercle. Cardiac region inflated, with large median tubercle, separated from metagastric region by shallow groove; posterior portion gradually depressed into intestinal region. Intestinal region not inflated. Pterygostomial region partially exposed, not excavated, tuberculate. Epimeral line (or moult line) bordered by numerous small tubercles (Fig. 4B, C).

Markedly heterochelous (Figs. 3, 4E, F); major cheliped (right) strong. Merus not well preserved, tuberculated; carpus not well preserved, slightly higher than long; surface slightly tuberculated, with spine on inner margin. Manus longer than high, slightly divergent distally, not triangular in cross section; outer margin with 5 triangular spines, widely spaced (Fig. 4H, I); lower margin slightly concave at base of fixed finger, with small aligned tubercles (Fig. 4H, I); inner margin not well developed, with 3 widely spaced, ornamented tubercles (Fig. 4H, I); upper, inner surface smooth (Fig. 4H, I); row of 4 ornamented tubercles on outer side aligned in central part plus several tubercles irregularly distributed over surface (Fig. 4H). Fixed finger short, slightly oblique downward, triangular, tip pointing slightly upward (Fig. 4E); lateral row of granulation extending to articulation with dactylus. Dactylus strong, curved (Fig. 4E); upper surface with 2 granular crests. Lateral surface slightly granular, with row of pores; occlusal margin with molariform teeth, becoming smaller distally.

Left cheliped more slender (Fig. 4E) than right cheliped. Merus strongly tuberculated; carpus not well preserved, slightly higher than long; surface slightly tuberculated, with spine on inner margin. Manus longer than high, slightly divergent distally; outer margin with 3 triangular teeth, widely spaced; lower margin slightly concave at base of fixed finger, with small aligned tubercles; inner margin not well developed, with 3 ornamented tubercles widely spaced; upper, inner surface smooth. Fixed finger shorter than palm, 3 times longer than high, oblique downward, with 2 longitudinal grooves on the outer margin and 2 on mesial part; dactylus curved, longitudinal rows of setae along edge, with longitudinal groove in upper mesial part; occlusal margin with small teeth, becoming smaller distally.

Etymology: The specific name is dedicated to Dr. Joe S.H. Collins, recently deceased, in recognition to a lifetime dedicated to the study of fossil brachyurans.

DISCUSSION

Modern Parthenopidae are mainly tropical or subtropical in distribution and are usually associated with mobile siliciclastic substrates from the intertidal to deep water (i.e. Zariquiey, 1968; Garth, 1993; Davie & Turner, 1995; Tan *et al.*, 1999; Ng & Rahayu, 2000; Tan & Ng, 2003, 2007a, b; McLay & Tan, 2009). Most of these species show derived characters, with highly developed chelipeds as in *Parthenope macrochelos* (Fig. 2). This species digs into sandy substrates and remains motionless with only the eyes, apex of the rostrum, and a respiratory passage exposed (see Tan *et al.*, 1999; Tan & Ng 2007a). It is important to emphasize that one of the few fossil species described with large chelipeds associated with the carapace (*Eurolambrus mainensis* De Angeli & Beschin, 2010), also inhabited siliciclastic soft bottoms.

There are nevertheless several modern genera showing characters similar to those of *Aragolambrus* **n. gen.**, such as the reduced size of the chelipeds (i.e. *Furtipodia* Tan & Ng, 2003, *Neikolambrus* Tan & Ng, 2003, *Ochtholambrus* Tan & Ng, 2007a, and *Pseudolambrus* Paul′son, 1875). Species belonging to these genera inhabit reefs, fore reefs, or coral rubble at depths of about 20–30 m (see Ng & Rahayu, 2000; Tan & Ng, 2003, 2007a; Tan, 2008). Such morphology of the chelipeds can also be observed in some species of *Daldorfia*, which live among corals, sponges, and bryozoans (Tan *et al.*, 1999; Tan & Ng, 2007b). Based on sedimentological data, *Aragolambrus collinsi* **n. gen., n. sp.** probably inhabited isolated coral-red algae pinnacle reefs and associated rubble that developed in the mesophotic zone, below wave-base, at depths that did not exceeded 40 m.

The fossil record of parthenopids suggest that they had at least an Eocene origin with 19 fossil species described (Table 1). Many of these fossil species from the Eocene come from basins located in the Mediterranean area, and are related to reef or coral-algal environments. These species have been found associated with a high diversity of other brachyuran species (i.e., Beschin *et al.*, 2017 and references therein). These horizons of high diversity support the idea that in the Eocene vast marine areas in the Mediterranean were occupied by patch reefs (Beschin *et al.*, 2017), environmental conditions similar to those currently occurring in the central Pacific (Klompmaker *et al.*, 2016).

Aragolambrus **n. gen.**, like most species associated with coral-algal buildups of warm latitudes, is small in size, an advantage for finding refuge and food between live corals and in coral rubble (i.e., Klompmaker *et al.*, 2016). Such traits can be observed in modern parthenopids with morphologies similar to that of *Aragolambrus* **n. gen.:** *Daldorfia dimorpha* Tan & Ng, 2007 (Tan & Ng, 2007b), *D. leprosa* (Nobili, 1905), *Niobafia erosa* (Miers, 1879), *Olenorfia cariei* (Bouvier, 1914), and *Neikolambrus polemistes* Tan & Ng, 2003.

Table 1 summarizes occurrences of parthenopids in the fossil record, with special emphasis on the age, substrate preferences, and distribution. We have used similar methodology than that proposed by Schweitzer & Feldmann (2014, 2015) tabulating the different species according to their environmental preferences and rock type.

Representatives of Eocene parthenopids occupied either siliciclastic (58%) or carbonate substrates (42%). These data suggest that the wide range of environmental tolerance observed in modern parthenopids was already established during the Eocene. During the Ypresian (lower Eocene) parthenopids had reefal and carbonate facies preferences, and all published occurrences come from such environments. This is probably related to the appearance and development of modern reef complexes, due to climatic and environmental conditions at that time (see Pomar *et al.*, 2017). By the Lutetian onwards parthenopids mostly occupied siliciclastic environments in shallow platforms. A high proportion of Lutetian-Bartonian (Middle Eocene) parthenopids from Italy were preserved in volcanoclastic sediments. According to Schweitzer & Feldmann (2015) these assemblages were usually associated with carbonate rocks, but it is not possible to determine if decapods were living in carbonate environments or on bottoms characterized by a mix of volcanoclastic sediments and carbonates. According to the fossil record, parthenopids did not re-occupied the reef environments until the Oligocene (De Angeli & Beschin, 2008).

ACKNOWLEDGEMENTS

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The oldest dairoidid crab (Decapoda: Brachyura: Parthenopoidea) from the Eocene of Spain

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Abstract

Eubrachyurans, or ‘higher’ true crabs, are the most speciose group of decapod crustaceans, and have a rich fossil record extending back into the Early Cretaceous. Despite this, is during the Palaeogene—and particularly the Eocene—, that most extant families are first known from fossils. Unfortunately, most early eubrachyuran fossils, tend to be sparse and fragmentary, and only a few works have combined extinct and extant taxa in a phylogenetic context using different optimality criteria. Here, we report the dairoidid crab *Phrynolambrus sagittalis* n. sp., an enigmatic eubrachyuran from the upper Eocene of Huesca (Northern Spain), whose completeness and exquisite preservation allowed us to examine aspects of its anatomy in a phylogenetic context. Dairoidids have been previously considered among the oldest stone crabs (Eriphioidea) or elbow crabs (Parthenopoidea), two disparate and distantly related groups of true crabs living today. Mechanical preparation and CT-scanning of the fossil material revelaed several diagnostic features that facilitate detailed comparissons with families across the crab tree of life, and test hypotheses about its phylogenetic affinities. *Phrynolambrus sagittalis* n. sp. is the first record of the genus in the Iberian Peninsula, and represents one of the oldest crown parthenopoidean crabs worldwide, expanding our knowledge of the biogeographic distribution of elbow crabs during the Paleogene and their early origins, anatomical diversity, and systematic affinities. Understanding the anatomical diversity or disparity of Eocene eubrachyurans is pivotal to disentangle the systematic relationships among crown families, and to investigate spatio-temporal patterns leading to the evolution of modern faunas.

Key words: fossil crabs, phylogeny, Priabonian, Pyrenees, Iberian Peninsula.

INTRODUCTION

The origin of modern families of ‘higher’ true crabs (Eubrachyura) and how they relate to other extant and extinct clades is matter of ongoing discussion (Luque et al., 2021). Phylogenetic analyses based on molecular and morphological data offer a good opportunity to quantitatively investigate the relationships among crab groups beyond alpha-taxonomy-based inferences of relatedness (e.g., Tsang et al., 2008; Wolfe et al., 2019; Luque et al., 2019, 2021). However, reliable well-preserved fossils of early crown groups are crucial to accurately calibrate molecular trees, and to reduce the uncertainty of anatomical data recorded for morphological phylogenies. Moreover, to date, there are few works that combine fossil and extant taxa in a phylogenetic context using different optimality criteria (Luque et al., 2019, 2021).

Here, we describe *Phrynolambrus sagittalis* n. sp., a new species of enigmatic parthenopid or elbow crabs found in the upper Eocene (Priabonian) Pamplona Fm of Huesca (southern Pyrenees), Northern Spain (Fig. 1), and discuss (i) its phylogenetic affinties with other eubrachyurans, and (ii) its importance for understaindg the early evolution of one of the most iconic groups of crabs. Mechanical preparation and CT-scanning of the new fossil material revealed anatomical features well-preserved and in-volume, such as dorsal carapaces and its regions, the orbits and rostrum, the epistome and pterygostome, cuticular ornamentation, sternum, pleon, and the ventral carapace and the chelipeds. These and other characters are crucial for taxonomic and phylogenetic studies, especially since most fossil elbow crabs are known only from isolated carapaces, and rarely from ventral carapaces or even legs and chelipeds associated to the body. In addition, based on a review of previous occurrences of *Phrynolambrus* and other parthenopoids in the fossil record, we discuss aspects of its paleoecology as well as for extinct and extant relatives.

Modern representatives of the superfamily Parthenopoidea MacLeay, 1838, have received significant systematic attention in recent decades, and there is a good understanding of the morphology and ecology of the group (i.e., Tan, 2004; Tan & Ng, 2007a, b). However, to date, there are no detailed studies exploring the phylogenetic relationships between members of Parthenopoidea (Tan & Ng, 2007a; Ferratges et al., 2019), especially considering extinct taxa, despite their anatomical character richness (Schweitzer et al., 2006). The oldest crown Parthenopoidea known to date are all Eocene in age (Ferratges et al., 2019 and references), and show that elbow crabs were relatively diverse early on (see Ferratges et al., 2019; Schweitzer et al., 2020a). However, fossil material assigned to this group of odd-looking crabs usually consists of only carapaces (see exceptions in Ferratges et al., 2019 and references therein), hampering the interpretation of its origin and evolution.

The new species occurs in a diverse assemblage of decapod crustaceans recorded in siliciclastic sediments derived from a pro-delta environment. The outcrop focus of this study has yielded specimens belonging to at least eighteen superfamilies of decapods, and some of these taxa have been studied by various authors (Artal et al., 2013; Ossó et al., 2014; Ossó & Domínguez, 2017; Ossó et al., 2020). Although eubrachyurans have a rich fossil record extending back into the Early Cretaceous, is during the Eocene that the oldest representatives of most extant families are first known (e.g. Schweitzer & Feldmann, 2015; Luque et al., 2017). For this reason, understanding the anatomical diversity or disparity of Eocene brachyurans and how they relate to other extinct and extant groups is pivotal to investigate spatio-temporal patterns leading to the evolution of the modern groups seen today.

GEOLOGICAL SETTING

The decapod specimens here studied come from the marly-dominated succession of the Pamplona Fm (Puigdefabregas, 1975), which forms part of the sedimentary infill of the Jaca Basin, located in the central part of the South Pyrenean zone (Fig. 1). Specifically, this material was collected along the road N-260 located 400 m east-southeast of the village of Fanlillo, in the municipality of Yebra de Basa, Huesca province, Aragon, Spain. Data on the biostratigraphy (Canudo & Molina, 1988;

Canudo et al., 1988) and magnetostratigraphy (Hogan, 1993) indicate a Bartonian-Priabonian age for the Pamplona Fm, and the calibration of Pueyo et al. (2002), establish the lower and upper limits of this formation from 40.32 to 37.17 Ma, which corresponds to a Bartonian-early Priabonian age.

This formation consists of a thick grey and blue marl succession deposited in a distal offshore environment. The succession grade upwards into sandstone delta-mouth bars with abundant vegetal remains in the uppermost levels. According to Montes-Santiago (2009), the distribution of fauna in the stratigraphic log of the Pamplona Fm, with bryozoans, nummulitid foraminifera, pelecypods, siliceous sponges, and crustacean decapod remains in the lower levels, and corals, algae, gastropods, and remains of crustacean decapods and fishes in the upper ones (outcrop levels), indicates a progressive upwards decrease of the bathymetry, with sedimentation probably within the euphotic zone, above storm wave base.

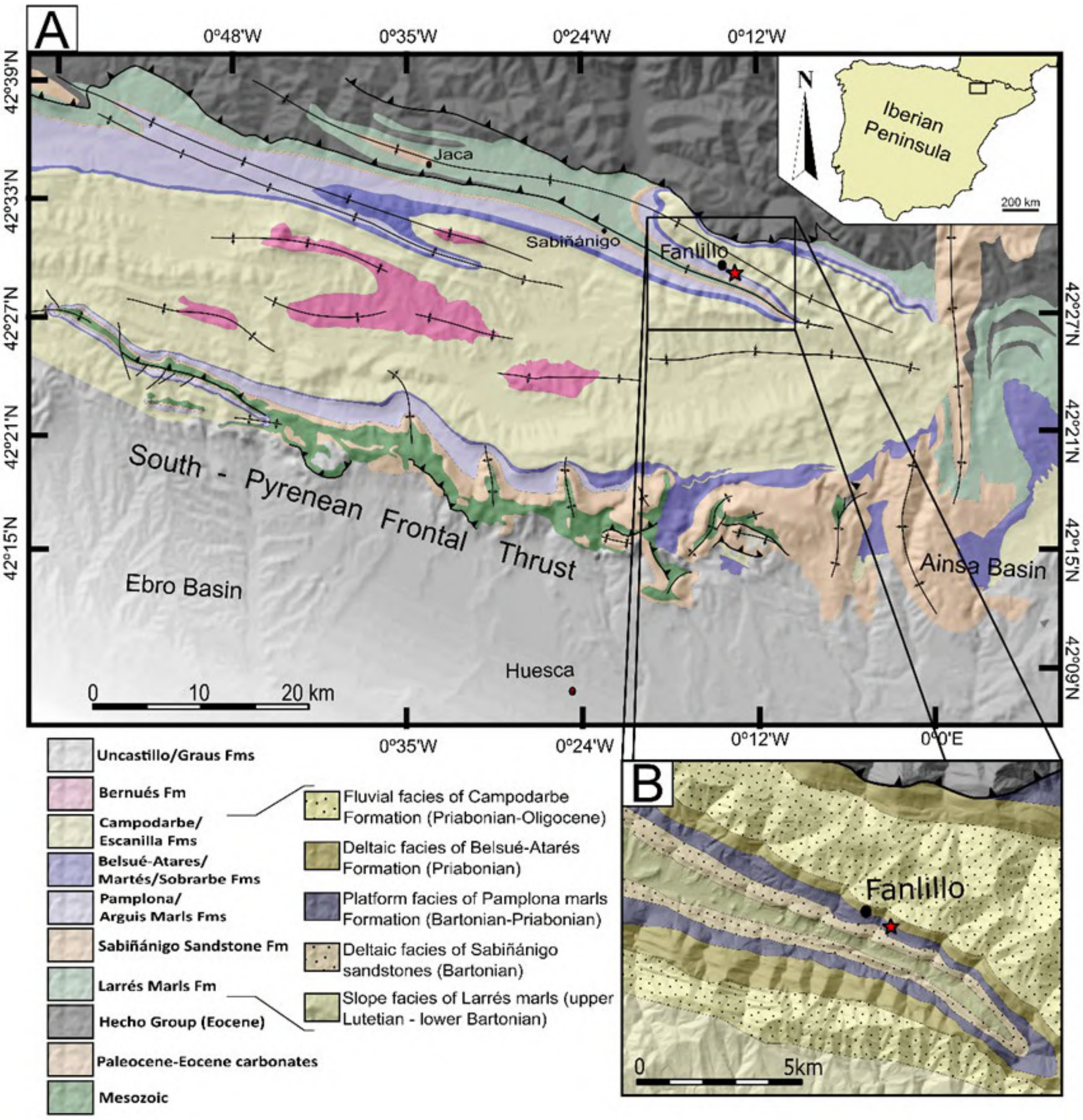

Figure 1. A: Simplified geological map of the Jaca Basin in the South Central Pyrenean zone (modified from Coll et al., 2022). B: Detail of the studied area. The red star near to Fanlillo shows the location of the studied outcrop.

MATERIAL AND METHODS

Material and preparation

Ten studied specimens were collected from bioclastic interval found in the upper part of the Pamplona Fm exposed near the village of Fanlillo. Measurements of carapace length-carapace width are given in millimetres (mm). Specimens are deposited in the palaeontological collection of the Museo de Ciencias Naturales de la Universidad de Zaragoza under acronym MPZ. The location of the outcrop is shown in Fig. 1.

Specimens were prepared using a needle under a 40x magnification binocular magnifying glass, and in some cases (specimens MPZ2022/204, MPZ2022/763), chemically, using potassium hydroxide (KOH). The specimens were then photographed dry and coated with ammonium chloride sublimate. Detailed photography of the carapace surfaces was made using a Nikon d7100 camera (Nikon, Tokyo, Japan) with a macro 60 mm lens. One specimen (holotype, MPZ2022/761) preserving a complete carapace and chelipeds was selected to scan in the Micro-Computed Tomography Laboratory (Micro-CT scan) model V|Tome|X s 240 from GE Sensing & Inspections Technologies Phoenix X-Ray, from the Centro Nacional de Investigación sobre la Evolución Humana (CENIEH, Burgos, Spain). Specimen matrix was reduced in order to get more contrast between rock and fossil and later scanned. As a result, we obtained 1680 sections of the fossil specimen. To process the data, image reconstruction software SPIERSedit 3.1.0 has been used

Phylogenetic analyses

The dataset, contain 46 taxa from 13 brachyuran families, and 113 adult morphological characters, was built in Mesquite 2.75 (appendix X), and modified from the datasets in Luque et al. (2019, 2021). Although most of the characters used to distinguish modern parthenopids are not preserved in the fossil record (i.e., antennal articles, ambulatory legs), Tan and Ng (2007a,b) listed usefull morphological characters that can be recognized in fossil species, including *Phrynolambrus sagittalis* n. sp. (e.g., carapace shape, carapace ornamentation, shape and distribution of the dorsal regions, shape of the rostrum and orbits, and cross-section shape and ornamentation of the chelipeds). Undetermined and not preserved characters were scored as “?”, and inapplicable characters were scored as “–”. Multiple character states present in a given terminal were scored as polymorphisms.

The final data set was analyzed under Bayesian Inference (BI), as implemented in MrBayes v. 3.2.6. The data set was analyzed under the traditional Mk model with an ascertainment bias correction to account for scoring only variable morphological characters. Each analysis was performed with two independent runs of 3×10^7 generations each. We used the default settings of four chains (one cold and three heated) per each independent run. The relative burn-in fraction was set to 25% and the chains were sampled every 200 generations. We used Tracer v.1.6 to determine whether the runs reached stationary phase, and to ensure that the effective sample size for each parameter was greater than 200. Results of the Bayesian runs were summarized as a majority-rule consensus tree of the post-burn-in sample with a node support threshold of 75% (nodes with posterior probability support < 75% were collapsed).

SYSTEMATIC PALAEONTOLOGY

Terminology used herein follow Tan and Ng (2007b) and is summarized in Fig. 2.

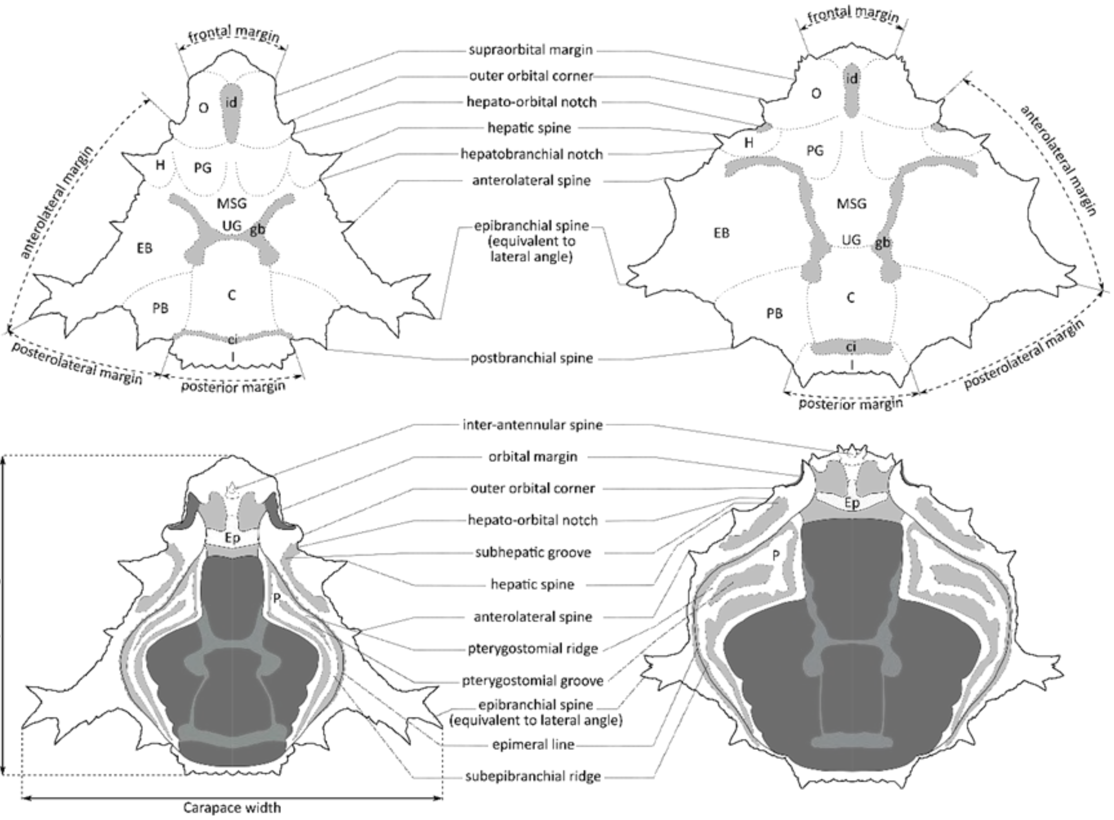

Figure 2. Anatomical comparison between the extinct genus *Phrynolambrus* (left) and the extant genus *Dairoides* (right), and terminology used in the text. Shaded areas represent depressed areas not covered by mushroom-shaped tubercles. C: cardiac region; ci: cardiointestinal groove; EB: epibranchoial region; Ep: epistome; gb: gastrobranchial groove; H: hepatic region; I: intestinal region; id: inter-orbital depresion; MSG: mesogastric region; O: orbital region; P: pterygostomial region; PB: postbranchial region (meso- and metabranchial region); PG: protogastric region; UG: urogastric region.

Infraorder BRACHYURA Latreille, 1802
Section EUBRACHYURA de Saint Laurent, 1980
Superfamily PARTHENOPOIDEA MacLeay, 1838
Family DAIROIDIDAE Števčić, 2005

Type species. Dairoides margaritatus Stebbing, 1920, by monotypy; gender masculine.

= *Asterolambrus* Sakai, 1938 (type species *Asterolambrus kusei* Sakai, 1938, by original designation; gender masculine.

Remarks. The extinct genus *Phrynolambrus*, previously included within the family Parthenopidae MacLeay, 1838, shares with species of the extant genus *Dairoides* (i.e., *D. kusei* (Sakai, 1938); *D. margaritatus* Stebbing, 1920; and *D. seafdeci* Takeda & Ananpongsuk, 1991), the similar general morphology, with a triangular frontal margin, a spinose lateral angle, a similar position of the spines and dorsal regions, the distribution of the grooves (dorsal and ventral), the morphology and structure of the cuticle, and the morphology of the chelipeds. The family Dairoididae, and thus the genus *Dairoides*, have been previously assigned to the superfamily Eriphioidea MacLeay, 1838, or stone crabs, based on their overall similarities (Ng et al., 2008; De Grave et al., 2009; Davie et al., 2015; Schweitzer et al., 2020b). This assignment, however, was questioned by some authors (Lai et al., 2014; Jagt et al., 2015) and suggest that the diagnostic characters are the result of convergence. Our re-evaluation of the anatomy and phylogenetic relationships of *Dairoides* supports that the family Dairoididae belongs to the superfamily Parthenopoidea, also known as elbow crabs, and that both *Dairoides* and *Phrynolambrus* constitute the family Dairoididae, highlighting the anatomical disparity seen among early parthenopoids during the Eocene (see below under "Discussion").

Genus *PHRYNOLAMBRUS* Bittner, 1893

Type species. Phrynolambrus corallinus (Bittner, 1893).

Included species in the genus. P. corallinus (Bittner, 1893)*; P. italicus* De Angeli & Beschin, 2008; *P. sagittalis* n. sp.

Phrynolambrus sagittalis n. sp.

Figs 3–5, 7.

Type material. The holotype, MPZ 2022/761, is a complete carapace (length and width, 15.1 and 12.2 mm, respectively) and chelipeds, with well-preserved cuticle. Additional specimens include the paratypes, MPZ 2022/203, 2022/204, 2022/762, 2022/763, 2022/764, 2022/765, 2022/766, 2022/767 and 2022/768.

Etymology. From the Latin *sagitta*, in reference to its arrowhead carapace shape.

Diagnosis. Carapace triangular, wider than long; projected frontal margin; orbits inflated; anterolateral margins almost straight, with small conical spine; posterolateral margin converging backward, with strong spine and marked concavity behind epibranchial spine; armed epibranchial spine, oriented obliquely backwards; straight posterior margin; depressed postbranchial region; carapace surface densely tuberculated by mushroom-shaped tubercles.

Description. Cephalothorax triangular in outline, anteriorly narrowing (Fig. 3). The dorsal regions are well defined and strongly convex. Dorsal surface is almost completely covered with mushroom-shaped tubercles that abut around the edges leaving pores leading into subsurface canals (Fig. 3B), except in the interorbital depression, in which a "window" is formed, and the grooves that separate the gastric and cardiac regions from the branchial regions, and from the intestinal of the cardiac region. Front narrow, triangular. Below the frontal margin, between the antennular pits, there is a forward-facing oriented spine (interantennular spine). Orbits small, deep and rounded, laterally directed, bordered by a row of tubers. Ocular peduncle short, ornated. Antennular and orbital cavities in communication. Hepatic margin distinct, not continuous with epibranchial region, with one prominent spine bearing covered with mushroom-shaped tubercles. The anterolateral margins are strongly diverging and longer than the posterolateral ones, with hepato-orbital and hepatobranchial notch; on each lateral angles, there is a large projecting epibranchial expansion (epibranchial spines), directed slightly backwards. In the distal part they present 4 spines; 3 oriented in a lateral plane and a fourth spine oriented upwards. The posterior margin is broad and concave; it occupies about half the carapace greatest width.

The regions are defined by wide grooves, but on the dorsal surface it is masked by the tubercles; seen from the inside view they are much more evident (Fig. 4). The small epigastric lobes are very apparent: they are inflated at the base of the front; the protogastric regions are large, vaulted. Mesogastric region flattened. Urogastric region short, arched, anterior portion undifferentiated, lateral and posterior margin bounded by deep grooves. The cardiac region is large, subrectangular, widening posteriorly, strongly convex, swollen and prominent. The hepatic region narrow, triangular, depressed slightly lower than epibranchial and gastric regions. The epibranchial regions are very large; dorsally it has a conical central part. Laterally, approximately in the first third of the epibranchial region there is a pointed conical tubercle that stands out among the others (anterolateral spine). Towards the posterior part of the epibranchial region is the lateral expansion with four spines, equivalent to the lateral angle that has *Daldorfia* (see Tan & Ng, 2007b). Postbranchial regions, formed by meso- and metabranchial regions, undifferentiated, laterally surround the cardiac region, and smaller than epibranchial region, depressed and have a subtriangular shape. Intestinal region subrectangular, wide and separated from cardiac region by a deep cardiointestinal groove. Subhepatic region bordered by a subhepatic groove that separates the hepatic spine from the inferior border. Subepibranchial region narrow, covered with tubercles in shape of “petaloid” mushrooms, with very marked epibranchial ridge. Epimeral line (or moult line) bordered by numerous small mushroom-shaped tubercles in the upper margin, and by a smooth groove in the pterygostomial region (Fig. 3-D). Pterygostomial region ornated with two rows of small mushroom-shaped tubercles, that converge both anteriorly and posteriorly, forming the pterygostomial and subepibranchial ridges and the pterygostomial groove.

The chelipeds are markedly heterochelous (Figs 4, 5); major cheliped (right) robust. Carpus slightly higher than long; surface equipped with various complex long spines, with a narrowing at the base. Manus longer than high; outer margin with five spines (Fig. 4); lower margin slightly concave at base of fixed finger, with seven small aligned spines (Fig. 4); inner margin not well developed, with four tubercles (Fig. 4); upper, inner surface with spaced tubercles (Fig. 4); row of 4 long spines on outer side aligned in central part plus several spines irregularly distributed over surface (Fig. 4). Fixed finger short, slightly oblique downward, triangular, tip pointing slightly upward (Fig. 4). Dactylus strong, curved. Lateral surface with a small ridge; occlusal margin with molariform teeth, becoming smaller distally. Left cheliped slender (Fig. 4). Carpus slightly higher than long; surface armed with various long spines. Manus longer than high, slightly divergent distally; outer margin with four triangular spines, widely spaced; lower margin slightly concave at base of fixed finger, with eight small aligned spines; inner margin not well developed, with four tubercles; upper, inner surface with spaced conic tubercles. Fixed finger shorter than palm, 3 times longer than high, oblique downward, with a longitudinal groove on the mesial part; dactylus curved, with longitudinal groove in upper mesial part; occlusal margin with small teeth, becoming smaller distally.

Occurrences. The genus *Phrynolambrus* is only known from the upper Eocene of Italy, Hungary, and Romania (Bittner, 1893; Lörenthey & Beurlen, 1929; Beschin et al., 2009) and the Oligocene of Italy (De Angeli & Beschin, 2008). In this work, we expand its distribution to the upper Eocene of the Iberian Peninsula.

Remarks. Phrynolambrus sagittalis n. sp. can be differentiated from congeners on the basis of 1) its projected and triangular front, with a deep and narrow interorbital depression (Figs 2; 3A, C and F; 4A-C; and 5A), 2) a large hepatic spine and one conical spine in the anterolateral margin (Figs 2, 3A, C; 4A-F; and 5), 3) robust epibranchial spines backwards oriented (Figs 2; 3A, C, D-F; 4A-F, P; and 5), and 4) a well-developed postbranchial spine on the posterolateral margin oriented (Figs 2; 3A, C, D, F; 4A, C, E, F; and 5). *Phrynolambrus sagittalis* n. sp. is morphologically close to *P. corallinus,* the type species of the genus; both have a triangular outline, carapace surface covered with mushroom-shaped tubercles, and similarly distributed dorsal regions. However, the latter is distinguished in having wider interorbital depression, anterolateral margin more convex, epibranchial spines oriented laterally instead of back, apparently lacks anterolateral spine and postbranchial spine.

The species *Phrynolambrus corallinus* was erected by Bittner (1893) based on three specimens from the upper Eocene of Romania. However, the poor state of conservation of specimens of the type material, resulted in both the original description and the reconstruction drawing not corresponding faithfully with the true morphology of *Phrynolambrus*. Subsequently, other authors (Lörentey, 1898; Lörentey & Beurlen, 1929; De Angeli & Beschin 2008; Beschin et al., 2009) carefully analyse other carapaces from Italy and Hungary, and correct some of the inaccuracies of the original description. Anyway, almost all previous studies on the genus *Phrynolambrus* are based on carapaces that have lost the external part of the cuticle (Beschin et al., 2007, 2009; De Angeli & Beschin, 2008) and consequently do not preserve the structure of the tubercles and the actual external appearance. It is important to mention because the presence of cuticle is a key for the appearance of crabs (see Klompmaker et al., 2015).

The new species is also close to *P. italicus* De Angeli & Beschin, 2008, but that species differs in having a wider and prominent frontal margin, and wider interorbital depression. In addition, the gastrobranchial groove and cardiointestinal groove are wider than in the new species. Dorsal granulation is also dense, but with smaller tubercles (only preserved as internal mold in *P. italicus*). The poor state of conservation of *P. italicus* does not allow further comparisons.

The species *Parthenope (Pseudolambrus) pentagonus* Quayle & Collins, 1981, is considered as a species of *Phrynolambrus* in Schweitzer et al. (2010). However, does not show the characteristic structures of this genus (i.e., very marked interorbital depressions and dorsal grooves), show a much more circular outline of the carapace than other species of *Phrynolambrus*, and little marked lateral angle. For all this reasons we are excluding *Parthenope (Pseudolambrus) pentagonus* Quayle & Collins, 1981 from the genus *Phrynolambrus*, and hence from the phylogenetic analysis.

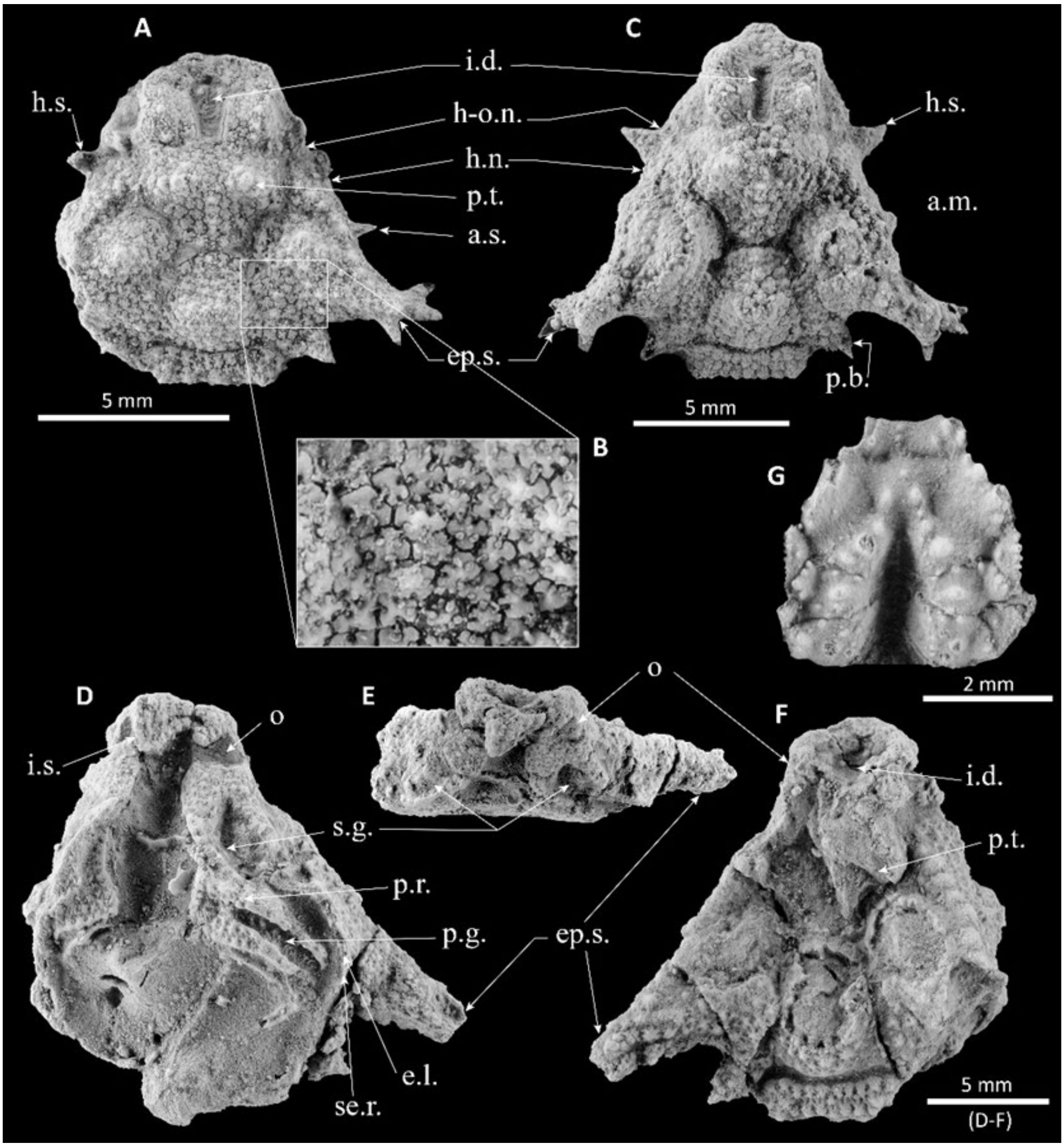

Figure 3. Paratypes of *Phrynolambrus sagittalis* **n. sp.** from the upper Eocene (Pamplona Fm) of Huesca, Spain. A: Paratype MPZ 2022/763 in dorsal view; B: detail of the cuticle with mushroom-shaped tubercles (with puzzle-like hats); C: (MPZ 2022/203). D-F: paratype MPZ 2022/204 in ventral (D), dorsal (E), and frontal (F) views; detail of ventral view of the carapace (F). G: isolated sternum (MPZ 2022/767) assigned to the new species due to similarities with the modern *Dairoides* and other parthenopoids. Abbreviations: a.s., anterolateral spine; e.l., epimeral line; ep.s., epibranchial spine (equivalent to lateral angle); h.n., hepatobranchial notch; h-o.n.: hepato-orbital notch; h.s., hepatic spine; i.d., interorbital depression; i.s., interantennular spine; o: orbit; p.b., postbranchial spine; p.g., pterygostomial groove; p.r., pterygostomial ridge; p.t., protogastric tubercles; s.g., subhepatic groove; se.r., subepibranchial region.

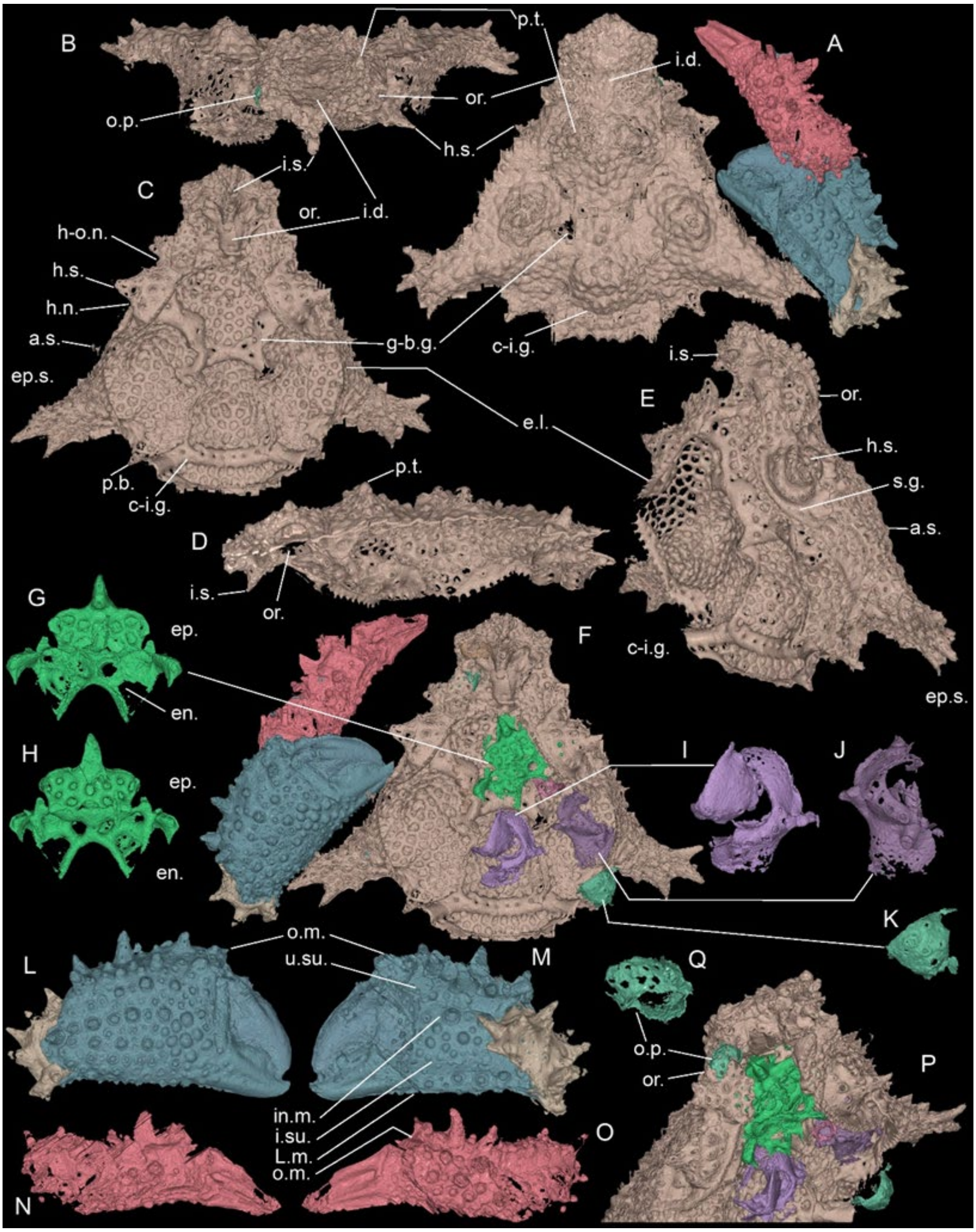

Figure 4. CT Scan of the holotype of *Phrynolambrus sagittalis* **n. sp.** (MPZ 2022/761). A-D: Carapace in dorsal (A), frontal (B), ventral (C), oblique ventral (D) and lateral views, with the other anatomical parts that hinder the view of the cephalothorax digitally extracted. F: ventral view with ventral unremoved remains. G-H: Epistome in outer and inner view respectively. I-J: Coxa-ischium, of both chelipeds. K: isolated ischium. L-M: Right cheliped in outer (L) and inner (M) surfaces. N-O: Left cheliped in inner (N) and outer (O) surfaces. P: oblique antero-ventral view, showing the orbit (or.) and the position of the ocular peduncle (o.p.). Q: Detail of the ocular peduncle. The holes both of carapace, coxa, ischium and ocular peduncle correspond to mushroom-shaped tubercles, with less contrast. Abbreviations: c-i.g.: cardio-intestinal groove; L.m., lower margin; o.m., outer margin; in.m., inner margin; i.su., inner surface; O.s., outer surface; or. orbit; o.p.: ocular peduncle; u.su., upper surface. The rest of the abbreviations are the same as in the figure 3.

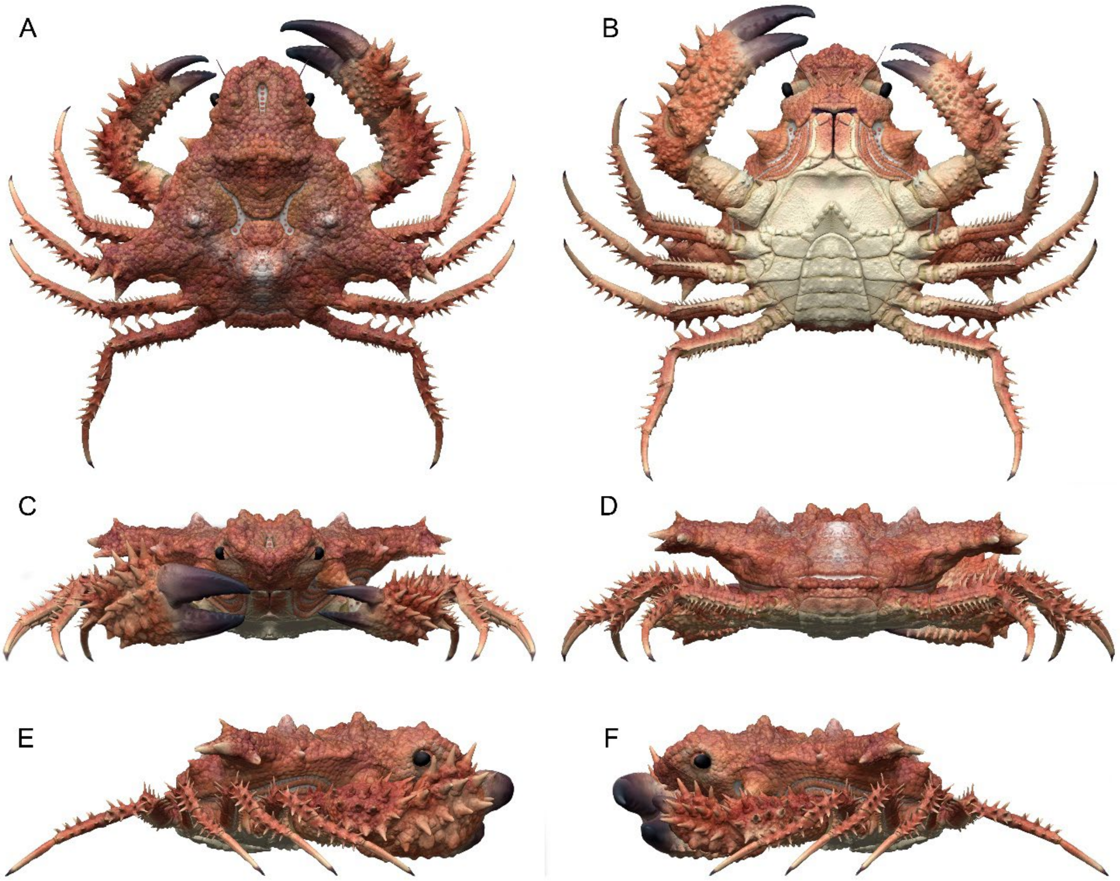

Figure 5. 3D artistic reconstruction of *Phrynolambrus sagittalis* n. sp. based on the type material and the CT scan in dorsal (A), ventral (B), frontal (C), posterior (D) and lateral (E-F) views. The ambulatory legs and colour pattern have been based on the modern genus *Dairoides*. Drawings by Hugo Salais (Metazoa Studio).

POSITION OF *PHRYNOLAMBRUS* AND ITS RELATIONSHIP WITH *DAIROIDES*

The genus *Phrynolambrus* was originally included within the family Parthenopidae based on dorsal characters that resemble other parthenopids (Bittner, 1893). Later, other authors (Lőrenthey & Beurlen, 1929; Roger, 1954; Glaessner, 1969; Via, 1969; De Angeli & Beschin, 2008; Beschin et al., 2009) have included *Phrynolambrus* in the same family. Due to the peculiar ornamentation, Guinot (1967, 1978, 1979) proposed the possible relationship between this genus and the modern genera *Dairoides* Stebbing, 1920, *Daira* De Haan, 1833, and *Actaea* De Haan, 1833. In fact, Guinot (1979) suggested that different evolutionary branches would develop and differentiate from a common ancestor, giving rise to the branch of the modern Parthenopidae, also related to *Phrynolambrus* and *Dairoides*, and a second branch, already differentiated during the Eocene, associated to *Daira*, possibly related within the Xanthoidea. However, molecular phylogenetic works have shown that parthenopoids and xanthoids are not closely related, and that any common ancestor for both superfamilies, likely rooted into the 'mid'-Cretaceous, would also have been ancestor to several other superfamilies in between (e.g., Ahyong et al., 2007; Lai et al., 2014; Tsang et al., 2014).

The genus *Phrynolambrus* has clear affinities with Parthenopidae, but it shows some characteristics that in turn are diagnostic features of Dairoididae (i.e., the genus *Dairoides*), such as: a dorsal surface covered with fused mushroom-like perforate vesicular tubercles, with deep grooves (interorbital, gastrobranchial and cardiointestinal grooves, in dorsal view); a narrow front, deflexed; small orbits, deep, and rounded; antennular and orbital cavities in communication; strong chelipeds, not pressed tightly against the anterolateral margin; and the junction between the anterolateral and posterolateral margins (lateral angle) produced and armed with teeth (see Števčić, 2001, 2005).

The new material from Spain offers not only the morphology from the dorsal carapace but also information about the ventral view of the carapace and the chelipeds. The ventral morphology provides critical information, including: **i.** a characteristic ornamentation and distribution of tubercles in the pterygostomial region that give rise to grooves and ridges; these characteristic grooves are not observable in any other brachyuran representative with the exception of *Dairoides* and *Aragolambrus*; **ii.** the shape and delimitation of the hepatic spine in his lower margin with a groove; and **iii**. the cuticle with its mushroom-shaped petaloid tubercles. In addition, the presence of the semi-articulated chelipeds in one specimen (MPZ 2022/761) allows us to observe the relative size in comparison to the cephalothorax, the type of ornamentation, and the distribution and number of spines that conform it. All these conservative characters have not been mentioned in previous works.

On the other hand, the genus *Dairoides* (sole representative of the Family Dairoididae) has been previously included in Parthenopidae (see Sakai, 1976; Ng et al., 2001). However, a number of authors have discussed relationships between *Dairoides* and other genera— mainly *Daira* and *Dacryopilumnus*—without reaching a consensus (Serene, 1984; Guinot, 1967; Sakai, 1976; Ng & Tan, 1984, 1985; Dai & Yang, 1991; Ng et al., 2001; Števčić, 2005; Ng et al., 2008; Lai et al., 2014). Guinot (1967, 1979) noted that *Dairoides* seems to have more in common with parthenopids than with *Daira*, and suggested its possible inclusion with the family Parthenopidae. Subsequently, Ng & Rodríguez (1986) described the family Dairidae to accommodate *Daira* and *Dairoides* and included it in the superfamily Parthenopoidea. Števčić (2005) defined the family Dairoididae to accommodate *Dairoides* and placed both families (Dairidae and Dairoididae) in the superfamily Dairoidea. Later, Ng et al. (2008) placed Dairoididae (with only the genus *Dairoides*) within Eriphioidea, and considered the similarities between *Dairoides* and many parthenopid genera as convergence. More recently, Lai et al. (2014), suggest that there may be a phylogenetic basis for the relationship between Dairoididae and Parthenopidae since *Dairoides* is a moderately well-supported sister group of *Daldorfia*.

The obtained results with the distribution of anatomical characters suggest that *Phrynolambrus* is closely related to modern *Dairoides* Stebbing, 1920, both genera nested within crown Parthenopoidea, and phylogenetically distant from somewhat similar, convergent forms such as those seen among some Eriphioidea (as proposed by Ng et al., 2008) (Fig. 6). Our results support the conclusions of Lai et al. (2014), in which they suggest that *Dairoides* is a well suported sister group to *Daldorfia*. Therefore, we consider both *Dairoides* and *Phrynolambrus* as members of the Superfamily Parthenopoidea, but forming a clade that is different from Parthenopidae and thus the subfamilies Parthenopinae and

Daldorfinae (Fig. 6). Thus, *Phrynolambrus* is here considered as fossil member of the modern Family Dairodidae Števčić, 2005, and in turn part of the superfamily Parthenopoidea (Fig. 6). Future molecular works based on *Dairoides*, and parthenopids could provide some light in the relationships of those groups and how much are they related to each other.

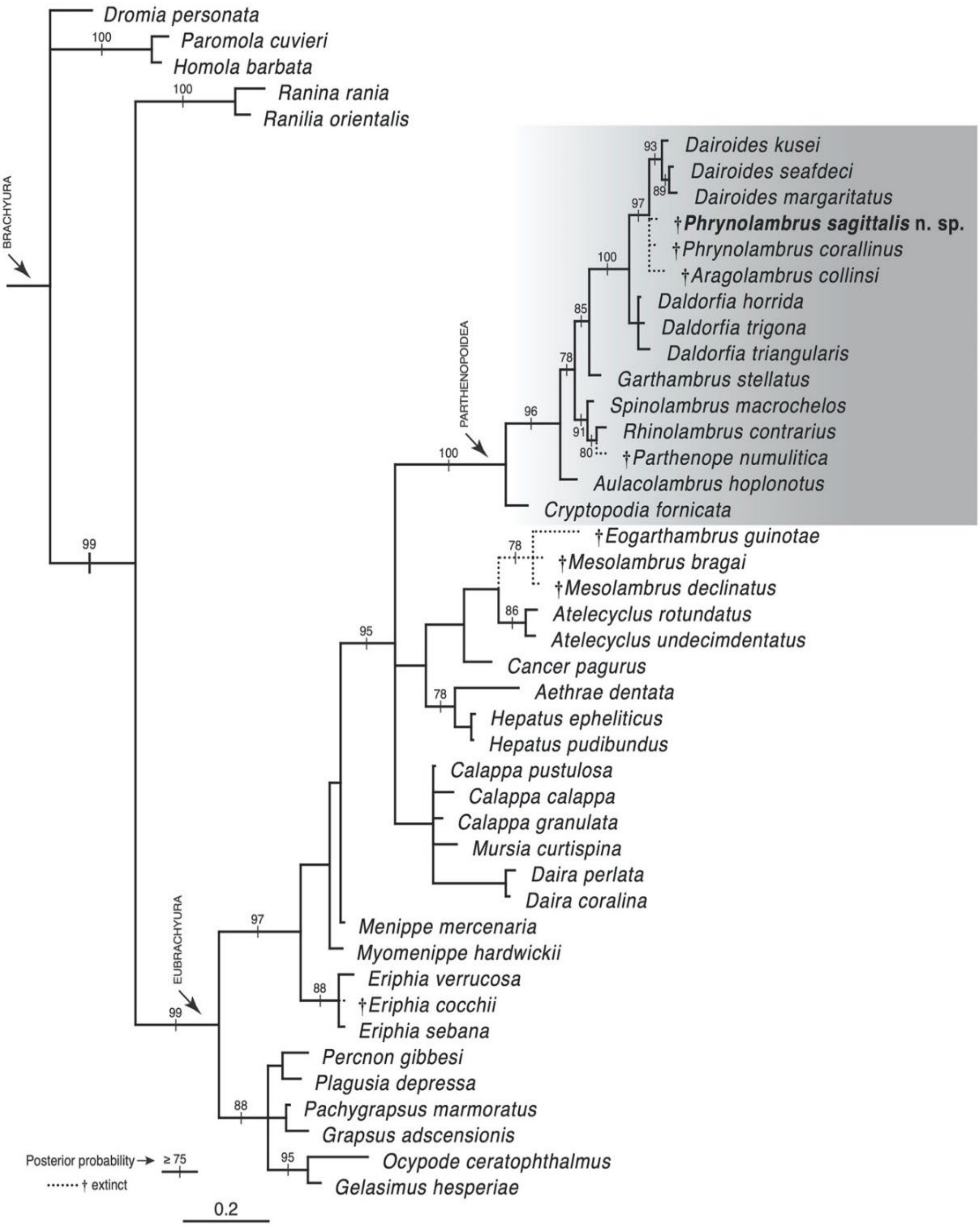

Figure 6. Bayesian majority-rule consensus topology of the post-burnin sample of trees for selected fossil and extant brachyuran families, including *Phrynolambrus sagittalis* n. fam. Posterior probability support values indicated above branches. Branches with posterior probability support < 75% are collapsed. Terminal taxa indicated by a dagger (†) are extinct. Grey box indicates the monophyletic family Parthenopoidea.

ECOLOGICAL IMPLICATIONS

Modern parthenopids are usual inhabitants at tropical or subtropical latitudes, from the intertidal to deep water, and are usually associated with siliciclastic substrates where they dig and remain motionless (see Tan et al., 1999; Tan & Ng 2007a; Ferratges et al., 2019 and references herein). Eocene parthenopoids are supposedly represented by 20 species in 14 genera, although some of them need to be revised in the future, since the phylogenetic results reveal that some of them are far from Parthenopoidea (see Fig. 7). In any case, these taxa are mainly from basins located in the Mediterranean region, associated to diferent depositional settings. Based on sedimentological data, the Eocene parthenopoids occupied either siliciclastic or carbonate depositional settings, being more abundant on reef environments during the lower Eocene (see Ferratges et al., 2019 and references herein). However, based solely on the information available to date, during the middle and upper Eocene, this trend appears to have reversed, with higher diversities then occurring in siliciclastic depositional settings over shallow platforms (see Ferratges et al., 2019).

In contrast, extant dairoidids represent a rare and controversial group (see above), represented by only three species reported from sandy and muddy soft bottoms, front reef and outer reef (at depths up to 400 m). These taxa are distributed in tropical or subtropical latitudes (i.e., Clarke, 1972; Takeda & Ananpongsuk, 1991; Padate et al., 2020), and to date, no other representatives were known in the fossil record.

The three species belonging to the genus *Phrynolambrus* currently known come from reef environments from the upper Eocene of Italy and Budapest (Bittner 1893; Beschin et al., 2007) and the lower Oligocene of Italy (De Angeli & Beschin, 2008). The palaeoenvironmental reconstruction of the locality herein studied, indicates a relatively low energy sedimentary environment dominated by clay sedimentation, with eventual episodes of high energy. Based upon the sedimentological and palaeoecological data, the studied outcrop can be related to an relatively shallow environment, and suggest that *P. sagittalis* n. sp. inhabited soft bottoms in siliciclastic environments with briozoan, small and isolated spherical coral colonies (*Stylocoenia* sp.), and seagrass meadows (Fig. 7). These probably developed in the euphotic zone, above storm wave base level, at depths that did not exceeded 20-30 m as represented in Fig. 7. All of the above seems to suggest a gradual transition from shallow environments inhabited by the oldest taxa, to deeper platform environments, as is seen today for the genus *Dairoides*.

Figure 7. Reconstruction of the *Phrynolambrus sagittalis* n. sp. in the lower Priabonian (upper Eocene) benthos of the Pamplona Fm (Huesca province, Spain), on a hypothesized muddy bottom and seagrass meadow. Parts nor preserved in the fossil are idealized from comparison with the closest modern representative. Reconstruction by Hugo Salais (Metazoa Studio).

CONCLUSIONS

Phrynolambrus sagittalis n. sp., from the upper Eocene of Spain, is the first record of fossil crabs of the enigmatic family Dairoididae. The completeness and exquisite preservation of the new fossil material allowed us to examine aspects of the anatomy of *Phrynolambrus* and *Dairoides*—the type and only genus of Dairoididae previously known—, and to place them in a phylogenetic context. We conclude that Dairoididae is indeed a type of elbow crab, or Parthenopoidea, rarher than a type of stone crab, superfamily Eriphioidea, and only superficillay similar due to convergence.

The recognition of *Phrynolambrus* as sister group to *Dairoides* pushes back the origins of the family Dairoididae more than 40 million years into at least the late Eocene, and provides a reliable calibration point of the family for molecular phylogenetic studies. The new species is also second report of Eocene elbow crabs from the Iberic Peninsula, and one of the oldest parthenopid crabs discovered to date.

Our results 1) expand our understanding on the stratigraphic and paleobiogeographic distribution of Paleogene elbow crabs, 2) highlight the Eocene as a time of rapid evilution of higher eubrachyuran groups, and 3) shed lights on the early origins, anatomical diversity, and systematic affinities of ancient Parthenopoidea, one of the most emblematic and anatomically distinctive groups of true crabs. Understanding the anatomical diversity or disparity of Paleogene eubrachyurans is pivotal to disentangle the systematic relationships among several of the main crown families, and to investigate spatio-temporal patterns leading to the evolution of modern faunas.

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AUTHOR CONTRIBUTIONS

S.Z., F.A.F. and J.L. designed the study. F.A.F. prepared the specimens. F.A.F., S.Z. processed the CT-scans. F.A.F. and J.L. built the dataset and performed the phylogenetic analysis. All authors described and interpreted the specimens. F.A.F. and J.L. prepared the figures. F. A. Ferratges, S. Zamora, J. Luque wrote the first draft of the manuscript with input from all co-authors.

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6.1.2.6. Systematics and palaeoecology of a new Varunidae H. Milne Edwards, 1853 (Decapoda, Brachyura) from the lower Eocene of Spain.

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Systematics and paleoecology of a new species of Varunidae H. Milne Edwards, 1853 (Decapoda: Brachyura) from the lower Eocene of Spain

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ABSTRACT

The Roda Formation (early Eocene Ypresian, Huesca, Aragón, northern Spain) records successive levels including rich decapod faunas relevant for the understanding of Ypresian decapod assemblages. *Asthenognathus fernandezi* **n. sp.** is described from one of these levels, representing the oldest report of a fossil Asthenognathinae, and the first report from the Iberian Peninsula. Fossil members of Asthenognathinae Stimpson, 1858, are difficult to distinguish from other families, especially when they lack preserved pereiopods, sternum, and abdomen. The new taxon shows important features that include reduced pereiopods, small and subcylindrical carapace, and absence of protruding ornamentation. This combination of characters indicates a possible early adaptation of *Asthenognathus* Stimpson, 1858 to life in cylindrical cavities. *Asthenognathus fernandezi* **n. sp.** occurred on poorly consolidated siliciclastic substrates associated with a rich benthic fauna, including echinoderms, molluscs, and other crustaceans.

Key Words: Crustacea, fossil crabs, thoracotreme brachyurans, Ypresian

INTRODUCTION

The lower Eocene of the south-central Pyrenees (northeastern Spain) has provided an important diversity of fossil crabs (Vía, 1969, 1973; Artal *et al.*, 2005, 2013a, b; Fraaije & Pennings, 2006; Schweitzer *et al.*, 2007; van Bakel *et al.*, 2012; Ferratges *et al.*, 2019, 2021a, b, c), with some representatives that help elucidate the origin of some modern families (Ferratges *et al.*, 2019). This development is in part related to the excellent outcrop conditions exposing a large variety of shallow marine facies ranging from carbonate-dominated reefal environments to deltaic siliciclastic facies (Ferratges *et al.*, 2021c).

The subfamily Asthenognathinae Stimpson, 1858 consists of a small group of thoracotreme brachyurans comprising the genus *Asthenognathus* Stimpson, 1858 and *Globihexapus* Schweitzer & Feldmann, 2001 (see Kato, 2005; Feldmann *et al.*, 2011; Schweitzer *et al.*, 2022). Modern representatives of this genus occupy tropical-temperate seas (East China and Korea Seas, western Mediterranean Sea, and eastern Atlantic (see Falciai & Minervini, 1992; Lee *et al.*, 2010; Jourde *et al.*, 2012)), but its fossil record shows a wider geographical distribution extending from Argentina, Hungary, Italy, and Japan. The oldest records of *Asthenognathus* has so far been reported from Oligocene levels of Argentina, Italy, and Washington state (Fig. 1) (Schweitzer & Feldmann, 1999, 2001; Casadio *et al.*, 2004; De Angeli & Garassino, 2006), and only nine fossil species have been described, ranging from the Oligocene to the Pleistocene (Karasawa, 1993, 2018; Schweitzer & Feldmann, 1999, 2001; De Angeli & Garassino, 2006; Feldmann *et al.*, 2011; Pasini *et al.*, 2017). The discovery of articulated specimens of *Asthenognathus* in the lower Eocene of the south-central Pyrenees (Huesca, Spain) provides a unique opportunity to understand the morphology of the earliest known representatives of *Asthenognathus* and extends back the record of the genus c.a. 25 mya from the Oligocene to the early Eocene.

Asthenognathus shows several morphological adaptations, like a transversally elongated carapace with subcylindrical shape, reduced chelae and ambulatory legs (especially the first and last pair) and in general, absence of marked and salient ornamentation. These adaptations and general morphology are very similar to hexapodid crabs (see Guinot, 2006; De Angeli *et al.*, 2010; Guinot *et al.*, 2013 and references therein), which sometimes makes them difficult to differentiate from this and other families and subfamilies in the fossil record when they lack preserved pereiopods or sternum (see Schweitzer & Feldmann, 2001), especially Hexapodidae Miers, 1886, Chasmocarcininae Serène, 1964, Tritodynamiinae Števčić, 2005, and Scalopidiidae Števčić, 2005. In the case of Hexapodidae, these adaptations allow the animal to move inside tubular spaces (Zehntner, 1894; Tesch, 1918; Gordon,

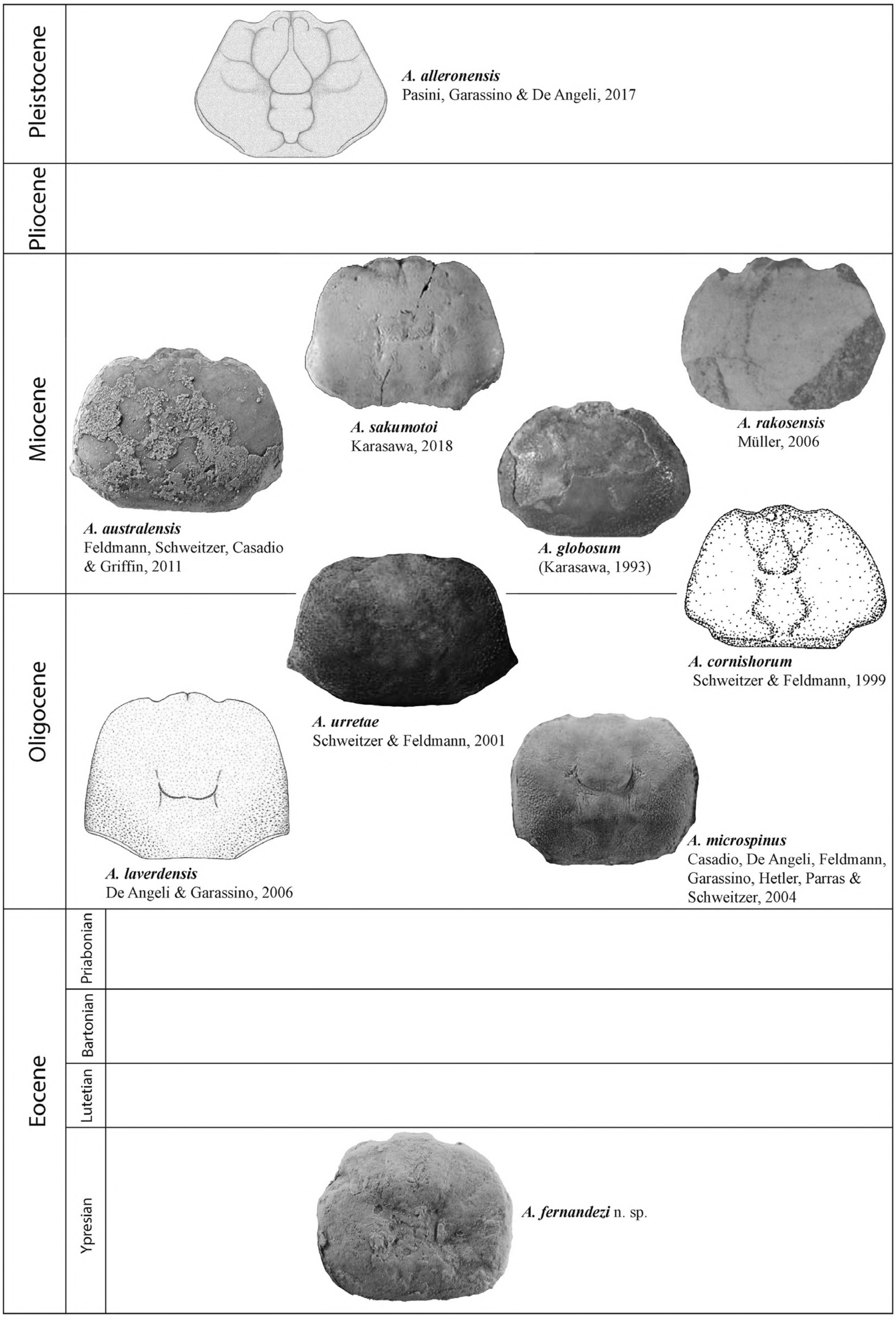

Figure 1. Fossil representatives of the genus *Asthenognathus* Stimpson 1858 and their stratigraphic distribution. Time not to scale.

1971; Manning & Holthuis, 1981; Pereyra Lago, 1988), but some species are found living free in soft and intertidal sandy muddy bottoms (see Guinot *et al*., 2013 and references therein; Rahayu & Ng, 2014).

The aim of the present work is the description of new material of *Asthenognathus* discovered in the Roda Formation (middle Ypresian, lower Eocene) from the southern Pyrenees, Spain. This peculiar crab occurs in a remarkable assemblage of decapod crustaceans adapted to live on soft bottoms deposited in a pro-delta environment (Callianassidae indet., *Ctenocheles* sp., *Periacanthus ramosus* Artal & Castillo, 2005, *Zanthopsis dufouri* (H. Milne Edwards, 1850), *Glyphithyreus* sp., *Micromaia* sp.). Based on a review of previous occurrences of *Asthenognathus* in the fossil record, the paleoecology of this new material and other fossil occurrences is compared with modern representatives of the genus.

GEOLOGICAL SETTING

The studied material comes from the upper Ypresian (lower Eocene) marine sediments recorded in the Tremp-Graus Basin (south-central Pyrenees, northeastern Spain). This new material comes from the Roda Formation, in the outcrop known as Barranco de Bacamorta, in the neighbourhood of the village of Bacamorta (Fig. 2A). In this locality, the Roda Formation consists of an approximately 500 m-thick succession of marls and sandstones including highly fossiliferous intervals, which have provided several important assemblages of decapods in different associations (see Fig. 2B); *Zanthopsis dufouri*, *Periacanthus ramosus*, *Eosymethis aragonensis* van Bakel, Guinot, Artal, Fraaije & Jagt, 2012 (van Bakel *et al.*, 2012), *Collinscarcinus obliquesulcatus* Artal & van Bakel, 2020, *Titanocarcinus decor* Schweitzer, Artal, van Bakel, Jagt, & Karasawa, 2007 (Schweitzer *et al.*, 2007); *Gaudipluma bacamortensis* Artal, van Bakel, Fraaije & Jagt, 2013 (Artal *et al.*, 2013b), *Parapetrochirus robustus* Ferratges, Artal & Zamora, 2021 (Ferratges *et al.*, 2021a), have been previously documented. *Archaeoportunus isabenensis* Artal, Ossó & Domínguez, 2013 (Artal *et al.*, 2013a), was originally reported from the Roda Formation, but new observations suggest a placement in the carbonate characteristic levels of the Morillo Formation (Fig. 2B).

The Roda Formation is a coarsening and shallowing upwards succession (Molenaar & Martinius, 1990) and shows a general progradational pattern to the south and southwest (Puigdefàbregas *et al.*, 1985; Molenaar *et al.*, 1988; López-Blanco *et al.*, 1991, 1996; Nio & Yang, 1991; Molenaar & Martinius, 1996; López-Blanco *et al.*, 2003; Leren *et al.*, 2010). This formation is late Ypresian in age (Samso *et al.*, 1990; Tosquella *et al.*, 1990) and consists of an

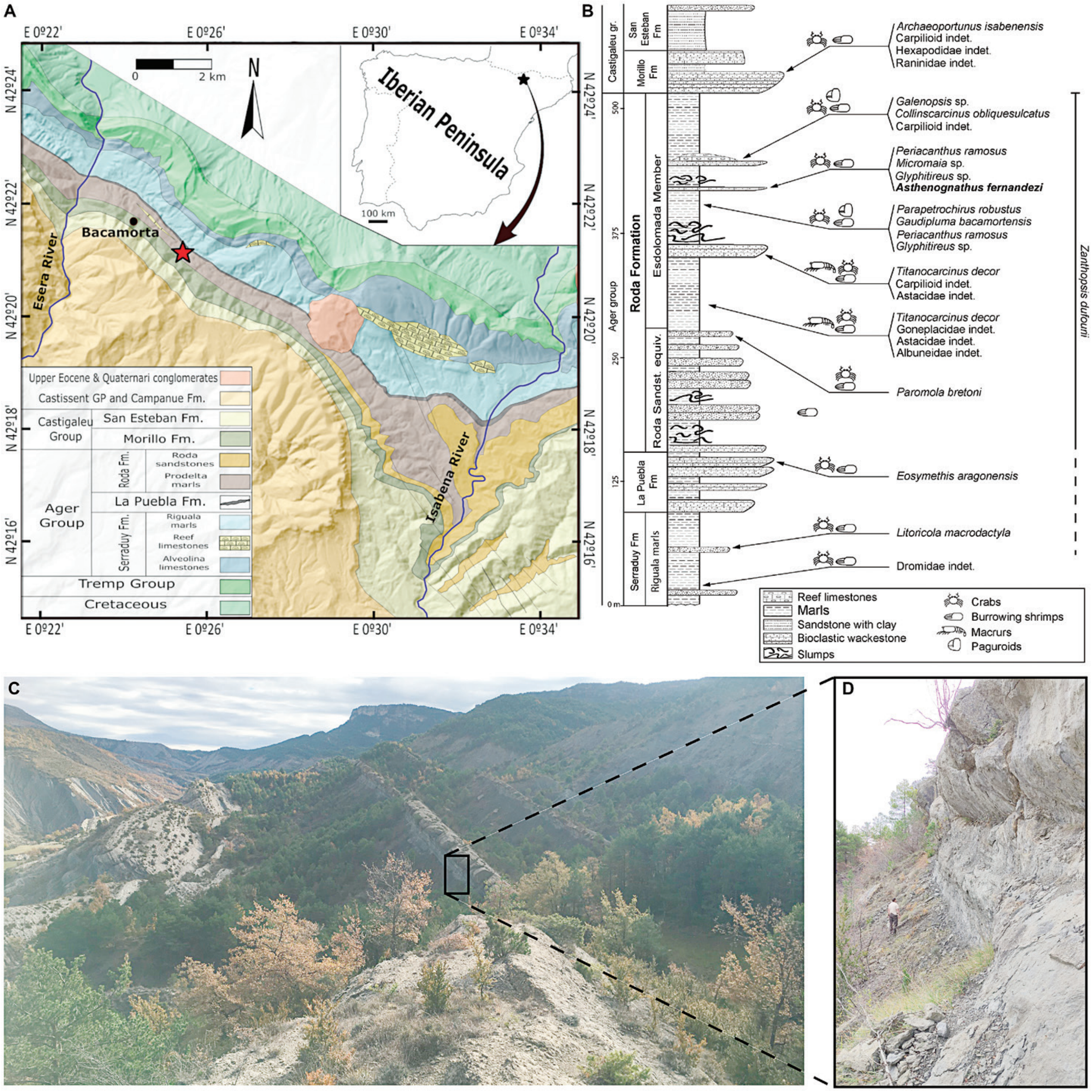

Figure 2. Geological setting of the studied material in the prodelta marls of the Roda Formation East to the Bacamorta village (south-central Pyrenean zone) (**A**). The red star indicates the location of the studied outcrop. Synthetic stratigraphic log of the Bacamorta locality indicating the main lithological features of the Ypresian (lower Eocene) formations and the successive levels with recorded decapod associations (**B**). Field views of the studied outcrop (**C**-**D**). Panoramic view of the studied site (**C**). Detail of the outcrop (**D**).

up to 250 m-thick mixed siliciclastic-carbonate, shallow-marine succession (Martinius & Molenaar, 1991).

MATERIALS AND METHODS

The four studied specimens were collected from the outcrops exposed along the valley known as Barranco de Bacamorta, specifically from a bioclastic wackestone level found in the upper part of the Roda Formation (see Fig 2B).

Measurements of carapace length-carapace width are given in millimetres (mm), respectively. Abbreviations used are as follows: CL, carapace length; CW, carapace width; fm, frontal margin; wf, width of frontal margin (Fig. 3); mxp3, third (external) maxilliped; P2–P4, pereiopods.

The specimens were prepared mechanically using a Micro Jack (Paleotools, Brigham, UT, USA) and, chemically, using potassium hydroxide (KOH). The specimens were then photographed dry and coated with an ammonium chloride sublimate. Detailed photography of the carapace surfaces and appendages was done using a Nikon d7100 camera (Nikon, Tokyo, Japan) with a macro 60-mm lens.

The specimen MPZ 2022/44 was legally sampled under permit EXP: 032/2018 from the Servicio de Prevención, Protección e Investigación del Patrimonio Cultural (Gobierno de Aragón). The specimens MPZ 2022/42-2022/43 and MPZ 2022/41 were found by Manuel Fernández and Ricard Lladó, respectively, and then donated to the Museo de Ciencias Naturales de la Universidad de Zaragoza for this study. Specimens are deposited in the palaeontological collection of the aforementioned museum under acronym MPZ. The location of the outcrop is shown in Figure 2.

SYSTEMATICS

Superfamily Grapsoidea MacLeay, 1838
Family Varunidae H. Milne-Edwards, 1853
Subfamily Asthenognathinae Stimpson, 1858
Genus *Asthenognathus* Stimpson, 1858

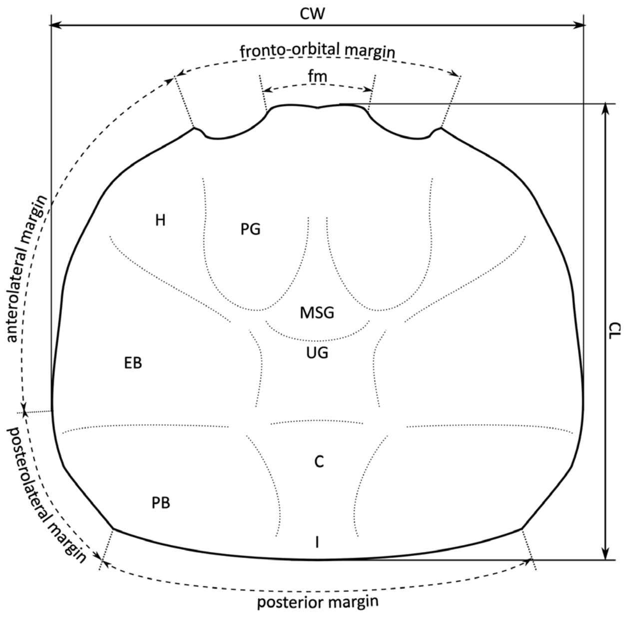

Figure 3. Morphological scheme and terminology used in the text: fm, frontal margin; PG, protogastric region; MSG, mesogastric region; UG, urogastric region; H, hepatic region; C, cardiac region; EB, epibranchial region; PB, postbranchial regions (meso- and metabranchial regions); I, intestinal region.

Type species

Asthenognathus inaequipes Stimpson, 1858, by original designation.

Included species

Asthenognathus atlanticus Monod, 1933 (extant); *A. alleronensis* Pasini, Garassino & De Angeli, 2017 (Pasini *et al.*, 2017); *A. australensis* Feldmann, Schweitzer, Casadio & Griffin, 2011 (Feldmann *et al.*, 2011); *A. cornishorum* Schweitzer & Feldmann, 1999; *A. fernandezi* **n. sp.**; *A. globosus* (Karasawa, 1990); *A. hexagonum* Rathbun, 1909 (extant); *A. inaequipes* (extant); *A. laverdensis* De Angeli & Garassino, 2006; *A. microspinus* Casadio, De Angeli, Feldmann, Garassino, Hetler, Parras & Schweitzer, 2004 (Casadio *et al.*, 2004); *A. rakosensis* Müller, 2006; *A. sakumotoi* Karasawa, 2018; *A. urretae* Schweitzer & Feldmann, 2001.

Remarks

The material herein described is referred to the genus *Asthenognathus*. Species of this genus possess a trapezoidal carapace slightly wider than long, posterolateral margins straight or slightly concave (posterolateral facets of Sakai, 1976), and a weak rim paralleling the posterolateral and posterior margins. The species also possess a triangular mesogastric region, a small inflated area on the anterior portion of the protogastric region, sightly inflated branchial regions, and a subhexagonal cardiac region. The new specimens possess all these aforementioned characteristics and are therefore referred to the genus *Asthenognathus*.

Based on dorsal features from the carapace only, fossil members of the subfamily Asthenognathinae are not easily differentiated from similar forms (i.e., Schweitzer & Feldmann 2001; Müller, 2006; Hyžný & Schlögl, 2011). Dorsal characters are not always useful to assign and differentiate taxa of this group from other families such as Chasmocarcinidae Serène, 1964) and Pinnotheridae De Haan, 1833, and the subfamilies Tritodynamiinae and Chasmocarcininae. For example, Asthenognathinae, Chasmocarcininae, and Scalopidiidae have representatives showing well-developed posterolateral re-entrants, or at least slightly concave posterolateral margins (see Ng, 1987, fig. 1A; Hyžný & Schlögl, 2011). Ventral characteristics are thus critical in order to ensure a proper systematic placement (see Schweitzer & Feldmann, 2001; Hyžný & Schlögl, 2011; Hyžný & Artal, 2018), which also poses problems in order to compare fossil taxa with modern representatives of the group. Despite these problems, Schweitzer & Feldmann (2001) listed clues for distinguishing these genera based on carapace morphology only.

In particular, *Asthenognathus* shows important similarities to *Tritodynamia* Ortmann, 1894, and some species of the former have been assigned to the later (see Schweitzer & Feldmann, 1999 and references therein). Both genera were synonymised by Bocquet (1963), which not is accepted due to the different morphology of their third maxillipeds (see Sakai, 1976; Schweitzer & Feldmann, 1999). The studied specimens can nevertheless be differentiated from *Tritodynamia* because the carapace is much wider than long in *Tritodynamia* and the different shape of the carapace regions cardiac and mesogastric regions less developed in *Tritodynamia*, protogastric region semicircular in *Tritodynamia* but subtrapezoidal in *Asthenognathus*.

The dorsal carapace of *Asthenognathus* resembles that of the chasmocarciniod *Styrioplax* Glaessner, 1969 (included in Goneplacoidea, Chasmocarcinidae). The genera differ nevertheless in some respects because the pereiopods are shorter and thicker in *Asthenognathus* (compare Schweitzer & Feldmann, 2001: fig. 5.9), and the pleonal somites are free and there are no branchial ridges in *Styrioplax*, whereas the male pleonal somites 4–6 in Asthenognathinae are typically fused (Fig. 4) and usually the branchial regions have ridges (Schweitzer & Feldmann, 2001).

Asthenognathus also shows similarities with *Scalopidia* Stimpson, 1858 (Goneplacoidea: Scalopidiidae), but *Scalopidia* differs in some of the diagnostic criteria such as chelipeds prominently unequal and heteromorphic, the ambulatory legs are proportionally long, and the dorsal and ventral margins of the first and second merus has sharp granules and/or spines.

Asthenognathus fernandezi **n. sp.** (Figs. 4–7)

Type material: The holotype is a partially complete specimen (MPZ 2022/41).

Material examined: Four articulated specimens. Measurements: holotype (MPZ 2022/41): CW 12.31 mm, CL 10.45 mm. Paratype (MPZ 2022/42): CW 12.29 mm, CL 10.38 mm. Specimens MPZ 2022/43 and MPZ 2022/44 do not allow complete measurements of the carapace.

Etymology: In honour of Manuel Fernández-Expósito (Santa Margarida de Montbui, Catalonia, Spain) who found and donated critical studied specimens (MPZ 2022/42 and MPZ 2022/43).

Type locality: Barranco de Bacamorta, Bacamorta, Huesca, Aragón, Spain.

Type horizon: Roda Formation, upper Ypresian, lower Eocene.

Diagnosis: Carapace subtrapezoidal, slightly wider than long (L/W ratio ~0.85); surface smooth, with some small pits; front downturned, straight (frontal width/total width 0.20), axially sulcate, projecting beyond the orbits; orbits small, sub-oval, weakly rimmed; fronto-orbital width occupying 47% total frontal width; anterolateral margin smooth, diverging distally, rounded; posterolateral margin with subtle re-entrant; posterior margin convex, rimmed, posterior width/total width 0.74.

Description: Carapace wider than long, subquadrate; dorsal surface convex longitudinally, smooth, cervical and branchio-cardiac grooves noticeably shallow; round branchiocardiac depressions. Dorsal regions not well-defined, separated by shallow grooves; protogastric region elongated, swelling anteriorly along axis, subtrapezoidal; mesogastric region triangular, sulcate, narrow anteriorly; urogastric region slightly defined; cardiac region triangular, weakly elevated, bounded by shallow grooves. Branchial regions not differentiated (Figs. 5, 6).

Surface ornamented by spaced pits. Front depressed, narrow, downturned, extending beyond orbits, widened distally, sulcate; margin straight in front view. Orbits small, rounded; supraorbital border sinuous, rimmed; anterolateral margin convex. Posterolateral margins converging posteriorly.

Thoracic sternum with granular surface, broadening posteriorly, widest at sternite 6; sternites 1,2, 8 unknown; sternites 3–7 granular. Sternite 3 distinct, demarcated by suture; sutures 4/5 to 6/7 equidistant; sternites 5–7 much wider than long, similar in size and shape, with anterior and posterior margins nearly parallel; sternite 5 directed slightly anterolaterally. Sternites 4–6 with posterolaterally episternal projection defining sinuous margin.

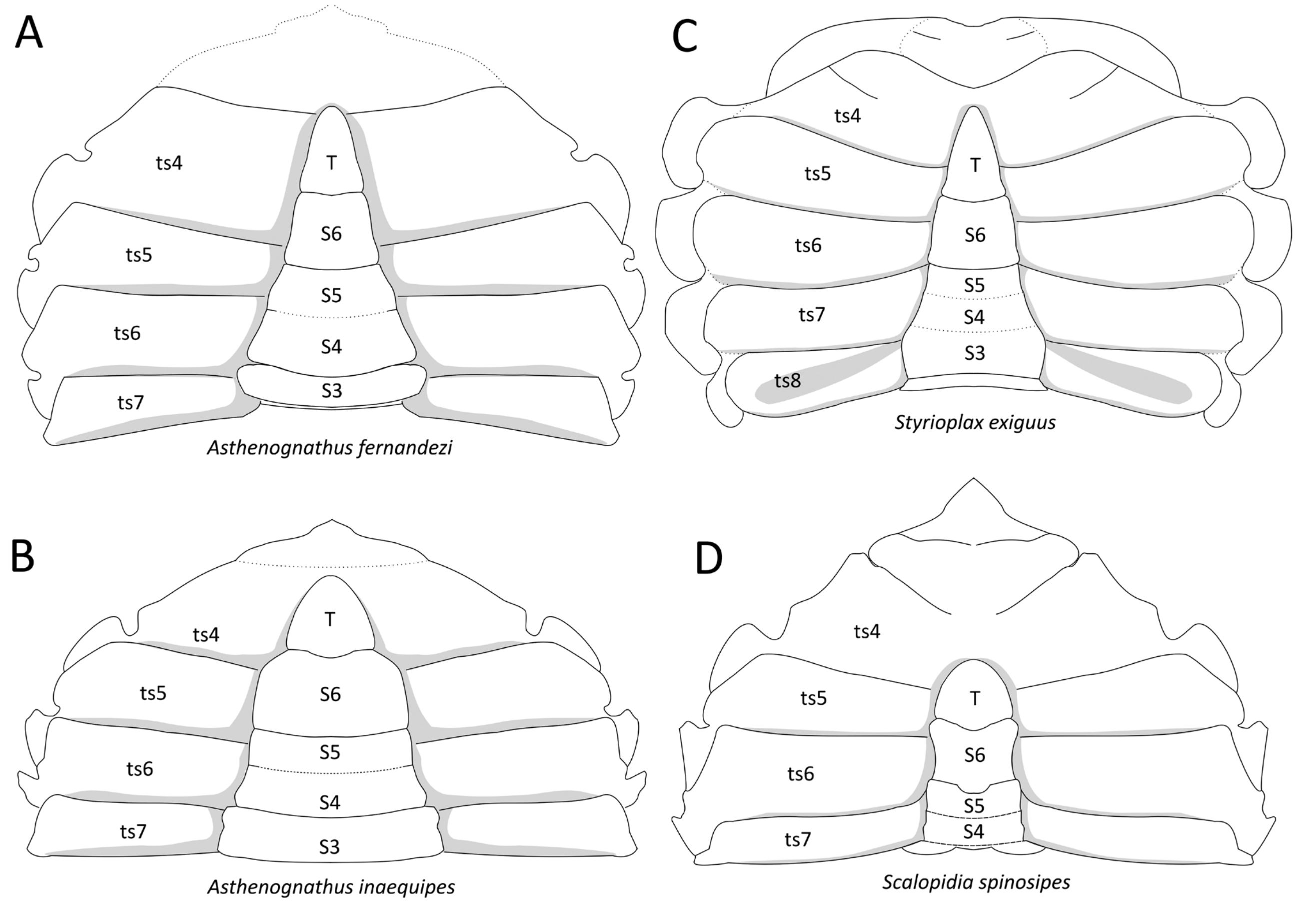

Figure 4. Morphological scheme of ventral views of four taxa with similar dorsal morphology but belonging to different families: *Asthenognathus fernandezi* **n. sp.** (Varunidae) (**A**), *A. inaequipes* Stimpson, 1858 (Varunidae) (**B**), *Styrioplax exiguus* Glaessner, 1928 (Chasmocarcinidae) (**C**), *Scalopidia spinosipes* Stimpson, 1858 (Scalopidiidae) (**D**). Abbreviations: ts4–8, thoracic sternites; S3–6, pleonal somites; T, telson.

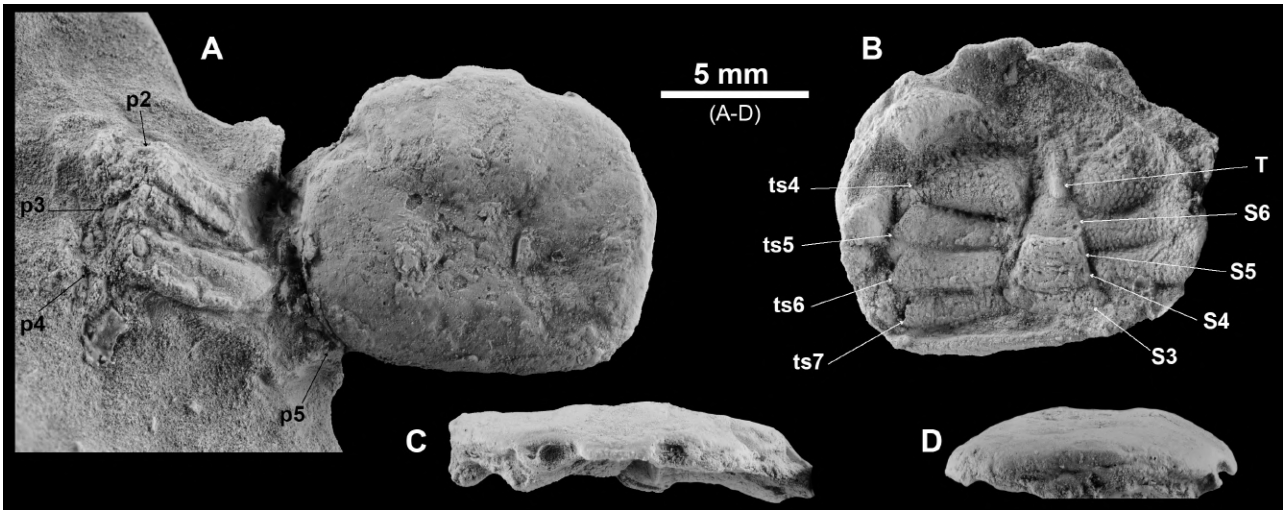

Figure 5. *Asthenognathus fernandezi* **n. sp.** in dorsal (**A**), ventral (**B**), frontal (**C**), and lateral views (**C**) (holotype MPZ 2022/41). Abbreviations: ts4–7, thoracic sternites; S3–6, pleonal somites; P2–5, pereiopods; T, telson.

Sternite 8 not observed in studied specimens, probably because of collapsed specimens.

Telson elongated, subtriangular, not well preserved. Pleonal somites 3–6 smooth, with some small pits. Pleonal somites 6, 5 trapezoidal, wider than long; anterior and posterior margins parallel, lateral margins converging anteriorly. Somites 5, 4 fused. Somites 3, 4 nearly rectangular in shape, wider than long. Pleonal somites 1, 2 unknown.

Chelipeds similar in size and shape. Propodus ~0.3 times as long as high, granular. Fixed finger not well preserved, shorter than palm; dactylus slightly longer than fixed finger; granular; occlusal margin with conical teeth regularly arranged. Carpus short, about as long as high, about a third of the propodus length, smooth laterally. Merus longer than high. Pereiopods 1–3 similar in size and shape; short, robust; flattened in lateral view. Ischium short, triangular. Merus of pereiopods 1–3 longer than high, oval in cross section, upper margin convex, granular; lower margin slightly convex. Carpus short, narrow proximally, widening distally. Propodus short, subquadrate, upper and lower margins appearing parallel. Dactylus thin, not very long, slightly curved. Pereiopod 5 not well preserved, but apparently shorter and thinner than pereiopods 2–4 (Fig. 7).

Remarks: The new species possesses the general shape of the carapace of *Asthenognathus microspinus* from the Oligocene of Argentina, but the latter differs from the new taxon by presenting a series of small spines on the anterolateral margin, a granular surface, a more prominent epibranchial region, and more marked posterolateral margins (see Casadio *et al.*, 2004: fig. 8). *Asthenognathus australensis* also shows similarities with the new taxon in the general outline of the carapace and the shape of the orbits and front, but the carapace is wider, with the posterolateral margins slightly more marked, and it does not present the pits in the dorsal surface (see Feldmann *et al.*, 2011: fig. 13).

Asthenognathus globosus also has important similarities with *A. fernandezi* **n. sp.** in the shape and size of the orbits and front, rounded anterolateral margins, with a reasonably well defined cervical groove. The dorsal surface of the carapace, however, is ornamented with small granules, the posterolateral margins are well marked, and the oval outline is wider than long (see Karasawa, 1990: pl. 8, fig. 12a-c).

Asthenognathus fernandezi **n. sp.** can be easily distinguished from *A. cornishorum*, *A. urretae*, *A. sakumotoi*, *A. laverdensis*, and *A. alleronensis* because the carapaces in these taxa have broader posterolateral margins, clearly differentiated from the anterolateral margin and are more strongly concave than in the new species. Both fossil species *A. sakumotoi* and *A. urretae* also show pereiopods longer than those in the new species. *Asthenognathus rakosensis* can be differentiated from the new taxon by having a much wider than long carapace, wider orbits that occupy almost the entire anterior margin, and the surface of the cephalothorax is completely smooth.

The new taxon shows similarities with the modern species A. inaequipes and A. atlanticus. The fronts of all three species are furrowed by a shallow longitudinal crevice with reduced suboval orbits, the chelae are reduced, the pereiopods are short and robust, and the P5 have a similar morphology and are reduced. The new species, however, can be distinguished from the modern species because it has a narrower carapace, with a less marked posterolateral margin, more spherical sternite 4, the sternites are granular, and the telson is more elongated. The carapace of another modern species, *A. hexagonum*, is strongly hexagonal, but subquadrate in the new species.

DISCUSSION

Distinguishing between members of Asthenognathinae, Hexapodidae and Chasmocarcininae is difficult in fossil specimens that lack preserved pereiopods or sterna. The modern species of Scalopidiidae and Tritodynamiinae also show many similarities with fossil and modern species of Asthenognathinae.

Asthenognathus occurs in shallow-water modern ecosystems throughout temperate and tropical seas, with species are distributed in the Indo-West Pacific (Japan, China, and Korea), western Mediterranean and North Sea (France), and eastern Atlantic (northwestern Africa) (see Monod, 1956; Sakai, 1976; Manning & Holthuis, 1981; Falciai & Minervini, 1992; Lee *et al.*, 2010; Jourde *et al.*, 2012)). The genus includes only three living species: *A. inaequipes*, *A. atlanticus*, and *A. hexagonum* (see Ng *et al.*, 2008). These species are commonly commensals within the mantle cavity of molluscs, as well as cnidarians and echinoderms, lives in polychaete tubes or in callianassid burrows (Woodward & Barrett, 1858; Schmitt *et al.*, 1973; Glémarec & Hily, 1979; Jourde *et al.*, 2012). Some specimens, however, have been observed free-living, and most species spend some part of their lives independent from their hosts (Jourde *et al.*, 2012). There are records of individuals associated with mobile siliciclastic substrates and mud bottoms (Falciai & Minervini, 1992; Lee *et al.*, 2010; Jourde *et al.*, 2012).

The outcrop that provided *Asthenognathus fernandezi* **n. sp.** corresponds to prodelta marls of the Roda Formation, with sediments composed of fine calcareous sandstones and clays, with moderate

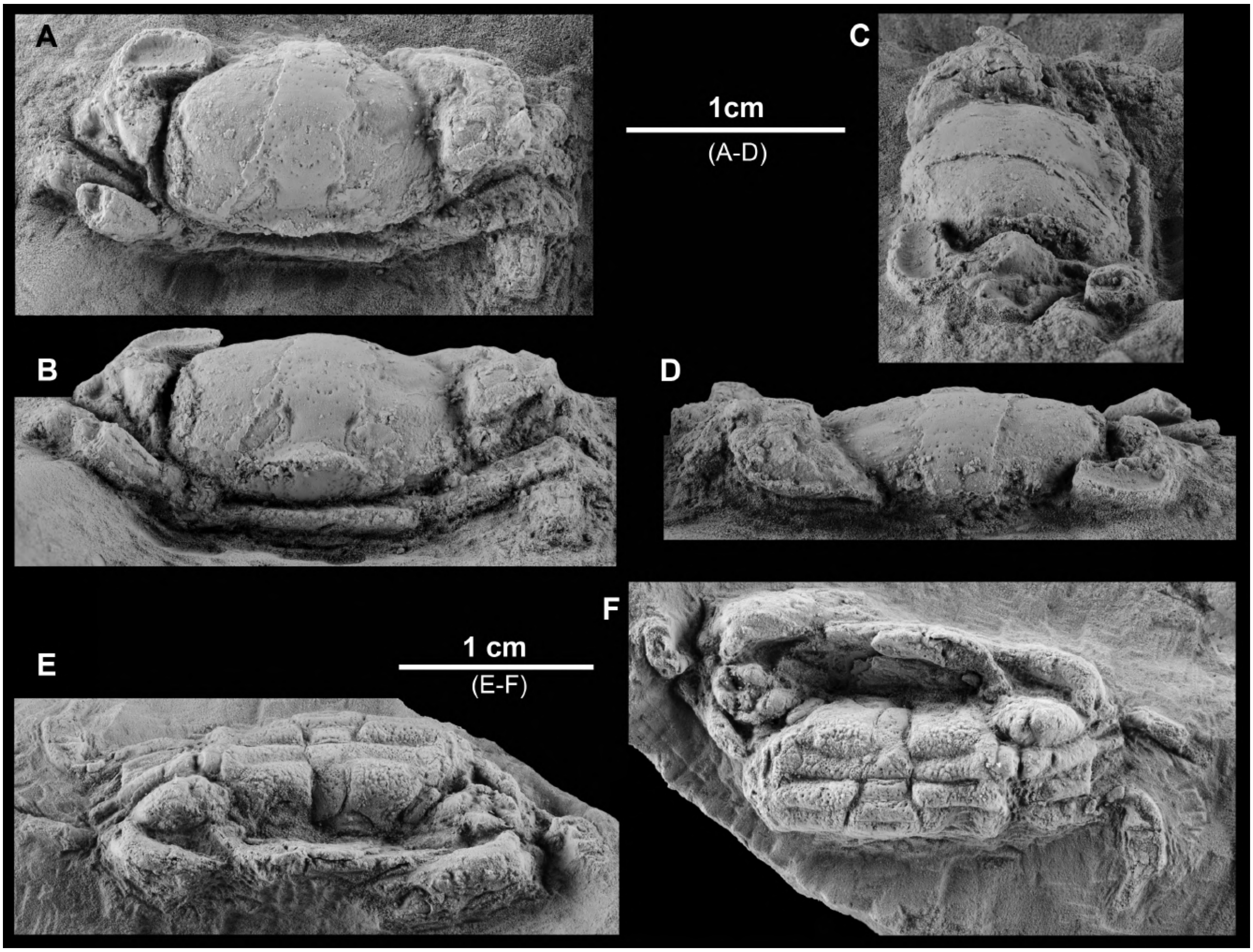

Figure 6. *Asthenognathus fernandezi* **n. sp.** in dorsal (**A**), posterior (**B**), oblique lateral (**C**) and frontal views (**D**) paratype MPZ 2022/42 preserving ventral view with; (**E-F**) paratype MPZ 2022/43 in frontal ventral (**E**) and ventral view (**F**).

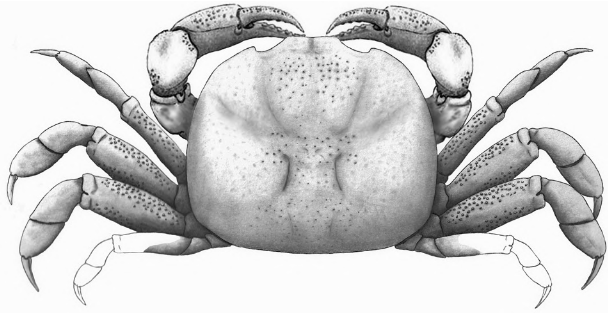

Figure 7. Reconstruction of *Asthenognathus fernandezi* **n. sp.** based on holotype and paratypes.

bioturbations, molluscs, abundant regular and irregular echinoids, and other decapod crustaceans. The presence of delicate and articulated specimens suggests relatively little transportation prior to burial. Bioturbation is present but disperse at these levels, especially for vertical burrows of sections ranging from few millimetres to two centimetres.

According to the fossil record, representatives of *Asthenognathus* only occupied sand and soft bottoms (siliciclastic environments) in shallow platforms. Fossil *Asthenognathus* generally appear associated with other crabs (i.e., Schweitzer & Feldmann, 1999; Casadio *et al.*, 2004; Müller, 2006). The samplings undertaken at the studied site show some decapod species that always appear disarticulated (*Periacanthus ramosus* and *Micromaia* sp.), suggesting a possible parautochtonous origin, but other taxa appear fully articulated (*Zanthopsis dufouri*, *Glyphithyreus* sp., and the new species described herein). This distribution suggests the episodic occurrence of high-energy events affecting the offshore setting, transporting material from nearby areas and accumulating both complete specimens and disarticulated carcasses. Based upon the faunal content and sedimentology of the area, the depositional environment corresponds with a muddy bottom within the mesophotic zone.

Previous fossil records of *Asthenognathus* from the Mediterranean area were limited to *A. laverdensis* from the early Oligocene of Veneto (northeastern Italy) and *A. alleronensis* from the early Pleistocene of Terni (central Italy). Both taxa differ notably in the shape of the carapace and ornamentation from the species described herein (see above).

The new species also represents the oldest record of this genus and the first report in the Eocene. Schweitzer & Feldmann (2001) suggested a high southern latitude for the origin of the subfamily Asthenognathinae, dispersing towards the Pacific and North Atlantic. This new discovery indicates the presence of this genus in temperate latitudes of the Northern Hemisphere and in older strata, and based on the shape of its body and limbs, suggest an early adaptation to live inside cylindrical cavities.

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6.2. Distribución y diversidad de los crustáceos decápodos del Eoceno

Las fluctuaciones en la diversidad y abundancia del registro fósil de crustáceos decápodos y otros invertebrados marinos preservados en facies marinas poco profundas dependen de múltiples factores, como los cambios en el nivel del mar, factores ecológicos particulares, o procesos tafonómicos que afectan a su conservación (p. ej., Peters, 2005; Hannisdal y Peters, 2011; Smith *et al*., 2012; Peters y Heim, 2011; Klompmaker *et al*., 2013a, 2013b; Dunhill *et al*., 2014 y sus referencias; Luque *et al*., 2019). Por este motivo, algunos autores consideran a los decápodos como buenos indicadores zoogeográficos (Müller, 1979; Schweitzer 2001; Feldmann y Schweitzer 2006; Hyzny, 2015, 2016). Al estar restringidos a condiciones sedimentarias particulares (suministro de alimento, profundidad, etc), la distribución de los decápodos está controlada por el tipo de facies (p. ej., Bertini y Fransozo, 2004; Pallas *et al*., 2006; Rufino *et al*., 2006; Furlan *et al*., 2013; Cartes *et al*., 2014). Algunos autores han intentado comprender la distribución de las faunas de decápodos a nivel de afloramiento (Via, 1959; Hyžný 2015, 2016; Klompmaker *et al*., 2013b, 2016; Ferratges *et al*., 2020a, 2021c) o a nivel regional más amplio (Via, 1959; Hyžný, 2016). Los primeros estudios proporcionan datos importantes a pequeña escala, mientras que los últimos proporcionan un panorama general de la distribución de decápodos en áreas relativamente grandes.

Un ejemplo de factor ecológico es el desarrollo de arrecifes, que representan hábitats ideales para estos organismos, proporcionando refugio y alimento. La mayor proliferación de arrecifes en ciertos períodos geológicos se correlaciona con la diversidad de crustáceos decápodos, mientras que las caídas en la diversidad de estos parece haber coincidido con el colapso de los arrecifes (p. ej., Klompmaker *et al*., 2013b, 2016). Esto ha sido bien contrastado en algunos periodos clave como el Jurásico Superior (arrecifes de esponjas) o el Albiense (arrecifes de corales), pero poco se sabe de qué ocurre en el Eoceno. Por otra parte, el tipo de arrecifes es otro factor importante que afecta la diversidad y distribución de los decápodos (Franțescu, 2011). Por ello, la diversidad encontrada en cada tipo de arrecife es muy dispar (ver por ejemplo Ferratges *et al*., 2020 y 2021c). Además, la abundancia y diversidad de decápodos en los arrecifes de coral es mayor que en los biohermos de esponjas y algas, en la misma área geográfica y de la misma edad (ver Franțescu, 2011, 2013). Esta diferencia de diversidad sostiene la idea de que la diversidad de los decápodos está influenciada por condiciones ambientales como la profundidad del agua, la cantidad de nichos ecológicos, la estructura del arrecife, la abundancia de luz, etc. La mayor abundancia y diversidad de decápodos en los ambientes coralinos puede reflejar un mayor número de nichos disponibles, aguas menos profundas con mayor contenido de oxígeno y alimento, diferencia en los niveles de energía, etc., haciendo que los arrecifes de coral sean uno de los ambientes más adecuados para la diversificación de los decápodos (Klompmaker, 2013; Franțescu, 2013).

Las unidades del Eoceno de las cuencas Surpirenaicas ofrecen la oportunidad de llevar a cabo un análisis comparativo de la fauna de invertebrados bentónicos preservada desde entornos deposicionales someros a relativamente profundos. Estos afloramientos permiten la reconstrucción de diversos transectos de proximal a distal que muestran un amplio espectro de facies y representan diferentes entornos de sistemas mixtos siliciclásticos-carbonatos. Estos entornos varían progresivamente desde niveles siliciclásticos costeros proximales, intervalos siliciclásticos marinos poco profundos, plataformas carbonatadas que incluyen arrecifes de coral, praderas de briozoos-esponjas en la plataforma externa, hasta ambientes siliciclásticos relativamente profundos con escasa fauna bentónica.

El conjunto de estudios que se presenta trata de comprender la distribución de los crustáceos decápodos en diversas formaciones que se extiende sobre una gran área geográfica, que abarca afloramientos de las cuencas de Tremp-Graus y de Jaca principalmente, con datos comparativos de la cuenca de Ainsa. Los datos presentados se adquirieron después de un muestreo intensivo en diferentes transectos de plataforma para analizar la diversidad, la abundancia y el estado de conservación de los crustáceos decápodos. En los transectos estudiados es posible establecer correlaciones detalladas entre diferentes áreas debido a las excelentes condiciones de afloramiento y los datos sedimentológicos detallados. Se ha realizado una numeración de subcapítulos no cronológica a cada artículo:

6.2.1. Unravelling the distribution of decapod crustaceans in the Lower Eocene coral reef mounds of NE Spain (Tremp-Graus Basin, southern Pyrenees).

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Unravelling the distribution of decapod crustaceans in the Lower Eocene coral reef mounds of NE Spain (Tremp-Graus Basin, southern Pyrenees)

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ABSTRACT

Modern reefs are considered important hot spots of biodiversity, but the analysis of the distribution of the invertebrate fauna across different reefal domains in ancient ecosystems can be challenging, because the fossil record is usually affected by strong taphonomic biases. The lower Eocene coral reef in the well-exposed outcrops of Ramals (Tremp-Graus Basin, southern Pyrenees, northeast Spain), preserve a high diversity of invertebrate groups, including decapod crustaceans. In Ramals the reefal facies belt is formed by a 100–200 m width E–W trending facies belt, including a set of closely spaced reef mounds up to five meters high, surrounded by the skeletal-rich (packstones, rudstones) inter-reef facies. These outcrops also allow the analysis of the fossil-association present in the inner and outer fore-reef facies, which are dominated by skeletal packstones with molluscs, foraminifera, corals, bryozoans, decapod crustaceans, echinoderms and vertebrate fragments (fishes and crocodiles). The reef framework consists of framestones with bioclastic wackestone to packstone matrix, including abundant colonial corals, as well as crustose red algae, encrusting foraminifera (*Solenomeris*), solitary corals and bryozoans. These reef mounds developed within the mesophotic zone, disturbed by the episodic activity of storm-induced waves.

The distribution of decapod crustaceans across the different reefal domains was subjected to extensive paleontological and statistical analyses. The 911 specimens of decapod crustaceans include 41 species belonging to 21 families. Most crustaceans were concentrated in the periphery of the mound reefs and suggest that the core of the reef hosted the highest diversity and abundance of decapod crustaceans. Carpilioids were the most abundant group within the reefal facies belt, *Ctenocheles* sp. dominated the inner fore-reef areas, and *Litoricola macrodactylus pyrenaicus* showed preferences for outer fore-reef environments. Decapod crustaceans and associated faunas lived in close association with coral reefs but disappeared from the area after the demise of the reefs due to the increase of the depositional depth and fine terrigenous sedimentary input, illustrating how diversity changes at local scale due to extrinsic factors.

1. Introduction

The fluctuations in the diversity and abundance of the fossil record of decapod crustaceans and other marine invertebrates which are eventually preserved in shallow marine facies is dependent on multiple factors, such as sea level changes, ecological factors and preservation processes (e.g. Peters, 2005; Hannisdal and Peters, 2011; Smith et al., 2012; Peters and Heim, 2011; Klompmaker et al., 2013a, 2013b; Dunhill et al., 2014 and references therein; Luque et al., 2019). One example ecological factor is the increase of reef development in certain geological periods, which correlates with the diversity of decapod crustaceans, while drops in decapod diversity coincided with the collapse of reefs several times in Earth history (e.g., Klompmaker et al., 2013b, 2016). Indeed, reefs represent ideal habitats for decapods, providing prevalent shelter and feeding opportunities. In a well-documented case study, the peak of decapod diversity in Albian reefs of the southwestern Pyrenean domain correlated with ecological factors, and was not a preservational artefact (Klompmaker et al., 2013a).

The coralgal reef record around the Paleocene-Eocene transition is scarce, and is dominated by isolated reefs, subordinate to other buildups dominated by calcareous algae and large benthic foraminifera (Rasser et al., 2005; Zamagni et al., 2012; Scheibner and Speijer, 2008; Vescogni

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et al., 2016). Following the Paleocene-Eocene Thermal Maximum (PETM), the Eocene was a critical epoch in the development of many modern-day features of the Earth, for example palaeogeographical configurations, ocean circulation patterns and several climatic conditions (e.g., Hallock et al., 1991; Hallock and Pomar, 2008; Stickley et al., 2009). Cenozoic Earth surface temperatures attained their warmest state during the early Eocene (Zachos et al., 2001; Payros et al., 2015). In addition, modern-style coral reefs were fully established by the Eocene (see Pomar et al., 2017). These external and ecological factors probably affected the diversification of brachyurans, and consequently many

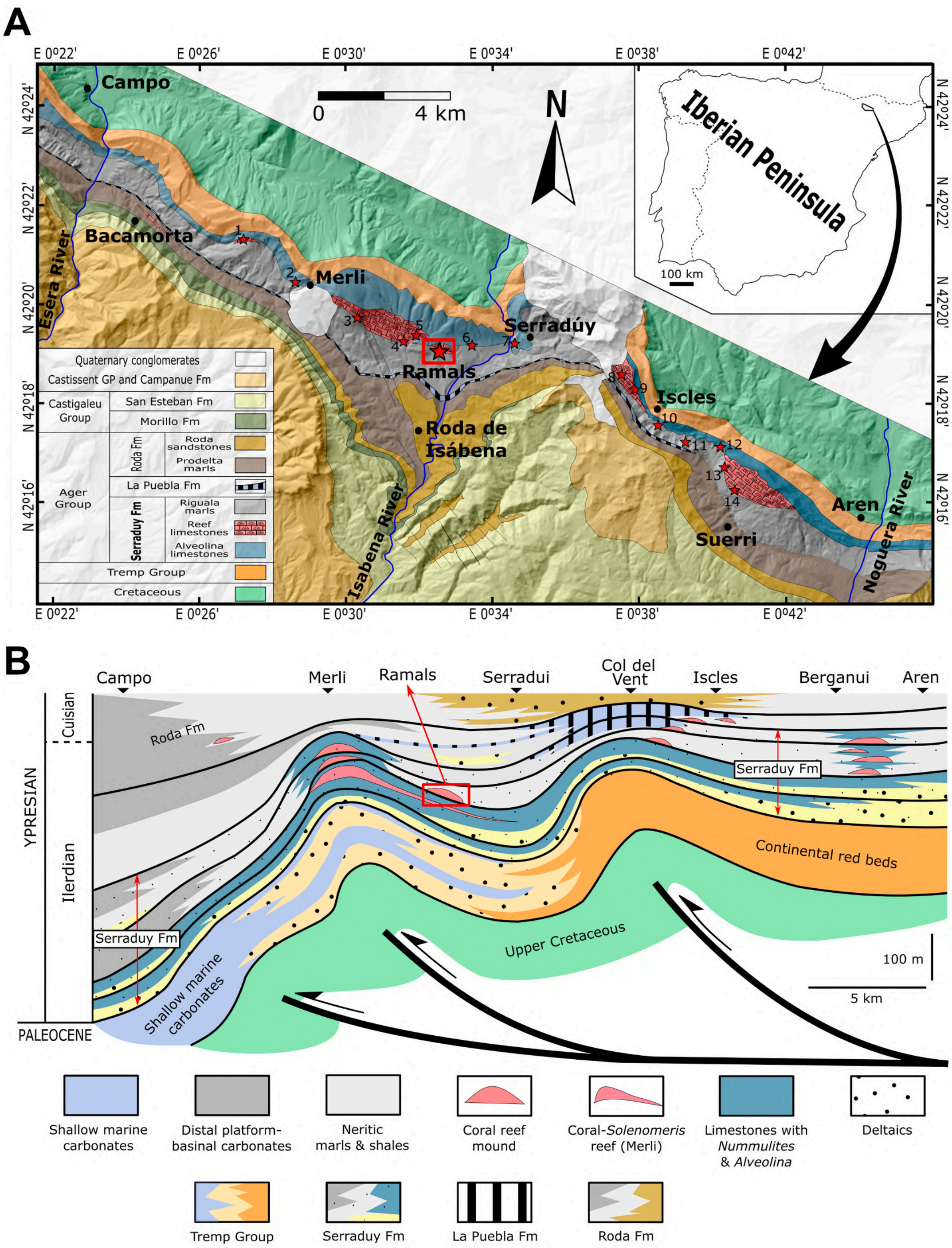

Fig. 1. A: Simplified geological map of the western sector of Tremp-Graus Basin (modified after Serra-Kiel et al., 1994). The red box shows the location of the studied Ramals outcrop (expanded in Fig. 2). The red stars of smaller size indicate other localities that supplied complementary material B: Synthetic stratigraphic cross-section of the northern margin of the Tremp area during the lower Eocene, with main facies types and the location of the main reefal complexes indicated. Equivalence with the lithostratigraphic units used by Serra-Kiel et al. (1994) is indicated in the legend of the different facies types. Modified from Einchenseer (2003) and Pomar et al. (2017). Coordinates of the sampled outcrops: 1: 42°21′19.94″N, 0°26′52.69″E; 2: 42°20′33.29″N, 0°29′01.84″E; 3: 42°19′33.82″N, 0°29′59.48″E; 4: 42°19′14.82″N, 0°31′26.14″E; 5: 42°19′17.92″N, 0°31′45.10″E; 6: 42°19′10.13″N, 0°33′47.05″E; 7: 42°19′19.60″N, 0°34′46.21″E; 8: 42°18′12.66″N, 0°37′22.81″E; 9: 42°17′47.03″N, 0°37′47.24″E; 10: 42°17′29.11″N, 0°38′13.69″E; 11: 42°17′20.35″N, 0°38′40.21″E; 12: 42°16′54.85″N, 0°39′55.02″E; 13: 42°16′23.87″N, 0°39′41.08″E; 14: 42°16′08.42″N, 0°39′45.72″E. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

families of modern species originated in the Eocene (e.g., Brösing, 2008; Tsang et al., 2014; Schweitzer and Feldmann, 2015).

The foreland basins that developed during the Eocene in the southern Pyrenean domain preserve an extraordinary record of shallow marine carbonate successions, including reefs and associated facies (e.g. Pomar et al., 2017; Garcés et al., 2020). In particular, previous studies have addressed the general stratigraphic framework and sedimentary features of the lower Eocene reef mounds exposed in the marginal areas of Tremp-Graus Basin of the southern Pyrenees (i.e. Eichenseer, 1988; Pomar et al., 2017). These previous studies provide the framework forthe characterization of the lower Eocene reef mounds and associated facies in the Ramals outcrop (Tremp-Graus Basin, southern Pyrenees, northeast Spain) performed here.

These Eocene rocks have provided a rich decapod assemblage including anomurans and brachyurans, but few papers have dealt with the relationships between the development of coral reefs and decapod distribution (but see Ferratges et al., 2020 and references therein). Previous studies in Ramals have reported several species of decapod crustaceans (Vía-Boada, 1973; Artal and Vía, 1988; Artal and Castillo, 2005; Fraaije and Pennings, 2006; Artal and Van Bakel, 2018a, 2018b; Ferratges et al., 2019), but none of them focus on the analysis of the distribution of decapods related to the different environments and successive evolutionary stages of the coevally developed reef mounds. The present work provides a well-documented case study demonstrating the relationship between early Eocene reef mound development and coeval setting of an abundant and diverse shallow marine benthic fauna, including a rich association of decapod crustaceans.

The main aims of this work are: (1) to characterize the overall framework and architecture of the coral reef mounds of Ramals, showing the main sedimentological and paleontological features of the associated inter- and fore-reef facies, (2) to describe the relative abundance and diversity of the different groups of marine invertebrates and vertebrates, with particular attention to the characterization of the decapod crustacean assemblages associated to the different reefal environments, and (3) to understand the interaction of the different factors controlling the fluctuations on the diversity of the invertebrate fauna, including decapod crustaceans.

2. Geological setting

The southern Pyrenean Paleogene foreland basins (i.e. Tremp-Graus, Ainsa and Jaca basins) developed in tropical latitudes (e.g. Hay et al., 1999; Silva-Casal et al., 2019). During the Eocene these basins formed part of an elongated gulf connected to the west to the Bay of Biscay and were bounded to the north by the axial zone of the Pyrenees (Plaziat, 1981; Garcés et al., 2020). Sedimentation in these basins has resulted in a well-exposed and complete Eocene succession, showing a great diversity of sedimentary environments, which range from proximal alluvial to shallow marine in the eastern Tremp-Graus basin, to slope and deep marine in most of the Ainsa and Jaca basins, to the abyssal plains of the oceanic basin of the Bay of Biscay (e.g. Garcés et al., 2020).

The lower Eocene reefal unit studied herein is in the middle part of the Serraduy Formation, exposed in the north-western margin of the Tremp-Graus basin. Around the study area of Ramals, the Serraduy Formation forms an almost continuous ESE-WNW trending outcrop (Fig. 1.A). This formation consists of three lithostratigraphic intervals (Serra-Kiel et al., 1994). The lower member is early Ypresian in age and is traditionally known as *Alveolina limestones.* This unit was deposited after the widespread transgression that occurred at the onset of the Eocene. The topography, together with the warm temperatures, favoured the setting of a low-relief carbonate ramp across the marginal areas of the Tremp-Graus basin at the earliest Eocene, in which the *Alveolina Limestones* was deposited (Ferrer, 1971; Robador et al., 1991; Luterbacher et al., 1991; Eichenseer and Luterbacher, 1992; Payros et al., 2000; Miller et al., 2005; Zachos et al., 2008; Martinius, 2011; Garcés et al., 2020).

The *Alveolina limestones* are overlain by a submarine hard-ground surface, formed after a widespread flooding event. This flooding event reached the marginal areas of the Tremp-Graus basin and was related to the southward migration of the plate flexure (Fonnesu, 1984; Garcés et al., 2020). Low sedimentary rates during this period of sea level rise favoured the development of a hardened surface that allowed the growth of reef mounds variable in size and morphology (Eichenseer and Luterbacher, 1992). These reefs and the associated facies characterize the middle member of the Serraduy Formation studied here (i.e. the *Reef limestones* member; Serra-Kiel et al., 1994). Analysis of the reef framework and the associated facies, combined with the characterization of the associated invertebrate assemblage, indicates that these reefs were developed at deep euphotic to mesophotic depths, around or below storm wave base (Gaemers, 1978; Eichenseer, 1988; Pomar et al., 2017).

The mid-Ypresian deepening event resulted in the eventual flooding of the platform and the sedimentation of *Riguala marls* of the upper part of the Serraduy Formation (Fig. 1). These marls were deposited in a relatively deep, open marine platform, transitioning to a slope-basin environment, and supported a lower concentration of benthic communities (Serra-Kiel et al., 1994). The *Riguala marls* were dated as lower to middle Ilerdian, which corresponds to the global Ypresian Stage (Pujalte et al., 2009). At a regional scale, most of the studied reef mounds grew over the hardened discontinuity surface found on top of the *Alveolina limestone* (Fig. 1). However, coral-reefs isolated within the *Riguala marls* have been also found near Suerri. There is also the local record of younger coral-reefs in the prodelta marls of the Roda Formation in Bacamorta (Fig. 1).

3. Material and methods

Most of the data presented here is based on analysis of fossil specimens collected from the outcrops exposing the *reef limestones* member and the lower part of the *Riguala marls* in the Ramals outcrop ($42^0$18′57’’N, $0^0$32′34″E). The collected specimens are generally recorded in a series of skeletal-rich levels including remains of different invertebrate and vertebrate groups. Further skeletal levels have been sampled westwards and eastwards to Ramals, from the municipalities of Merli to Suerri (see Fig. 1.A). This allowed a broader picture of the overall facies distribution and the recognition of lateral variations related to different reefal environments. Detailed sampling information from these areas is not included in the present study.

Detailed sampling and mapping of the reefs and inter-reef areas around Ramals was performed. This provided information on the geometry and the distribution of the different types of reef facies. Sampling was carried out by surface collecting both in the studied sections and their lateral equivalents. This was accomplished during approximately thirty field sessions during the years 2018 and 2019, with two researchers expending eight hours per day (average), and the same amount of time in each sampled area. Active extraction and splitting of rocks has been an adequate technique elsewhere for controlled sampling in some reef facies with decapod crustaceans (e.g. Klompmaker et al., 2013a) but was not the case at our fieldwork sites because of the characteristics of the fossil material (the cuticle of crustaceans is not easily visible in fresh fracture), and the siliciclastic nature of the facies. Mapping in Ramals was facilitated by the excellent outcrop condition and supported by aerial photos. The program QGIS 2.18 was used to construct maps. In addition, three stratigraphic successions representative of the different sedimentary domains in the Ramals outcrop were logged and sampled (see Fig. 2 for locations). The characterizations of the reef mound facies are based on field observation combined with core rock sampling around section A, and in a reef mound located in the western part of the outcrop (see P1 in Fig. 2). From these samples, 36 representative thin sections were studied to characterize the microfacies and microfossil association.

The identification of the different sedimentary domains represented in the Ramals outcrop is based in the lateral variation of facies and the

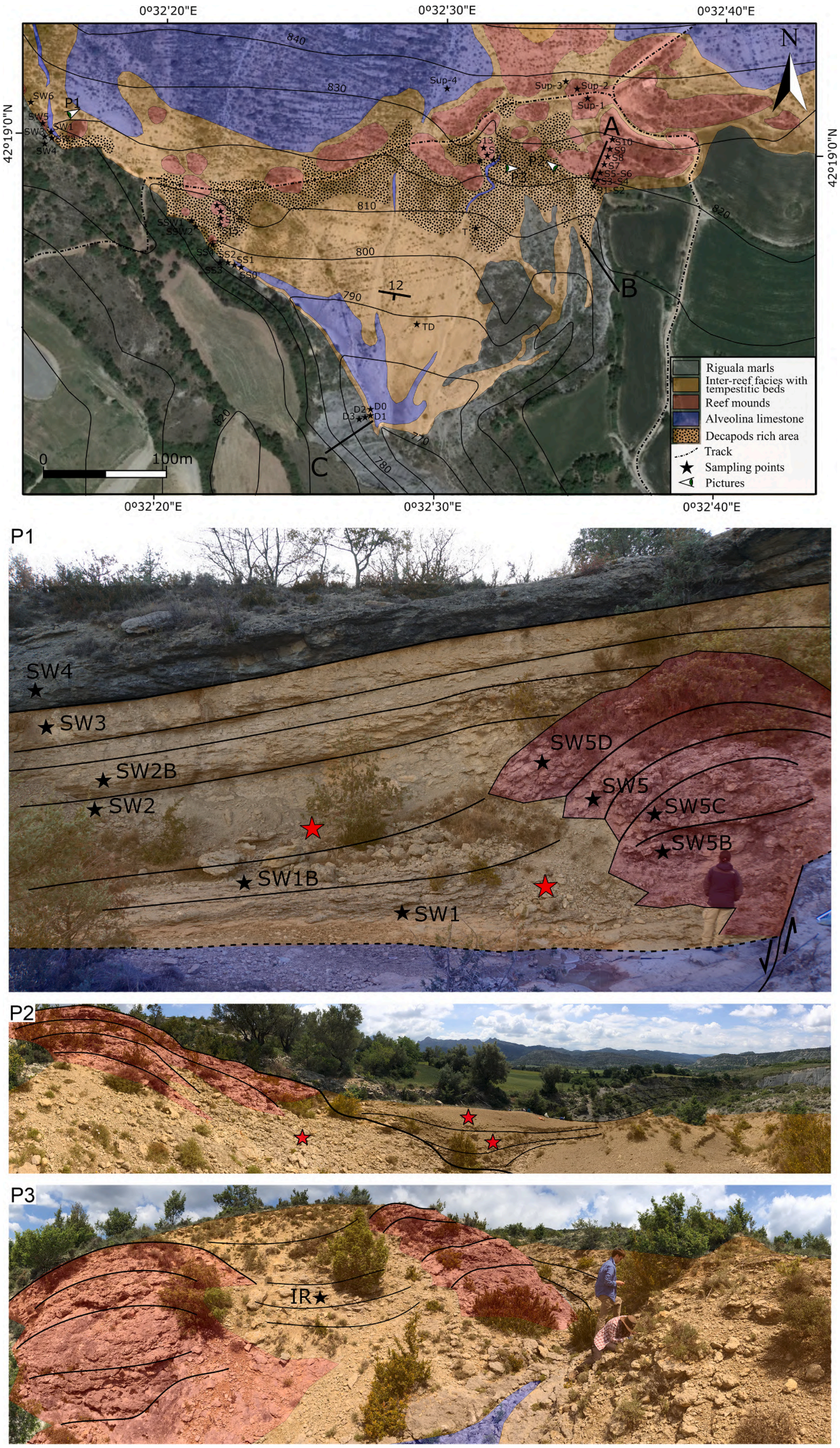

Fig. 2. Detailed map of the three members of the Serraduy Formation in Ramals (see Fig. 1.A for location). A, B and C correspond to the different logged sections represented in Fig. 3. The field views P1, P2 and P3 show the relationship between reef (red) and inter-reef (orange) facies (see location of the photos in the upper map). The *Alveolina limestones* (dark blue) and the *Riguala marls* (transparent) are the pre- and post-reef deposits respectively. The levels marked with a red star are those that provided the largest number and diversity of decapod crustaceans; the black stars indicate the rock samples collected for thin sections. The acronyms SW and IR refer to the location of the samples (SW: western section; IR: inter-reef). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

recorded fossil assemblages. A thorough sampling of fossil specimens was carried out in the areas of the outcrop representing the reefal facies belt (including the reef mounds and inter-reef facies) and the fore-reef areas. The area located in the transition between the reefal facies belt and the inner fore-reef environment includes the largest abundance of decapods (Fig. 2. A). The invertebrate assemblage and the taxa identified in each domain also helped to support the palaeoenvironmental interpretation.

Remains of a total of 911 decapod crustaceans were collected. Decapods were most commonly recovered as disarticulated carapaces and claws. In general specimens show little abrasion or breakage. Claw remains are usually incomplete, most lack important diagnostic characteristics, and only a few are articulated to a carapace (see exceptions in Artal and Vía, 1988; Artal and Van Bakel, 2018a, 2018b; Ferratges et al., 2019). Although most remains are disarticulated, the cuticle is well preserved, which is uncommon in reef environments (e.g., Klompmaker et al., 2013b, 2016) and allows better identification (Klompmaker et al., 2015). Specimens were counted using the following criteria: (1) carapaces assignable to a specific taxon (from approx. > 30% preserved) were counted as specimens, either at the species level or in open nomenclature; (2) chelae were taken into account only for taxa that preserve this part of the anatomy (i.e., Axiidea and Paguridea). In the case of Axiidea, only the left chelae were counted to avoid overcounting (they correspond to approximately 70% of the total sample for this taxon). In the case of Paguroidea, we only have either left or right chelae for each morphotype, so all specimens were counted; (4) the isolated chelae of brachyura (true crabs) were not included because they cannot be assigned with certainty to specific taxa; (5) remaining fragments or appendages were not counted.

The decapod crustacean specimens were prepared using a Micro Jack 2 air scribe (Paleotools) in combination with a microscope. In some cases potassium hydroxide (KOH) was used to remove the matrix. The specimens were then photographed dry and coated with an ammonium chloride sublimate. Detailed photography of the specimens was made using a Nikon D7100 camera (Nikon, Tokyo, Japan) with a macro 60-mm-lens. Specimens were legally sampled under permit EXP: 032/2018 from the *Servicio de Prevención, Protección e Investigación del Patrimonio Cultural (Gobierno de Aragón)* and deposited in the palaeontological collection of the *Museo de Ciencias Naturales de la Universidad de Zaragoza* under the acronym MPZ (see Canudo, 2018). The exact locations of the different outcrops are marked in Fig. 1.

To explore the diversity of the decapod crustacean species distribution in each sedimentary domain chi-squared tests and Principal Component Analyses (PCA) were performed using statistical program Past 4.03 (Hammer et al., 2001). Decapod groups were used as variables of each environment. By performing PCA, the dimensionality of these variables was reduced to determine which were the most characteristic of each environment. To perform these calculations, fossils not assignable to any group (129 specimens corresponding to indeterminate chelae and isolated fragments) were not taken into account. The remaining data were standardized and graphically represented in plots of PC1 vs PC2 and PC1 vs PC3. The information obtained with this method was contrasted with the habits of known taxa to deduce their most probable origin and thus determine whether they correspond to remains transported from adjacent facies (parautochthonous) or if they are characteristic of each facies (autochthonous). The density of each group of decapod crustaceans was calculated by dividing the number of collected specimens by the surface area of the respective zone. The surface areas were calculated using *Iberpix*.

To investigate differences in diversity among zones within the outcrop, multiple measures of diversity were calculated and all samples per site were combined to create an adequate sample size for comparisons among sites. All specimens identified to the species-level were included in the analyses. In addition all taxa that have been identified as different species but left in open nomenclature were included in the analysis (indeterminate fragments were not used for the analysis). Diversity per site was calculated using the methodology described in Klompmaker et al. (2013a):

"1. Taxa richness: the number of taxa found at each zone.

2. Individual rarefaction curves with 95% confidence intervals were computed for each of the samples using PAST 4.03.

3. Shannon–Wiener Index or Shannon Index or Shannon–Weaver Index $H = -\Sigma pi(\ln(pi))$, where pi is the proportion of the ith species, thus additionally taking into account the number of specimens per species.

4. Margalev's $d = (S - 1)/\ln(N)$, where S is the number of species and N is the number of specimens found at the site to account for the fact that more specimens yield more species in general.

5. Simpson's Index of Diversity $= 1 - (\Sigma n(n - 1))/(N(N - 1))$, where n is the number of specimens of a species and N again is the total number of specimens found at the site. This measure accounts not only for the number of specimens involved, but also for the number of specimens per species.

6. The Sorensen Index $= SI = 2c/a + b$, where a is the number of species from the zone 1, b is the number of species from the zone 2, and c is the number of species that share two zones. This measure has been used to determine the degree of similarity between zones.

7. The Chao1 Index (Chao, 1984) estimator of the absolute number of species in an assemblage: $SChao1 = Sobs+(F1^2/2F2)$, where Sobs is the number of species in the sample, F1 is the observed number of species represented by one specimen, and F2 is the observed number of species represented by two specimens. This measure calculates the theoretical number of species if an infinite number of specimens had been collected.

8. Pielou's evenness index was also calculated: $E = H/\ln(S)$, where E is the evenness index and H is the Shannon Index (see above)."

4. The reef mounds and associated facies

The reconstruction of the lateral relationship of the reef, inter- and fore-reef facies characterized in the outcrop exposed around Ramals provided the overall sedimentological and stratigraphic framework, in which the different collected decapod crustacean assemblages are located. The three logged and sampled stratigraphic sections (Fig. 3) cover the reef facies (section A), the inner fore-reef facies (section B) and the outer fore-reef facies (section C), as well as the basal levels of the post-reefs facies (*Riguala marls;* sections B and C).

In the northern part of the Ramals outcrop, a set of closely spaced reef mounds form a 100–200 m width E–W trending belt (Fig. 2.A). The reefs consist of isolated or agglutinated mounds up to five meters high. They sit directly on over the hardground surface that developed on top of the *Alveolina limestones*. In addition, the initial growth of some of these reefs can be related to local step faults (Fig. 2-P1).

The reef framework consists of coral framestones with bioclastic wackestone to packstone matrix (Fig. 4). Coral colonies are rarely preserved in growth position within the reef framework, indicating the episodic activity of currents, probably related to storm-induced waves. The reef is dominated by massive and tabular colonies, represented by the genera *Actinacis*, *Astreopora*, *Colpophyllia* and *Cyathoseris*. Branching colonies (such as the genus *Actinacis*) are also abundant. Other identified colonial corals include *Stylocoenia*, *Astrocoenia, Agaricia* and *Caulastraea*. Solitary corals (*Placosmilopsis, Leptophyllia*) are also found. Other relevant organisms that helped to build the reef framework are crustose coralline red algae, encrusting foraminifera (*Solenomeris*) and bryozoans (Figs. 4-B, C and 5-B, E).

At some points the reef mounds overlapped and growing over each other. This allowed the accumulation of sediments underneath them (Fig. 2-P2). At other points sediment accumulated in inter-reef spaces (Fig. 2-P3). These inter-reef areas include a large number of redeposited bioclastic levels with poorly sorted rudstone to packstone textures (Fig. 5.B, C, D), with a relative abundance of glauconite. The areas attached to the pinnacles include large blocks of coral reef framework rubble. The branching colonies (such as the genus *Actinacis*) are particularly abundant in the rubble redeposited in the skeletal-rich levels found a few tens of meters away in the main reefal facies belt.

The central and southern part of the Ramals outcrop corresponds to deeper fore-reef areas, in which reef mounds are absent and the proportion of skeletal grains is lower, resulting in wackestone to packstone textures (Fig. 2). The inner fore-reef facies attached to the northern reefal facies belt, consists of decimetre-thick rudstone to packstone levels interbedded with bioclastic marls, and contains a great abundance and diversity of fossils (Fig. 5.D, E, F). These coarse-grained and poorly sorted skeletal levels gradually pass to finer-grain skeletal packstone beds that eventually pinch out offshore (southwards), further away from the reef. This lateral gradation indicates that most of the skeletal components found in these levels were sourced from the reef mounds, and were transported downslope, most probably by storm-induced currents.

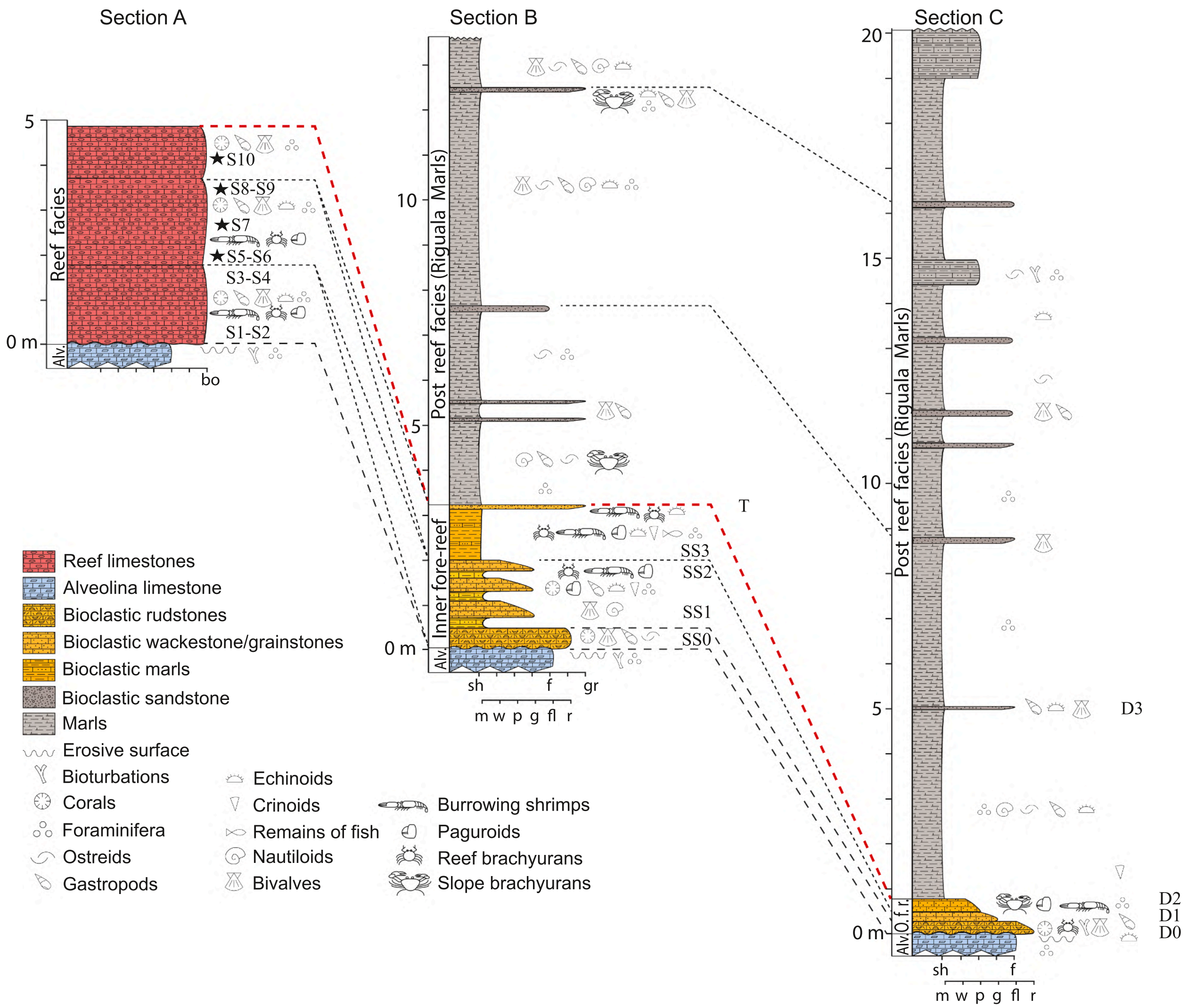

Fig. 3. Correlation of stratigraphic logs (see Fig. 2 for exact location of the logs). The red dashed line shows the boundary between the reef and fore-reef facies to the post-reef facies of the *Riguala marls*. The stars indicate the levels sampled for thin section analysis. Legend: sh: clays; f: fine-grained sandstone; gr: coarse-grained sandstone; m: mudstone; w: wackestone; p: packstone; g: grainstone; fl: floatstone; r: rudstone; bo: boundstone; O.f.r.: Outer fore-reef facies. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The inner fore-reef facies grade upwards to finer-grain bioclastic beds (decimetre-thick wackestone and packstone), with intercalated marls. These levels contain a low diversity, composed mostly of bivalves (ostreids), gastropods and occasionally echinoderms and decapods. The decrease in grain size and increase of muddy matrix up section indicates a decrease in hydrodynamic energy, probably related to the coeval increase in the depth of deposition.

Southwards, the outer fore-reef deposits are reduced to less than one meter (Fig. 3, section C). These deposits are mostly formed by skeletal packstones dominated by benthic foraminifera (Fig. 5F, G). There is some significant lateral variation in the dominant skeletal grains compared to the inner fore-reef facies. As a general rule, the diversity and concentration of skeletal debris is lower in the outer fore-reef areas, and there is a rapid decrease in the abundance and diversity of invertebrate fossils. The lateral variation on the recorded invertebrate fossil association across the fore-reef domains indicates that these skeletal levels are in fact a mixture of redeposited (parautochthonous) and autochthonous material.

The sedimentation of the *Riguala marls* occurred after the demise of reef mounds. These post-reef facies onlap and cover the reefs and associated bioclastic facies, and show an important decrease in the number of benthic fossils. The marls include interbedded decimetre-thick fine-grained detrital levels with scarce skeletal grains, which pinch out laterally towards the South.

5. The fossil association of the reefal facies belt

The analysis of the skeletal grains recorded in the inter- and fore-reef facies provided precise information about the fossil groups that developed coeval to the coral reef mound development. Among these groups are molluscs, foraminifera, corals, bryozoans, decapod crustaceans, echinoderms and vertebrates (see Figs. 6 and 7). The diversity and abundance of the recorded fossil assemblage indicates a favourable environment for the development of the benthic fauna while the reef was actively growing. The remains of decapods and other marine invertebrate groups are frequently disarticulated and fragmented, with local colonization by epibenthic fauna. In the case of decapods we cannot discard the possibility that some epibionts (mostly serpulids) attached during life, but in the case of echinoids most epibionts attached post-mortem because they affected parts originally covered with spines (Fig. 6). About 40% of echinoids were colonized by epibionts.

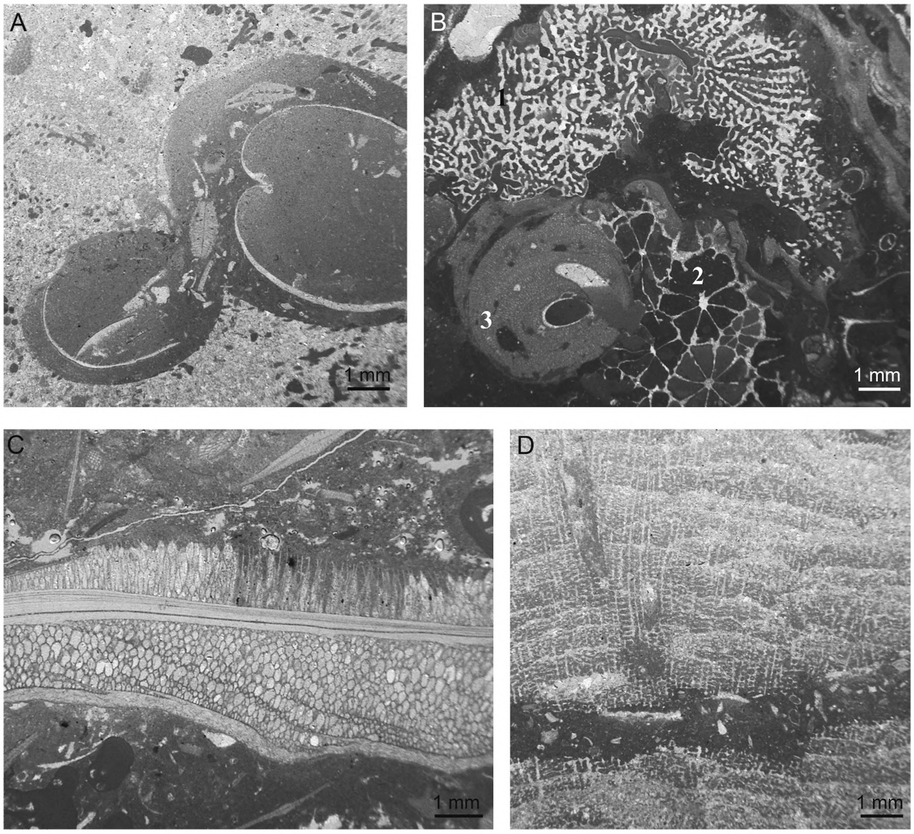

Fig. 4. Thin section pictures representative of the reef framework. A (sample S1): Scleractinian coral framestone with lithophagous bivalves; B (sample S8): Framestone with scleractinian corals (1), *Astrocoenia* (2) and *Solenomeris* (3); C (sample S6): the wackestone-packstone matrix of the reefal framestone, with discocyclinids, *Acervulina*,?*Sporolithon* and oysters; D (sample S2): Boundstone of tangential section of *Actinacis* with a cavity filled with micritic matrix. Location of samples in Fig. 3.

5.1. *Decapod crustaceans*

Decapod crustaceans were abundant both in the inter-reef and fore-reef environment (Table 1). A total of 41 different decapod species were recognized that are included in 21 families: Callianassidae, Ctenochelidae (Axiidae); Diogenidae, Paguridae (Anomura); Basinotopidae, Dynomenidae, Sphaerodromiidae, Homolidae, Raninidae, (podotreme brachyurans); Aethridae, Calappidae, Goneplacidae, Matutidae, Carpiliidae, Hexapodidae, Pilumnidae, Panopeidae, Parthenopidae, Portunidae, Tumidocarcinidae, Xanthidae (heterotreme brachyurans). This decapod assemblage has similarities with material collected from other European localities associated with Eocene reef facies (see, e.g., Beschin et al., 2007, 2015; Tessier et al., 2011).

5.2. *Echinoderms*

Among the echinoderms, marginal plates of goniasterid asteroideans (?*Calliderma* sp.; Fig. 6 V) and abundant crinoids were found (*Bourgueticrinus* sp.; Fig. 6 W-X) (see Zamora et al., 2018). In the studied area, these levels provided a great diversity of regular and irregular echinoids (Bataller, 1937; Gurrea, 1999; Carrasco, 2003, 2006, 2015, 2017). Among them (Fig. 6), the following taxa of regular echinoids were identified: *Ambipleurus* sp., *Baueria angelae* Carrasco, 2006; *Arachniopleurus reticulatus* Duncan & Sladen, 1882*; Fellius pouechi* (Cotteau, 1863)*; Cidaris gourdoni* Cotteau, 1889;?*Thylechinus frossardi* (Cotteau, 1889); *Salenia* sp.; Irregular echinoid fauna includes: *Ditremaster nux* (Desor, 1853); *Eurhodia* sp.; *Maretia arogonensis* (Cotteau, 1887); *Trachyaster* sp.; *Cyclaster gourdoni* (Cotteau, 1887); *Linthia aragonensis* (Cotteau, 1887); *Linthia hovelacquei* Cotteau, 1889; *Amblypygus dilatatus* Agassiz, 1840; *Echinocyamus* sp.; *Echinolampas leymeriei* Cotteau, 1863; *Echinolampas* sp.; *Gitolampas cotteaui* (Hébert, 1882); *Holcopneustes* sp.; *Prenaster* sp.; *Pygorhynchus aragonensis* Cotteau, 1889; *Schizaster rousseli* Cotteau, 1887*; S. vicinalis* (Agassiz and Desor, 1847).

5.3. *Foraminifera, other invertebrates and vertebrate remains*

The foraminifera include both benthic (free-living and encrusting) and planktonic forms. The species of benthic foraminifera were identified as discocyclinids (Figs. 4.C and 5), assilinids (?*Heterostegina*), *Alveolina*, orthophragminids, textularids (biseriate?), fiserinids, *Operculina*, *Nummulites*, possibly Discorbidae,?*Amphistegina*, *Gibsina* (?*Esferogibsina*), and abundant rotalids (of different species), *Solenomeris* (Fig. 4.B), *Acervulina* sp. (Figs. 4.C) and miliolids (Fig. 5).

Gastropods were found in great abundance (Cypraeidae, Xenophoridae, Fasciolariidae, Rostellariidae, Naticidae and Neritidae), most preserved as internal moulds. Epifaunal and infaunal bivalves were also identified. Epifaunal bivalves include groups with a free mode of life (Spondylidae, Chamidae, Pectinidae) and some that cemented to hard substrates (Ostreidae). Among the infaunal bivalves, taxa adapted to different substrates were found, like Mytilidae (*Lithophaga*) for hard substrates; Cardiidae, Carditidae, Lucinidae, Crassatellidae and Pinnidae for soft substrates; and *Teredolites* for wood substrates (Carrasco, 2004).

In addition, several species of terebratulid, ostracods (Fig. 5 D—H), bryozoans (Fig. 5 B—F) and serpulids were found. Some internal moulds of large nautiloids (larger than 30 cm), probably of the genus *Eutrephoceras*, and parts of their mouth apparatus (*Rhyncholites* sp.; Fig. 6 D) were also retrieved. In some cases, the shell of these nautiloids were associated with other organisms, which used these shells for shelter (Fraaije and Pennings, 2006).

Fish remains, mainly teeth of sharks and rays, indeterminate bones, otoliths and teeth of teleost fishes, rostral fragments of *Cylindracanthus* sp. and isolated bones of Crocodylia indet. (Eusuchia indet.) were less abundant (Fig. 6). The single specimen of Crocodylia indet. Was encrusted by oysters and bryozoans.

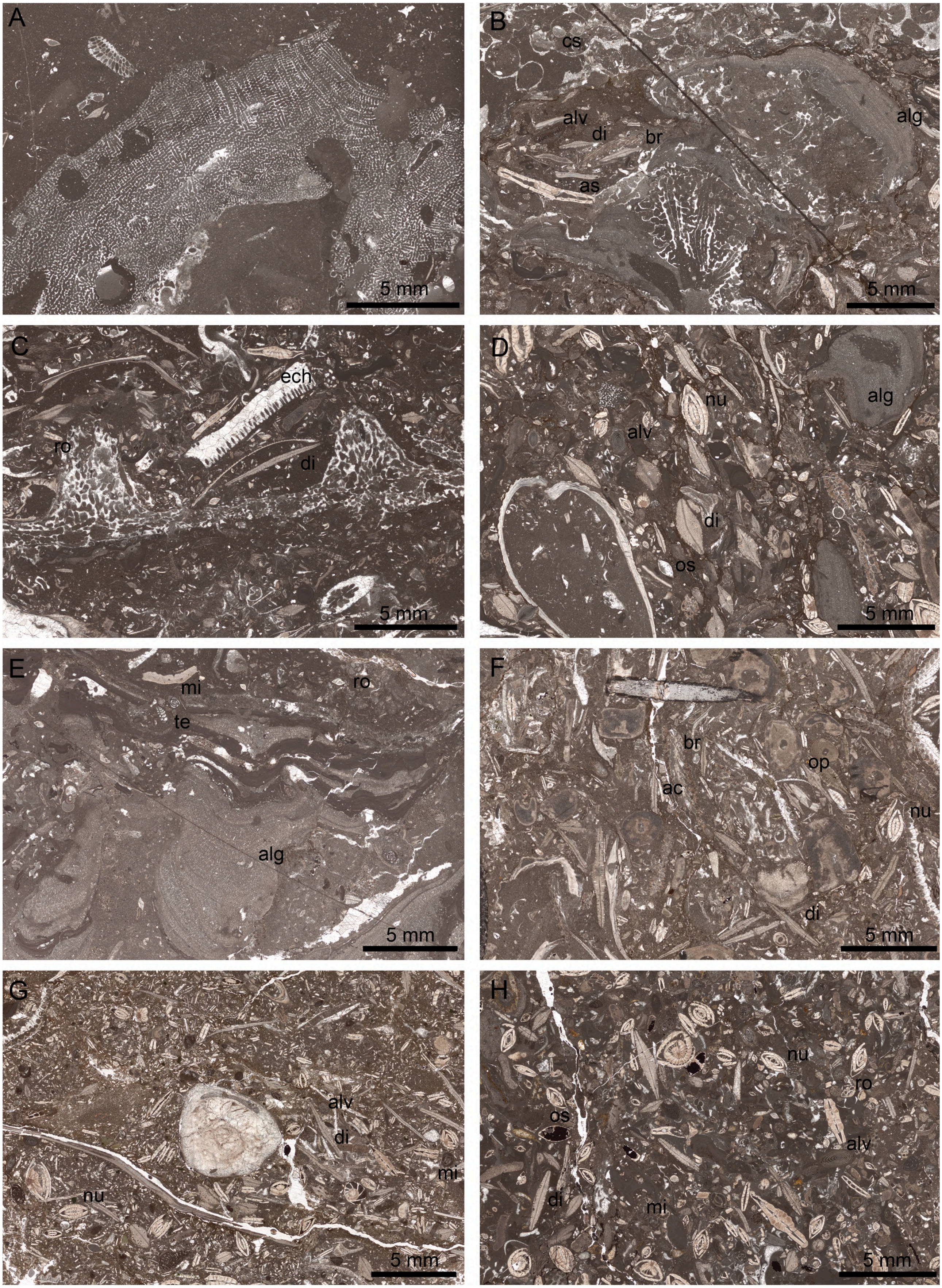

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Fig. 5. Thin section images showing the microfacies representative of the reef mounds (A), inter-reef (B, C, D), inner fore-reef (E, F) and outer fore-reef facies (G, H). A (sample SW5C): Scleractinian coral framestones with wackestone matrix; B (sample SW6): Poorly-sorted packstone with foraminifera and red algae (coralinacean) encrusting scleractinian coral; C (sample IR): Poorly sorted packstone with fragments of foraminifera, molluscs and echinoderms; D (sample SW3): Poorly sorted packstone with foraminifera, fragments of red algae and molluscs; E (sample ALG): Red coralinacean algae with foraminifera; F (sample T): Skeletal packstone with foraminifera; G (sample TD): Skeletal packstone with foraminifera and mollusc remains; H (sample D-1): Skeletal packstone dominated by foraminifera. Legend: ac: acervulinids; alg: red algae; alv: *Alveolina*; as: *Assilina*; br: bryozoans; cs: calcispheres; di: discocyclinids; ech: echinoderms; mi: miliolids; nu: *Nummulites*; op: *Operculina*; os: ostracods; ro: rotalids. Location of samples in Fig. 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

6. Palaeoenvironmental interpretations

A palaeoenvironmental reconstruction is provided for the shallow marine carbonate platform that developed during the early Eocene (middle Ypresian) around the Ramals area, in the northern margin of the Tremp-Graus basin (Fig. 8). Two stages of platform evolution were differentiated. A first stage with coral reef mound development involved a great abundance and diversity of the invertebrate marine fauna (Fig. 8 A). The paleoenvironment in which the reef mounds and inter-reef facies developed (reefal facies belt, see 1 in Fig. 8 A) grades offshore to the fore-reef setting (i.e., the inner- and outer fore-reef facies; see 2 and 3 respectively, Fig. 8 A). Abundance gradually decreases from the reefal facies belt to the outer fore-reef setting.

The first stage favourable for reef development coincides with a period of relative tectonic stability in which there was a low, fine-grained, terrigenous clastic input. These conditions had to be maintained long enough to allow the growth of reef mounds several meters in diameter. At the onset of the second stage, sedimentation rate and depositional depth increased suddenly (Fig. 8.B), probably due to an increase in tectonic activity. A deepening platform combined with an increase of terrigenous input due to the progradation of a deltaic system that moved westward in the Tremp-Graus basin (Serra-Kiel et al., 1994), to trigger the rapid disappearance of the reef and the collapse of the reef-induced ecosystem.

During the reef stage, the presence of assilinids, *Discocyclina* and planktonic foraminifera, combined with the absence of the typical inner platform organisms (such as green algae), suggest that the reefal facies belt developed in the euphotic to mesophotic zone, below the normal-wave base zone but above storm-wave base level (Scheibner et al., 2007; Morsilli et al., 2012; Pomar et al., 2017). This is further supported by the presence of *Solenomeris* in the reef framework, which is a relatively deep-water foraminifer (Plaziat and Perrin, 1992). In addition, the abundance of encrusting red algae within the reef framework is an indicator of deeper waters than reefs predominantly composed by corals (e.g., Baceta et al., 2005).

The diversity and abundance of benthic groups coeval to the reef development indicates that the seabed was rich in nutrients, thus allowing the presence of organisms feeding at different levels of the trophic scale: primary producers (such as red algae), suspension feeders (brachiopods, corals, crinoids, etc.), detritivores (some irregular echinoids), primary consumers (regular echinoids), scavengers and active predators (mainly fish, crocodiles and decapods).

Coral colonies are rarely preserved in growth position within the reef framework. Waves and storm-induced currents broke the coral colonies, which accumulated as rubble in the inter-reefs areas, but also over the reef substrate (Massel and Done, 1993; Madin and Connolly, 2006). These high-energy events limited the presence of mechanically unstable corals, and allowed a great diversity of other corals to continue to grow (Connell, 1978). These mechanically unstable coral species, susceptible to waves, offered more shelter and food for other organisms (Madin et al., 2012).

The relative abundance of glauconite in the inter-reef facies, along with the mode of preservation of the skeletal grains suggests that sedimentation rates were low. Further support for reduced sedimentation rates is provided by the presence of encrusting foraminifera such as *Acervulina* (see Scheibner et al., 2007) and epibionts on post-mortem echinoid skeletons (Fig. 6G). The bioclastic material produced in the reef was transported by storms to the fore-reef area where most of the studied fossils were found, commonly disarticulated and often fragmented. The low abundance of articulated material is explained by long periods of exposure on the seafloor to storm-induced waves and currents, which resulted in the fragmentation and disarticulation of decapods and other marine invertebrate groups (i.e., Mutel et al., 2008; Krause Jr et al., 2011; Klompmaker et al., 2015, 2017). Low sedimentation rates also explain the colonization by epibenthic fauna of echinoid skeletons following the disarticulation of their spines.

The degree of degradation that a specimen presents can provide clues to the mechanism of transport, scavenging and other factors (Mutel et al., 2008). The state of preservation of the crustacean remains found in the studied area can be explained, at least partially, from the taphonomic studies carried out by some authors (Jakobsen and Feldmann, 2004; Mutel et al., 2008; Krause Jr et al., 2011; Klompmaker et al., 2017). Most decapod crustacean remains are limited to the cephalothorax or isolated chelae, with only few examples preserving partial articulated specimens (Artal and Vía, 1988; Artal and Van Bakel, 2018a, 2018b; Ferratges et al., 2019). The collected remains, both of decapod crustaceans and echinoderms, suggest a relatively complex taphonomic history, with re-sedimentation events and long periods of exposure in the water-sediment interface that lengthened the biostratinomic phase (e.g., Nebelsick, 2004; Smith and Rader, 2009; for echinoderms; Allison, 1986; Mutel et al., 2008; Parsons-Hubbard et al., 2008; Krause Jr et al., 2011; for decapods). Occasional high-energy events, which were not enough to completely destroy relatively delicate specimens, transported material to the inter- and fore-reef areas where it was finally buried.

7. Abundance and distribution of decapod crustaceans

The decapod assemblage collected in Ramals corresponds largely to taxa associated with reef environments. The most abundant genus in the reefal complex is *Ctenocheles* (55.10%), followed by representatives of the superfamily Xanthoidea (5.27%), paguroids (5.49%), *Ilerdapatiscus* (5.05%) and carpilioids (3.74%). Minor components include some species of dromioids (1.98%), portunoids (1.43%), parthenopoids (genus *Aragolambrus*) (0.66%), calappoids (0.55%), raninoids (0.55%), pilumnoids (0.44%), and remains of homoloids (0.22%).Two independent taxa were represented by a single specimen each (0.22%) and 129 isolated remains could not be assigned with confidence to any group (14.16% of the total sample) (see Table 1).

Other localities in the Eocene of Europe have broadly similar carcinologic associations in terms of diversity and abundance (see e.g., Beschin et al., 2007, 2015, 2018; Tessier et al., 2011). However, the exceptional state of preservation of the Ramals outcrop and its optimal exposure in three dimensions, allowed a detailed sampling of different lithofacies and different sectors of the reefal environment. This allowed the quantification of the appearance of each taxon and study of its lateral and vertical variation. The number and diversity of decapod crustaceans in the studied area is not random. Faunal changes were observed from the three sampled intervals (reefal facies belt, inner- and outer fore-reef facies; Fig. 9).

The reefal facies belt, including the reef mounds and adjacent inter-reef areas (Fig. 8 A-1) has an intermediate diversity and the lowest abundance of decapod crustaceans (Table 2 and Fig. 9). In this lithofacies, the dominant group is the carpilioids (37.9%) followed by paguroids (17.24%), *Ctenocheles* (13.79%), aethroids (10.34%),

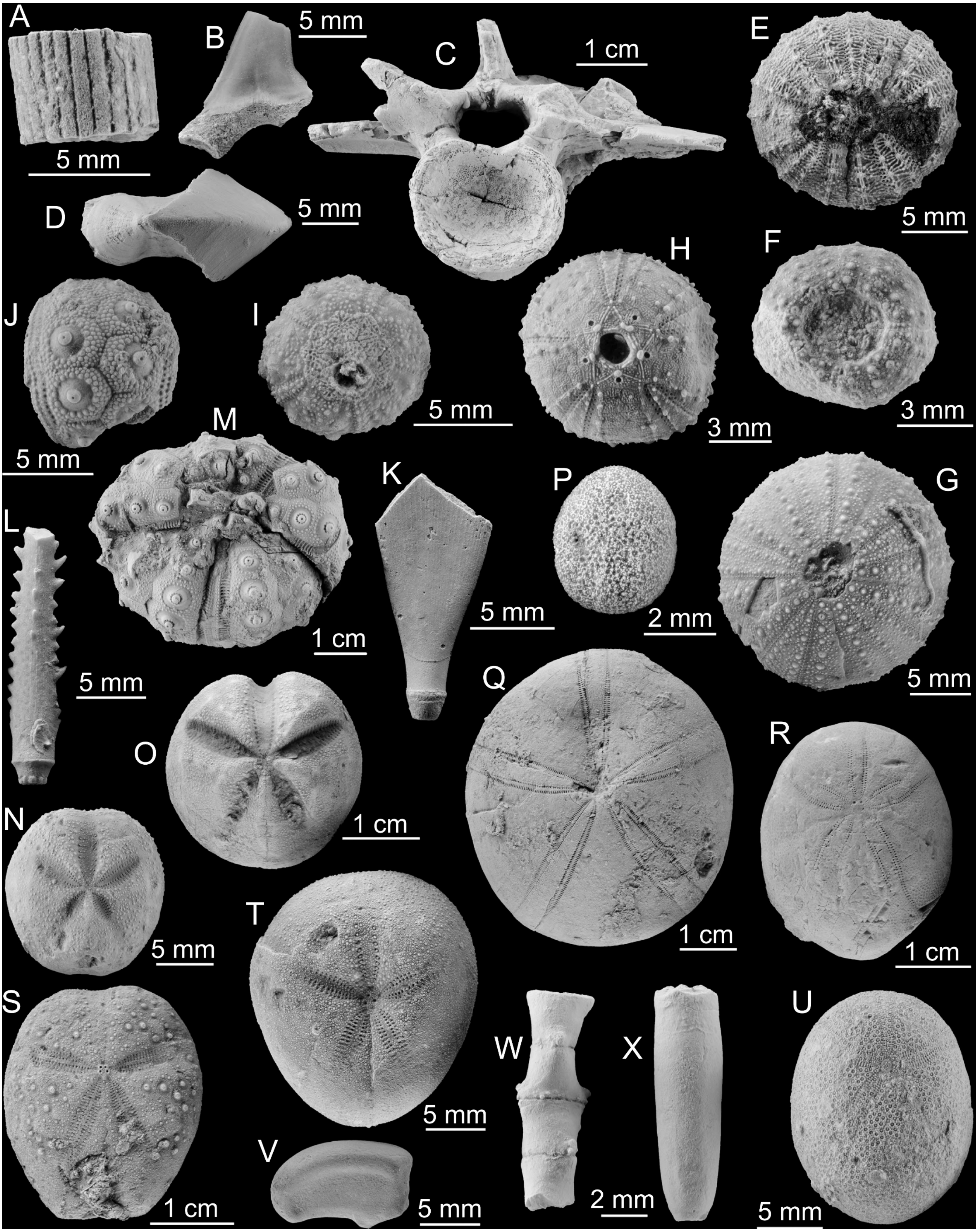

Fig. 6. Invertebrate and vertebrate fauna from the Ramals outcrop. A: Rostral fragment of *Cylindracanthus* sp. MPZ 2021/3; B: indeterminate shark tooth, MPZ 2021/4; C: Crocodylia indet. (Eusuchia indet.) MPZ 2021/2; D: *Rhyncholites* sp. (Nautiloidea) MPZ 2021/5; E: *Arachniopleurus reticulatus* Duncan & Sladen, 1882 MPZ 2021/6; F:?*Ambipleurus* sp. MPZ 2021/7; G:?*Thylechinus frossardi* (Cotteau, 1889) MPZ 2021/8; H: *Baueria angelae* Carrasco, 2006, MPZ 2021/9; I: *Salenia* sp., MPZ 2021/10; J-K: *Cidaris gourdoni* Cotteau, 1889, MPZ 2021/11, MPZ 2021/12; L-M: *Fellius pouechi* (Cotteau, 1863), MPZ 2021/13, MPZ 2021/14; N: *Ditremaster nux* (Desor, 1853), MPZ 2021/15; O: *Linthia aragonensis* (Cotteau, 1887), MPZ 2021/16; P:?*Echinocyamus* sp., MPZ 2021/17; Q: *Amblypygus dilatatus* Agassiz,1840, MPZ 2021/18; R: *Gitolampas cotteaui* (Hébert, 1882), MPZ 2021/19; S: *Maretia aragonensis* (Cotteau, 1887), MPZ 2021/20; T:?*Trachyaster* sp., MPZ 2021/21; U: *Echinolampas leymeriei* Cotteau, 1863, MPZ 2021/22; V: ossicle of?*Calliderma*, MPZ 2021/23; W-X: *Bourgueticrinus* sp., MPZ 2021/24, MPZ 2021/25.

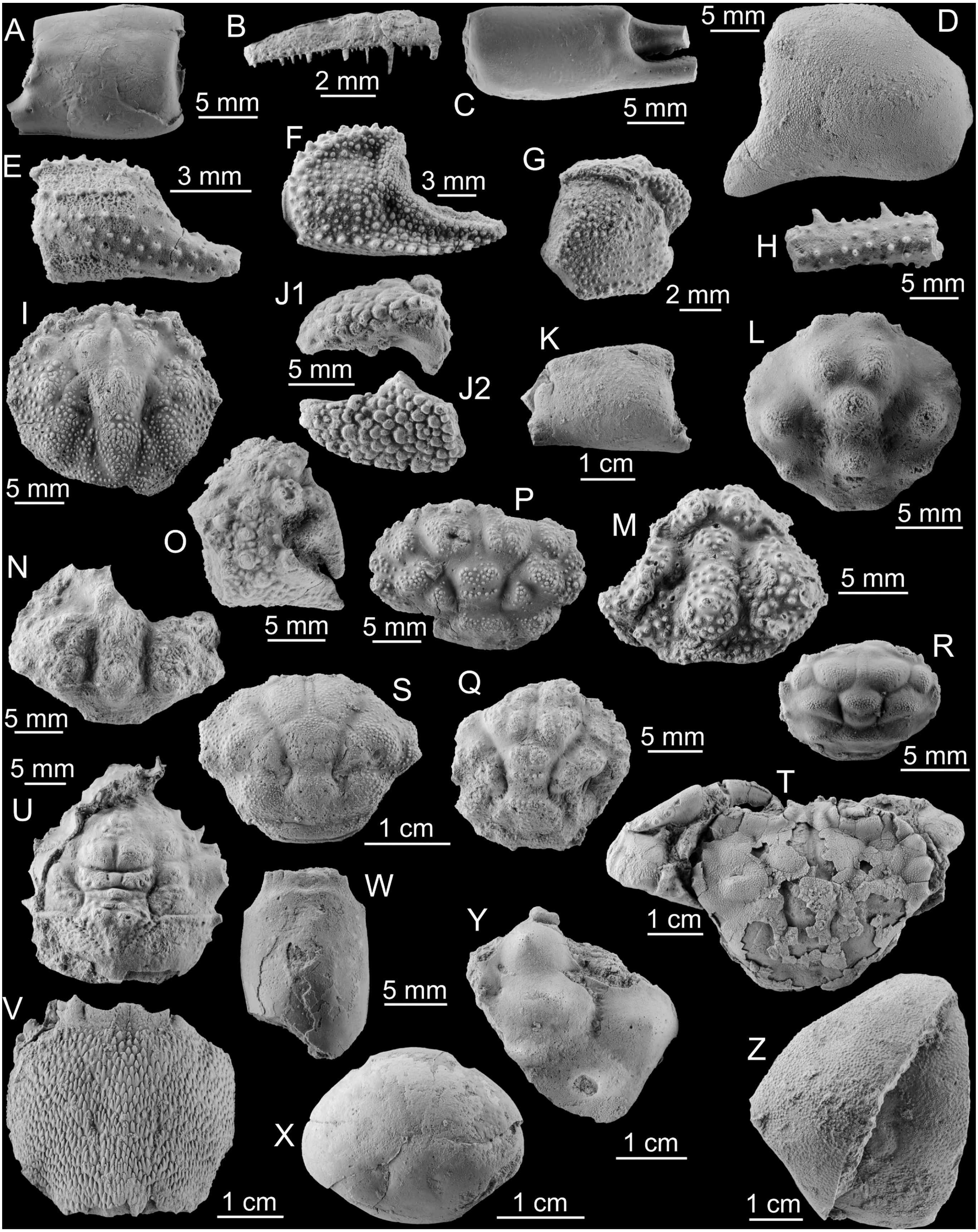

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Fig. 7. Representatives of decapod crustaceans found in the Ramals outcrop. A: Callianassidae indet., MPZ 2021/26; B-C: *Ctenocheles* cf. *cultellus* (Rathbun, 1935), MPZ 2021/27, MPZ 2021/28; D: *Eocalcinus* sp. MPZ 2021/29; E: *Pagurus* sp., MPZ 2021/30; F:?*Rhodochirus* sp., MPZ 2021/31; G: Paguridae indet., MPZ 2021/32; H: indeterminate merus, MPZ 2021/33; I: Calappidae indet. 1, MPZ 2021/34; 1 J1-J2: *Petrolistes* sp., MPZ 2021/36, MPZ 2021/37; K:?Majidae, MPZ 2021/38; L: *Ilerdapatiscus guardiae* Artal and Van Bakel, 2018a, 2018b, MPZ 2021/39; M: *Aragolambrus collinsi* Ferratges et al., 2019, MPZ 2019/211; N-O: Calappidae indet. 2, MPZ 2021/35, MPZ 2021/40; P: Xanthidae indet. 1, MPZ 2021/41; Q: Xanthidae indet. 2, MPZ 2021/42; R: *Glyphithyreus almerai* Artal and Van Bakel, 2018a, 2018b, MPZ 2021/43; S: Xanthilites sp., MPZ 2021/44; T: *Litoricola macrodactylus pyrenaicus* (Artal and Vía, 1988), MPZ 2021/45; U: *Dromilites* cf. *alpina* Glaessner, 1929, MPZ 2021/46; V: *Ranina* sp., MPZ 2021/47; W: *Quasilaeviranina* sp., MPZ 2021/48; X: *Oscacarpilius rotundus* Artal and Van Bakel, 2018a, 2018b, MPZ 2021/49; Y: Dromidae indet., MPZ 2021/50; Z: *Eocarpilius ortegai* Artal and Van Bakel, 2018a, 2018b, MPZ 2021/51.

Table 1
Number of specimens and percentage (%) of different decapod crustacean taxa in the different facies of the Ramals outcrop. The reefal facies belt includes both the reef core facies and the inter-reef deposits.

Taxon		reefal facies belt		Inner fore-reef		outer fore-reef		Total	% of total
		Specimens	%	Specimens	%	Specimens	%		
Axiidea	Callianassidae		0	2	0.27		0	2	0.22
	Ctenocheles sp.	5	6.94	456	60.88	41	45.56	502	55.10
Paguroidea	Paguridae indet. 1		0	1	0.13		0	1	0.11
	Paguridae indet. 2	1	1.39	5	0.67		0	6	0.66
	Paguridae indet. 3		0	1	0.13		0	1	0.11
	Paguridae indet. 4		0	2	0.27		0	2	0.22
	Paguridae indet. 5		0	2	0.27		0	2	0.22
	Paguridae indet. 6		0	2	0.27		0	2	0.22
	? *Paguritta* sp.		0	3	0.40		0	3	0.33
	Eocalcinus sp.	4	5.56	18	2.40	4	4.44	26	2.85
	Eocalcinus sp. 2		0	1	0.13		0	1	0.11
	Petrochirus sp. 1		0	3	0.40		0	3	0.33
	Petrochirus sp. 2		0	3	0.40		0	3	0.33
Dromioidea	Dromidae indet. 1		0	9	1.20	1	1.11	10	1.10
	Dromidae indet. 2		0	1	0.13		0	1	0.11
	Dromidae indet. 3		0	1	0.13		0	1	0.11
	Dromidae indet. 4	1	1.39	3	0.40		0	4	0.44
	Kromtitis sp.		0	2	0.27		0	2	0.22
Homoloidea	Homolidae indet.		0	2	0.27		0	2	0.22
Raninoidea	*Antonioranina ripacurtae* (Artal and Castillo, 2005)		0	1	0.13		0	1	0.11
	Quasilaeviranina sp.		0	1	0.13		0	1	0.11
	Ranina sp.		0	3	0.40		0	3	0.33
Aethroidea	*Ilerdapatiscus guardiae*Artal and Van Bakel, 2018a, 2018b	3	4.17	37	4.94	6	6.67	46	5.05
Calappoidea	Calappidae indet.		0	3	0.40		0	3	0.33
	Matutidae?		0	1	0.13	1	1.11	2	0.22
Carpilioidea	*Eocarpilius ortegai*Artal and Van Bakel, 2018a, 2018b	3	4.17	8	1.07	3	3.33	14	1.54
	Carpilius sp.	6	8.33	6	0.80		0	12	1.32
	*Oscacarpilius rotundus*Artal and Van Bakel, 2018a, 2018b	1	1.39	5	0.67	1	1.11	7	0.77
	Carpiliidae indet.	1	1.39		0		0	1	0.11
Goneplacoidea	Goneplacidae indet.		0	1	0.13		0	1	0.11
Hexapodoidea	Hexapodidae indet.		0	1	0.13		0	1	0.11
Parthenopoidea	*Aragolambrus collinsi* Ferratges. Zamora & Aurell, 2019		0	5	0.67	1	1.11	6	0.66
Pilumnoidea	*Galenopsis* sp.	3	4.17	1	0.13		0	4	0.44
Portunoidea	*Litoricola macrodactylus* (Artal and Vía, 1988)			1	0.13	10	11.11	11	1.21
	Ceronectes sp.		0	1	0.13		0	1	0.11
	Liocarcinus sp.		0	1	0.13		0	1	0.11
Xanthoidea	*Glyphithyreus almerai*Artal and Van Bakel, 2018a, 2018b		0	9	1.20		0	9	0.99
	Xanthidae indet. 1		0	1	0.13		0	1	0.11
	Xanthidae indet. 2		0	2	0.27		0	2	0.22
	Xanthilites sp.	2	2.78	31	4.14	3	3.33	36	3.95
	Indet fragments.	28	38.89	40	5.34	16	17.78	84	9.22
	Morphotype 1	3	4.17	15	2.00	3	3.33	21	2.31
	Morphotype 2		0	7	0.93		0	7	0.77
	Morphotype 3	3	4.17	6	0.80		0	9	0.99
	Morphotype 4		0	5	0.67		0	5	0.55
	Morphotype 5		0	5	0.67		0	5	0.55
	Morphotype 6		0	8	1.07		0	8	0.88
	Morphotype 7		0	8	1.07		0	8	0.88
	Morphotype 8	1	1.39		0		0	1	0.11
	Morphotype 9		0	1	0.13		0	1	0.11
	Morphotype 10		0	7	0.93		0	7	0.77
	Morphotype 11		0	2	0.27		0	2	0.22
	Morphotype 12 (carpiliids)	7	9.72	9	1.20		0	16	1.76
	TOTAL	72	100	749	100	90	100	911	100

pilumnoids (10.34%), xanthoids (6.9%) and dromioids are very rare (3.45%) (Fig. 9). Several unidentified chelae have also been found, representing 58.32% of the total assemblage. These are difficult to identify at the species level because they correspond mainly to disarticulated and broken fragments.

The inner fore-reef facies (Fig. 8 A-2) hosts the greatest diversity and abundance of decapod crustaceans (Fig. 9) and is mainly composed of small crabs. The most abundant taxon is *Ctenocheles*, only represented by

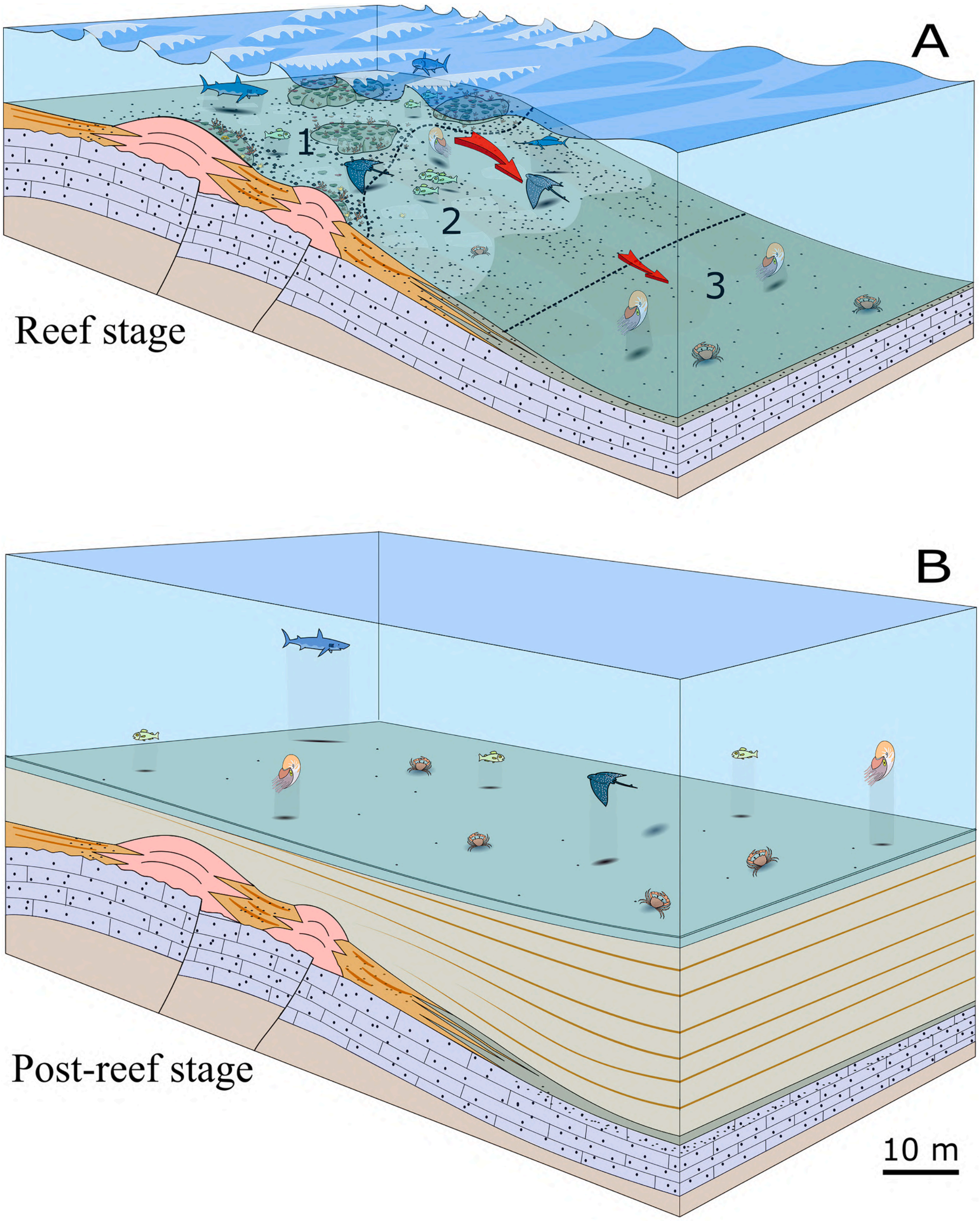

Fig. 8. Simplified diagram showing the facies belt distribution. In the reef stage (A), the reefal and inter-reef facies (1), inner fore-reef facies (2), and outer fore-reef facies (3) are differentiated. The development of the reef mound is occasionally controlled by the steep relief generated by the faults affecting the lower unit (*Alveolina limestone*). The red arrows show the dominant offshore transport of skeletal remains by episodic storm-induced currents. In the second stage (B), the reefs were covered by the post-reef *Riguala marls* and there was a significant decrease in the diversity of the benthic fauna. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

fragments of chelipeds, representing 65.51% of the sample, followed by paguroids (8.37%), aethrioids (*Ilerdapatiscus*) (7.55%), some species of xanthoids (6.94%), carpilioids (3.88%), dromioids (3.27%), parthenopoids (*Aragolambrus*) (1.02%), raninoids (1.02%), calappoids (0.82%), portunoids (0.61%), homoloids (0.41%), pilumnoids (0.2%), hexapoids (0.2%) and goneplacoids (0.2%). There are also abundant remains of several indeterminate taxa, which represent 15.09% of the total assemblage (Table 1).

The outer-fore reef facies (Fig. 8.A-3) shows the lowest diversity and intermediate abundance (Table 1). In this lithofacies, the most abundant taxon is represented by fragmented claws of *Ctenocheles* (47.54%) followed by *Litoricola macrodactylus pyrenaicus* (16.39%). Minor components belonging to seven different families represent the remaining 36.07% (Table 2). Indeterminate taxa represent 21.11% of the total assemblage.

The faunal distribution of decapods in Ramals shows important differences in terms of both relative abundance and diversity in each of the differentiated facies belts. In order to explore if there was a relationship among the distribution of the species in each facies, a Principal Component Analysis (PCA) was performed. To simplify the calculations, the different recognized taxa were grouped into superfamilies (Table 2). Taking these groups as variables, we were able to infer which groups had

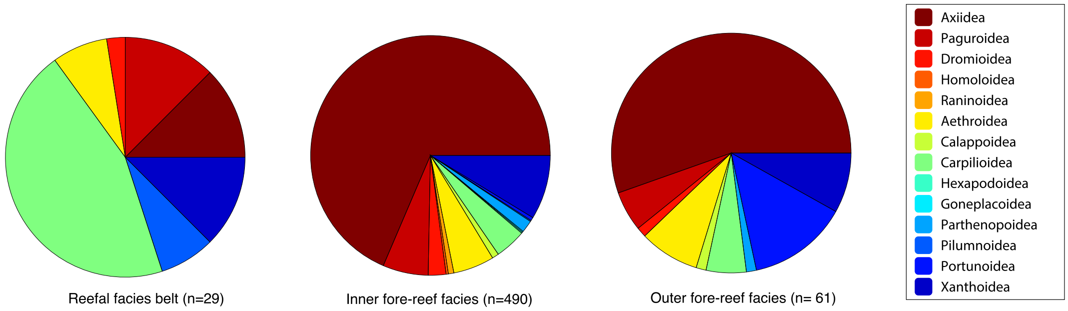

Fig. 9. Pie charts showing the relative abundance and diversity of the different decapod crustacean groups in the different facies. Indeterminate remains were excluded from the analysis.

Table 2
Corrected percentages indicating the relative abundance and distribution of main groups of decapod crustaceans the different facies of the Ramals outcrop. The indeterminate taxa are not included.

	Reefal facies belt	%	Inner fore-reef facies	%	Outer fore-reef facies	%	total	%
Axiidea	4	13.79	321	65.51	29	47.54	354	61.03
Paguroidea	5	17.24	41	8.37	4	6.56	50	8.62
Dromioidea	1	3.45	16	3.27	1	1.64	18	3.10
Homoloidea	0	0	2	0.41	0	0	2	0.34
Raninoidea	0	0	5	1.02	0	0	5	0.86
Aethroidea	3	10.34	37	7.55	6	9.84	46	7.93
Calappoidea	0	0	4	0.82	1	1.64	5	0.86
Carpilioidea	11	37.93	19	3.88	6	9.84	36	6.21
Hexapodoidea	0	0	1	0.20	0	0	1	0.17
Goneplacoidea	0	0	1	0.20	0	0	1	0.17
Parthenopoidea	0	0	5	1.02	1	1.64	6	1.03
Pilumnoidea	3	10.34	1	0.20	0	0	4	0.69
Portunoidea	0	0	3	0.61	10	16.39	13	2.24
Xanthoidea	2	6.90	34	6.94	3	4.92	39	6.72
Total	29	100	490	100	61	100	580	100

preferences for a specific environment. The three main principal components (PC1, PC2 and PC3) are visualised in Fig. 10.

By reducing the dimensionality of variables using PCA, it is shown that certain taxa have strong affinity for particular environments. For example carpilioids occupy a position in the top left of the plot of PC1 against PC2, indicating a much more positive PC2 value compared to other groups. This is mainly explained by the diversity of this group in the reefal facies belt environment (Fig. 10 A). It can also be observed that the portunoids (specifically the species *Litoricola macrodactylus pyrenaicus*) occupy a position in the top left of the plot of PC1 against PC3, indicating a much more positive PC3 compared to the other groups. This is mainly explained by the diversity of this group in outer-fore reef facies (Fig. 10 B). Also notable is the distribution of Axiidea which is markedly much more positive on the PC1 axis than any other group. This is mainly explained by the diversity of this group in inner fore-reef facies (Fig. 10 A and B). The distribution (and high concentration) of Axiidea is not surprising, because members of this infraorder are mostly represented by *Ctenocheles*, considered a bioturbator taxon typical of soft or sandy bottoms of shallow waters (i.e. Hyžný and Klompmaker, 2015 and references therein).

On the other hand, the remaining groups are more or less clustered in PCA space (Fig. 10). Thus, groups such as Pilumnoidea, Xanthoidea, Paguroidea, and Aethroidea show a trend resulting from their reef facies belt facies (positive in PC 2) (Fig. 10 A). Similarly, Dromioidea, Parthenopoidea (*Aragolambrus*), Calappoidea and Raninoidea are more representative of the inner fore-reef facies (positive in PC1) (Fig. 10 A

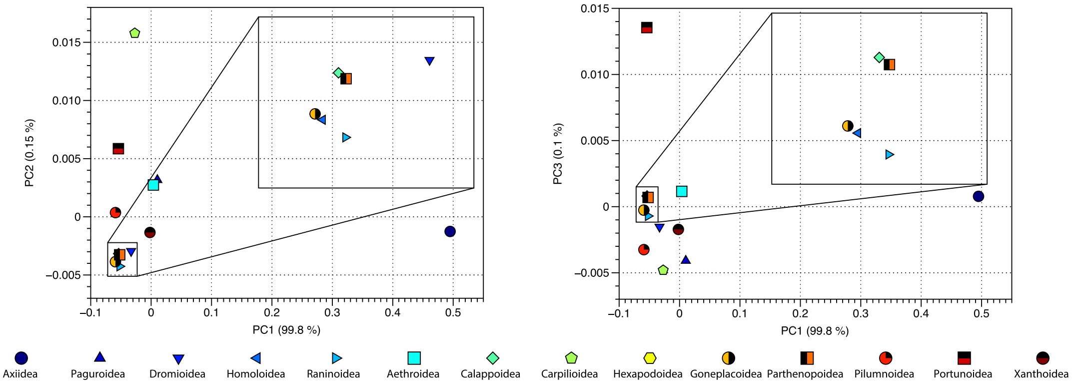

Fig. 10. Distribution of decapod crustacean groups in the different facies. The affinity of each group to the different environments shows how closely they are related to these facies. Plots obtained from Principal Component Analysis (PCA) when processing data with Past4.03. PC1: inner fore-reef; PC2: reefal facies belt; PC3: outer fore-reef.

and B). Some groups may show a greater dispersion to the outer fore-reef facies (for example Aethroidea, Xanthoidea and Axiidea). This may be because they are the more abundant taxa and therefore easier to collect during the sampling, but we cannot discount that these groups were more widespread in different facies. In contrast, the only taxon showing complete and articulated specimens in the outer fore-reef facies is L. *macrodactylus* suggesting rapid burial by episodically high sedimentary events. This taxon probably lived in this area.

To demonstrate that some areas contained more specimens of certain groups than others, the number of specimens in each group was normalized, and their densities calculated. The number of specimens was divided by the total area of the different sampling zones. Following this normalization, areas of higher abundance of some groups than others can be determined. The values obtained for the density of decapod crustaceans in each sector of the outcrop vary by one or two orders of magnitude (Table 3), which supports the idea that some groups showed preferences for facies type. For example the density of Axiidea and Dromioidea varies by two orders of magnitude, suggesting that these groups are strongly linked to inner fore-reef facies.

Table 3

Density of crustacean remains obtained after the division of the number of specimens by the surface area of each sector of the outcrop (1: reefal facies; 2: Inner fore-reef facies; and 3: Outer fore-reef facies). Note that the density between representatives of the same group in different areas can vary by several orders of magnitude.

	Zone	Number of specimens	Area (m^2)	Density (specimen/ m^2)
Axiidea	1	5	18,500	$2{,}70\cdot10^{-4}$
	2	458	12,800	$3{,}58\cdot10^{-2}$
	3	41	36,400	$1{,}13\cdot10^{-3}$
Paguroidea	1	5	18,500	$2{,}70\cdot10^{-4}$
	2	41	12,800	$3{,}20\cdot10^{-3}$
	3	4	36,400	$1{,}10\cdot10^{-4}$
Dromioidea	1	1	18,500	$5{,}41\cdot10^{-5}$
	2	16	12,800	$1{,}25\cdot10^{-3}$
	3	1	36,400	$2{,}75\cdot10^{-5}$
Homoloidea	1	0	18,500	0
	2	2	12,800	$1{,}56\cdot10^{-4}$
	3	0	36,400	0
Raninoidea	1	0	18,500	0
	2	5	12,800	$3{,}91\cdot10^{-4}$
	3	0	36,400	0
Aethroidea	1	3	18,500	$1{,}62\cdot10^{-4}$
	2	37	12,800	$2{,}89\cdot10^{-3}$
	3	6	36,400	$1{,}65\cdot10^{-4}$
Calappoidea	1	0	18,500	0
	2	4	12,800	$3{,}13\cdot10^{-4}$
	3	1	36,400	$2{,}75\cdot10^{-5}$
Carpilioidea	1	11	18,500	$5{,}95\cdot10^{-4}$
	2	19	12,800	$1{,}48\cdot10^{-3}$
	3	4	36,400	$1{,}10\cdot10^{-4}$
Hexapodoidea	1	0	18,500	0
	2	1	12,800	$7{,}81\cdot10^{-5}$
	3	0	36,400	0
Goneplacoidea	1	0	18,500	0
	2	1	12,800	$7{,}81\cdot10^{-5}$
	3	0	36,400	0
Parthenopoidea	1	0	18,500	0
	2	5	12,800	$3{,}91\cdot10^{-4}$
	3	1	36,400	$2{,}75\cdot10^{-5}$
Pilumnoidea	1	3	18,500	$1{,}62\cdot10^{-4}$
	2	1	12,800	$7{,}81\cdot10^{-5}$
	3	0	36,400	0
Portunoidea	1	0	18,500	0
	2	3	12,800	$2{,}34\cdot10^{-4}$
	3	10	36,400	$2{,}75\cdot10^{-4}$
Xanthoidea	1	2	18,500	$1{,}08\cdot10^{-4}$
	2	43	12,800	$3{,}36\cdot10^{-3}$
	3	3	36,400	$8{,}24\cdot10^{-5}$
Indeterminate	1	42	18,500	$2{,}27\cdot10^{-3}$
	2	113	12,800	$8{,}83\cdot10^{-3}$
	3	19	36,400	$5{,}22\cdot10^{-4}$

Several analyses (see below) were performed in order to investigate links between diversity with type of facies. Our null hypothesis (H_0) was that species composition does not differ between facies (Table 4). The alternative hypothesis (H_1) was that species composition does differ between facies. The *p*-values of chi-squared tests were < 0.05 in all cases (reefal facies vs inner fore-reef facies: 4.84E-13; reefal facies vs outer fore-reef facies: 3.05E-4; and inner fore-reef facies vs outer fore-reef facies: 1,37E-06), which suggests that there is a significant link between species and the different facies (acceptance of H_1). Both the PCA and the pie-charts clearly reflect that it is mainly carpilioid taxa that differentiate the reefal facies. The PCA and the pie-charts indicate that the raninoids and a greater relative abundance of Axiidae are characteristic of the inner fore reef. Differences and relative abundances of portunoids characterize the outer fore reef.

8. Discussion: taphonomic biases affecting decapod crustacean diversity

The data compiled from the lower Eocene outcrop of Ramals confirms that the coral reef mounds which grew in the relatively shallow warm waters (mesophotic zone), combined with episodic storm-wave reworking, provided a favourable conditions for the development of a diverse and abundant decapod assemblage. This diversity suddenly dropped after the reef mounds were drowned and covered by sediments -the *Riguala marls* (Fig. 8B)- only a single species of decapod (*Litoricola macrodactylus pyrenaicus*) remained. The loss of capacity of the environment to sustain a rich and complex ecosystem is explained by the disappearance of ecological niches offered by the reef due to sediment clogging.

The Ramals outcrop offers an excellent opportunity to discuss the interplay of factors preserving fossil decapod communities affected by different taphonomic processes in different facies. Depending on the depositional processes and taphonomic bias, decapod remains can be preserved close to their living site (e.g., Allison, 1986; Krause Jr et al., 2011). Disarticulated carcasses or exuviae of crustaceans can be exposed in the sediment-water interface for long periods of time without degrading (Allison, 1986, 1988; Plotnick, 1986; Briggs and Kear, 1994; Mutel et al., 2008; Parsons-Hubbard et al., 2008; Krause Jr et al., 2011; Klompmaker et al., 2017). In the case of "burrowing shrimp" (Callianassidae and Ctenochelidae), only the hardened parts are preserved (i.e., the chelae), due to the delicate nature of the rest of the cuticle (Hyžný and Klompmaker, 2015; Klompmaker et al., 2017). In the case of the Ramals reefal facies belt, the state of preservation and the sedimentological data suggest that most specimens were exposed for long periods of time before burial. This is also supported by observations in other invertebrate groups like echinoids, that appear colonized by serpulids and bryozoans, suggesting a prolonged residence time on the sediment-water interface (Nebelsick and Kroh, 2002; Nebelsick, 2004). Furthermore, some vertebrate bones were colonized by oysters and bryozoans.

Preferential preservation occurred mostly in inner fore-reef facies. This environment hosts the greatest abundance and diversity of decapods in Ramals, and this is probably correlated with the most favourable

Table 4

Diversity metrics and an evenness index for the three studied zones (highest values in bold). The indeterminate taxa are not included.

	Reefal facies	Inner fore-reef facies	Outer fore-reef facies
Specimens	29	**499**	59
Species	11	**39**	10
Superfamilies	7	**14**	9
Simpson's Index of Diversity	**0.877**	0.578	0.708
Shannon–Wiener Index	**2.225**	1.7	1.644
Chao1 Index	14	**52.13**	16
Pielou's evenness index	**0.841**	0.14	0.517

taphonomic conditions. This facies belt accumulated most of the bioclastic sediment transported by episodic storm-induced currents, and hosted autochthonous and parautochthonous taxa that lived within the reef and in the soft sediment of the attached fore-reef domain. This is the case of some decapods, whose modern relatives are adapted to soft substrates like raninoids (e.g. Goeke, 1985; Kasinathan et al., 2007) and Axiidae (Fig. 7 A-C) (e.g., Dworschak, 2000, 2005; Hyžný and Klompmaker, 2015). Other taxa were adapted to live among coral rubble, like the genus *Aragolambrus* (Ferratges et al., 2019) and calappoids (e.g. Schweitzer and Feldmann, 2000).

The low diversity and abundance of fauna in the reefs and inter-reef areas is probably related to taphonomic factors. This sedimentary domain represents areas of high energy and low preservation potential of crustacean decapods. Mainly carpilioids, some aethrids (*Ilerdapatiscus*), rare dromioids and fragments of chelipeds have been found, whereas most of the autochthonous fauna was probably transported to the inner fore-reef facies belt (Fig. 8-A).

Finally, the outer fore-reef facies recorded the lowest sedimentation rates, although episodically affected by distal storm events, and also hosted the lowest diversity of decapods, including *Litoricola macrodactylus pyrenaicus* (Artal and Vía, 1988); *Ctenocheles* sp.; xanthoids; rare dromioids and fragments of indeterminate chelipeds. All fossil remains from these facies, except those belonging to *Litoricola macrodactylus pyrenaicus*, are disarticulated and often broken, so it can be deduced that most of the fauna from this interval was probably transported from proximal facies. The specimens of L. *macroactylus* are an exception, and they are completely preserved, with carapaces articulated to chelipeds and locomotory legs. In addition, this species was the only one found in the post-reef sediments, suggesting that it did not have a close relationship with coral environments.

Species that are always found in all zones are *Ctenocheles* sp., *Ilerdapaticus guardiae* Artal and Van Bakel, 2018a, *Eocarpilius ortegai* Artal and Van Bakel, 2018b, *Carpilius* sp., and *Xanthilites* sp. (Fig. 7; Table 1). *Ctenocheles* sp. is the most common species in all zones, except for reefal facies where *Carpilius* sp. is represented by eleven specimens (Table 1).

Although the rarefaction analysis indicates that sampling has not

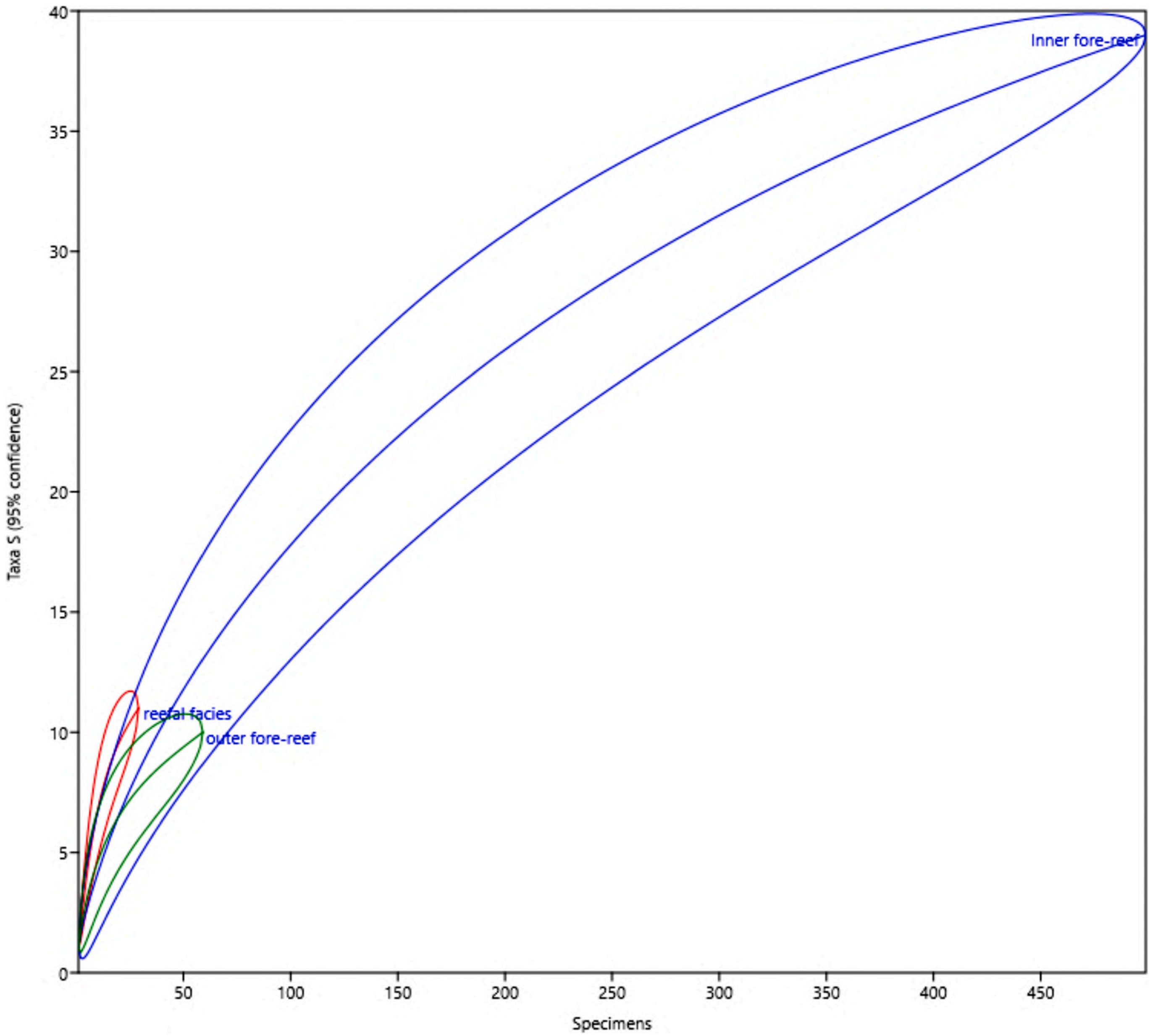

Fig. 11. Rarefaction curves for decapod crustaceans from the three zones with 95% confidence intervals based on specimens collected between 2018 and 2019. The slopes of the means (middle lines) suggest that inner fore-reef facies preserves the highest diversity.

stabilized (Fig. 11), the curves of the three zones have stopped growing exponentially, and indicate a different stabilization point in each zone. Based on our sampling and the Shannon index, the data obtained suggests that the greatest diversity is concentrated on the reefal facies (Fig. 12). On the other hand our sedimentological analysis suggests that most specimens from the core reef were transported to the inner fore-reef facies by storm events. Taken together, these lines of evidence could explain why some taxa are represented by a small number of individuals (see Fig. 9 and Fig. 11).

The Chao1 index (Fig. 13), which estimates abundances, is highest in the inner fore-reef. However, the fact that several taxa are represented by a low number of specimens suggests that these taxa have been transported from the core reef. Tables 1 and 2 shows that inner fore-reef facies contained the highest number of species. Thus, based on a variety of diversity measures our hypothesis is that inner fore-reef facies preserved the most abundant assemblage; although some species preserved in such zone were transported from the core of the reef. However, for the Simpson's Index of Diversity and Shannon–Wiener Index, the inner fore-reef facies came in third and second position respectively (Table 4). These indices are highest for the reefal facies.

The Shannon index measures specific biodiversity. Our study areas show a Shannon index of 2.225 for the reefal facies, 1.7 for the inner fore-reef, and 1.644 for the outer fore-reef (see Table 4 and Fig. 12), showing that the zone with the greatest diversity of taxa corresponds to the reefal facies. In order to compare whether these differences in the Shannon index are significant between the studied areas we performed a *t*-test. Comparisons of the reefal facies vs the inner fore-reef and the reefal facies vs outer fore-reef facies (see supplementary material), resulted in *P* values of 0.001 and 0.003 respectively. The *P* value in both cases falls below the significance threshold (0.05) and thus indicate significant differences between the facies. On the other hand, a comparison of the inner fore-reef vs outer fore-reef, resulted in a *P* value of 0.735, which indicates that the differences in the Shannon index obtained in the inner- and outer fore-reef are not significant. In terms of evenness, all sites have an evenness ranging from 0.14 to 0.841, which implies that more than one species are important contributors to the decapod diversity at each zone (Table 4).

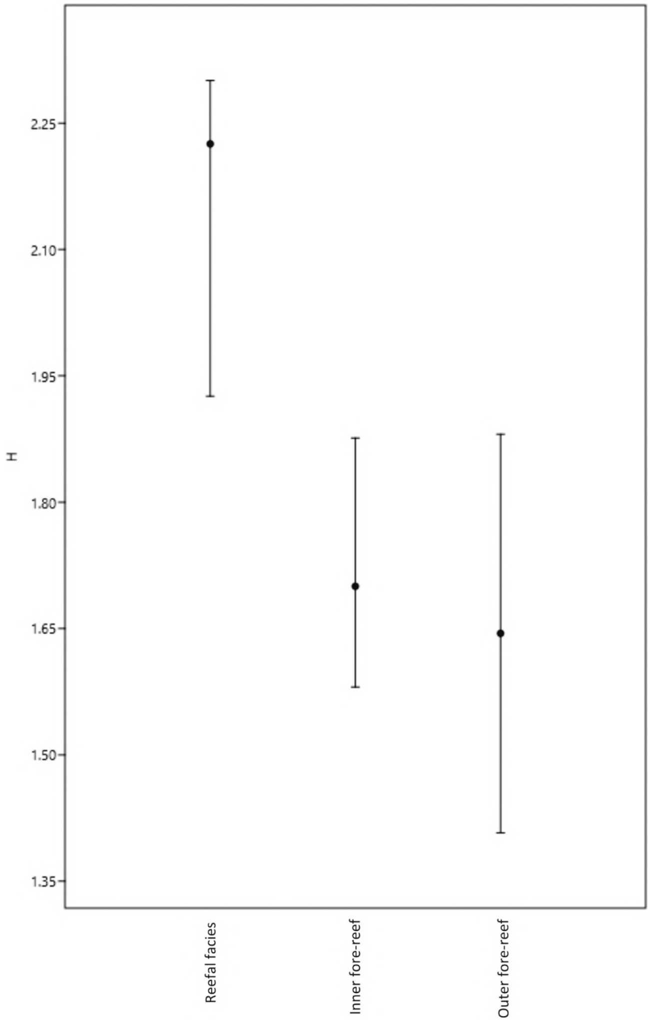

Fig. 12. Shannon index for decapods of the three zones.

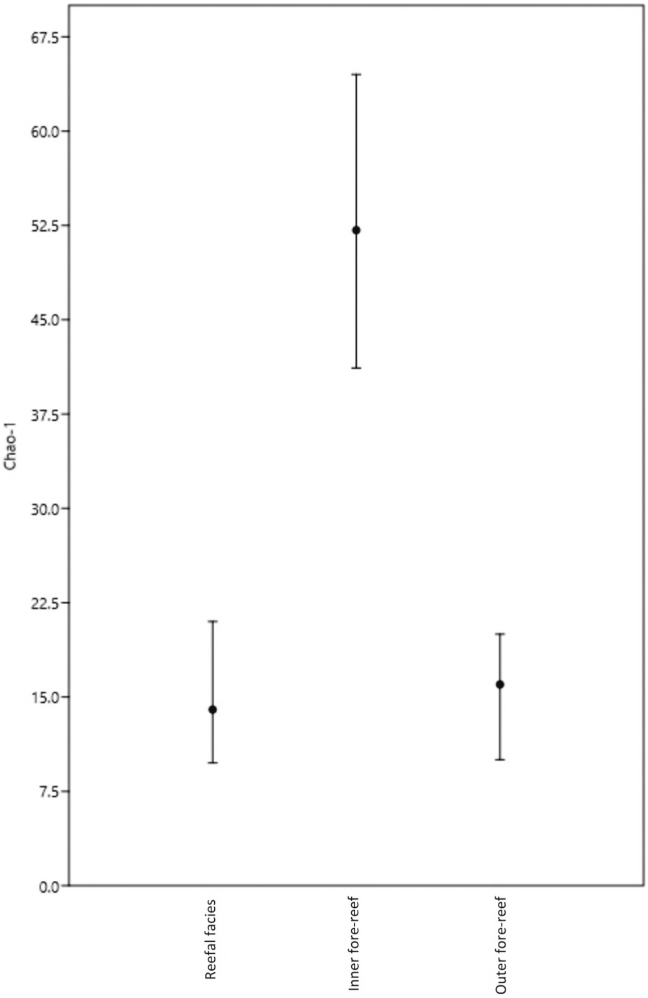

Fig. 13. Chao1 Index giving the estimated number of species for each site and the standard deviations.

9. Conclusions

The lower Eocene (Ypresian) outcrop of Ramals (Graus-Tremp basin, southern Pyrenees, Spain) exposes a reefal facies belt including closely spaced mounds up to five meters high, and associated inter- and fore-reef facies. The reef framework consists of coral framestones with bioclastic wackestone to packstone matrix, with colonial corals (*Stylocoenia, Astrocoenia, Astreopora, Agaricia, Actinacis, Cyathoseris, Colpophyllia* and *Caulastraea)*, solitary corals (*Placosmilopsis, Leptophyllia*), crustose red algae, encrusting foraminifers (*Solenomeris*) and bryozoans.

The reef mounds and associated facies developed within the euphotic to mesophotic zone (a few tens of meters deep), with some nutrient content to maintain the diversity of associated benthic organisms. Evidence of episodic activity of storm-induced waves and currents is provided by abundant coral rubble within the reef framework and the skeletal-rich beds accumulated on the inter- and fore-reef domains. These beds are dominated by molluscs, foraminifera, corals, bryozoans, decapod crustaceans, echinoderms and vertebrate fragments. The presence of epibionts in some skeletal remains (such as echinoderms and fragments of vertebrates) indicates long periods of time on the sea floor.

The studied reef mounds and associated facies allowed the establishment of a rich association of decapods consisting of 41 species. These are mostly preserved as claw fragments or isolated carapaces, although little abrasion or breakage has been observed. A Principal Component Analysis (PCA) suggests that superfamilies were distributed across different facies. Thus, in the reef and inter-reef areas, the most representative groups are: Carpilioids, pilumnoids, xanthoids, *Ilerdapatiscus* and paguroids; the inner fore-reef are dominated by Axiidae, dromioids, parthenopoids, calappoids and raninoids; in the outer fore-reef area, the most representative taxon is *Litoricola macrodactila pyrenaicus*. The only decapod that remained in the post-reef marls deposited after the collapse of the reef mounds is *Litoricola macrodactylus pyrenaicus*.

Statistical analyses of diversity indicate that the studied areas are significantly different, corroborating the sedimentological analysis. These analyses also strength the hypothesis that the greatest diversity was found in the reefal facies belt and that an important part of the generated remains in such area were transported to fore reef facies.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2021.110439.

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Article

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

Fernando A. Ferratges, Samuel Zamora, and Marcos Aurell

With 9 figures and 3 tables

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

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

1. Introduction

The Eocene Epoch was crucial in the development of many present-day features of the Earth. In particular, new palaeogeographical configurations and ocean circulation patterns forced by tectonic plate rearrangement, led to the initial development of Antarctic ice sheets during the late Eocene and a progressive switch from greenhouse to icehouse climatic conditions (e.g., Hallock et al. 1991; Hallock & Pomar 2008; Stickley et al. 2009). These climatic changes had an impact on the evolution of reefs and associated metazoan communities (Pomar et al. 2017). Coral reefs were fully established in this period (Pomar et al. 2017), hosting decapod crustacean communities with taxa that are similar to those that inhabit modern reefs (Müller & Collins 1991; De Angeli & Garassino 2002; Busulini et al. 2006; Beschin et al. 2007; Tessier et al. 2011; Beschin et al. 2012, De Angeli & Ceccon 2012; De Angeli & Ceccon 2013a, De Angeli & Ceccon 2013b; De Angeli & Ceccon 2014; De Angeli & Garassino 2014; Beschin et al. 2015; De Angeli & Ceccon 2015; Beschin et al. 2016; De Angeli & Ceccon 2016; Beschin et al. 2017). The Eocene is also considered an important period in the evolution of brachyurans (e.g., Fraaije 2003; Brösing 2008; Tsang et al. 2014; Schweitzer & Feldmann 2015). Despite a good understanding of the taxonomic

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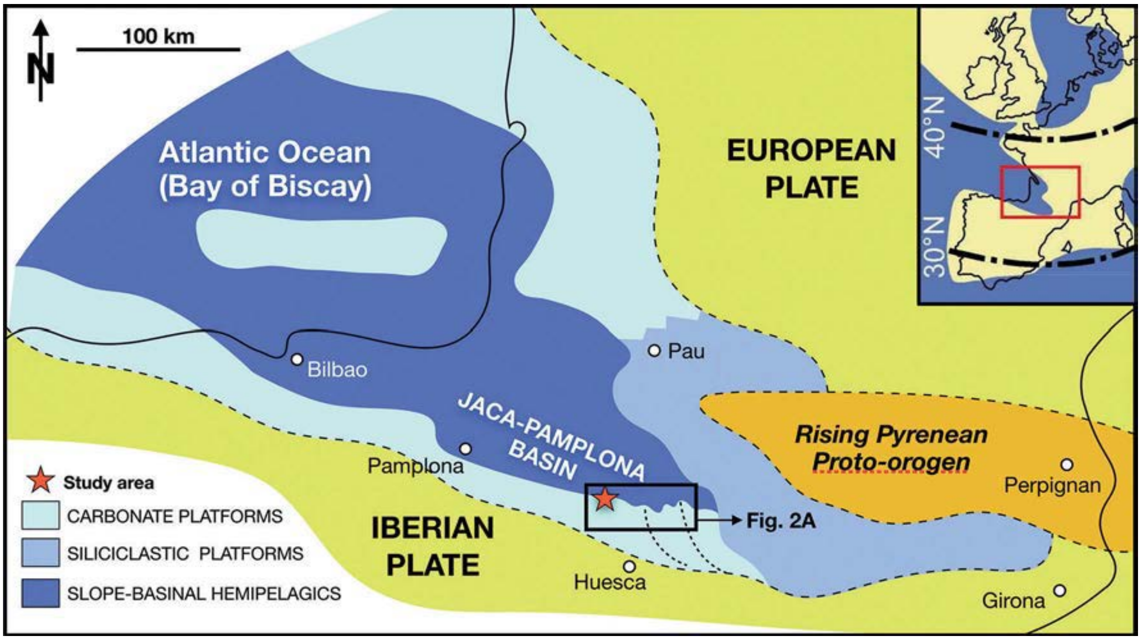


Fig. 1. Mid-Eocene palaeogeographical map of the Pyrenean area, showing the location of the Jaca-Pamplona Basin (modified from Silva-Casal et al. 2017). The squared area in the southern part is enlarged in Fig. 2.

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

Outcrops located in the central part of the southern Pyrenees include an extraordinary record of middle–upper Eocene rocks with coral buildups and associated benthic faunas at several time intervals (Puigdefabregas 1975; Millán et al. 1994; Pomar et al. 2017). Upper Eocene reefs are well represented in the upper portion of the Arguis-Pamplona Marls Formation, along the southern margin of the Jaca-Pamplona Basin (Fig. 1). The upper part of the prodeltaic, clay-dominated succession represented by the Arguis Formation includes levels with early Priabonian (latest Eocene) mesophotic coral buildups. These buildups, between the localities of Rasal and La Peña (province of Huesca, northern Spain), were characterised by Morsilli et al. (2012). In order to understand decapod crustacean composition and their distribution in these lower Priabonian reefs, detailed sampling in the La Peña reef was carried out. Specimens were collected in association with specific microfacies (see 'Materials and methods' below). The aim of the present study is to describe all material collected and discuss the presence of certain taxa in different parts of the reef.

2. Geological setting

The southern Pyrenean basins record one of the most complete Eocene marine sedimentary successions in Europe, with decapod crustaceans previously described from several outcrops (see e.g., Vía 1969; Vía-Boada 1973; Artal & Vía 1988; Artal & Castillo 2005; Artal et al. 2013; Ossó et al. 2014; Domínguez & Ossó 2016; López-Horgue & Bodego 2017; Ossó & Domínguez 2017; Artal & Van Bakel 2018a; Artal & Van Bakel 2018b; Ferratges et al. 2019). Palaeogeographically, the southern Pyrenean basin was located at approximately 35°N palaeolatitude during the Eocene (e.g., Hay et al. 1999; Silva-Casal et al. 2017) and corresponded to an elongated gulf connected towards the west by the Bay of Biscay, located on the southern limit of the axial zone of the Pyrenees. The gulf was flanked by shallow-water carbonate platforms, with accumulations of hemipelagic sediments at the bottom of the basin (Fig. 1).

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

The Sierras Exteriores includes outcrops located along the southern margin of the Jaca-Pamplona Basin (Fig. 2A). The middle and upper Eocene (Lutetian–Priabonian) units form a *c*. 2-km-thick succession, including shallow-marine limestones of the Guara Formation, the prodelta/outer ramp marls/clays of the Arguis Formation, the deltaic Belsue-Atares Formation and its lateral counterpart (i.e., coastal siliciclastics of the Yeste-Arres Formation) and the fluvial Campodarbe Formation (Puigdefabregas 1975; Silva-Casal et al. 2019). These units are diachronous and record the late-stage infilling of the foreland basin (Millán et al. 1994; Millán et al. 2000). Coeval to basin infill, a series of thrust ramps and oblique folds with a north-south axis started to develop during the Lutetian and progressively propagated westwards until the Bartonian to early Priabonian with variable shortening rates (Millán et al. 1994; Castelltort et al. 2003; Huyghe et al. 2009). The uppermost Lutetian–lower Priabonian sedimentary units coevally deposited with these growth structures are arranged in four Depositional Sequences I–IV (Fig. 2A). Their boundaries correspond to flooding surfaces, which grade basinwards into correlative conformities. These boundaries are related to tectonic pulses, as indicated by the presence of both angular unconformities and onlap geometries (Millán et al. 1994). These sequences were correlated across a nearly dip-section which displays the transition from the inner areas located to the east to the outer areas towards the west. Their age is constrained by magnetostratigraphical and palaeontological data (Canudo et al. 1988; Canudo et al. 1991; Hogan 1993; Pueyo et al. 2002; Silva-Casal et al. 2019). As a whole, each depositional sequence consists of a lower, poorly fossiliferous to barren clayey-marly unit and an upper shallow-marine siliciclastic or carbonate unit that yields abundant benthic fossils. The lateral extent of the shallow-marine units overlying the relatively deep marly facies is progressively larger in younger sequences, with progradation advancing from east to west. Siliciclastic components also increase according to the same pattern and they become clearly dominant in the uppermost depositional sequence (Fig. 2A). Specifically, the decapod crustaceans studied for the present paper come from lower Priabonian coral buildups developed in the middle part of Sequence IV. These buildups form discontinuous outcrops between the localities of Rasal and La Peña (Fig. 2B). These coral buildups provided a good opportunity for other invertebrates to colonise such a specific environment (e.g., echinoderms, molluscs, decapod crustaceans etc). Although several outcrops have been sampled for decapod crustaceans, only the one located east of La Peña provided fresh rock and enough material to be analysed in detail.

3. The early Priabonian coral reefs of La Peña

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

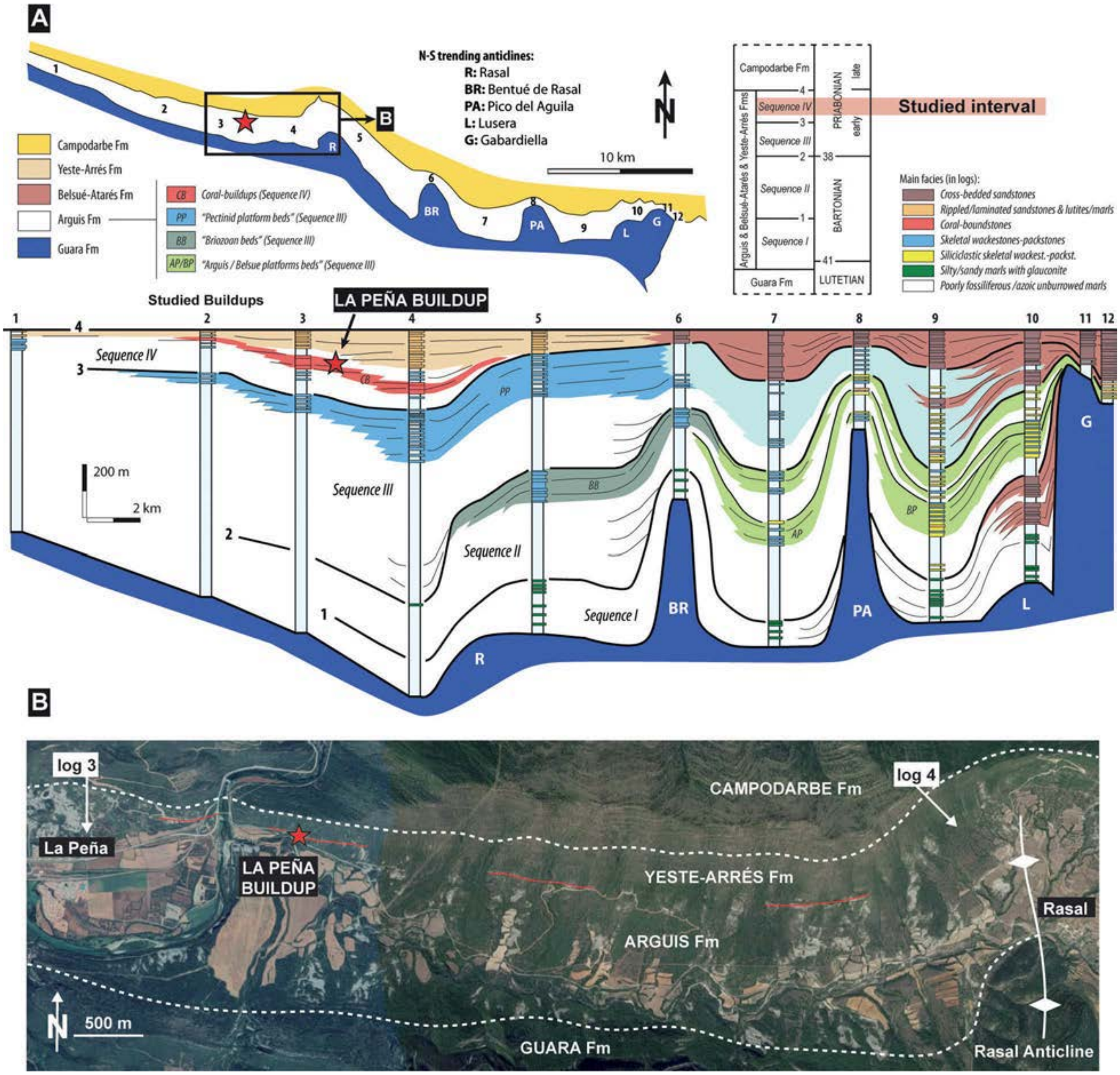


Fig. 2. **A** – Location of logs 1–12 studied by Millán et al. (1994) in the Sierras Exteriores area (for location, see Figure 1). These logs are used as a reference for correlation of Sequences I–IV within the Arguis, Belsué-Atares and Yeste-Arres formations that are shown in the central part of the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

The skeletal matrix commonly consists of floatstone/rudstone with fine-grained, poorly sorted packstone to mud-dominated wackestone. Red algae are conspicuous as both laminar and branching forms, and coral and echinoid fragments are abundant. Bryozoans, bivalves (oysters, pectinids and *Spondylus*), serpulids, ostracods and, locally, chaetetid sponges are common. In addition, regular and irregular echinoids, gastropods and brachiopods have been found. Planktonic and smaller to large benthic foraminifera are present (genera *Nummulites, Heterostegina, Asterocyclina* and *Operculina*). Polygenic laminar red algae and encrust-

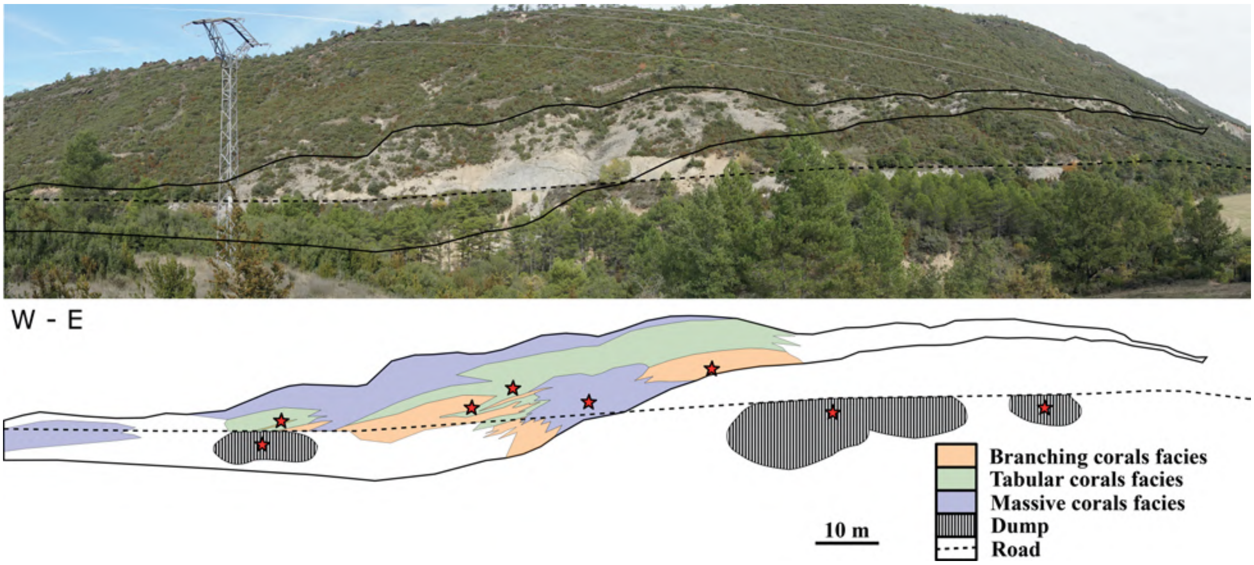


Fig. 3. General view of the outcrop studied (La Peña reef) in a west-east (or distal-proximal) panoramic view. The sketch shows the distribution of the three facies identified on the basis of predominant coral morphologies. Red stars correspond to sample points (for location, see Fig. 2B). Dumped material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

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

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

4. Materials and methods

The specimens studied were collected directly from outcrop in the section along the road between the villages of Rasal and La Peña (Fig. 3). This locality corresponds to the coral buildup developed in the middle part of the lower Priabonian Sequence IV, which is referred here as the La Peña buildup (Fig. 2). The La Peña buildup includes a diverse invertebrate fauna associated with corals, including a diverse assemblage of decapod crustaceans associated with several lithofacies.

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

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

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

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

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

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

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

Only specimens preserving complete carapaces have been treated systematically. Other material, including partial chelipeds and limbs have been treated only in the discussion (see below) and formal description awaits the discovery of more complete material.

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

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

5. Decapod crustacean composition

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

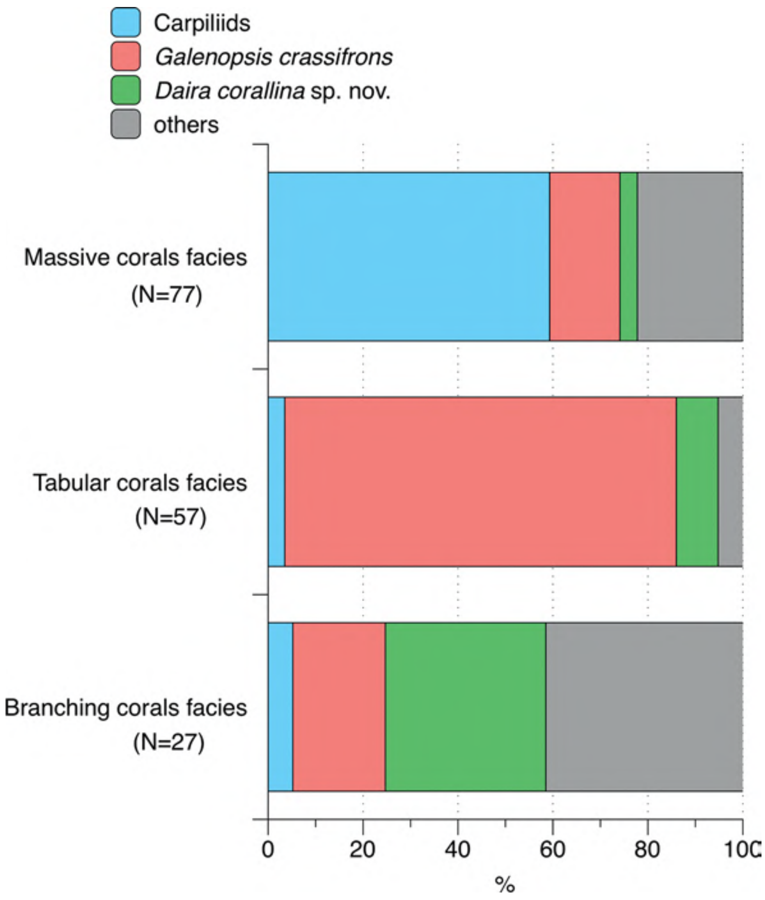


Fig. 4. Relative abundance of the main decapod crustacean taxa in the three different facies within the La Peña reef.

in the different facies identified within the La Peña reef (Fig. 4). These taxa include representatives of the genera *Enoploclytia*? McCoy, 1849 (Fig. 5I), *Petrochirus* ? Stimpson, 1858 (Fig. 5J), *Gemmellarocarcinus* Checchia-Rispoli, 1905 (Fig. 5A–C), *Liopsalis* von Meyer, 1862 (Fig. 6C, D), *Ocalina* ? Rathbun, 1929 (Fig. 5E), *Galenopsis* A. Milne-Edwards, 1865 (Figs. 6E–G, 7), *Lobogalenopsis* Müller & Collins, 1991 (Fig. 6H–J), and *Daira* De Haan, 1833 (Figs. 8B–K, 9). In addition, representatives of the family Trapeziidae? Miers, 1886 (Fig. 5H), carpiliids (Figs. 5D, 6A, B) and remains of four other indeterminate taxa have been found (Table 1; Fig. 5F, G).

This decapod assemblage has similarities to material collected at some localities with Eocene strata in Italy where they appear associated with reef facies (see e.g., Beschin et al. 2007; Tessier et al. 2011; Beschin et al. 2015). However, the exceptional state of preservation of the outcrop described herein and its optimal exposure, have allowed a detailed sampling of different lithofacies in order to quantify the occurrence of each taxon.

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

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

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

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

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

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

In order to analyse which distribution of the species are significantly linked to a specific facies we applied the command "fisher.multcom" from the same R-package (see above) to apply a pairwise comparison of the Fisher's-exact test. We detected significant differences in the distribution of carpiliids and *Galenopsis crassifrons* in branching corals facies and massive corals facies (p=2.04e^{-03}), and carpiliids and *Daira corallina* sp. nov. in the same facies (p=3.20e^{-07}). There were significant differences in the distribution of *Galenopsis crassifrons* and *Daira corallina* sp. nov. in the branching corals facies and massive corals facies (p=1.87e^{-07}). Finally, we also found significant differences in the distribution of carpiliids and *Galenopsis crassifrons* in the massive corals facies and tabular corals facies (p=9.22e^{-09}) and carpiliids and *Daira corallina* sp. nov. in the same facies (p=6.12e^{-03}). The rest of species distribution are not significantly linked to any specific facies.

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

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

The branching corals facies shows the highest diversity and abundance, and this may have been controlled by both biological and taphonomic factors. The branching corals of the genus *Acropora*, *Pocillopora* and *Stylophora* identified in the La Peña reef (Morsilli et al. 2012) are also common in the modern Indo-Pacific and host a diverse community of decapod crustaceans (Patton 1994). Branches between corals provide a large number of places for refuge to decapod crustaceans, especially to small forms like *Daira* and this can be the reason why the branching corals facies shows the highest diversity. This is also the area with the lowest energy within the reef, favouring preservation of the smallest taxa within the sediment accumulating in the spaces between the coral branches. Small-sized specimens of *Goniodromites laevis* were also found particularly in between coral branches in the Albian of northern Spain (Klompmaker et al. 2013) supporting the idea that branching corals are favourable places for small decapods. Coral species with tabular growth forms are particularly important ecosystem engineers on wave-exposed Indo-Pacific reefs (Madin et al. 2012). The La Peña reef tabular facies was dominated by *G. crassifrons*, which is the largest form collected; it probably lived in the spaces under and between tabular corals. The massive coral facies shows the lowest abundance and this was probably a consequence of both taphonomic and biological reasons. Massive corals provide little space for sediment accumulation between the colonies and also fewer opportunities for refuge than other type of colonies. Despite the fact that there are still many uncertainties in our understanding of zonation patterns of different species within the reef, carefully collected material associated with sedimentological information could provide important data for future palaeoecological studies. The La Peña reef decapod community is a small, yet interesting example.

6. Systematic palaeontology

The classification used here follows Guinot et al. (2013) and Jagt et al. (2015).

Infraorder Brachyura Linnaeus, 1758
Section Podotremata Guinot, 1977
Superfamily Dromioidea De Haan, 1833
Family incertae sedis
Genus *Gemmellarocarcinus* Checchia-Rispoli, 1905

Type species: *Gemmellarocarcinus loerentheyi* Checchia-Rispoli, 1905, by monotypy.

Other species included: *Gemmellarocarcinus disalvoi* Beschin, Busulini & Tessier, *in* Beschin, Busulini, Fornaciari, Papazzoni & Tessier, 2018 and *G. riglosensis* sp. nov.

Gemmellarocarcinus riglosensis sp. nov.
Fig. 5A–C

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

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

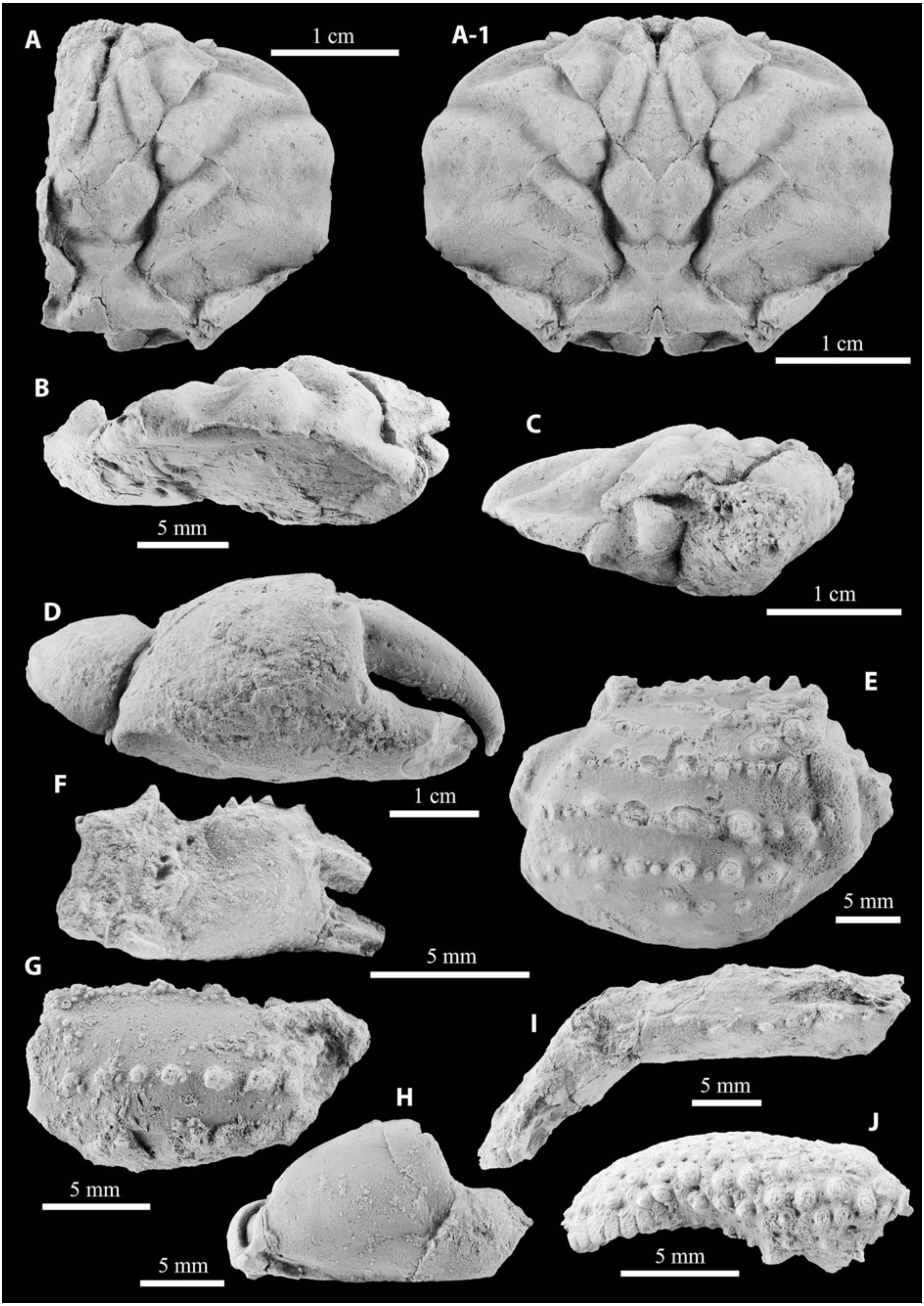
Diagnosis: Carapace slightly wider than long (L/W ratio about 1.41), slightly swollen, descending rapidly in the anterior part; orbits small, suboval and deep, with a blunt suborbital tooth. Anterolateral margins depressed, strongly convex. Dorsal regions well defined. Cervical groove wide and deep,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

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

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

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

The placement of *Gemmellarocarcinus* at family level is problematic (Karasawa et al. 2011) because of the absence of sternal and pleonal elements. We consider *Gemmellarocarcinus riglosensis* sp. nov. to be *incertae sedis* within the superfamily Dromioidea.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Section Eubrachyura de Saint Laurent, 1980
Subsection Heterotremata Guinot, 1977
Superfamily Carpilioidea Ortmann, 1893
Family Carpiliidae Ortmann, 1893
Genus *Liopsalis* von Meyer, 1862

Type species: *Cancer klipsteini* von Meyer, 1842, by monotypy.

Other species included: *L. anodon* (Bittner, 1875) and *L. simplex* (Stoliczka, 1871).

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

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

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

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

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

Superfamily Pilumnoidea Samouelle, 1819
Family Pilumnidae Samouelle, 1819
Genus *Galenopsis* A. Milne-Edwards, 1865

Type species: *Galenopsis typica* A. Milne-Edwards, 1865, by subsequent designation of Glaessner (1929).

Other species included: *Galenopsis crassifrons* A. Milne-Edwards, 1865, *G. depressa* (A. Milne-Edwards, 1872), *G. murchisoni* A. Milne-Edwards, 1865, *G. pustulosa* (A. Milne-Edwards, 1865), *G. ristorii* Checchia-Rispoli, 1905, *G. schopeni* Checchia-Rispoli, 1905, and *G. similis* Bittner, 1875.

Galenopsis crassifrons A. Milne-Edwards, 1865
Figs. 6E–G, 7

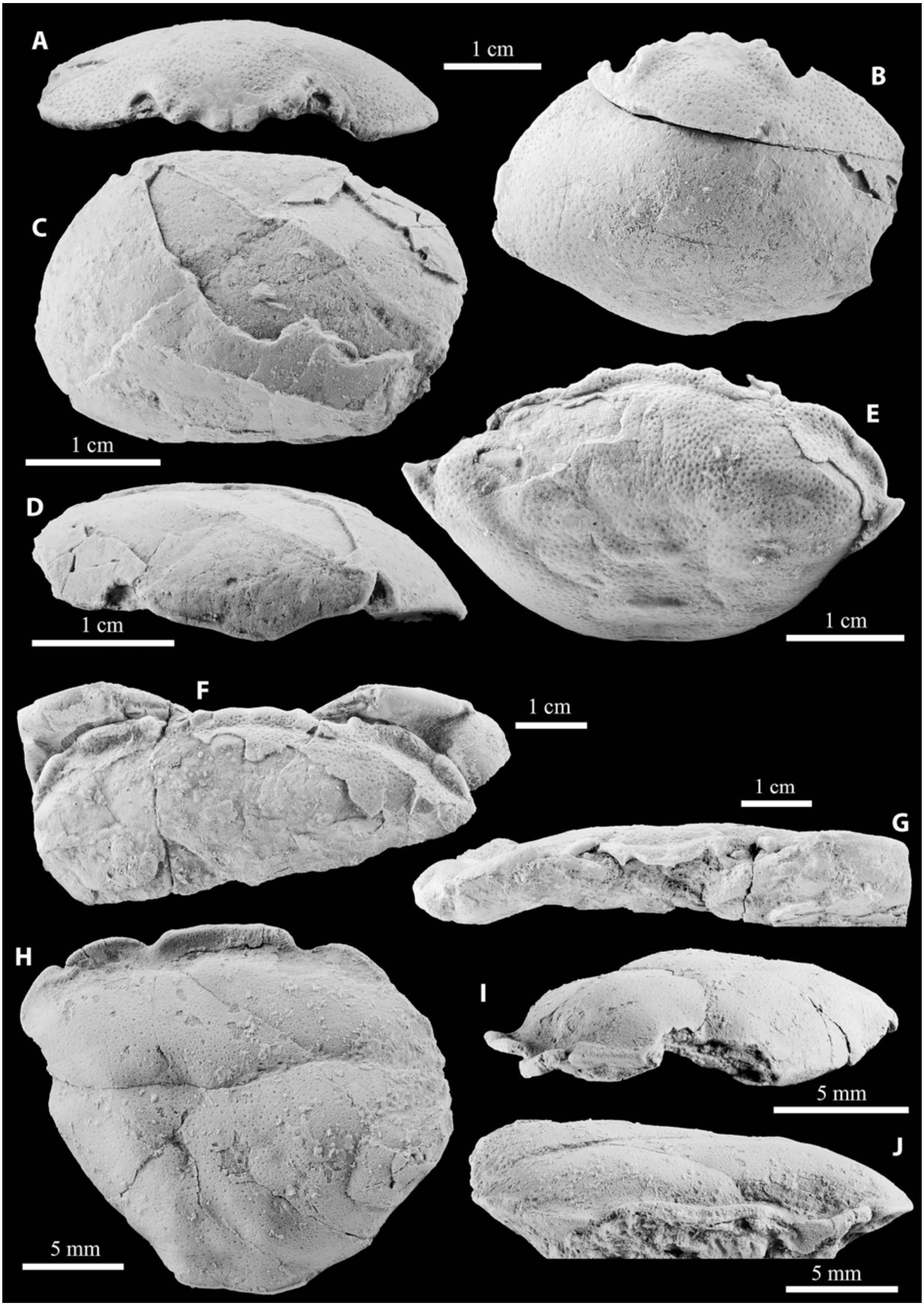
1865 *Galenopsis crassifrons* A. Milne-Edwards, p. 319, pl. 7, fig. 2a–d.
1901 *Galenopsis crassifrons*. – Oppenheim, p. 284.
1908 *Galenopsis crassifrons*. – Fabiani, p. 211.
1929 *Galenopsis crassifrons* – Glaessner, pp. 177, 178.
1991 *Galenopsis crassifrons*. – Vía-Boada, p. 184, pl. 1, fig. 7a, b.

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

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

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

Fig. 5. A–C – *Gemmellarocarcinus riglosensis* sp. nov., holotype (MPZ 2019/1722), in dorsal, right lateral and frontal views, respectively (A-1: mirrored reconstruction). **D** – Cheliped of a carpiliid (MPZ 2019/1805). **E** – Propodus of *Ocalina* ? sp. (MPZ 2019/1723). **F, G** – Indeterminate chelipeds (MPZ 2019/1852 and MPZ 2019/1837, respectively). **H** – Cheliped of a trapeziid? (MPZ 2019/1724). **I** – *Enoploclytia* ? sp. (MPZ 2019/1730). **J** – *Petrochirus* ? sp. (MPZ 2019/1734).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The type material of *G. crassifrons* was recovered from the upper Eocene of Vicenza (Italy) (A. Milne-Edwards 1865); subsequently, it has also been recorded from the middle Eocene of Alicante (Spain; see Vía-Boada1991: pl. 1, fig. 7). Its discovery in the La Peña buildup (Huesca) extends the range of the species to the upper Eocene of northern Spain.

Genus *Lobogalenopsis* Müller & Collins, 1991

Type species: *Galenopsis quadrilobatus* Lőrenthey, 1898, by the subsequent designation of Müller & Collins (1991).

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

Lobogalenopsis joei sp. nov.
Fig. 6H–J

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

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

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

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

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

- carapace convex, elliptical with a sharp keel along the anterolateral margin;
- straight front in top view, depressed below gastric regions;
- orbits small;
- anterolateral margin lobate.

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

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

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

Superfamily Dairoidea Serène, 1965
Family Dairidae Serène, 1965
Genus *Daira* De Haan, 1833

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

Other species included: *Daira americana* Stimpson, 1860, *D. depressa* (A. Milne-Edwards, 1865), *D. coccoi* Beschin, De Angeli, Checchi & Zarantonello, 2012, *D. Coronata* Beschin, De Angeli, Checchi & Zarantonello, 2005, *D. eocaenica* (Lőrenthey, 1898), *D. iugata* Beschin, Busulini & Tessier, *in* Beschin, Busulini, Fornaciari, Papazzoni & Tessier, 2018, *D. pseudovulgaris* Beschin, Busulini & Tessier, *in* Beschin, Busulini, Fornaciari, Papazzoni & Tessier, 2018, *D. Salebrosa*

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

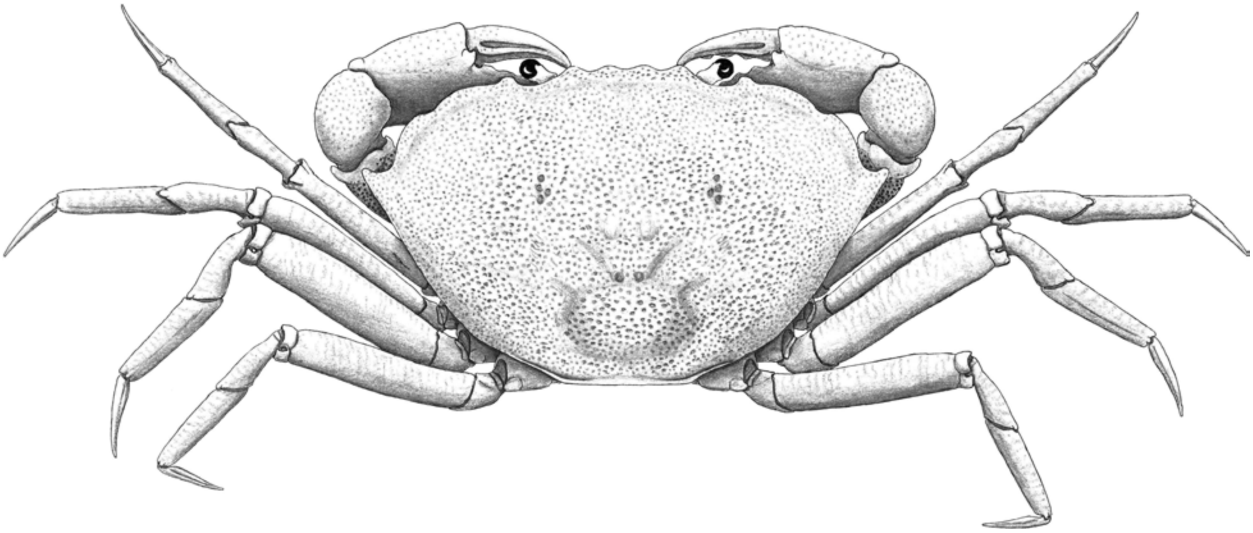


Fig. 7. Reconstruction of *Galenopsis crassifrons* A. Milne-Edwards, 1865, on the basis of material recovered from the outcrop studied (see also Fig. 6E–G).

Beschin, Busulini, De Angeli & Tessier, 2002, *D. sicula* (Di Salvo, 1933), *D. speciosa* (Reuss, 1871), *D. vestenanovensis* Beschin, Busulini & Tessier, 2015, and *D. vulgaris* Portell & Collins, 2004.

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

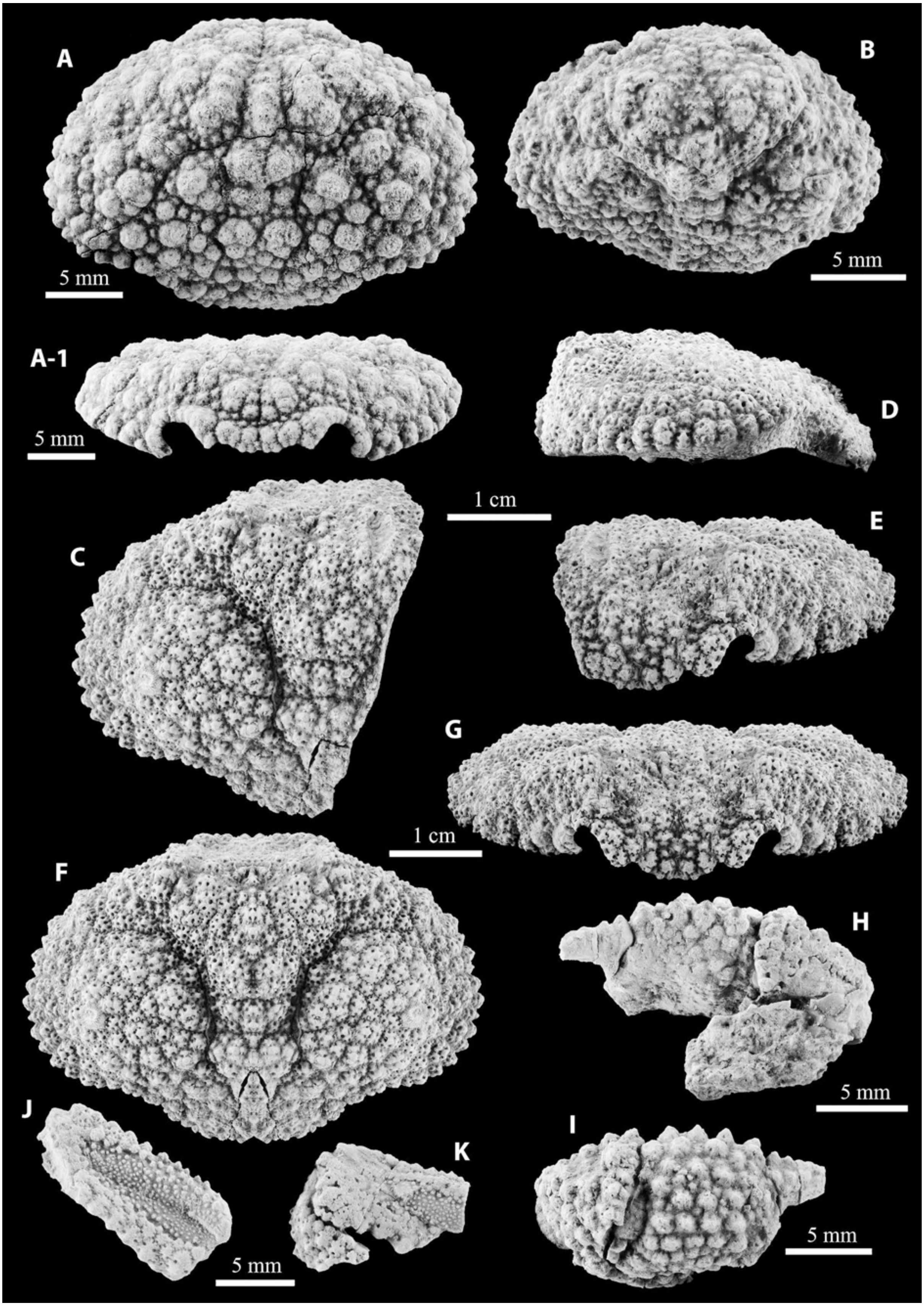
Etymology: Latin *corallium*, meaning coral, in reference to the preference of this taxon for coral reef environments.

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

Diagnosis: Carapace suboval, wider than long, very convex longitudinally, transverse convexity less pronounced. Front sinuous. Orbits circular, with supraorbital margins covered with coalescent tubercles with micropores. Anterolateral margins convex, with conical tubercles; posterolateral margins concave, ornamented with slightly smaller tubercles. Regions well differentiated by grooves. Dorsal surface covered with mushroom-shaped tubercles with micropores.

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

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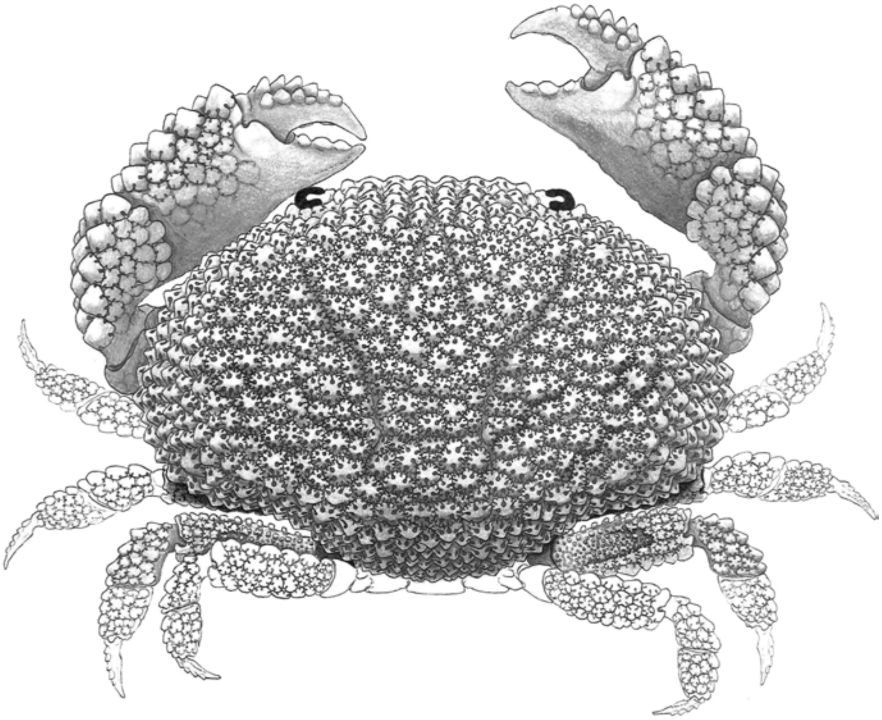

Fig. 9. Reconstruction of *Daira corallina* sp. nov., on the basis of material recovered from the outcrop studied. Parts without shading correspond to those that have been not found and have been reconstructed on the basis of a comparison from modern species.

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

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

The genus *Daira* comprises only two extant species, *D. perlata* from coralline settings in the Indo-Pacific (e.g., Peyrot-Clausade 1989; Morgan & Berry 1993), and *D. americana*, which typically occurs in rocky or coral habitats along the Pacific coasts of central America, from southern California to Ecuador (Rathbun 1930). As far as extinct species are concerned, the genus *Daira* appears to have preferred coral or reef environments. Frequently, its presence is indicative of a diverse reefal decapod crustacean assemblage (see Beschin et al. 2002; Portell & Collins 2004; Beschin et al. 2005; Beschin et al. 2017; De Angeli et al. 2010; Gatt & De Angeli 2010; Beschin et al. 2012; Beschin et al. 2015, Beschin et al. 2016, Beschin et al. 2018; Tessier et al. 2011).

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

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

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

	Branching corals facies	Massive corals facies	Tabular corals facies
Carpiliids	4	15	2
Galenopsis	15	4	47
Daira	26	1	5

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

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

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

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

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

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

7. Conclusions

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

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

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6.2.3. Decapod crustacean diversity through time and space from a middle-upper Eocene carbonate-siliciclastic platform system (southern Jaca Basin, Pyrenees, Spain).

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Decapod crustacean diversity through time and space from a middle-upper Eocene carbonate-siliciclastic platform system (southern Jaca Basin, Pyrenees, Spain)

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Abstract

The well exposed outcrops in the south-central margin of the Jaca Basin (South-central Pyrenees, Spain) allows evaluation of the decapod crustacean distribution across a mixed carbonate-siliciclastic system during the middle-late Eocene (Bartonian-Priabonian). The studied units were deposited in a wide range of environments in an area of 1000 km^2, ranging from siliciclastic coastal plains, deltaic complexes, shallow carbonate to mixed platforms (including coral reef complexes) to prodelta/outer platform deeper conditions. The observed sedimentary evolution was mostly controlled by compressional syntectonic activity, which involved the progressive shallowing and eventual uplift of the western margin of the basin, with the coeval eastward progradation of the deltaic complexes. This progradation was episodic and resulted in the formation of four sequences bounded by unconformities. Detailed sampling on these sequences has provided a total of 339 fossil decapod crustaceans from different lithofacies in 20 different localities. The analysis of the reported data provides an extraordinary example of ecological zonation of decapod crustaceans within a shallow to relatively deep transect, with a total of 39 different decapod species included in 22 families.

Results show that major peaks in diversity are correlated with siliciclastic shallow areas in the proximal prodelta environments, followed by carbonate bryozoan meadows. The number of species associated with carbonate or siliciclastic facies in this middle and upper Eocene is apparently similar, although with completely different taxonomic composition. However, the mean size of reef species is significantly smaller than that of species associated with siliciclastic environments (except in relatively deep proximal areas where size is considerably reduced). Articulated specimens mostly appear in proximal shallow and in relatively distal deep areas associated with siliciclastic sediments resulted from sudden sedimentary inputs and high sedimentary rates.

These data provide a unique opportunity to understand, in a kilometre-size area, the distribution in time and space of a single invertebrate group and help to understand the control factors for such distribution during the middle and upper Eocene.

Key words: Crustacea, taxonomy, Bartonian, Priabonian, paleoenvironments, paleoecology

1. Introduction

Understanding how diversity of a single systematic group evolves through space and time across a sedimentary succession is not always possible, especially when outcrops are limited or the group has little potential of fossilisation (i.e., Via, 1959; Klompmaker et al., 2013, 2016; Meyer and Ausich, 2019; Ferratges et al., 2020a, 2021a). The middle-upper Eocene units exposed in the External Sierras of northern Spain (South-Central Pyrenees) offer the opportunity to carry out a comparative analysis of the benthic invertebrate fauna preserved from shallow to relatively deep depositional settings. These exposures have allowed the reconstruction of a c. 30 km long proximal to distal transect (from west to east) that show a wide spectrum of facies representing different settings of a mixed siliciclastic-carbonate system (Millán et al., 2004; Silva-Casal et al., 2017). These settings range (upwards and basinwards) from proximal coastal siliciclastics, shallow marine siliciclastic, carbonate platforms including coral reefs developed in the mesophotic zone (Morsilli et al., 2012; Pomar et al., 2017; Ferratges et al., 2020a), distal bryozoan-sponges meadows on the external platform, to relatively deep marls with a very scarce benthic fauna.

One of the groups that is present in a wide range of facies from this platform transect are decapod crustaceans. Some authors consider them to be good zoogeographic indicators (Müller, 1979; Schweitzer, 2001; Feldmann and Schweitzer, 2006; Hyzny, 2015, 2016) and their distribution is highly controlled by facies types, because decapods can be restricted to particular sedimentary conditions, food supply, depth, etc (i.e., Bertini and Fransozo, 2004; Pallas et al., 2006; Rufino et al., 2006; Furlan et al., 2013; Cartes et al., 2014). For this reason, some authors have tried to understand the distribution of decapod faunas at outcrop level (Via, 1959; Hyžný 2015, 2016; Klompmaker et al., 2013, 2016; Ferratges et al., 2020a, 2021a) or at larger regional scales (Via, 1959; Hyžný, 2016). The former studies provide important data at small scales while the later provide a big picture of decapod distribution in relatively large areas. This study presents an intermediate level of detail, and tries to understand the distribution of decapod crustaceans in a single formation which spreads over a large area of a sedimentary basin. In the studied transect, detailed correlations between the decapod sites are possible due to the excellent outcrop conditions and detailed sedimentological data.

The data herein were acquired after an intensive sampling in a c. 30 km long platform transect to analyse diversity, abundance and state of preservation of decapod crustaceans from more proximal siliciclastic-dominated environments to more distal carbonate facies. The aims of this study are: (1) to provide a preliminary description of all collected material, (2) to give further information of the previously known framework and architecture of the studied middle-late Eocene syntectonic sequences, showing some key sedimentological and paleontological features of different facies, (3) to describe the relative abundance and diversity of the different groups of the decapod crustacean assemblages associated to the different paleoenvironments, and (4) to understand the interaction of the different factors controlling the fluctuations on the diversity of decapod crustaceans.

2. Geological setting

The studied area is located in the Sierras Exteriores, in the southern margin of the piggyback Jaca basin attached to the South Pyrennean Frontal Thrust (Fig. 1A). This thrust forms the northern boundary of the Ebro foreland basin. In Eocene times, the

Jaca basin corresponded to an elongated gulf opened to the west (to the Bay of Biscay), which was located at approximately 35ºN palaeolatitude (e.g., Hay et al., 1999; Silva-Casal et al., 2017). The formation of this basin was caused by the southward propagation of the Pyrenean fold and thrust belt structures during the Palaeogene (Millán et al., 1994; Muñoz et al., 1994; Castelltort et al., 2003; Huyghe et al., 2009). The propagation of these structures resulted in the formation of a coeval relief, acting as a sediment source area for deltaic complexes (e.g., Plaziat, 1981; Dreyer et al., 1999; Pujalte et al., 2002; Barnolas et al., 2004). These deltaic complexes prograded westward in the southern part of the Jaca basin, progressively covering the turbiditic systems of the lower and middle Eocene Hecho Group (Mutti et al., 1985; Remacha et al., 2003, 2005).

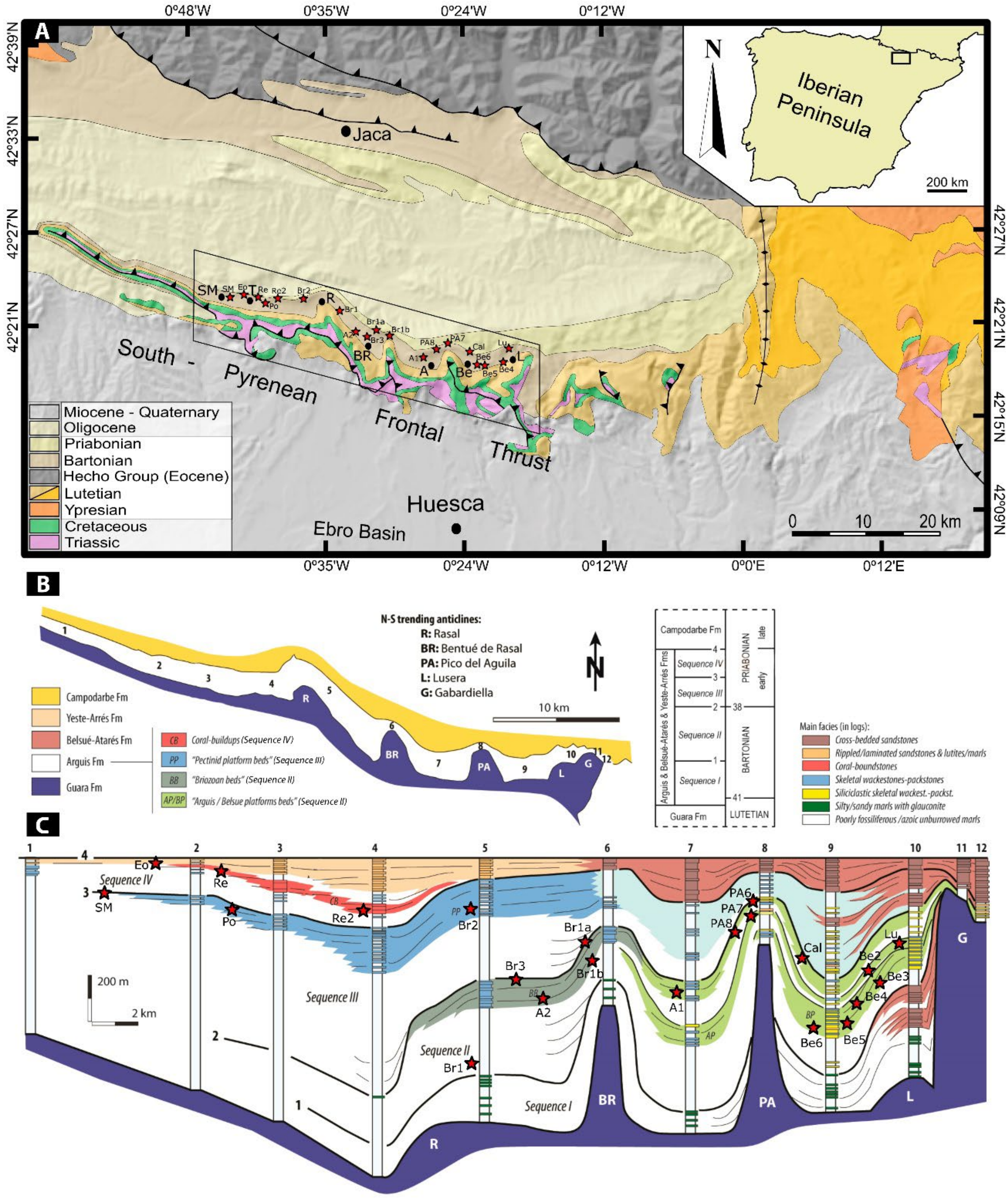


Figure 1. **A**: Geological map in Southern Central Pyrenees with location of the studied area and the different sampled outcrops. The area included inside the rectangle corresponds to the studied area in the south-central Jaca Basin, enlarged in section B and C. Coordinates of the sampled outcrops: 1: 42°26′8″N, 0°55′14″W; 2: 42°23′45″N, 0°44′9″W; 3: 42°23′45″N, 0°42′6″W; 4: 42°23′14″N, 0°40′7″O; 5: 42°22′55″N, 0°40′6″W; 6: 42°23′17″N, 0°34′46″W; 7: 42°20′22″N, 0°31′32″W; 8: 42°20′18″N, 0°31′17″W; 9: 42°20′36″N, 0°31′3″W; 10a: 42°20′30″N, 0°30′17″W; 10b: 42°20′26″N, 0°30′17″W; 11: 42°19′2″N, 0°26′40″W; 12: 42°19′35″N, 0°24′44″W; 13: 42°19′31″N, 0°25′27″W; 14: 42°18′58″N, 0°22′23″W; 15: 42°18′31″N, 0°22′20″W; 16:42°18′52″N, 0°20′37″W; 17: 42°19′21″N, 0°19′42″W. **B**: Location of logs 1–12 studied by Millán et al. (1994) in the Sierras Exteriores area. These logs are used as a reference for correlation of Sequences I–IV within the Arguis, Belsué-Atares and Yeste-Arres formations that are shown in the central part of the figure. The inset in the upper right-hand side shows the age of these sequences [modified from Millán et al. (1994) and Silva-Casal et al. (2017)]. **C**: Distribution of uppermost Lutetian–Priabonian lithostratigraphical units between the villages of La Peña and Nocito (see A for location), and sampling points (red stars) which have provided crustaceans fossils. Acronyms: SM: Santa María de la Peña; T: Triste; R: Rasal; A: Arguis; Be: Belsué; L: Lúsera.

The middle and upper Eocene (Lutetian–Priabonian) units of the southern margin of the Jaca basin form a c. 2 km thick succession that includes the shallow marine limestones of the Guara Formation and the prodelta/outer ramp marls/clays of the Arguis Formation, which laterally (eastwards) and upwards grades into the deltaic Belsue-Atares Formation and its lateral counterpart (i.e., coastal siliciclastics of the Yeste-Arres Formation) (Fig. 2). These units are in turn overlain by the fluviatile Campodarbe Formation (Puigdefabregas, 1975; Silva-Casal et al., 2019). This set of units are diachronous and record the late-stage infilling of the piggyback Jaca basin (Millán et al., 1994, 2000).

In the studied southern margin of the Jaca basin, a series of thrust ramps and oblique anticlines with a north-south axis began to develop since the Lutetian and progressively propagated westward through the early Priabonian with varying rates of shortening (Millán et al., 1994; Castelltort et al., 2003; Huyghe et al., 2009). In particular, the anticlines of Gabardiella, Lusera, Pico del Aguila and Bentue de Rasal (G, L, PA and BR in Fig. 1B) created a syndepositional relief and giving rise to a compartmentalization of the basin, with the presence of barriers between different sectors of the studied area. The setting of these topographic highs led to the proliferation of different palaeoenvironments in a relative small area, with marked differences in the sedimentation recorded in the intermediate Belsúe, Arguis and Bentue de Rasal subsiding syncline areas (see Fig. 1 for location; Millán et al., 1994).

Following Millán et al. (1994), the sedimentary units coevally deposited to the growth anticlines are arranged in four third-order depositional sequences I–IV (Fig. 1C). The age of these sequences is constrained by palaeontological and magnetostratigraphic data (Canudo et al. 1988, 1991; Hogan 1993; Pueyo et al. 2002; Silva-Casal et al. 2019; Garcés et al., 2020). The four distinguished depositional sequences have a deepening-shallowing trend, and consist of a lower poorly fossiliferous to azoic clayey-marly unit, and an upper shallow marine siliciclastic and carbonate unit bearing abundant benthic fossils. The marly-clayed dominated interval is highly variable in thickness, with frequent onlap geometries over the flanks of the syndepositional anticlines, whereas the shallow marine interval is highly progradational and has a more homogeneous thickness.

The good tectonic and stratigraphic control of the study area allows very precise control of the sedimentary and structural evolution, and the syntectonic character of each sequence in relation to its associated growth fold (see Millán et al., 1994, 2000; Morsilli et al., 2012; Silva-Casal et al., 2019). The tectonic activity had a major impact on the coeval sedimentary record controlling the depositional sequence formation, the terrigenous input and the distribution of depositional depths. Sequence boundaries are related to episodic tectonic pulses with the formation of local angular unconformities in proximal areas, and drowning unconformities in the shallow platforms developed in relatively distal areas (Millán et al., 1994). The onlap geometries would reflect the sharp growing of the anticlinal structures at the onset of the sequences. The rapid accommodation gain created significant differential subsidence from the hinges of the anticlines to the synclines, which was filled up by the azoic blue marls because of the high sedimentary rates. Basinward progradation of shallow facies took place in subsequent periods of decrease in tectonic activity, resulting in a more homogeneous accommodation. The lateral extent of the shallow marine units overlying the relatively deep marly facies is progressively larger in younger sequences, with progradation advancing from east to west (Figs. 1C,2; Millán et al., 1994; Ferratges et al., 2020a).

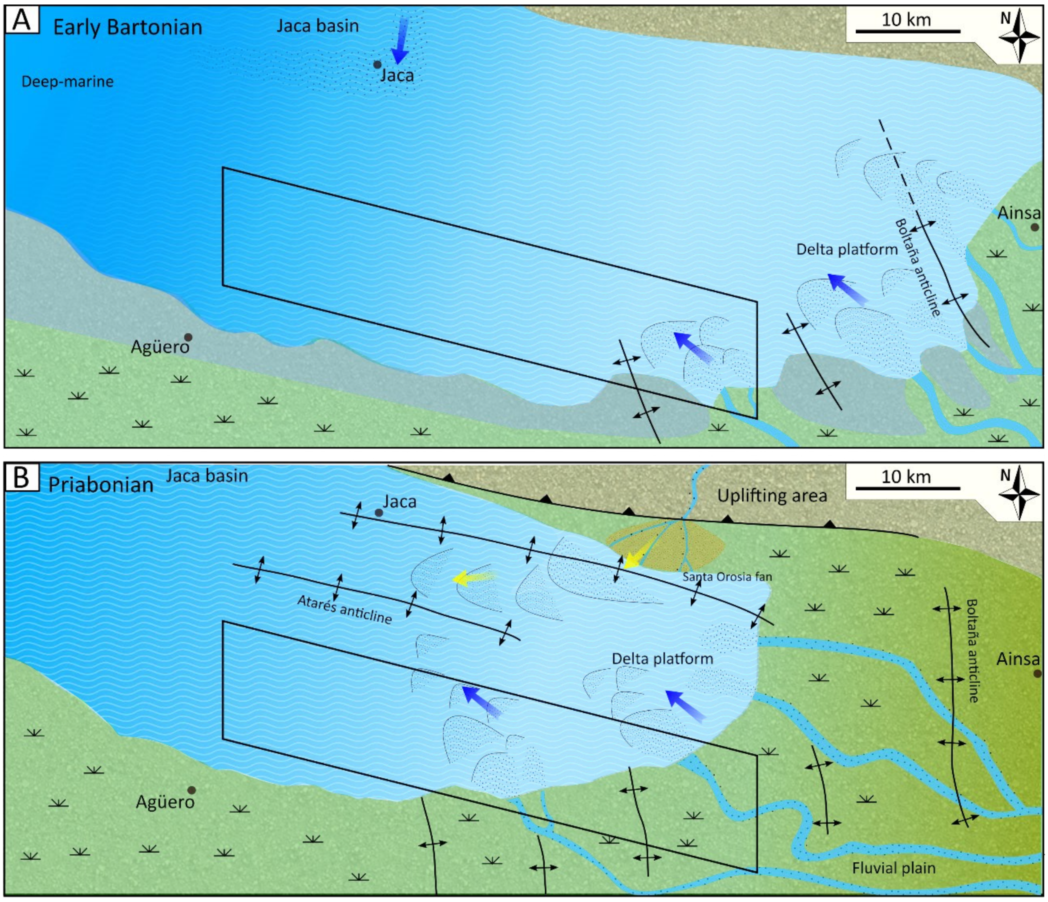


Figure 2. Paleogeographic scheme of the Jaca basin during Bartonian–Priabonian times. **A**: Early Bartonian. **B**: Priabonian. The box shows the location of the studied area (modified from Coll et al. 2022).

3. Materials and methods

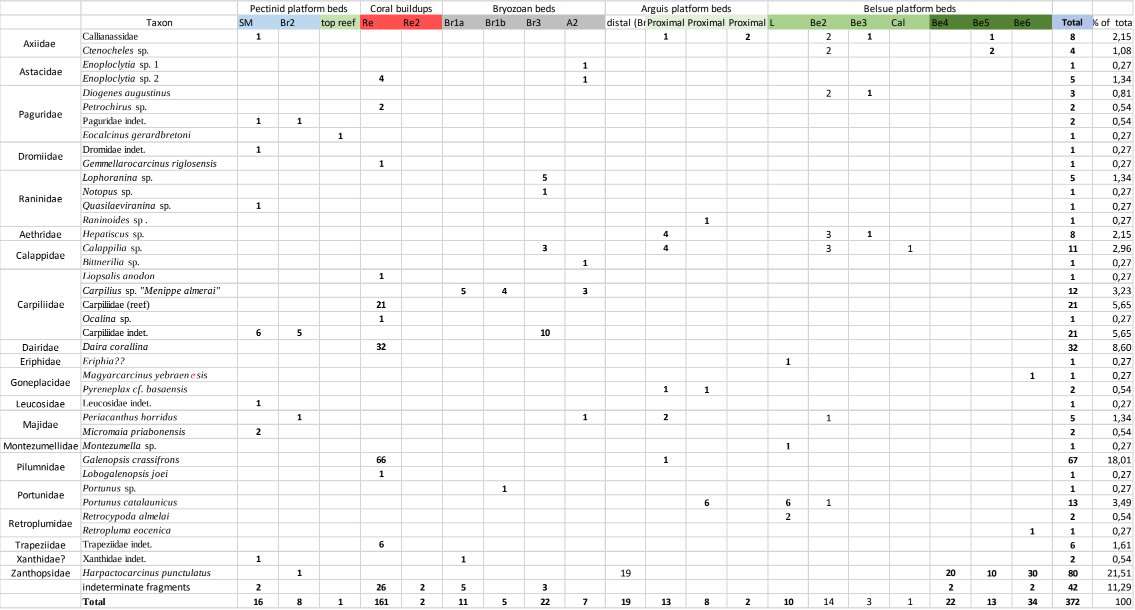
The fossil assemblages studied herein come from the three successive depositional sequences II–IV exposed between the localities of Lusera and Santa María de la Peña.

Twenty-two sites located in the Arguis Formation across a transect of 30 kilometres in length have been sampled for decapod crustaceans (Table 1). All sampled points are included into five main facies, representing distinctive palaeoenvironments (see below). More than 330 decapod crustacean specimens have been collected from sequences II–IV. To carry out the sampling, the outcrops were regularly prospected during approximately twenty-five field sessions from 2018 to 2020, with 6 to 8 consecutive hours of superficial sampling in groups of 2 to 5 people. Due to the scarcity of decapods and the great dispersion of the material, together with the large area we focused on surface collecting (see alternatives in Klompmaker et al. 2013a, 2016). The exact locations of the different crustacean sites are indicated in Figure 1.

The samples were counted following Ferratges et al. (2021a), with minor modifications: (1) all carapaces assignable to a specific taxon were counted as specimens, either at the species level or in open nomenclature; (2) indeterminate remaining fragments or appendages were not counted; (3) identifiable remains (isolated chelae) were taken into account; (4) chelae were taken into account for taxa that usually only preserve this part of the anatomy (i.e., Axiidea and Paguroidea) and other decapods for which we have only found this part (i.e., *Enoploclytia*, *Bittnerilia* and ?*Eriphia*). In case of having several isolated chelae of the same taxon, only the major cheliped has been taken into account.

The studied material has been prepared mechanically using a Micro Jack 2 air scribe (Paleotools; Brigham, UT, USA). The specimens were then photographed dry and coated with an ammonium chloride sublimate. Detailed photographs of carapaces and appendages were made using a Nikon d7100 camera (Nikon, Tokyo, Japan) with a 60 mm macrolens. Specimens were legally sampled under permit EXP: 032/2018 from the Servicio de Prevención, Protección e Investigación del Patrimonio Cultural (Gobierno de Aragón) and are deposited in the palaeontological collection of the Museo de Ciencias Naturales de la Universidad de Zaragoza under the acronym MPZ.

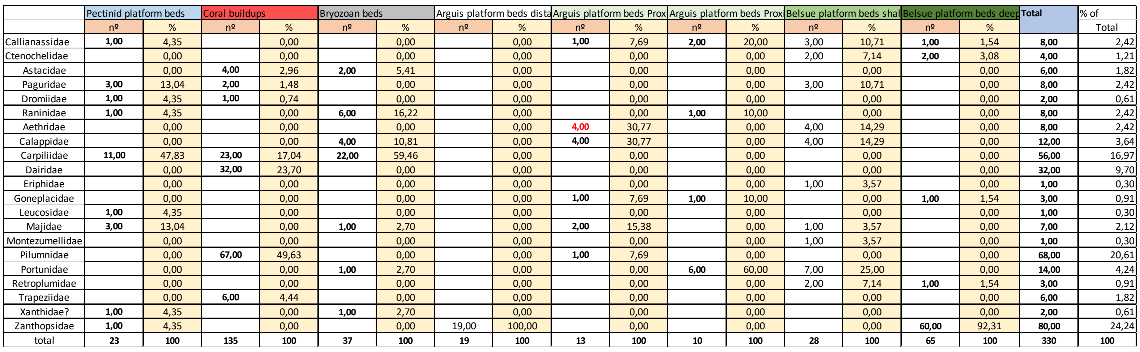
To explore the diversity of the decapod crustacean species distribution in each sedimentary domain and site, we used the statistical program Past 4.03 to obtain Shannon–Wiener Index (or Shannon Index or Shannon–Weaver Index H), Simpson's Index of Diversity, Sorensen Index, Chao1 Index, and the Pielou's evenness index. To investigate differences in diversity among zones within the outcrop, multiple measures of diversity were calculated and all samples per site were combined to create an adequate sample size for comparisons among sites. All specimens identified to the familiar level were included in the analyses (indeterminate fragments were not used for the analysis). Diversity per site was calculated using the methodology described in Klompmaker et al. (2013a) and employed in Ferratges et al. (2021a).



		Pectinid platform beds			Coral buildups		Bryozoan beds				Arguis platform beds				Belsue platform beds								
	Taxon	SM	Br2	top reef	Re	Re2	Br1a	Br1b	Br3	A2	distal (Br	Proximal	Proximal	Proximal	L	Be2	Be3	Cal	Be4	Be5	Be6	**Total**	% of tota
Axiidae	Callianassidae	**1**										**1**		**2**		2	**1**			**1**		**8**	2,15
	Ctenocheles sp.															2				**2**		**4**	1,08
Astacidae	*Enoploclytia* sp. 1									**1**												**1**	0,27
	Enoploclytia sp. 2				**4**					**1**												**5**	1,34
Paguridae	*Diogenes augustinus*															2	**1**					**3**	0,81
	Petrochirus sp.				**2**																	**2**	0,54
	Paguridae indet.	**1**	**1**																			**2**	0,54
	Eocalcinus gerardbretoni			**1**																		**1**	0,27
Dromiidae	Dromidae indet.	**1**																				**1**	0,27
	Gemmellarocarcinus riglosensis				**1**																	**1**	0,27
Raninidae	*Lophoranina* sp.								**5**													**5**	1,34
	Notopus sp.								**1**													**1**	0,27
	Quasilaeviranina sp.	**1**																				**1**	0,27
	Raninoides sp .												**1**									**1**	0,27
Aethridae	*Hepatiscus* sp.											**4**				3	**1**					**8**	2,15
Calappidae	*Calappilia* sp.								**3**			**4**				3		1				**11**	2,96
	Bittnerilia sp.									**1**												**1**	0,27
Carpiliidae	*Liopsalis anodon*				**1**																	**1**	0,27
	Carpilius sp. *"Menippe almerai"*						**5**	**4**		**3**												**12**	3,23
	Carpiliidae (reef)				**21**																	**21**	5,65
	Ocalina sp.				**1**																	**1**	0,27
	Carpiliidae indet.	**6**	**5**						**10**													**21**	5,65
Dairidae	*Daira corallina*				**32**																	**32**	8,60
Eriphidae	*Eriphia??*														**1**							**1**	0,27
Goneplacidae	*Magyarcarcinus yebraenesis*																				**1**	**1**	0,27
	Pyreneplax cf. basaensis											**1**	**1**									**2**	0,54
Leucosidae	Leucosidae indet.	**1**																				**1**	0,27
Majidae	*Periacanthus horridus*		**1**							**1**		**2**				1						**5**	1,34
	Micromaia priabonensis	**2**																				**2**	0,54
Montezumellidae	*Montezumella* sp.														**1**							**1**	0,27
Pilumnidae	*Galenopsis crassifrons*				**66**							**1**										**67**	18,01
	Lobogalenopsis joei				**1**																	**1**	0,27
Portunidae	*Portunus* sp.							**1**														**1**	0,27
	Portunus catalaunicus												**6**		**6**	1						**13**	3,49
Retroplumidae	*Retrocypoda almelai*														2							**2**	0,54
	Retropluma eocenica																				**1**	**1**	0,27
Trapeziidae	Trapeziidae indet.				**6**																	**6**	1,61
Xanthidae?	Xanthidae indet.	**1**					**1**															**2**	0,54
Zanthopsidae	*Harpactocarcinus punctulatus*		**1**								19								**20**	**10**	**30**	**80**	21,51
	indeterminate fragments	**2**			**26**	**2**	**5**		**3**										**2**		**2**	**42**	11,29
	Total	**16**	**8**	**1**	**161**	**2**	**11**	**5**	**22**	**7**	**19**	**13**	**8**	**2**	**10**	14	**3**	1	**22**	**13**	**34**	**372**	100

Table 1. Number of specimens and percentage (%) of different decapod crustacean taxa in the different facies of the studied area.

To simplify the calculations, the recognized taxa were grouped into their respective families (Table 2). Several analyses (see below) were performed to investigate the links between diversity and composition with type of facies and palaeoenvironment. Our null hypothesis (H^0) was that species diversity and composition does not differ between proximal vs distal facies and siliciclastic vs carbonate facies. The alternative hypothesis (H^1) was that species composition does differ between proximal vs distal facies and siliciclastic vs carbonate facies.



	Pectinid platform beds		Coral buildups		Bryozoan beds		Arguis platform beds dista		Arguis platform beds Proxi		Arguis platform beds Proxi		Belsue platform beds shal		Belsue platform beds deep		**Total**	% of
	nº	%	nº	%	nº	%	nº	%	nº	%	nº	%	nº	%	nº	%		Total
Callianassidae	**1,00**	4,35		0,00		0,00		0,00	**1,00**	7,69	**2,00**	20,00	3,00	10,71	**1,00**	1,54	**8,00**	2,42
Ctenochelidae		0,00		0,00		0,00		0,00		0,00		0,00	2,00	7,14	**2,00**	3,08	**4,00**	1,21
Astacidae		0,00	**4,00**	2,96	**2,00**	5,41		0,00		0,00		0,00		0,00		0,00	**6,00**	1,82
Paguridae	**3,00**	13,04	**2,00**	1,48		0,00		0,00		0,00		0,00	3,00	10,71		0,00	**8,00**	2,42
Dromiidae	**1,00**	4,35	**1,00**	0,74		0,00		0,00		0,00		0,00		0,00		0,00	**2,00**	0,61
Raninidae	**1,00**	4,35		0,00	**6,00**	16,22		0,00		0,00	**1,00**	10,00		0,00		0,00	**8,00**	2,42
Aethridae		0,00		0,00		0,00		0,00	**4,00**	30,77		0,00	4,00	14,29		0,00	**8,00**	2,42
Calappidae		0,00		0,00	**4,00**	10,81		0,00	**4,00**	30,77		0,00	4,00	14,29		0,00	**12,00**	3,64
Carpiliidae	**11,00**	47,83	**23,00**	17,04	**22,00**	59,46		0,00		0,00		0,00		0,00		0,00	**56,00**	16,97
Dairidae		0,00	**32,00**	23,70		0,00		0,00		0,00		0,00		0,00		0,00	**32,00**	9,70
Eriphidae		0,00		0,00		0,00		0,00		0,00		0,00	1,00	3,57		0,00	**1,00**	0,30
Goneplacidae		0,00		0,00		0,00		0,00	**1,00**	7,69	**1,00**	10,00		0,00	**1,00**	1,54	**3,00**	0,91
Leucosidae	**1,00**	4,35		0,00		0,00		0,00		0,00		0,00		0,00		0,00	**1,00**	0,30
Majidae	**3,00**	13,04		0,00	**1,00**	2,70		0,00	**2,00**	15,38		0,00	1,00	3,57		0,00	**7,00**	2,12
Montezumellidae		0,00		0,00		0,00		0,00		0,00		0,00	1,00	3,57		0,00	**1,00**	0,30
Pilumnidae		0,00	**67,00**	49,63		0,00		0,00	**1,00**	7,69		0,00		0,00		0,00	**68,00**	20,61
Portunidae		0,00		0,00	**1,00**	2,70		0,00		0,00	**6,00**	60,00	7,00	25,00		0,00	**14,00**	4,24
Retroplumidae		0,00		0,00		0,00		0,00		0,00		0,00	2,00	7,14	**1,00**	1,54	**3,00**	0,91
Trapeziidae		0,00	**6,00**	4,44		0,00		0,00		0,00		0,00		0,00		0,00	**6,00**	1,82
Xanthidae?	**1,00**	4,35		0,00	**1,00**	2,70		0,00		0,00		0,00		0,00		0,00	**2,00**	0,61
Zanthopsidae	**1,00**	4,35		0,00		0,00	19,00	100,00		0,00		0,00		0,00	**60,00**	92,31	**80,00**	24,24
total	**23**	**100**	**135**	**100**	**37**	**100**	**19**	**100**	**13**	**100**	**10**	**100**	**28**	**100**	**65**	**100**	**330**	**100**

Table 2. Corrected percentages indicating the relative abundance and distribution of main groups of decapod crustaceans at the different facies of the studied outcrops. The indeterminate taxa specimens are not included.

The criteria used to determine proximal and distal environment are based on the general decrease in grain size and the position further west (E-W progradation, see Fig. 2). For example, *Portunus catalaunicus* has only been found on or near the crests of anticlines, which correspond to underwater paleoreliefs (see Millán et al., 1994) that are shallower than surrounding areas, totally disappearing in the lateral ramp equivalents. In the case of *Harpactocarcinus punctulatus*, it is only found in the lower parts of the paleorelief, which also contain less diversity of benthic fauna.

4. RESULTS

The exhaustive sampling in different sites representing a wide spectrum of facies (Figs. 1, 3 and 4), as well as the detailed characterization of the different material present in different outcrops provides information about the fossil groups that developed coeval to different sedimentary environments. The available reconstruction of the lateral and vertical facies relationship provided the overall sedimentological and stratigraphic framework, in which abundant fauna and the different decapod crustacean assemblages are located from proximal to relatively distal platform areas. The different materials and their distribution are described below.

4.1. Facies description and distribution

In the studied sequences, there is an overall upwards and basinwards facies progradation in East-West direction (Fig. 1C; Millán et al., 1994). The lower part of each sequence formed during widespread basin deepening consists of grey and blue marls and clays mostly without macrofauna (see white intervals in Figure 1C). These monotonous successions of macrofauna barren poorly burrowed clay to marls form the bulk of the Arguis Formation. They either occur laminated or structureless (locally bioturbated), or locally contain interbedded centimetre-thick sandstone beds, locally cross-laminated due to diluted turbiditic currents or storm wave activity (Millán et al., 1994). In contrast, the shallow marine successions found in the upper part of sequences I–IV include lateral changes with progressive lithological/facies variations that are also coeval to certain variations of fossil content. These variations in different faunal associations are especially notable among crustaceans and echinoderms.

The shallow platform facies found in the upper part of the sequences are variable across space and time (Fig. 1; Millán et al., 1994). The sedimentary units located around the Arguis anticline (in the Belsue and Arguis syncline, see Fig. 1) include the episodic setting of shallow siliciclastic to mixed platforms. In the westernmost sector, Sequences I and II, and most of Sequence III are dominated by the blue marls deposited in a relatively deep marine platform transitioning to a slope-basin environment (Fig. 1). Detailed descriptions of different sequences are provided below.

- **Sequence I**

The lowermost depositional sequence is mainly composed of decimetre- to metre-thick beds of detrital components (quartz grains) and glauconite, interlayered with blue marls and sandy marls (Fig. 3C). In general, this sequence has a very variable thickness, pinching out in Pico del Aguila (PA) and Gabardiella (G) anticlines, and reaching thicknesses of up to 400 m in the Belsue syncline, and between 100 to 250 m in the Arguis and Rasal synclines (see Fig. 1).

Depositional setting of the blue marls has been interpreted by Millán et al. (1994) as a relatively deep and poorly circulated marine environment, located below the storm wave base level. The coarsening upward siliciclastic sequences correspond to shallow marine bars of a deltaic complex in a low angle depositional setting. Most of the sequence consists of nearly azoic blue marls. According to Canudo et al. (1988, 1991), the age of this depositional sequence is well constrained by both palaeontological and magnetostratigraphical data, and corresponds to latest Lutetian to early Bartonian. However, due to the scarcity of fossil remains and the absence of fossils decapod crustaceans in Sequence I after several days of sampling, the study of this sequence has not been deepened.

- **Sequence II**

Sequence II has a maximum thickness of up to 500 m in the Arguis syncline, which is sharply reduced towards the crests of the Pico del Aguila and Bentue de Rasal anticlines (PA and BR in Fig. 1C). According to Canudo et al. (1988, 1991), Sequence II spans the middle and upper part of the Bartonian. The Bartonian-Priabonian boundary is located near the top of the sequence (Montes Santiago, 1992).

The geometry reconstructed after outcrop restoration indicates the setting of a low angle carbonate ramp, with only a significant slope break west to the Rasal anticline (Millán et al., 1994). This sequence consists of two main stratigraphic intervals. The lower interval consists of nearly azoic blue marls with silty grains of quartz deposited in a relatively deep outer platform environment located below the storm wave base level. In the upper part of the sequence, the fossil content and bioturbation increases, and the upper interval is characterized by the frequent presence of c. metre-thick interbedded bioclastic sandy-limestones to sandstone graded beds (Millán et al., 1994). These beds are arranged in thickening upwards sequences, allowing the definition of three shallow platform-dominated intervals within Sequence II, which were called (from bottom to top) ***Belsue platform, Arguis platform,*** and ***Bryozoan beds***. These three platforms have particular faunal groups including abundant decapod crustaceans, and are prograding up to the Pico del Aguila, Bentue de Rasal and Rasal anticlines, respectively (Fig. 1C).

The Belsue and Arguis platforms mostly correspond to burrowed tabular sandstones of variable thickness interbedded with marls and clays (Fig. 4H). Its faunal content consists of a great diversity of organisms (macro- and microfauna) that indicate favourable conditions in a shallow marine setting for the development of a benthic community. Plant remains are also frequent, among which occasional fruits of the mangrove palm genus *Nypa* and wood fragments stand out (Fig. 3F). The thick sandstone to sandy-limestones bodies of the Belsue and Arguis platforms found in the Belsue syncline gradually thin towards the west into the Pico del Aguila anticline, where only the Arguis platform is preserved. The Belsue syncline is dominated by terrigenous sediments (Fig. 3B), with high sedimentation rates, as it is shown by evidence of sudden burial events (Ferratges et al., 2020b).

The uppermost platform of Sequence II is well preserved in the Bentue de Rasal syncline (BR, Fig. 1C). There, a well-cemented carbonate-rich interval dominated by skeletal-rich floatstones with a wackestone to packstone matrix (Fig. 4A-B) called “***Bryozoan beds***” in Puigdefabregas (1975). The sedimentation rates in the shallow platform domains appear to be variable. Eventual stops in sedimentation or low sedimentation rates favoured the episodic development of hardened surfaces that allowed the formation of highly burrowed glauconite-rich hard-grounds (see Br3 in Fig. 1 and Fig. 3D). Low sedimentation rates also favoured the growth of sponge bioherms with variable size and morphology. A great abundance and diversified siliceous sponge association includes *Laocoetis samueli* (d'Archiac, 1850), *Guettardiscyphia thiolati* (d'Archiac, 1846) (or *Pleuroguettardia iberica* Pisera and Busquets, 2002), *Phlyctia expansa* Pomel, 1872; *Centrosia viquensis* Pisera and Busquets, 2002; *Brachiolites munterensis* Pisera and Busquets, 2002; and *Callicylix eocenicus* Pisera and Busquets, 2002. This fauna is very similar to that described from the Bartonian (middle Eocene) of Navarre and Catalonia (see Pisera and Busquets, 2002; Astibia et al., 2014). Although some sponges have been found as isolated fragments, sometimes they are grouped in bioherms (Fig. 4D-E) in growth position, so it can be deduced that they correspond to autochthonous elements. Pisera and Busquets (2002) tried to deduce the bathymetric position of the sponge assemblage of the Bartonian of Catalonia based their taxonomic composition, and suggested a depth of 100 m for the sponge meadows. The depth estimation in the studied area based on faunal content indicates that the conditions were aphotic in the distal part of the platform (dominated by the blue marl facies), while shallower and euphotic conditions existed in more proximal areas (dominated by the carbonates of the Bryozoan beds) (see Millán et al., 1994; Morsilli et al., 2012). At these levels, a great abundance and diversity of echinoderms is also remarkable, some of them encrusted by calcareous algae (Fig. 4C). This sequence is thus a critic interval for the present study because ***Belsue*** and ***Arguis platforms*** are dominated by siliciclastic sediments while ***Bryozoan beds*** are mostly carbonatic with local development of bioherms. This allows to tackle important questions like changes in diversity depending on siliciclastic vs carbonate sediments, and changes in diversity related with depth.

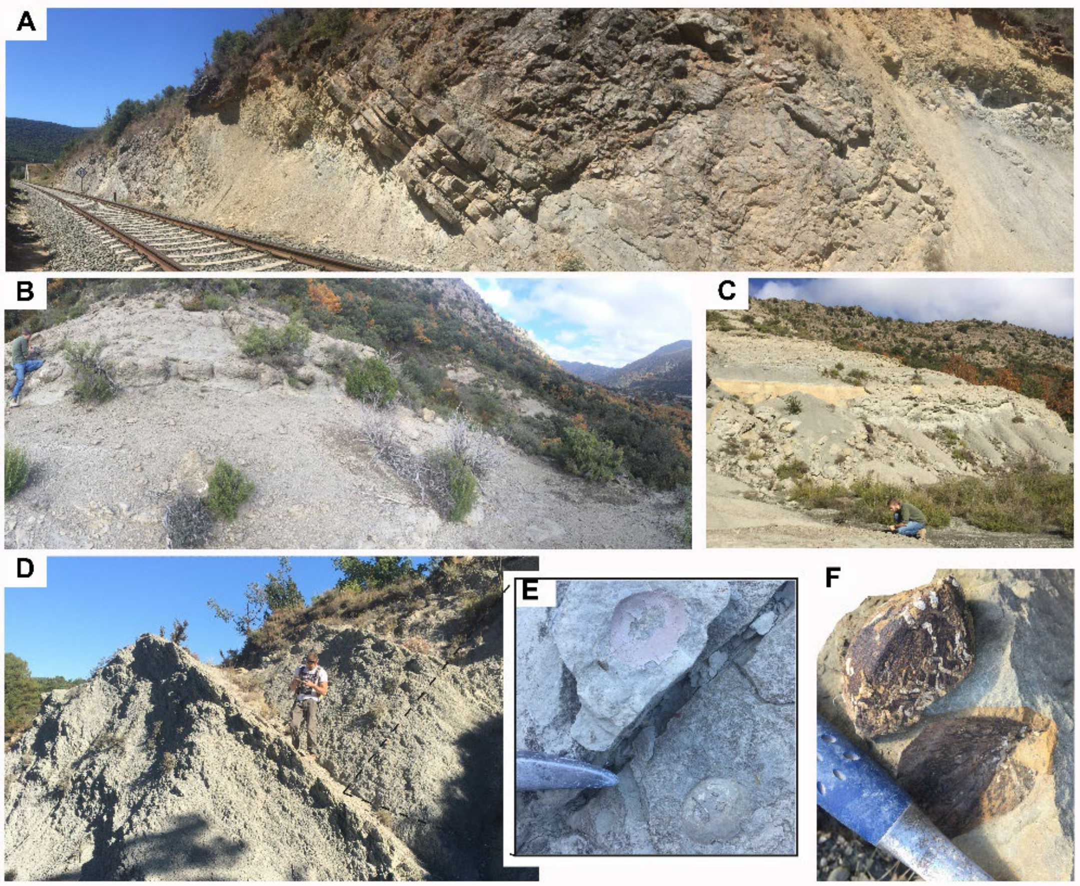


Figure 3. **A**: Sequence IV (near log 3, Fig. 1C): off-shore well-bedded sandstones overlying the reefal units where *Eocalcinus gerardbretoni* was found; **B**: panoramic view of *Belsue platform beds* (Sequence I) near Lusera (see Be4 in Fig. 1B); **C**: lower part of the Sequence IV, to the east of Triste (see T en Fig. 1A); **D**: Marls and sandstones from the lower part of Sequence II (see Br1b in Fig. 1B); **E**: Detail of *Harpactocarcinus punctulatus* (part and counterpart) found *in situ* in the lower part of Sequence II (Br1b). **F**: *Nypa* sp. colonized with *Teredolites* sp. found in the upper part of *Arguís platform* bed near the hinge of the Pico del Aguila anticline (see PA6in Fig. 1B).

- Sequence III

As in the previous sequences, the lower part of Sequence III consists of azoic marls. Further carbonate-dominated shallow marine facies in the Bentue de Rasal syncline are found in the upper part of the sequence, in the so-called ***Pectinid platform beds*** (Millán et al., 1994; see Fig. 4F). These beds are stacked in elemental parasequences formed by couplets of fossiliferous marls and decimetre to metre thick limestones (wackestones to packstones), arranged in turn in coarsening and shallowing upward sequences, between 10 and 20 m thick (Millán et al., 1994). Paleontological content is dominated by red algae, bivalves, echinoids (Fig. 4G), bryozoans, miliolids and other foraminifers. Decapods in this sequence are few and mostly fragmentary (see below).

- Sequence IV

Sequence IV consists of three different facies (see Millán et al., 1994). The more proximal one corresponds to sandy marls and cross-bedded sandstones (Belsué-Atares Formation) corresponding to successive delta lobes prograding onto prodelta marls. Blue marls (outer ramp facies) and interlayered skeletal graded beds are found at the base of the distal sector of Sequence IV. These sharply grade to a level with abundant coral buildups. Above these materials, marls and siliciclastic tabular beds with planar or low angle lamination deposited in a shallow marine to littoral environment (Fig. 3A), above storm wave base level and interlayered bioclastic beds (Fig. 1C), are found. This unit is included in the Yeste-Arres Formation, a lateral equivalent of the Belsué-Atares Formation (Puigdefábregas, 1975).

The facies interval of Sequence IV with the most diverse decapod fauna corresponds to the coral buildup facies (Ferratges et al., 2020a). Medium to large reef structures are overlying a relatively deep marly-clayed interval, and developed at euphotic to mesophotic depths, around or below the storm wave base (see Morsilli et al., 2012; Ferratges et al., 2020a). The coral buildups contain boundstone facies of scleractinian coral colonies mostly in growth position and are always encased in blue marly clays. This lithofacies occurs in nodular biostromal beds or in small bioherms, which may amalgamate to form up to 40 m thick buildups (Morsilli et al., 2012). Coral growth forms are diverse and can be platy, massive, branched or phaceloid-like (see Morsilli et al., 2012 for details), and each morphology harbours different associations of decapod crustaceans (Ferratges et al., 2020a).

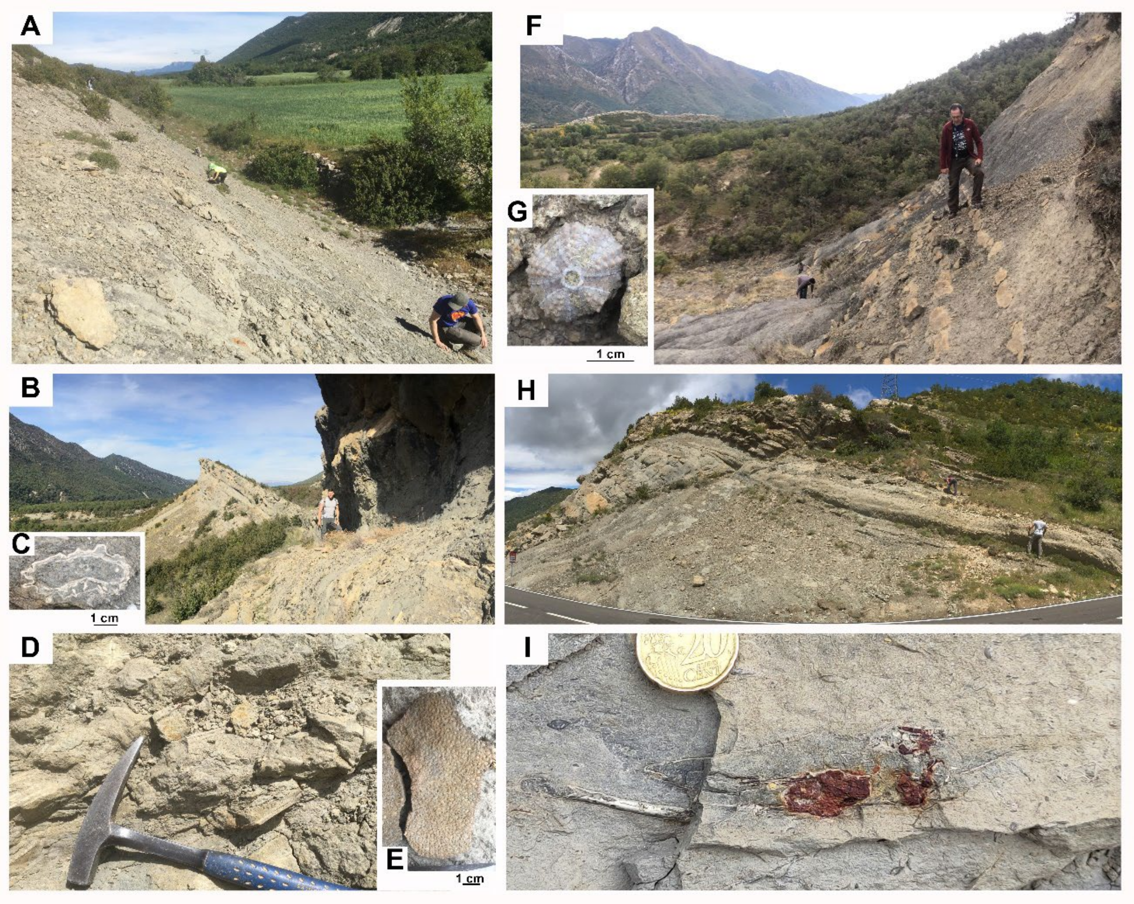


Figure 4. Views of different outcrops that have provided crustaceans. **A**: Hardground on the top of the Sequence II, in the upper part of the Bryozan beds (Br3 in Fig. 1C); **B**: Bryozoan beds near the BR section (Br1a in Fig. 1); **C**: Echinoid section incrusted by calcareous algae (in Br1a site); **D**: Small sponge bioherm included in the Bryozoan beds near to Bentué de Rasal (see Br1a in Fig. 1C); **E**: detail of a well-preserved sponge from Bryozoan beds; **F**: Alternating grey marls and skeletal sandy limestones in the lower part of Pectinid platform beds (Sequence III, see Br2 in Fig. 1C); **G**: detail of *Coelopleurus coronalis* found in situ in the Pectinid platform beds; **H**. The upper levels of Sequence II in the Pico del Aguila section (PA6 in Fig. 1A); **I**: in situ cross section of articulated Portunus catalaunicus in PA6.

4.2. Decapod composition

The facies described above have provided a significant diversity of invertebrates, including decapod crustaceans, showing different assemblages in different palaeoenvironments (see summary in Tables 1 and 2, and Fig. 5). The decapod assemblages of some beds of the studied area have similarities with decapods collected in other Eocene localities from Spain (e.g., Via, 1959, 1969, 1991), Italy (see, e.g., De Angeli and Caporiondo, 2009; Busulini et al., 2012; Beschin et al., 2013; Tessier et al., 2011), Slovenia and Croatia (Schweitzer et al., 2005, 2007). These decapod assemblages reflect a wide range of environments, ranging from soft bottoms with higher clay content, to sandy and carbonate bottoms including coral reefs.

Taking all facies together the most abundant species in the studied area is *Harpactocarcinus punctulatus* (21.5%), followed by representatives of the families Pilumnidae (18.3%), Carpilidae (15.1%), Dairidae (8.6%), Portunidae (3.8%), Axiidae (3.2%), Calappidae (3.2%), Raninidae (2.1%), Aethridae (2.1%) and Paguridae (2.1%). Minor components include taxa of ten families, corresponding to 9% of the total sample. Finally, 42 isolated remains could not be assigned with confidence to any group (11.3 per cent of the total sample) (see Table 1).

The area of the Belsue syncline located between the Lúsera and Pico del Águila anticlines (“L” and “PA” in Figure 1C) contains a great decapod diversity (Table 3). Specifically, the easternmost sector of *Belsue platform beds* located close to Lúsera is composed of siliciclastic sandstones (Fig 1C, outcrops L, Be2), with specimens of *Retrocypoda almelai*, *Portunus catalanicus*, isolated fragments of *Montezumella* sp. (probably *M. amenosi*) and unidentifiable crab remains (?*Eriphia*). This association is similar to that of the Catalonian central sector (Via, 1969). However, in the western flank of the syncline (Fig 1C, outcrops Be4-Be6), the sediments present a finer grain size and are greyish in colour. This lithological change is accompanied by a radical change in the faunas, with a predominance of *Harpactocarcinus punctulatus* in the lower sandstone beds and a poorly preserved associated fauna composed of irregular echinoids, molluscs and fish remains. Occasionally, other crabs like *Magyarcarcinus yebraensis* and *Retropluma eocenica* are found. The specimen of *M. yabraensis* (Fig. 5H, MPZ 2016/77) was incorrectly reported by Domínguez and Ossó (2016) from Yebra de Basa.

Upwards, the number of decapods progressively decreases and their diversity varies, gradually giving way to a predominance of *Portunus catalaunicus* in the upper layers (Fig. 4I), in association with Callianassidae indet. (some of these remains are associated with burrows), and occasionally ?*Raninoides* sp. This last association shows its bloom in the upper part of the PA and L anticlines (logs 8 and 10 of Fig. 1) and decreases again to the west (Fig. 6).

Both the Pectinid platform and the Bryozoan platform contain similar faunas, associated with siliciclastic bottoms and bio-construction organisms such as sponges, with the predominance of large carpiliids (“*Menippe*” *almerai*). Other components of the Bryozoan platform include raninids (both *Lophoranina* sp. and *Notopus* sp.), calappids (*Calappilia* sp. and *Bittnerilia* sp.), and occasional portunid remains, majids (*Periacanthus* sp.), xanthids and astacids (*Enoploclitia* sp.). In the Pectinid platform, additional taxa include paguroids, dromiids and leucosids.

Finally, reef complexes contain a relatively high diversity and abundance of remains (Tables 1-3) condensed in a relatively small section. They include *Enoploclytia*?, *Petrochirus*?, *Gemmellarocarcinus riglosensis, Liopsalis* cf. *anodon*, *Ocalina*?, *Galenopsis crassifrons*, *Lobogalenopsis joei*, and *Daira corallina*. In addition, representatives of the family Trapeziidae?, carpiliids and remains of four other indeterminate taxa have been found (Ferratges et al., 2020a). These faunas are not found outside the reef domain and correspond to specialized taxa in this type of environment. For this reason, we assumed they were autochthonous or suffered little transport (see Ferratges et al., 2020a, for details).

4.3. Preservation of decapod crustaceans

The preserved remains of decapod crustaceans are composed of both complete and fragmented carapaces (aprox. 50%) and isolated and broken fragments (aprox. 20%). Only approximately 30% of the remains appear articulated. Recent studies on taphonomic processes in decapod crustaceans show the rapid disarticulation of the remains under normal marine conditions (see Klompmaker et al., 2017, for variable periods under laboratory-controlled conditions; Mutel et al., 2008, Krause et al., 2015, for experiments at different depths during varied periods for a single species).

Apparently, the proximal areas, both shallow and deep, contain a greater number of articulated specimens. In the case of the distal zones, only the deep facies provide articulated material (with some occasional exceptions). This may be due to a high rate of sedimentation during sudden sedimentary input. In general, the more distal facies preserve more fragmentary material (see Fig. 5). However, near to the bottom of Sequence II in the distal zone (Log 5 of Fig. 1), articulated specimens of *H. punctulatus* are abundant in sandstones of decimetre-scale (Fig. 3D).

Most articulated specimens come from the proximal areas of the Arguis and Belsue platform beds, possibly due to rapid burial produced by high energy events (i.e., Ferratges et al., 2020b). Species like *Harpactocarcinus punctulatus*, *Portunus catalaunicus, Retrocypoda almelai*, *Pyreneplax* cf. *basaensis* and *Diogenes augustinus* can be found articulated in siliciclastic proximal areas. *Harpactocarcinus punctulatus* is especially abundant and almost always appears articulated (23.3% of the total assemblage).

The material found in the carbonate-dominated Bryozoan beds, the distal equivalent to the terrigenous-dominated Arguis and Belsue platform beds, presents a relatively greater diversity, but in general, represented by much more fragmented remains. Considering all data presented herein, it seems that the preservation of decapod crustaceans within the Bryozoan beds and Pectinid platforms was controlled by certain taphonomic aspects that favoured preservation of some groups (see above). In this area there are rare examples of large articulated carpiliids (probably the species "*Menippe*" *almerai*) and isolated carapaces and chelipeds of the same taxon (3.7% of the total assemblage). Development of sponges meadows normally require from low sedimentary rates (i.e., Busquets et al. 1991, 1994, 1997; Astibia et al. 2016). Finally, in the coral buildups from the sequence IV the remains correspond mainly to disarticulated specimens (isolated carapaces and disarticulated chelipeds or pereiopods), with the exception of some partially articulated specimens of *Galenopsis crassifrons*. Coral reefs are very sensible for high sedimentary inputs and remains of decapod crustaceans in these environments are often disarticulated or fragmented due to the large time of exposure in the sea floor (Ferratges et al., 2021a).

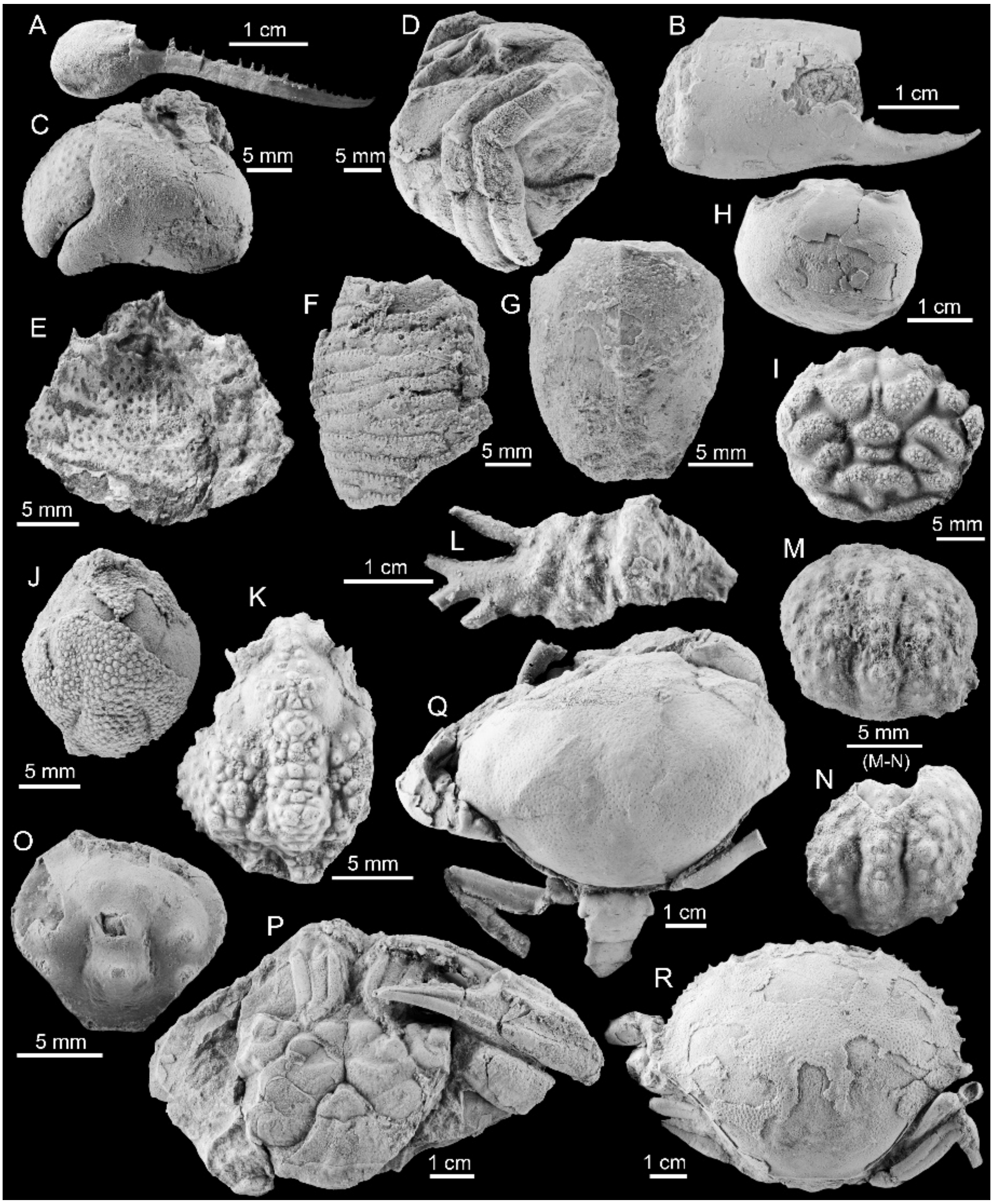


Figure 5. Some of the most characteristic taxa of the studied area. **A**: *Ctenocheles* sp. from Be4 site; **B**: Callianassidae from PA8 site; **C**: *Eocalcinus gerardbretoni* Ferratges, Artal & Zamora, 2021 (MPZ 2020/617) from Eo site (taken from Ferratges et al., 2021b); **D**: Left lateral view of *Diogenes augustinus* Ferratges, Zamora & Aurell, 2020 (MPZ2020/54) from Be4 site (taken from Ferratges et al., 2020b); **E**: Dromidae indet from SM site; **F***: Lophoranina ?straeleni* Vía, 1959 from Br3 site; **G**: *Notopus* sp. from Br3 site; **H**: *Magyarcarcinus yebraensis* Domínguez & Ossó, 2016 (MPZ 2016/77) from Be5 site; **I**: *Pyreneplax basaensis* Ossó, Domínguez & Artal, 2014 from A1 site; **J**: Leucosidae indet. from SM site; **K**: *Micromaia* cf. *priaboniensis* from SM site; **L**: *Periacanthus horridus* Bittner, 1875 from A2 site; **M-N**: *Calappilia ?verrucosa* A. Milne Edwards in Bouillé, 1873 from Cal and A1 sites respectively; **O**: *Hepatiscus* cf. *neumayri* Bittner, 1875 from Be4 site; **P**: male specimen of *Portunus catalaunicus* Via, 1941 from Be4 site; **Q**: Carpiliid indet. from Br1a site; **R**: *Harpactocarcinus punctulatu*s Desmarest, 1822 from Be5 site.

4.4. Decapod distribution

The decapod assemblages correspond to different palaeoenvironments, associated with clearly differentiated biotopes, and generally associated with shallow waters. Most of these taxa appear associated with unconsolidated bottoms (soft bottoms and sandy bottoms) with different benthic communities, and occasionally associated with biostructure-building organisms such as sponges (Bryozoan Beds and deep areas of Arguis/Belsue platform beds) and corals (Coral-buildups, see Ferratges et al., 2020a).

The **Arguis and Belsue platforms** host the greatest diversity and abundance of decapod crustaceans (Fig. 6) and is mainly composed of medium to large crabs (see Table 3). However, these facies have different decapod crustacean assemblages both laterally and vertically with a variable distribution. In fact, deeper facies can be distinguished from shallow facies on these platforms by differences in diversity and different assemblages of decapod crustaceans.

In the shallow and more proximal facies of Belsue and Arguis platform located in the Belsue syncline (Cal, Be2, Be3, L), the most abundant taxon is *Portunus catalaunicus,* represented by large and articulated specimens, representing 25.0% of the sample in this facies, followed by Axiidae and Ctenochelidae (both *Ctenocheles* and *Callianassa* sp.) (17.9%), Aethridae (14.3%), Calappidae (14.3%), Paguridae (10.7%). Minor components represent 17.9% of the total (Eriphidae, Majidae, Montezumellidae and Retroplumidae). On the other hand, in the deeper facies the most abundant taxon is *Harpactocarcinus punctulatus*, represented by large and articulated specimens, representing 87.0% of the sample in this facies. Minor components represent 7.3% of the total of this area (Axiidae, Goneplacidae and Retroplumidae). The indeterminate taxa represent 5.8% of the total assemblage (see Tables 1 and 2).

Table 3 summarizes the number of species found in the different facies. The highest number of species is contained both in the pectinid platform (PP) and Bryozoan beds (BB), followed by reef facies (CB), shallow areas of the Belsue platform (BP shallow) and proximal areas of the Arguis platform (AP prox.). Deep areas of the Belsue platform (BP deep) and distal areas of the Arguis platform (AP distal) contain a lower number of species (Table 3). In terms of evenness, all sites have an evenness ranging from 0.35 to 0.85, (except AP distal) which implies that more than one species are important contributors to the decapod diversity at each zone (Fig. 9C).

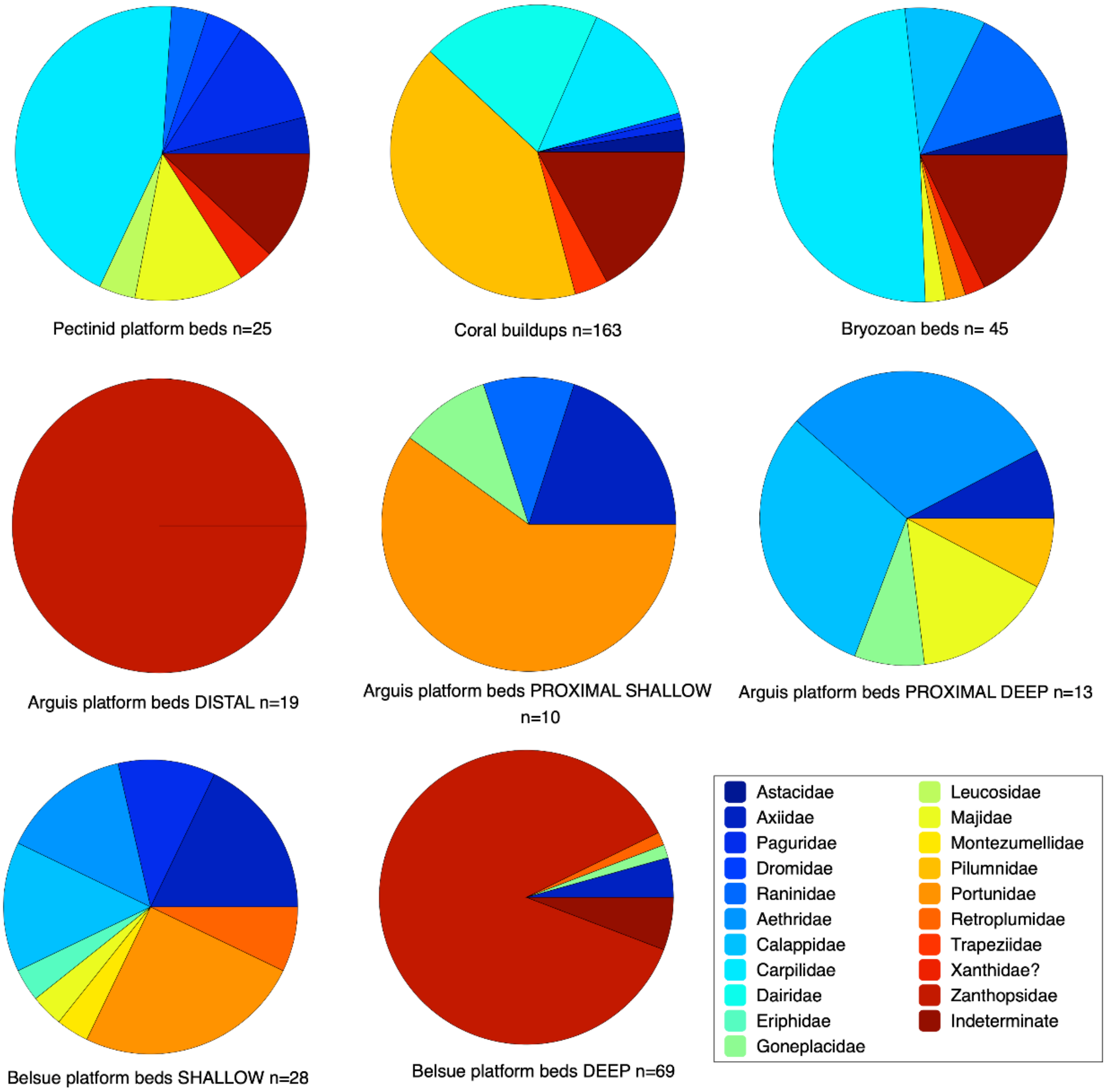


Figure 6. Pie charts showing the relative abundance and diversity of the different decapod crustacean groups in the different facies.

	Pectinid Plat.	Coral buildups	Bryozoan beds	Arguis Plat. dist.	Arguis Plat. prox. deep	Arguis Plat. prox. shallow	Belsue Plat. shallow	Belsue Pat. deep
Specimens	22	**135**	37	19	10	13	28	65
Species	**11**	10	**11**	1	6	4	10	5
Superfamilies	8	7	7	1	6	4	**9**	4
Simpson's Index	0,7025	0,6653	0,6034	0	0,58	0,7692	**0,8444**	0,1453
Shannon-Wiener index	1,592	1,332	1,295	0	1,089	1,605	**1,995**	0,3443
Chao-1 Index	**18**	7	8,5	1	4,5	7,5	10,5	5
Average size (Aprox) in mm	20,8	40	50,4	44,4	16,2	70,8	**77**	66

Table 3. Diversity metrics for the studied facies (highest values in bold). The indeterminate specimens are not included. Average size of the carapace in the different areas studied. The averages of each area have been calculated from the width of the carapace of the crabs of each area. The data is approximate since many specimens are incomplete due to erosion processes.

At the central sector of the studied area (in the Arguis syncline, between “PA” and “BR” in Figure 1) corresponding to the middle and distal area of the *Arguis platform*, an increase in diversity of the benthic organisms includes abundant bivalves (pectinids), gastropods, bryozoans (branched and dome-shaped) and echinoderms. Regarding decapod crustaceans, we have recognized *Galenopsis* sp., *Hepatiscus* sp., *Calappilia* sp., *Periacanthus* cf. *horridus*, *Pyreneplax* cf. *basaensis* and indeterminate Callianassidae. In addition, we found large crabs in proximal areas (*Harpactocarcinus punctulatus* and *Portunus catalaunicus*) that are absent in the distal equivalent layers. Also notable is the high degree of disarticulation of these remains, and the reduction in the body size of the taxa, with an average width of approximately 1.5 cm in distal areas to 6 cm on average in the proximal areas (Table 3).

In the distal lateral equivalent of the Belsue platform (log 5 of the Fig. 1C), near the base of Sequence II, decimetre-scale sandstone layers appear between the massive marly levels. The species *Harpactocarcinus punctulatus* is abundant here, but they are smaller than those of the proximal facies of the Belsué platform (see Appendix), and represent 100% of the sample for these facies (see Tables 1 and 2).

The **Bryozoan Beds** have an intermediate diversity (Fig. 6) and a relatively low abundance of decapod crustaceans (Tables 1, 2, 3 and Fig. 6). However, rarefaction curves suggest a high diversity for this area (Fig. 7). In this lithofacies, the dominant group is the carpiliids (48.9% of the total of this facies), mostly composed of broken fragments, followed by raninids (13.3%), and calappids (8.9%). Minor components (Astacidae, Majidae, Portunidae and Xanthidae) account 11.1% of the total of this facies. Several unidentified fragments have also been found, representing 17.8% of the total assemblage.

The association of decapod crustaceans in the **Bryozoan beds** is relatively diverse, but generally composed of disarticulated and usually fragmented material (Fig. 6). The presence of remains of large carpiliids stands out, which eventually appear articulated (Fig. 5P), accompanied by smaller-sized fauna (*Enoploclytia* sp., *Periacanthus* sp., *Calappilia* sp., *Bitnerilia* sp., *Lophoranina* sp. and *Notopus* sp.). Other macrofauna that we have been able to identify are tube-dwelling polychaetes (*Rotularia* sp.), bivalves, giant gastropods (Gisortiinae), diverse and large sponges (occasionally forming bioherms) and very abundant and diverse echinoderms (regular and irregular echinoids, and disarticulated ossicles of crinoids and goniasterid asteroideans). The bryozoan beds are bounded on top by a hardground surface rich in glauconite and fragmented remains of crabs. Among them are the presence of raninoids (*Lophoranina* sp. and *Notopus* sp.), calappids (*Calappilia* sp.) and very fragmented remains of large carpiliids as well as other fauna (small gastropods, echinoderms, shark teeth and isolated bones).

The **Pectinid Platform beds** have provided a great diversity and abundance of benthic groups like bivalves (pectinids and oysters), gastropods (*Pleurotomaria* sp., *Conus* sp., turritellids and others) nautiloids, and echinoderms like *Coelopleurus* sp. (Fig. 4G) and other minor components such as Brissidae, Cassidulidae, Cidaroidea, Clypeasteridae, ?Cyclasterinae, Echinolampadidae, Eupatangidae, ?Hemiasteridae, ?Laganinae, Micrasteridae, Palaeostomidae, ?Plesiolampadidae, Prenasteridae, Schizasteridae, Scutellinidae and ?Temnopleuridae. However, this interval has provided little abundance but relatively diverse decapod crustaceans (Fig. 6, Table 1), and almost all the remains are disarticulated or fragmented (except for a leucosid specimen that preserves the thoracic elements). In this lithofacies, the most abundant taxon is represented by very fragmented Carpiliids (44% of the crustacean remains of this levels) followed by pagurids (12%) and majids (12%). Minor components belonging to five different families (Tables 1 and 2) represent the remaining 20% (Axiidae, Dromiidae, Raninidae, Leucosidae and Xanthidae). Indeterminate taxa represent 12% of the total assemblage of these levels.

The decapod assemblage collected from the **Coral buildups** facies (mainly La Peña buildup) correspond to taxa associated with reef environments (see Ferratges et al., 2020a for details). This assemblage includes representatives of the genera ?*Enoploclytia* McCoy, 1849, ?*Petrochirus* Stimpson, 1858, *Gemmellarocarcinus* Checchia-Rispoli, 1905, *Liopsalis* Von Meyer, 1862, ?*Ocalina* Rathbun, 1929, *Galenopsis* A. Milne-Edwards, 1865, *Lobogalenopsis* Müller & Collins, 1991, and *Daira* De Haan, 1833, and representatives of the family ?Trapeziidae Miers, 1886, carpiliids and remains of four other indeterminate taxa have been found (Table 1). Recently, the distribution of different coral domains has been studied (Ferratges et al., 2020a), showing the preferential distribution of different groups of crabs in the same reef environment.

The sandstones above the Coral buildups have provided very little material of decapod crustaceans (*Eocalcinus gerardbretoni* Ferratges et al., 2021b). However, other benthic fauna is abundant, especially gastropods. Some of these correspond to giant gastropods such as *Campanile* sp. whose presence has been associated with marked seasonality and ideal conditions for the development of shallow marine biodiversity (i.e., Winter et al., 2020).

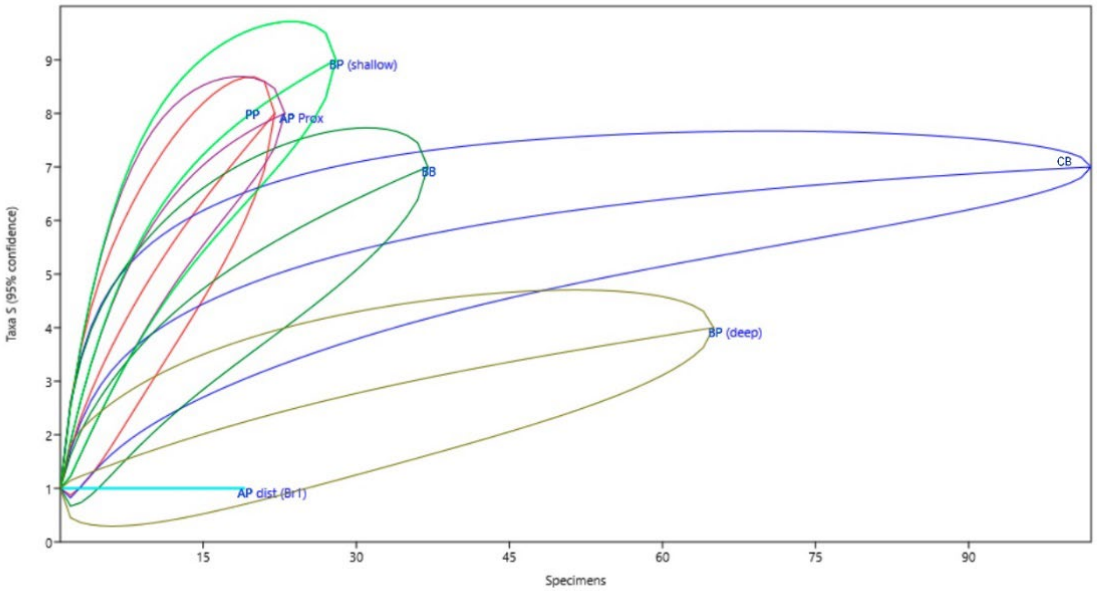


Figure 7. Rarefaction curves for decapod crustacean families from the studied zones with 95% confidence intervals based on collected specimens. The trajectory of the means (middle lines) may suggest that PP preserves the highest diversity.

5. Discussion

Understanding how diversity fluctuates in a single taxonomic group in relatively small areas is sometimes hampered by sampling and taphonomic biases. The exceptional exposure of four stratigraphic sequences allowed a detailed sampling of different lithofacies and intervals (Figs. 1, 3 and 4). This allows quantification of decapod occurrences of each taxon and their distribution. Results show that decapod distribution is not random but shows a pattern that might result from the original zonation of decapod crustaceans and their original preferences for certain environments coupled with specific taphonomic conditions (Figs. 6, 7 and 8). Stratigraphic studies of the areas in which decapod crustaceans occur allow us to correlate changes in sedimentary environments ultimately related to changes in the evolution of the basin.

The taxa recognised in the studied area have significant variation in their relative abundance in the different facies, identified as glauconitic sandy marl (Gl), bryozoan beds (Br), pectinid platform (Pc), siliciclastic platform (Sil) and coral growth (Cor) (Fig. 6). Relatively complete preservation with articulated specimens occurred mostly in proximal shallow and in relatively distal deep areas. This is probably related to the most favourable taphonomic conditions (higher sedimentation rates in shallow areas and less energy in the deep areas).

In modern ecosystems, changes in benthic fauna follow a depth gradient and are probably related to changes in sediments and the physical stability of local water bodies (Sumida and Pires-Vanin 1997). Some authors (i.e., Paiva, 1990; Pires, 1992; Pires-Vanin, 1993; Bertini and Fransozo, 2004) suggested that in the first tens of meters of depth (generally between 10 and 40 m, and up to 100 m) the sediment type is the most relevant factor in the distribution of benthic macrofauna, but from depths close to 40 m, temperature significantly affects their distribution. Other important parameters are local differences in hydrodynamics and high sedimentation rates, which can reduce the living space of decapods, varying the diversity and abundance of species (see Morgado and Tanaka, 2001). Based on the distribution and role of modern decapod crustaceans, some questions arise that are discussed below.

5.1. Are changes in decapod crustacean diversity correlated with the type of facies? (carbonate vs. siliciclastic environments)

Analyses of facies and diversity has been presented in previous studies (Ferratges et al., 2020a, 2021a), but in the current studied outcrops facies changed in a single area responding to sedimentary input and tectonic-induced sedimentary processes. Sampling in the different facies of the study area shows a very uneven distribution of taxa, showing different decapod assemblages associated with different facies (Fig. 8). This can be explained because the different facies of the study area correspond to different palaeoenvironments with very different ecological and taphonomic conditions (see Millán et al., 1994; Morsilli et al., 2012).

Eocene decapod crustaceans, like modern representatives, show adaptations to live in a wide range of environments, interacting with other organisms like algae, sponges and corals (i.e., Alves et al., 2012; Davie, 2021 for modern species). Some of the studied intervals preserve these types of environments and the decapod communities that inhabited them (Fig. 8). Decapod crustaceans in carbonate-dominated reef intervals of this area show species that are absent in other areas which correlate with the very specific conditions of reefs (see also Ferratges et al., 2020a).

In the *Bryozoan beds* dominated by carbonate fabrics, sponges constitute important bioherms that also host certain taxa. Sponges are an important component of benthic ecosystems in modern tropical and temperate regions (Wenner et al., 1983) and are inhabited by a wide diversity of invertebrates, including decapod crustaceans (Klitgaard, 1995; Duarte & Nalesso, 1996; Caruso et al., 2005; Bezerra & Coelho, 2006; Alves et al., 2012). Large carpiliids (the species "*Menippe*"*almerai*) are relatively abundant in this environment in the study area associated with sponge meadows. This taxon is represented in the siliciclastic materials of the *Pectinid platform beds,* but only by isolated fragments, which suggests that correspond to transported remains (allochthonous).

In particular, the species *Harpactocarcinus punctulatus* seems to show a greater ability to exploit their environment (occurs in large numbers in the intervals where this taxon is present) and is the most abundant taxon of the studied area, but it varies dramatically between the different sectors (only found on certain levels). This species has been well known for decades and is very abundant in different Tethyan areas during the Eocene (see Schweitzer et al., 2007, and references therein).

The environmental preferences of this species and other representatives of the family Zanthopsidae Via, 1959, have been studied by some authors (Schweitzer et al., 2005, 2007). These studies hypothesized that this group seemed to be restricted to off-shore habitats, below the wave base and in clear water. The presence of complete and articulated specimens of *H. punctulatus* at specific levels of the studied area seems to indicate that these animals are autochthonous and prefer relatively deep siliciclastic and sandy marl environments with sponges, bryozoans and molluscs. However, when carbonate facies are stablished *H. punctulatus* disappear.

Although the specimens of *H. punctulatus* found near to the bottom of Sequence II in the distal zone (Log 5 of Fig. 1) are articulated, the mode of preservation is different from those of the proximal areas and these appear compressed and with a much-degraded cuticle (Fig. 3E), probably due to diagenetic processes.

The new data provided here supports previous suggestions (Schweitzer et al., 2005, 2007) about the environmental preferences of *H. punctulatus*, but we also pointed out their tolerance to deeper waters, and that they could not cope with a change in conditions to a softer bottom consisting of lime mud.

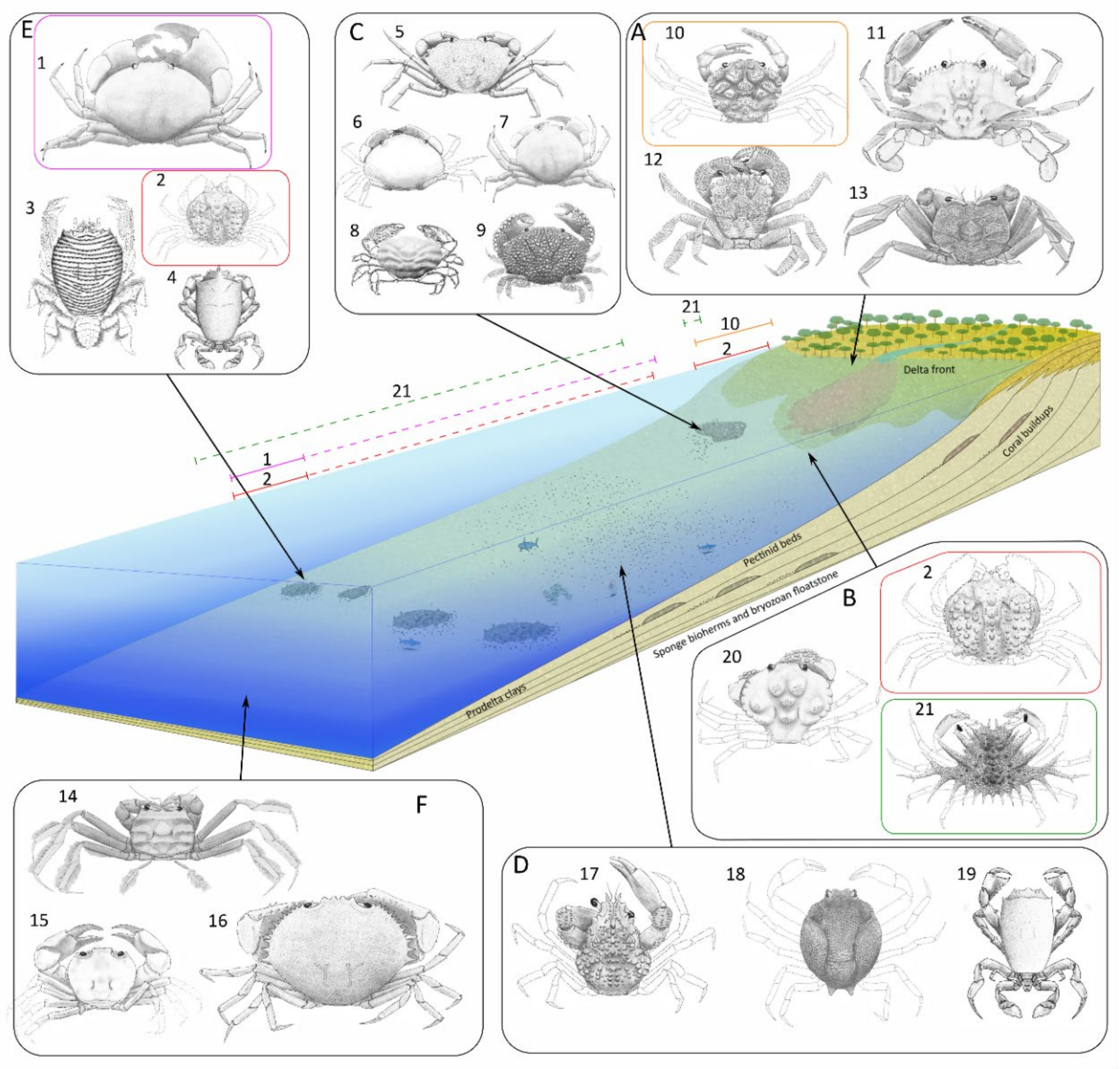


Figure 8. Simplified reconstruction of the study area with the distribution of different facies and the different assemblages of crabs found in different environments. **A-F**: different decapod assemblages of the studied area (only brachyura). The geographical subdivisions produced by the different anticlines have been omitted to simplify the scheme. Individually framed taxa have larger distribution areas, marked with a dashed line of the same colour as each box where their record is less fragmentary preservation and scattered remains, and a solid line of the same colour where their record is less fragmentary and continuous. Taxa: **1**: Carpilidae indet. 1; **2**: *Calappilia* sp.; **3**: *Lophoranina* sp.; **4**: *Notopus* sp.; **5**: *Galenopsis crassifrons*; **6**: *Liopsalis anodon*; **7**: Carpilidae indet. 2; **8**: *Gemmellarocarcinus riglosensis*; **9**: *Daira corallina*; **10**: *Pyreneplax* cf. *basaensis*; **11**: *Portunus catalaunicus*; **12**: *Montezumella* cf. *amenosi*; **13**: *Retrocypoda almelai*; **14**: *Retropluma eocenica*; **15**: *Magyarcarcinus yebraensis*; **16**: *Harpactocarcinus punctulatus*; **17**: *Micromaia priabonensis*?; **18**: Leucosidae indet.; **19**: *Quasilaeviranina* sp.; **20**: *Hepatiscus* sp.; **21**: *Periacanthus horridus*. (A11-13, B20-21, D17, E1-2, F14 and 16 taken from Ferratges, 2017; C5 and 9 taken from Ferratges et al., 2020a).

5.2. What is the influence of distal vs. proximal on faunal diversity?

Variations in diversity related to paleo-bathymetry and proximity to the coastline have been observed in this work. In the case of of the Arguis and Belsue platform beds there is a marked difference between the shallow proximal facies and the deeper facies.

Shallower facies are dominated by *Portunus* and deeper facies with *Harpactocarcinus*. The smaller size of the specimens of *Harpactocarcinus* found in the distal areas (Br1), equivalent to deeper zones, may be related to a lower supply of nutrients or other limiting factors that control their growth, but not their dominance in the benthic ecosystem.

Based on our sampling (Figs. 6 and 7) and the Shannon index (Fig. 9B), the data obtained suggests that the greatest diversity is concentrated on the shallow and proximal areas. The Chao1 index (Fig. 9D), which estimates the number of taxa, is highest in the Pectinid platform (PP). However, the fact that several taxa are represented by a low number of specimens (Table 1), and in general, very fragmented remains, suggests that most of these taxa have been transported from the shallow and proximal areas. These indexes (both Shannon and Chao1 index) are highest for the Belsue platform (BP shallow, corresponding to shallower waters). The Shannon index measures specific diversity. Our study area show a Shannon index of 1.995 for the shallow areas of Belsue platform (BP shallow), but only 0.3443 in the deeper and more distal areas of the same facies. The same result applies to the proximal areas of Arguis platform (AP proximal), with 1.922 in the proximal areas, and 0 in the distal ones. PP, CB and BB show intermediate values.

The *Bryozoan beds* correspond to sedimentation in a shallow platform area. The sequence boundary located atop of this unit (i.e., boundary between Sequences II and III) is a drowning unconformity with a glauconite-rich condensed and hardened interval formed due to very reduced sedimentary rates. This sedimentary stoppage could have allowed the establishment of a diverse benthic community, and the proliferation of decapod crustaceans like happens in modern ecosystems (Morgado and Tanaka, 2001). In general, the *Bryozoan beds* presents a rich and diverse benthic community, with an interesting diversity of decapod crustaceans, distributed in different areas (see Table 1).

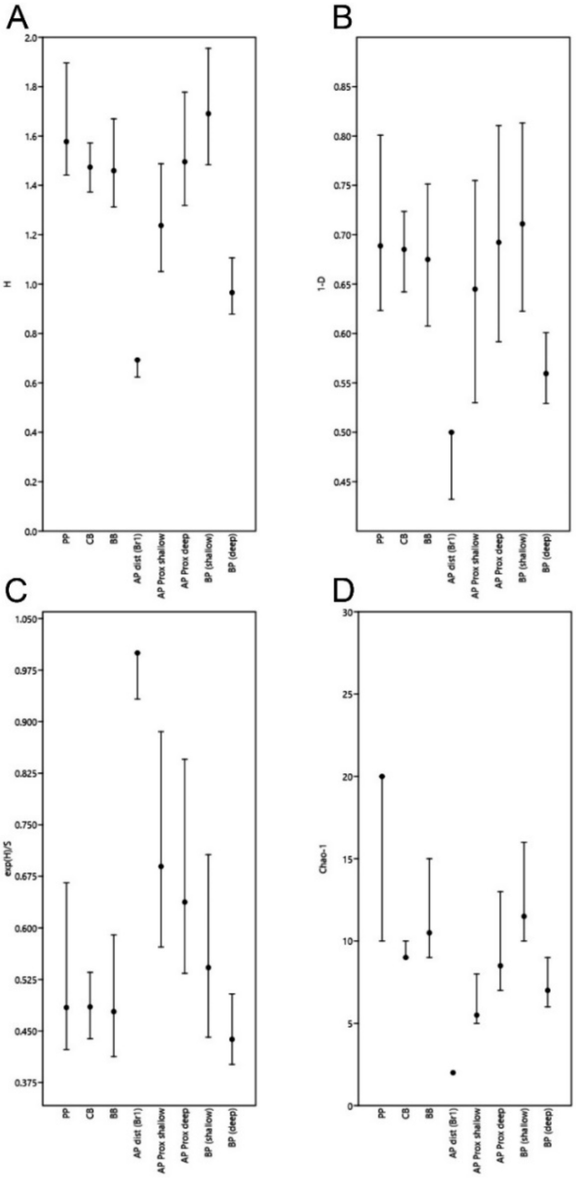


Figure 9. Diversity index: **A**: Shannon index for decapods of the main zones; **B**: Simpson index; **C**: Evenness index; **D**: Chao-1 index giving the estimated number of taxa for each site and the standard deviations. Legend: PP: Pectinid Platform; CB: Coral Buildups; BB: Bryozoan beds; AP dist (Br1): Arguis Platform distal; AP Prox shallow: Arguis Platform shallow area; AP Prox Deep: Arguis Platform deep area; BP (shallow): Belsue Platform shallow area; BP (deep): Belsue Platform deep area.

The crustacean site found in the glauconite level (Br3) records an increase in diversity in decapod crustaceans, but other remains such as endobenthonic echinoderms, crinoids and vertebrate remains (especially shark teeth) are also very abundant. Low sedimentation rates in a relatively shallow environment relatively far from the coastline, could allow the settlement of a complex benthic community. A dramatic and sudden disappearance of these faunas is observed above this level due to the widespread deepening giving rise to major platform flooding and the onset of the sedimentation of the outer ramp marl succession of the overlying Sequence III.

6. Conclusions

Distribution of decapod crustaceans from the Jaca-Basin, Southern Pyrennes is analysed in a carbonate-siliciclastic system with syntectonic activity that affected the distribution of different facies during the middle-late Eocene. A total of 39 species show heterogeneous distribution in different environments. They are mostly preserved as claw fragments or isolated carapaces, with different degrees of abrasion and breakage. The results suggest that the distribution of decapods in the Jaca basin was influenced by environmental factors and facies development. The faunal distribution of decapods shows important differences in terms of both relative abundance and diversity in each of the facies. The composition of the studied community suggests a complex structure, comprising of species from different superfamilies that exploit different niches.

The shallow and proximal facies show the highest diversity and abundance, and this can be controlled by both biological and taphonomic factors (higher production and higher sedimentation rate). These analyses reinforce the hypothesis that environments with bio-constructions (such as sponge bioherms, bryozoans or coral reefs) contain a great diversity of decapod crustaceans. All the data in the previous sections suggest that the zone with the greatest diversity of taxa corresponds to the proximal shallow areas.

Thus, based on a variety of diversity measures, we suggest that shallow areas preserved the most diverse assemblage. Some species preserved in distal/deep zones were transported from shallow areas. For the Simpson's Index of Diversity and Shannon–Wiener Index, the Coral buildups of this area came in third and fourth position respectively. The deep and distal areas contain by far the lowest diversity.

The composition of decapods per facies indicates that different families were distributed across different facies. The pie-charts indicate that the genus *Portunus* is characteristic of the proximal shallow facies. The genus *Harpactocarcinus* are characteristic and dominant in distal deeper facies. Differences and relative abundances and diversity of small and medium size crabs characterize the shallow siliciclastic facies. The coral buildups also appear to show high diversity but intermediate abundance. However, statistical calculations do not make it so clear.

Both the diversity index and the pie-charts clearly reflect that different composition of decapod faunas which suggests that the acceptance of H1.

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6.3. Resumen de resultados acerca de la distribución

A continuación, se resumen los datos más relevantes obtenidos en los casos estudiados. En los artículos correspondientes reproducidos en el apartado anterior se pueden consultar los aspectos más específicos.

6.3.1. Distribución de taxones en el Eoceno de la zona surpirenaica central

Los datos obtenidos a lo largo de esta investigación han permitido determinar algunos de los factores que condicionaron la distribución de los crustáceos decápodos en diferentes momentos y ambientes del Eoceno (ver Ferratges *et al.*, 2020a, 2021c, en preparación). Además, la gran diversidad de taxones asociados a determinados ambientes revela una alta variabilidad en las condiciones de los diferentes ambientes sedimentarios estudiados, tanto en el Eoceno inferior como en el Eoceno medio y superior. Esta diversidad indica diferencias en los niveles de energía, la disponibilidad de nutrientes y otros aspectos ambientales, como la batimetría (ver Ferratges *et al.*, 2021c).

La riqueza de ambientes registrados en el área de estudio es de gran interés, ya que la diversidad moderna está íntimamente ligada al tipo de hábitat. En este sentido, los arrecifes (ya sean coralinos, de esponjas o briozoos) son los hábitats con mayor diversidad (p. ej., Serène, 1972; Abele, 1974; Haig, 1976; Lindberg y Stanton, 1988; Mantelatto y Sauza-Carey, 1998; Morgado y Tanaka, 2001; Taylor y Schindler, 2004). Por otro lado, el conjunto de facies estudiadas, formadas en paleolatitudes tropicales, presenta especial relevancia en el estudio de los decápodos fósiles y la comprensión de su distribución es clave para entender el origen y diversificación de diversos grupos modernos. El motivo es que actualmente las regiones tropicales se consideran "*hot spots*" de biodiversidad (p. ej., Jablonski *et al.*, 2006; Marshall, 2006), concentrando la mayor diversidad de crustáceos, mientras que las menos diversas corresponden a zonas templadas y frías (p. ej., Boschi, 2000; Pohle *et al.*, 2011; Franțescu, 2013). Este hecho, puede haber jugado un papel fundamental en la diversificación y origen de varias familias de decápodos como se discute en el apartado de sistemática.

Para facilitar la lectura de esta Tesis y enmarcar los resultados obtenidos en cada caso de estudio (Eoceno inferior de la Cuenca de Tremp-Graus, y Eoceno medio-superior de la Cuenca de Jaca), se ha considerado adecuado hacer una exposición resumida de los datos más relevantes obtenidos. En los artículos correspondientes reproducidos en el apartado anterior (capitulo 6.2) se pueden consultar los aspectos más específicos. También se ha establecido una comparación entre los taxones registrados en los diferentes sistemas arrecifales analizados en la Tesis Doctoral (Ramals y La Peña), asi como en otros arrecifes Eocenos estudiados en otras cuencas del entorno.

6.3.1.1. Distribución en las plataformas del Eoceno inferior (Cuenca de Tremp-Graus)

El Eoceno inferior de la Cuenca de Tremp-Graus presenta facies asociadas a diversos ambientes, y son especialmente extensos y potentes los niveles de prodelta (miembro Margas de Riguala de la Formación Serraduy, Formación Roda) y las plataformas carbonatadas (miembro inferior de la Formación Serraduy y la Formación Morillo) que contienen una gran diversidad de crustáceos decápodos (ver compilación en Ferratges *et al*., 2022b en Zamora *et al*., 2022). Si bien se han prospectado estas formaciones durante la presente Tesis Doctoral y se ha estudiado parte del material recuperado (ver 7.2. (Tablas) y 7.3 Sistemática), el peso del estudio en este aspecto ha recaído en el afloramiento de la Formación Serraduy en Ramals (Eoceno inferior, Ypresiense), ya que presenta una excelente exposición (Fig. 37). Este afloramiento expone un cinturón de facies arrecifales que incluye biohermos de coral y algas incrustantes de escala métrica estrechamente espaciados y facies interarrecifales asociadas (Fig. 37A).

El afloramiento de Ramals ofrece una excelente oportunidad para entender la interacción de los factores que preservan las comunidades de decápodos fósiles afectadas por diferentes procesos tafonómicos en diferentes facies arrecifales. Según los procesos de depósito y el sesgo tafonómico, los restos de decápodos se pueden conservar cerca de su lugar de vida (p. ej., Allison, 1986; Krause Jr *et al*., 2011). Los restos desarticulados de crustáceos pueden quedar expuestos en la interfase sedimento-agua durante largos períodos de tiempo sin degradarse (Allison, 1986, 1988; Plotnick, 1986; Briggs y Kear, 1994; Mutel *et al*., 2008; Parsons-Hubbard *et al*., 2008; Krause Jr *et al*., 2011; Klompmaker *et al*., 2017). En el caso de los “camarones excavadores o gambas topo” (Callianassidae y Ctenochelidae), solo se conservan las partes endurecidas (es decir, las quelas) debido a la delicada naturaleza del resto de la cutícula (Hyžný y Klompmaker, 2015; Klompmaker *et al.*, 2017).

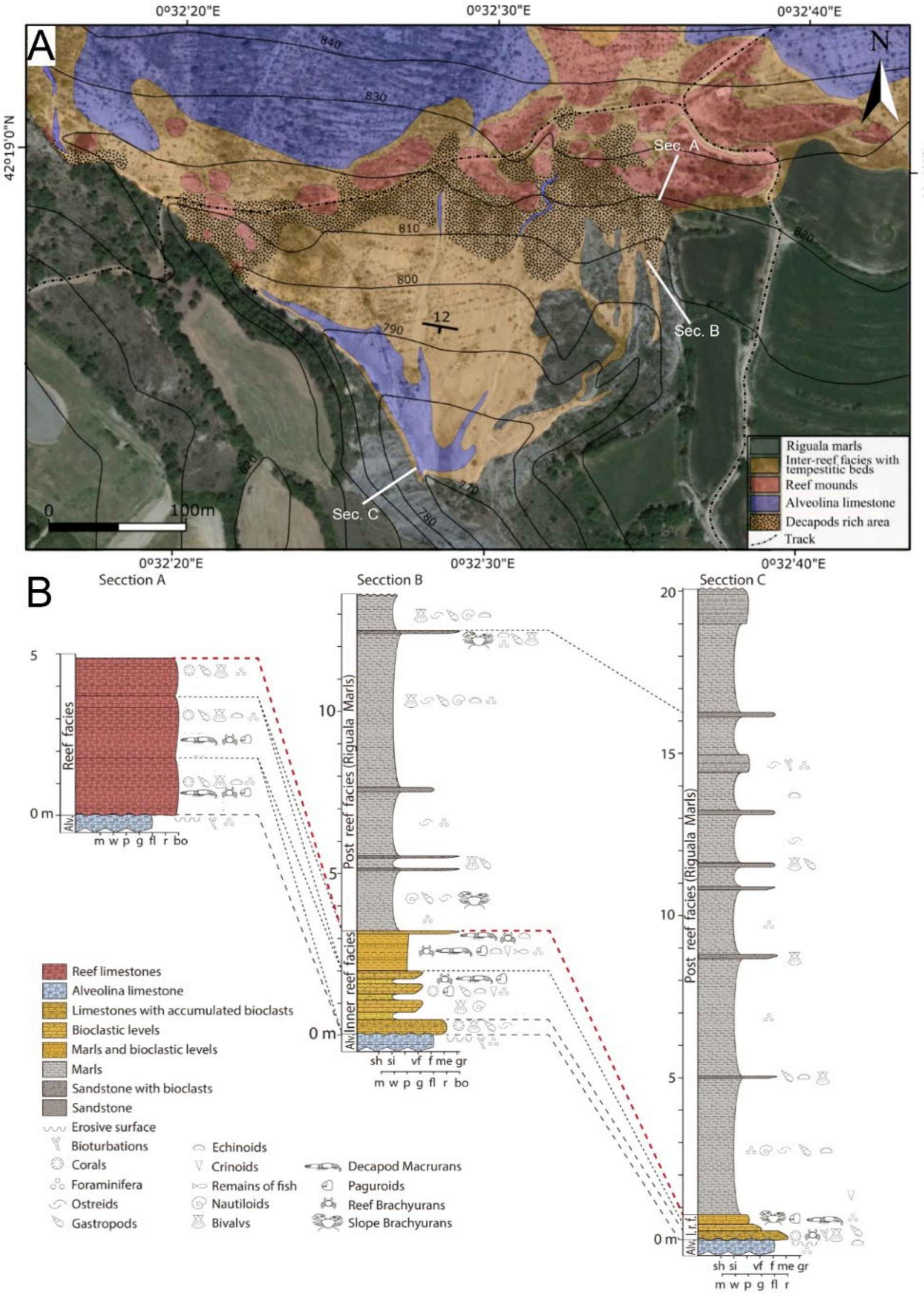


Figura 37: Distribución de facies y estratigrafía del afloramiento de Ramals. A: Mapa detallado de los tres miembros de la Formación Serraduy en Ramals. Sec. A, Sec. B y Sec. C corresponden a tres secciones analizadas en diferentes dominios sedimentarios. B: Correlación de secciones. Leyenda: sh: arcillas; f: arenisca de grano fino; gr: arenisca de grano grueso; m: lutita; w: wackestone; p: packstone; g: grainstone; fl: floatstone; r: rudstone; bo: boundstone; O.f.r.: Outer fore-reef facies.

Figure 37: Facies distribution and stratigraphy of the Ramals outcrop. A: Detailed map of the three members of the Serraduy Formation in Ramals. Sec. A, Sec. B and Sec. C correspond to the different logged sections represented below. B: Correlation of stratigraphic logs. Legend: sh: clays; f: fine-grained

sandstone; gr: coarse-grained sandstone; m: mudstone; w: wackestone; p: packstone; g: grainstone; fl: floatstone; r: rudstone; bo: boundstone; O.f.r.: Outer fore-reef facies. (Taken from Ferratges *et al*., 2022b).

Los domos arrecifales estudiados en Ramals están formados principalmente por un armazón de corales generalmente fragmentados, entre las que se encuentra sedimento interno bioclástico con texturas *wackestone* a *packstone,* con corales coloniales, corales solitarios, algas rojas incrustantes, foraminíferos incrustantes y briozoos (ver detalles en Ferratges *et al*., 2021c). Estos montículos arrecifales y las facies asociadas se desarrollaron en la zona eufótica a mesofótica (a algunas decenas de metros de profundidad), en un ambiente con cierto contenido en nutrientes que permitieron mantener una alta diversidad de organismos bentónicos asociados.

En Ramals, la preservación preferencial de crustáceos decápodos se dio en las facies adyacentes al arrecife (*inner fore-reef facies*). Esto probablemente se correlacione con las condiciones tafonómicas más favorables. Este cinturón de facies acumuló la mayor parte del sedimento bioclástico transportado por corrientes inducidas por tormentas episódicas y alberga taxones autóctonos y parautóctonos que vivían dentro del arrecife y en el sedimento blando del dominio del frente arrecifal adyacente (Fig. 37B). Este es el caso de algunos decápodos, cuyos parientes modernos están adaptados a sustratos blandos como los raninoideos (p. ej., Goeke, 1985; Kasinathan *et al*., 2007) y Axiidae (p. ej., Dworschak, 2000, 2005; Hyžný y Klompmaker, 2015). Otros taxones parecen mostrar adaptaciones a vivir entre escombros de coral (*coral rubble*), como el género *Aragolambrus* (Ferratges *et al*., 2019) y los calappidos (p. ej., Schweitzer y Feldmann, 2000).

En el cinturón de facies arreciles de Ramals (*reefal facies belt*), el estado de conservación y los datos sedimentológicos sugieren que la mayoría de los especímenes de crustáceos decápodos estuvieron expuestos durante largos períodos de tiempo antes de producirse su enterramiento. Esto también está respaldado por observaciones en otros grupos de invertebrados como los equinoideos, que parecen colonizados por serpúlidos y briozoos, lo que sugiere un tiempo de residencia prolongado en la interfase sedimento-agua (Nebelsick y Kroh, 2002; Nebelsick, 2004). Además, algunos huesos de vertebrados fueron colonizados por ostras y briozoos (ver Ferratges *et al*., 2021c).

La baja diversidad y abundancia de fauna en las áreas de arrecifes e inter-arrecifales (*inter-reef*) de Ramals probablemente esté relacionada con factores tafonómicos. Este dominio sedimentario representa áreas de alta energía y bajo potencial de conservación de crustáceos decápodos. Se han encontrado principalmente carpiliidos, algunos aethridos (*Ilerdapatiscus*), drómidos ocasionales (ver detalles en Artal *et al*., 2022) y fragmentos de quelípedos diversos, mientras que la mayor parte de la fauna autóctona probablemente fue transportada al cinturón de facies del frente arrecifal (Fig. 38).

La facies más alejadas al arrecife (*outer fore-reef facies*) registra las tasas de sedimentación más bajas, aunque episódicamente afectada por tormentas distales. Este ambiente albergó la diversidad más baja de decápodos, incluyendo *Litoricola macrodactyla* (Van Strelen, 1924) var. *pyrenaica* (Artal y Via, 1989); *Ctenocheles* sp.; xanthidos; dromioideos ocasionales (ver detalles en Artal *et al*., 2022) y fragmentos de quelípedos indeterminados. Todos los restos fósiles de esta facies, excepto los pertenecientes al género *Litoricola,* se encuentran desarticulados y frecuentemente rotos, por lo que se puede deducir que la mayor parte de la fauna de este intervalo probablemente fue transportada. Los ejemplares de *Litoricola macrodactyla* son una excepción, y se encuentran completos. Además, esta especie fue la única encontrada en los sedimentos post-arrecifes, lo que sugiere que no tuvo una relación cercana con los ambientes coralinos.

Las especies que se han encontrado en todas las zonas del yacimiento son *Ctenocheles* sp., *Ilerdapaticus guardiae* Artal y Van Bakel 2018a, *Eocarpilius ortegai* Artal y Van Bakel 2018b, *Carpilius* sp. y *Xanthilites* sp. (ver detalles en Ferratges *et al*., 2021c). *Ctenocheles* sp. es la especie más común en todas las zonas, excepto en facies arrecifales donde *Carpilius* sp. está mejor representada.

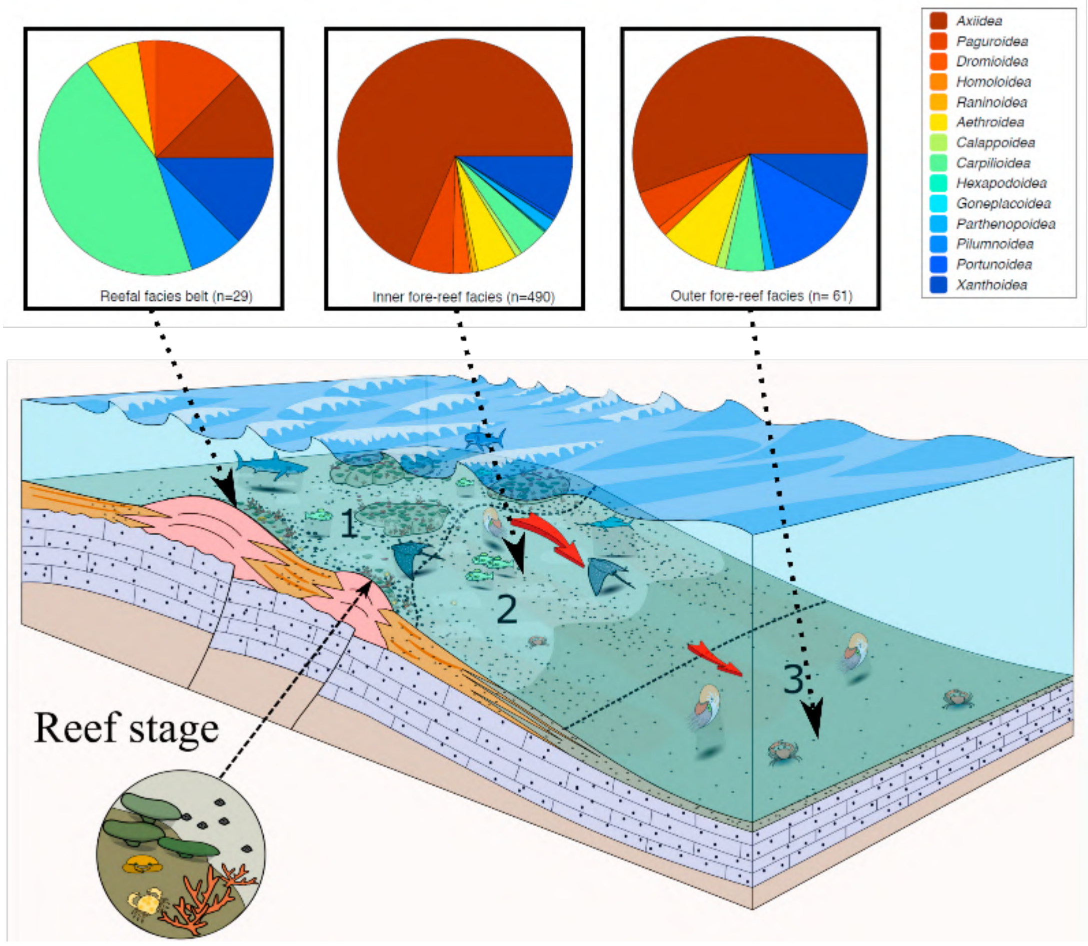


Figura 38: Diagrama simplificado que muestra la distribución del cinturón de facies. En la etapa de arrecife se diferencian las facies arrecifales e interarrecifes (**1**), facies de fore-reef proximales (**2**) y facies de fore-reef distales (**3**). Los gráficos circulares muestran la abundancia de los diferentes grupos en cada sector. El desarrollo de montículos arrecifales está ocasionalmente controlado por el relieve generado por las fallas que afectan a la unidad inferior (caliza Alveolina). Las flechas rojas muestran el transporte mar adentro dominante de restos esqueletales por corrientes episódicas inducidas por tormentas.

Figura 38: Simplified diagram showing the facies belt distribution. In the reef stage the reefal and inter-reef facies (**1**), inner fore-reef facies (**2**), and outer fore-reef facies (**3**) are differentiated. The pie charts show the abundance of the different groups in each sector. The development of the reef mound is occasionally controlled by the steep relief generated by the faults affecting the lower unit (Alveolina limestone). The red arrows show the dominant offshore transport of skeletal remains by episodic storm-induced currents.

6.3.1.2. Distribución en las plataformas del Eoceno medio y superior (Cuenca de Jaca)

En el estudio del **Eoceno medio y superior** de la Cuenca de Jaca, la exposición excepcional de cuatro secuencias estratigráficas (secuencias I a IV en Millán *et al.*, 1994; ver Fig. 39) incluidas en la Formación Arguis ha permitido realizar un muestreo detallado de diferentes litofacies e intervalos (Ferratges *et al.*, en preparación). Esto permite cuantificar la presencia de decápodos y su distribución. Los resultados obtenidos muestran que la distribución de los decápodos no es aleatoria, sino que muestra un patrón. Los estudios estratigráficos de las áreas en las que se encuentran los crustáceos decápodos nos permiten correlacionar los cambios en los ambientes sedimentarios relacionados en última instancia con los cambios en la evolución de la cuenca. La variación significativa en su abundancia relativa en diferentes facies de plataforma evidencia una relativa compartimentación de los distintos ambientes. Ocasionalmente, componentes formados en un ambiente particular podían sedimentarse en un medio adyacente, pero permitiendo la acumulación de restos cerca del lugar de producción.

Los conjuntos de decápodos recolectados en esta área corresponden a diferentes paleoambientes, y generalmente asociados a aguas poco o relativamente poco profundas. La mayoría de estos taxones, con la excepción de los conjuntos asociados a niveles arrecifales, aparecen asociados a fondos no consolidados (fondos blandos y fondos arenosos) con diferentes comunidades bentónicas, y ocasionalmente asociados a organismos constructores de biohermos como esponjas, briozoos y corales (Ferratges *et al.*, 2020a).

En las unidades estudiadas, se desarrollan una serie de plataformas someras, que se reciben diferentes denominaciones (Millán *et al.*, 1994). Dentro de la Secuencia II, las plataformas de Arguis y Belsue albergan una gran diversidad y abundancia de crustáceos decápodos (Ferratges *et al.*, en preparación que varían tanto lateral como verticalmente con una distribución variable. En las facies someras y más proximales de estas plataformas ubicadas en el sinclinal de Belsue (ver Fig. 39), el taxón más abundante es *Portunus catalaunicus*, representado por ejemplares grandes y articulados, que formal el 25,0% de la muestra en esta facies, seguida de Axiidae y Ctenochelidae (tanto *Ctenocheles* como *Callianassa* sp.) (17,9 %), Aethridae (14,3 %), Calappidae (14,3 %), Paguridae (10,7 %). Los componentes minoritarios representan el 17,9% del total (Eriphidae, Majidae, Montezumellidae y Retroplumidae). Por otro lado, en las facies más profundas de estas plataformas el taxón más abundante es *Harpactocarcinus punctulatus*, representado por ejemplares grandes y articulados, que formal el 87,0% de la muestra. Los componentes menores representan el 7,3% del total de esta área (Axiidae, Goneplacidae y Retroplumidae). Los taxones indeterminados representan el 5,8% del conjunto total (Ferratges *et al.*, en preparación).

En el sector central del área de estudio (en el sinclinal de Arguis, entre “PA” y “BR” en la Fig. 39) correspondiente a la zona media y distal de la plataforma de Arguis, se observa un aumento en la diversidad de organismos bentónicos, con abundantes bivalvos (pectínidos), gasterópodos, briozoos (ramificados y en forma de cúpula) y equinodermos. En cuanto a los crustáceos decápodos, se han reconocido ?*Galenopsis* sp., *Hepatiscus* sp., *Calappilia* sp., *Periacanthus* cf. *horridus*, *Pyreneplax* cf. *basaensis* y Callianassidae indet. Los cangrejos de mayor tamaño de las áreas más someras (*Portunus catalaunicus*) y profundas (*Harpactocarcinus punctulatus*) del sinclinal de Bentué están ausentes en estos niveles. También es destacable el alto grado de desarticulación de estos restos, y la reducción del tamaño corporal de los taxones, con aproximadamente 1,5 cm de media en las zonas distales a 6 cm de media en las zonas proximales.

En el equivalente lateral distal de la plataforma Belsue (columna 5 de la Fig. 39), cerca de la base de la Secuencia II, aparecen capas de arenisca de escala decimétrica entre los niveles margosos masivos. La especie *Harpactocarcinus punctulatus* es abundante aquí, pero son de menor tamaño que las de las facies proximales de la plataforma Belsué, y representan el 100% de la muestra para estas facies (ver Ferratges *et al*., en preparacion). Entre los braquiuros, la especie *H. punctulatus* es la especie más abundante en esta área (ver Garassino *et al*., 2009b). Sin embargo, los trabajos previos realizados en esta zona no han analizado su distribución y no se han realizado muestreos exhaustivos en las diferentes facies, por lo que hasta el momento se desconoce la distribución real.

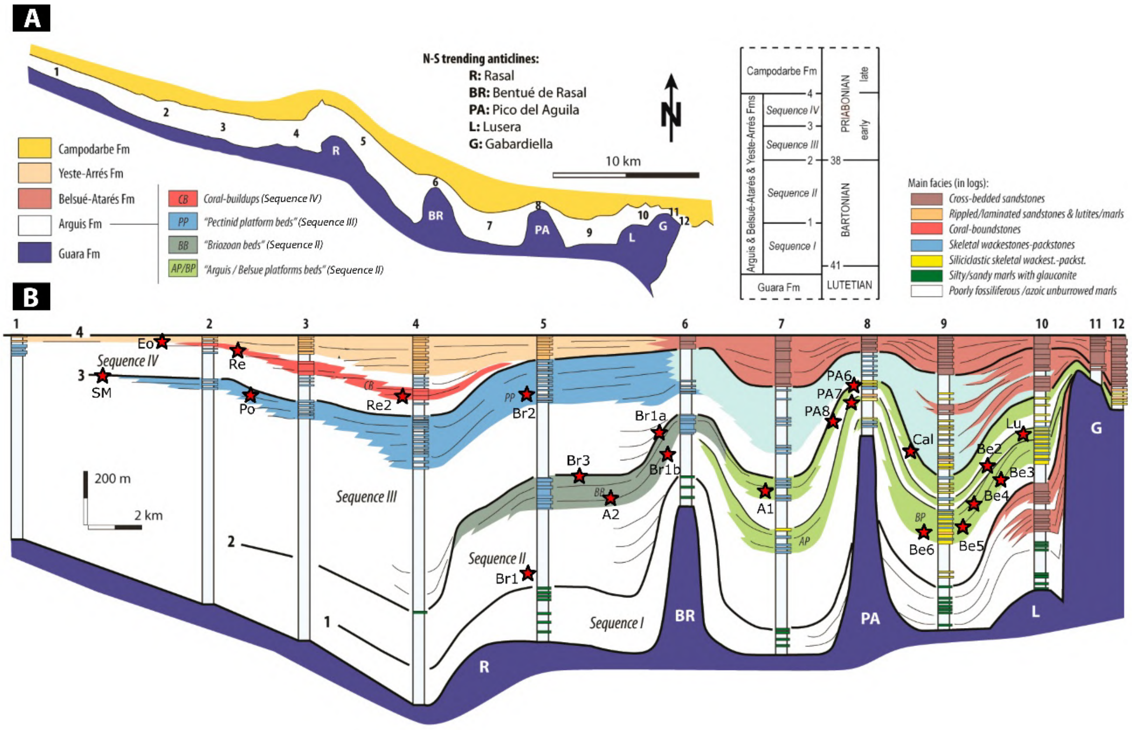


Figura 39: **A**: Ubicación de las columnas estratigráficas 1–12 estudiados por Millán *et al*. (1994) en el área de Sierras Exteriores. Estos registros se utilizan como referencia para la correlación de las Secuencias I–IV dentro de las formaciones Arguis, Belsué-Atares y Yeste-Arres que se muestran en la parte central de la figura. El recuadro en la parte superior derecha muestra la edad de estas secuencias [modificado de Millán *et al*. (1994) y Silva-Casal *et al*. (2017)]. **B**: Distribución de las unidades litoestratigráficas del Luteciense superior-Priaboniense entre los pueblos de La Peña y Nocito (ver Ferratges *et al*., en preparación para ubicación), y puntos de muestreo (estrellas rojas) que han proporcionado fósiles de crustáceos. Acrónimos: SM: Santa María de la Peña; T: Triste; R: Rasal; A: Arguis; Be: Belsué; L: Lúsera.

Figure 39: **A**: Location of logs 1–12 studied by Millán *et al*. (1994) in the Sierras Exteriores area. These logs are used as a reference for correlation of Sequences I–IV within the Arguis, Belsué-Atares and Yeste-Arres formations that are shown in the central part of the figure. The inset in the upper right-hand side shows the age of these sequences [modified from Millán *et al*. (1994) and Silva-Casal *et al*. (2017)]. **B**: Distribution of uppermost Lutetian–Priabonian lithostratigraphical units between the villages of La Peña and Nocito (see Ferratges *et al*., in preparation for location), and sampling points (red stars) which have provided crustaceans fossils. Acronyms: SM: Santa María de la Peña; T: Triste; R: Rasal; A: Arguis; Be: Belsué; L: Lúsera.

Al oeste del anticlinal del Bentue de Rasal (BR en Fig. 39), la secuencia II culmina con una caliza bioclástica, que en conjunto alcanzan hasta 40–50 de metros de espesor. Dichos niveles fueron denominados "Capas de Briozoos" por Puigdefábregas (1975) o "Bryozoan beds" (BB en Fig. 39) en Millán *et al*. (1994). Estos niveles de plataforma somera carbonatada tienen una diversidad intermedia y una abundancia relativamente baja de crustáceos decápodos (Fig. 40), además de estar generalmente compuesta por material desarticulado y fragmentado. En esta litofacies, el grupo dominante es el de los carpiliidos (48,9% del total de esta facies), compuestos en su mayoría por fragmentos, seguidos por los ranínidos (13,3%) y calápidos (8,9%). Los componentes menores (Astacidae, Majidae, Portunidae y Xanthidae) representan el 11,1% del total de la muestra. También se han encontrado varios fragmentos no identificados, que representan el 17,8% del conjunto total. Destaca la presencia de restos de grandes carpiliidos, que eventualmente aparecen articulados, acompañados de fauna de menor tamaño (*Enoploclytia* sp., *Periacanthus* sp., *Calappilia* sp., *Bitnerilia* sp., *Lophoranina* sp. y *Notopus* sp.) (Fig. 40). También se han identificado poliquetos tubulares (*Rotularia* sp.), bivalvos, gasterópodos gigantes (Gisortiinae), esponjas diversas y de gran tamaño (ocasionalmente formando biohermos) y equinodermos muy abundantes y diversos (equinoideos regulares e irregulares, crinoideos y asteroideos goniasteridos).

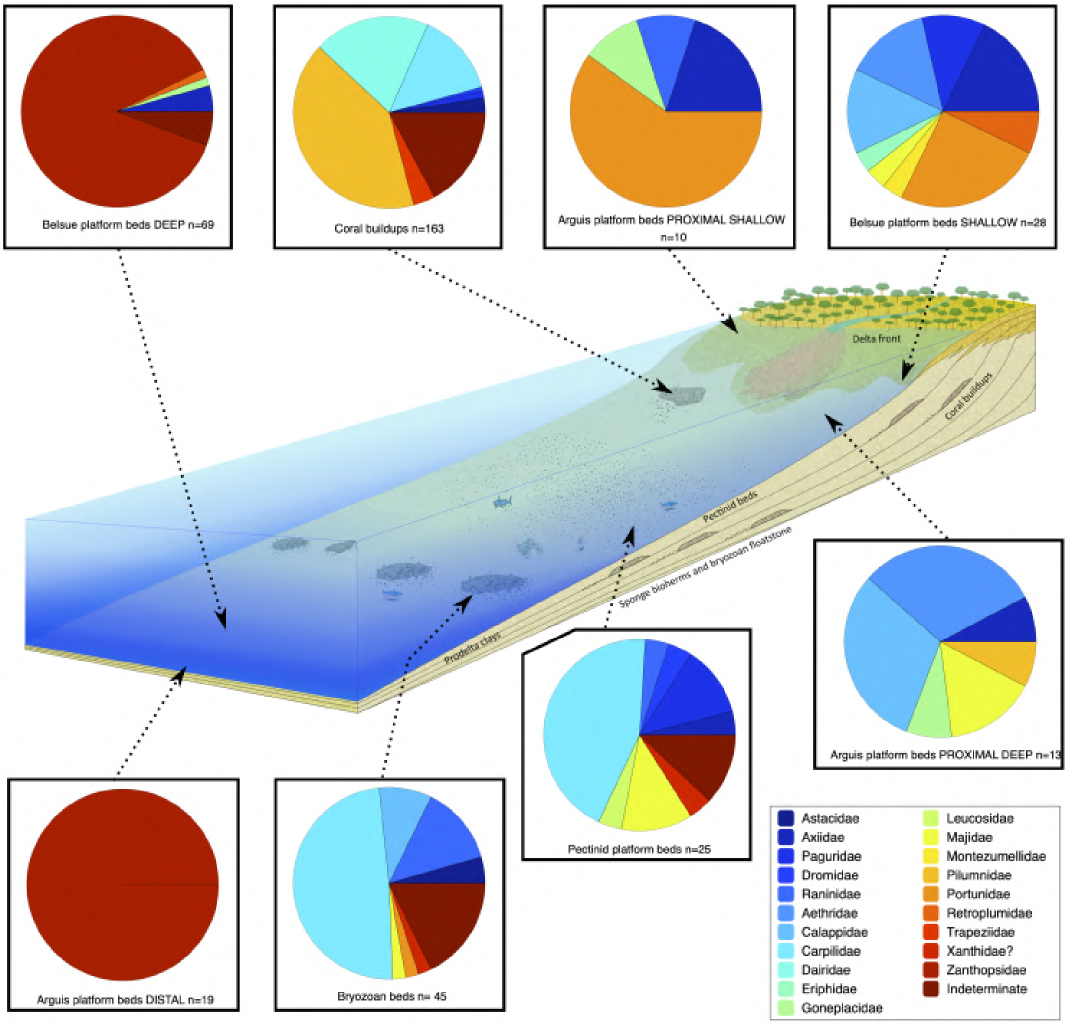


Figura 40: Modelo sedimentario simplificado del área de Arguis, mostrando los diferentes ambientes y facies. Gráficos circulares que muestran la abundancia relativa y la diversidad de los diferentes grupos de crustáceos decápodos en las diferentes facies.

Figure 40: Simplified sedimentary model of the Arguis area, showing the different environments and facies. Pie charts showing the relative abundance and diversity of the different decapod crustacean groups in the different facies.

En la parte superior de la Secuencia III se encuentran una serie de secuencias estratocrecientes y somerizantes de margas y calizas, que culminan con niveles potentes bioclásticos con abundates restos de bivalvos. Este conjunto de secuencias fue denominado por Millán *et al*. (1994) como Plataforma de Pectínidos (ver PP en Fig. 39). Esos niveles han proporcionado una gran diversidad y abundancia de grupos bentónicos como bivalvos (pectínidos y ostras), gasterópodos (*Pleurotomaria* sp., *Conus* sp., turritélidos y otros), nautiloideos y equinodermos como *Coelopleurus* sp. y otros componentes menores como Brissidae, Cassidulidae, Cidaroidea, Clypeasteridae, ?Cyclasterinae, Echinolampadidae, Eupatangidae, ?Hemiasteridae, ?Laganinae, Micrasteridae, Palaeostomidae, ?Plesiolampadidae, Prenasteridae, Schizasteridae, Scutellinidae y ?Temnopleuridae. Sin embargo, este intervalo ha proporcionado muy pocos crustáceos decápodos pero relativamente diversos (Fig. 40). Casi todos los restos están desarticulados o fragmentados, excepto un espécimen de leucosido que conserva los elementos torácicos. En esta litofacies, el taxón más abundante está representado por carpiliidos muy fragmentados (44% de los restos de crustáceos de este nivel) seguidos por los paguridos (12%) y majidos (12%). Los componentes menores pertenecientes a cinco familias diferentes (Cuadros 1 y 2) representan el 20% restante (Axiidae, Dromiidae, Raninidae, Leucosidae y Xanthidae). Los taxones indeterminados representan el 12% del conjunto total de estos niveles.

De particular interés para esta Tesis Doctoral fue el estudio del sistema arrecifal del Eoceno superior (Priaboniense inferior), desarrollado en la parte media de la Secuencia IV al oeste de la zona de estudio, en el entorno de las localidades de Rasal y La Peña (Coral-build ups en Millán *et al*., 1994; ver CB en la Fig. 39). Su estudio permitió complementar las observaciones realizadas en los arrecifes del Eoceno infeiror de Ramals explicado en el apartado anterior. El conjunto de decápodos recolectado en el arrecife de La Peña (ver Ferratges *et al*., 2020a) corresponde a taxones claramente asociados a ambientes arrecifales.

El análisis de las texturas, los componentes esqueleticos, la morfología de las bioconstrucciones y la arquitectura de las facies revela que las acumulaciones de coral del Priaboniense inferior se desarrollaron en un ambiente relativamente distal de prodelta (Morsilli *et al*., 2012). La detención episódica de los flujos terrígenos resultó en períodos de transparencia del agua, que permitieron el crecimiento y proliferación de corales coloniales. Morsilli *et al*. (2012) restringieron una posición batimétrica de estas acumulaciones alrededor de 15 a 25m de profundidad a partir del análisis de las comunidades dependientes de la luz y la distribución de litofacies dentro de las acumulaciones. Estas acumulaciones de coral ocurren como biohermos de bajo relieve, de hasta 20 a 30 m de espesor y unos pocos cientos de metros de ancho (ver detalles en Ferratges *et al*., 2020a). Los pulsos episódicos de alta actividad hidrodinámica proporcionaron la energía para reelaborar los sedimentos y producir los *rudstone* y *packstone* en torno de los biohermos.

El excepcional estado de conservación del afloramiento estudiado y su óptima exposición, han permitido un muestreo detallado de diferentes litofacies con el fin de cuantificar la presencia de cada taxón (Fig. 41A-B). En general, la especie más abundante es *Galenopsis crassifrons,* que representa el 41% del conjunto total, seguido de *Daira corallina* (19,9%) y carpiliidos (13,6%). Los componentes menores incluyen ?*Enoploclytia* sp. (2,5%), ?*Petrochirus* sp. (1,2%), *Gemmellarocarcinus riglosensis* (0,6%), ?*Ocalina* (0,6%), *Lobogalenopsis joei* (0,6%), ?Trapeziidae (3,7%), y 26 restos de taxones indeterminados que corresponden al 16,1% de la muestra total (ver Ferratges *et al*., 2020a). La facies de corales ramificados alberga la mayor diversidad y abundancia de crustáceos decápodos. El taxón más abundante es *Daira corallina* que representa el 34% de la muestra, seguido de *Galenopsis crassifrons* (19,5%) y Trapeziidae indet. (7,8%). Este último solo representado por fragmentos de quelípedos. También hay abundantes restos de varios taxones indeterminados, que representan el 27,3 % del conjunto total (Fig. 41C). La facies de corales tabulares muestra la diversidad más baja y la abundancia intermedia. En esta litofacies, el taxón más abundante es *Galenopsis crassifrons* (82,5%) seguido de *Daira corallina* (9%), carpiliidos (3,5%) y taxones indeterminados (4%) (Fig. 41C). La facies de corales masivos tiene una diversidad intermedia y la abundancia más baja. En esta litofacies, el grupo dominante corresponde a los carpiliidos (59,3%), seguido de *Galenopsis crassifrons* (15%) y ocasionalmente *Daira corallina* (3,7%) (Fig. 41C).

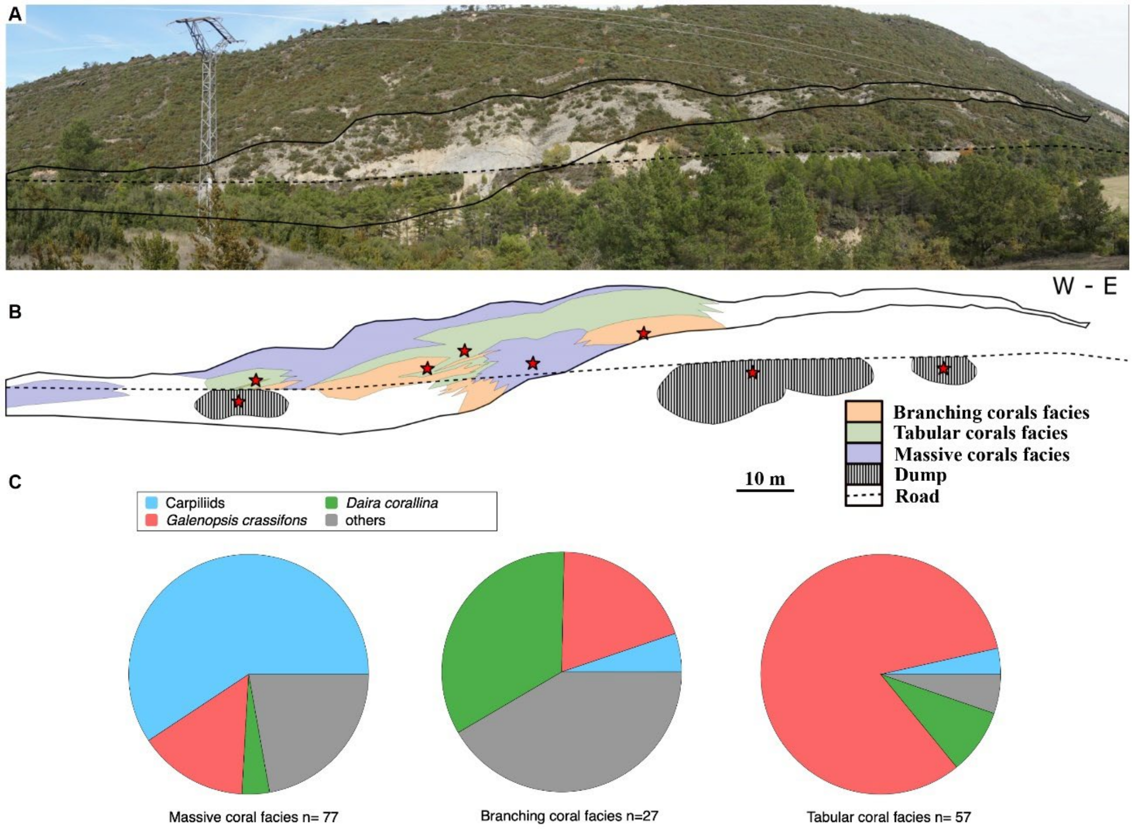


Figura 41: **A**: Vista general del afloramiento estudiado (arrecife de La Peña) en una vista panorámica oeste-este (o distal-proximal). **B**: El croquis muestra la distribución de las tres facies identificadas sobre la base de las morfologías coralinas predominantes. Las estrellas rojas corresponden a puntos de muestreo. Los materiales de escombrera corresponden a una mezcla de las diferentes facies del afloramiento, acumulados durante las obras. **C**: Abundancia relativa de los principales taxones de crustáceos decápodos en las tres diferentes facies dentro del arrecife La Peña (modificado de Ferratges *et al*., 2020a).

Figure 41: **A**: General view of the outcrop studied (La Peña reef) in a west–east (or distal–proximal) panoramic view. **B**: The sketch shows the distribution of the three facies identified on the basis of predominant coral morphologies. Red stars correspond to sample points. Dump materials correspond to a mixture of the different facies from the outcrop, accumulated during road works. **C**: Relative abundance of the main decapod crustacean taxa in the three different facies within the La Peña reef (modified from Ferratges *et al*., 2020a).

La distribución de fauna en el arrecife del Priaboniense inferior de Rasal-La Peña muestra diferencias importantes tanto en abundancia como en diversidad. Para probar si había una relación entre la distribución de las especies para cada facies, se realizó una prueba exacta de Fisher no paramétrica (debido a que el número de algunas especies es inferior a cinco), utilizando solo los tres grupos con mayor representación: carpiliidos, *Galenopsis crassifrons* y *Daira corallina* (ver detalles en Ferratges *et al*., 2020a). El análisis estadístico se computó con R (“RVAideMemoire” y la función “fisher.test”).

La hipótesis nula (H_0) fue que no había relación entre la distribución de especies y facies. Por el contrario, la hipótesis alternativa (H_1) fue que existía una relación entre facies y distribución de las especies. El valor de p o la prueba exacta de Fisher fue p=2.64e-14, lo que significa que existe una asociación significativa entre la distribución de las especies y las diferentes facies (aceptación de H_1) (ver Ferratges *et al*., 2020a).

Se han detectado diferencias significativas en la distribución de carpiliidos y *Galenopsis crassifrons* en facies de corales ramificados y facies de corales masivos (p=2.04e-03), y carpiliidos y *Daira corallina* en la misma facies (p=3.20e-07). También hubo diferencias significativas en la distribución de *Galenopsis crassifrons* y *Daira corallina* en facies de corales ramificados y facies de corales masivos (p=1.87e-07). Finalmente, también encontramos diferencias significativas en la distribución de carpiliidos y *Galenopsis crassifrons* en facies de corales masivos y facies de corales tabulares (p=9.22e-09) y carpiliidos y *Daira corallina* en la misma facies (p=6.12e-03). El resto de la distribución de las especies no está significativamente ligada a ninguna facies específica.

La facies con corales ramificados muestra la mayor diversidad y abundancia de cangrejos, y esto puede ser controlado por factores tanto biológicos como tafonómicos. Los corales ramificados del género *Acropora*, *Pocillopora* y *Stylophora* identificados en el arrecife La Peña (Morsilli *et al*., 2012) también son comunes en el Indo-Pacífico moderno y albergan actualmente una comunidad diversa de crustáceos decápodos (Patton, 1994). Las ramas de coral proporcionan refugio, especialmente para formas pequeñas como *Daira* y esta puede ser la razón por la cual las facies de corales ramificados muestran la mayor diversidad. Esta es también la zona de menor energía dentro del arrecife, favoreciendo la preservación de los taxones más pequeños dentro del sedimento acumulado en los espacios entre las ramas del coral. La facies con corales tabulares de La Peña estuvo dominada por *G. crassifrons*, que probablemente vivía en los espacios debajo y entre los corales tabulares. La facies de corales masivos muestra la menor abundancia y esto probablemente es consecuencia de razones tanto tafonómicas como biológicas. Los corales masivos brindan poco espacio para la acumulación de sedimentos entre las colonias y también menos oportunidades de refugio que otro tipo de colonias.

Por último, las areniscas que colmatan el nivel arrecifal han proporcionado muy poco material de crustáceos decápodos (*Eocalcinus gerardbretoni* Ferratges *et al*., 2021a). Sin embargo, es abundante otra fauna bentónica, especialmente gasterópodos. Algunos de estos corresponden a gasterópodos gigantes como *Campanile* sp. cuya presencia se ha asociado con una marcada estacionalidad y condiciones ideales para el desarrollo de biodiversidad marina somera (de Winter *et al*., 2020).

6.4. Tablas de diversidad

A continuación se hace un resumen en forma de tabla de todos los taxones identificados en las diferentes formaciones, haciendo énfasis en la correspondiente área donde se han localizado y su ambiente sedimentario.

6.4.1. Tabla de diversidad del Eoceno inferior de la Cuenca de Tremp-Graus (Formación Serraduy)

Superfamily	**Family**	**Subfamily**	**Taxon**	**Area**
Callianassoidea Dana, 1852	Callianassidae Dana, 1852		Callianassidae indet.	Inner fore-reef
	Ctenochelidae Manning & Felder, 1991	Ctenochelinae Manning & Felder, 1991	*Ctenocheles* cf. *cultellus* (Rathbun, 1935)	Inner fore-reef/outer fore-reef
Paguroidea Latreille, 1802	Diogenidae Ortmann, 1892		***Clibanarius isabenaensis* Ferratges Artal, van Bakel & Zamora, 2022**	Inner fore-reef
			***Parapetrochirus serratus* Ferratges Artal, van Bakel & Zamora, 2022**	Inner fore-reef
			?*Petrochirus* sp.	Inner fore-reef
	Annuntidiogenidae Fraaije, Van Bakel & Jagt ,2017		***Paguristes perlatus* Ferratges Artal, van Bakel & Zamora, 2022**	Inner fore-reef
	Calcinidae Fraaije, van Bakel & Jagt, 2017		***Dardanus balaitus* Ferratges Artal, van Bakel & Zamora, 2022**	Reefal facies belt/Inner fore-reef
			***Eocalcinus veteris* Ferratges Artal, van Bakel & Zamora, 2022**	Reefal facies belt to outer fore-reef
	Paguridae Latreille, 1802		?*Pagurus* sp.	Inner fore-reef
			***Anisopagurus primigenius* Ferratges Artal, van Bakel & Zamora, 2022**	Inner fore-reef
Dromioidea De Haan, 1833	Dromiidae De Haan, 1833	Basinotopinae Karasawa, Schweitzer & Feldmann, 2011	***Mclaynotopus longispinosus* Artal, Ferratges, van Bakel & Zamora, 2022**	Inner fore-reef
		Dromiinae De Haan, 1833	***Torodromia elongata* Artal, Ferratges, van Bakel &**	Inner fore-reef/outer

			Zamora, 2022	fore-reef
		Sphaerodromiinae Guinot & Tavares, 2003	***Basidromilites glaessneri* Artal, Ferratges, van Bakel & Zamora, 2022**	Inner fore-reef
			***Basidromilites* sp**	Inner fore-reef
	incertae sedis		**?*Basinotopus* sp.**	Inner fore-reef
	Dynomenidae Ortmann, 1892	Paradynomeninae Guinot, 2008	***Kromtitis isabenensis* Artal, Ferratges, van Bakel & Zamora, 2022**	Reefal facies belt/inner fore-reef
			***Sierradromia gladiator* Artal, Ferratges, van Bakel & Zamora, 2022**	Reefal facies belt/inner fore-reef
Homoloidea de Haan, 1839	Homolidae de Haan, 1839		***Paromola* cf. *bretoni* Ferratges, Domínguez & Ossó, 2021**	Outer fore-reef/post reef
Raninoidea de Haan, 1839	Raninidae De Haan, 1839	Cyrtorhininae Guinot, 1993	*Antonioranina ripacurtae* (Artal & Castillo, 2005)	Inner fore-reef
		Raninoidinae Lőrenthey in Lőrenthey & Beurlen, 1929	*Ranina* sp.	Inner fore-reef
			Quasilaeviranina sp.	Inner fore-reef
		Rogueinae Karasawa, Schweitzer, Feldmann & Luque, 2014	*Doraranina* sp.	Inner fore-reef
	?Orithopsidae Schweitzer *et al.*, 2003		?*Necrocarcinus* sp.	Inner fore-reef
Aethroidea Dana, 1851a	Aethridae Dana, 1851a		*Ilerdapatiscus guardiae*, Artal & Van Bakel, 2018	Reefal facies belt to outer fore-reef
Calappoidea H. Milne Edwards, 1837/ Cancridae Latreille, 1802	Matutidae De Haan, 1841		Matutidae indet.	Inner fore-reef/outer fore-reef
Cancroidea Latreille, 1802	Cancridae Latreille, 1802	Cancrinae Latreille, 1802	Cancridae indet.	Inner fore-reef
			Ceronnectes sp.	Inner fore-reef
Carpilioidea Ortmann, 1893	Carpiliidae Ortmann, 1893		*Carpilius* sp.	Reefal facies belt/inner fore-reef
			Eocarpilius ortegai Artal & Van Bakel, 2018	Reefal facies belt/inner fore-reef
			Oscacarpilius rotundus Artal & Van Bakel, 2018	Reefal facies belt/inner fore-reef
	Tumidocarcinidae Schweitzer, 2005		*Xanthilites* sp.	Reefal facies belt/inner fore-reef
Goneplacoidea MacLay, 1838	Euryplacidae Stimpson, 1871		?*Alponella* sp.	Inner fore-reef
Hexapodoidea Miers, 1886	Hexapodidae Miers, 1886		*Eohexapus* sp.	Inner fore-reef

Parthenopoidea MacLeay, 1838	Parthenopidae MacLeay, 1838	Daldorfiinae Ng & Rodríguez, 1986	***Aragolambrus collinsi* Ferratges, Zamora & Aurell, 2019**	Inner fore-reef/outer fore-reef
		Parthenopinae MacLeay, 1838	Parthenopidae indet.	Inner fore-reef
Pilumnoidea Samouelle, 1819	Pilumnidae Samouelle, 1819		*Galenopsis* sp.	Reefal facies belt
Portunoidea Rafinesque, 1815	Geryonidae Colosi, 1923		*Litoricola macrodactyla* (Van Strelen, 1924) var. *pyrenaica* (Artal & Via, 1989)	Outer fore-reef
	Carcinidae MacLeay, 1838		*?Lovaroides* sp.	Inner fore-reef
			?Liocarcinus sp.	Inner fore-reef
			?Boschettia sp.	Inner fore-reef
Xanthoidea MacLay, 1838	Panopeidae Ortmann, 1893	Eucratopsinae Stimpson, 1871	*Glyphithyreus almerai* Artal & Van Bakel, 2018	Inner fore-reef
	Xanthidae MacLeay, 1838		*Parhalimede* sp.	Inner fore-reef

Tabla 1. Diversidad de crustáceos decápodos en la Fm Serraduy y su distribución según las zonas descritas en Ferratges *et al*., 2021c del afloramiento Ramals (Ypresiense medio) y modificado de Ferratges *et al*. (2022b) en Zamora *et al*. (2022). En negrita aparecen las especies descritas en la Presente Tesis Doctoral.

Table 1. Diversity of decapod crustaceans at the Serraduy Fm and their distribution according to the areas described in Ferratges *et al*., 2021c of the Ramals outcrop (middle Ypresian). and modified form Ferratges *et al*. (2022b) in Zamora *et al*. (2022). The species described in this PhD appear in bold.

6.4.2. Tabla de diversidad del Eoceno inferior de la Cuenca de Tremp-Graus (Formación Roda)

Superfamily	**Family**	**Subfamily**	**Taxon**	**Area**
Callianassoidea Dana, 1852	Callianassidae Dana, 1852		Callianassidae indet.	Prodelta (marly sandstones)
	Ctenochelidae Manning & Felder, 1991	Ctenochelinae Manning & Felder, 1991	*Ctenocheles burlesoensis?*	Prodelta (marly sandstones)
Astacidae Latreille, 1802			Astacidae indet. 1	Prodelta (sandstones)
			Astacidae indet. 2	Prodelta (sandstones)
Paguroidea Latreille, 1802	Diogenidae Ortmann, 1892		***Parapetrochirus robustus* Ferratges, Artal & Zamora, 2021**	Prodelta (sandstones)
Hippoidea Latreille, 1825	Albuneidae Stimpson, 1858		*Albunea* sp.	Prodelta (marls)
Dromioidea De Haan, 1833			Dromidae indet.	Prodelta (marls)
Homoloidea de Haan, 1839	Homolidae de Haan, 1839		***Paromola bretoni* Ferratges, Domínguez & Ossó, 2021**	Prodelta (marly sandstones)
Raninoidea de Haan, 1839	Raninidae De Haan, 1839		*Pseudorogueus rangiferus* Fraaije, 1995	Prodelta (marly sandstones)
		Symethinae Goeke, 1981	*Eosymethis aragonensis* Van Bakel, Guinot, Artal, Fraaije &	Prodelta (marly

			Jagt, 2012	sandstones)
Carpilioidea Ortmann, 1893	Carpiliidae Ortmann, 1893		*Carpilius* sp.	Prodelta reef (sandstones)
	Zanthopsidae Via, 1959		*Zanthopsis dufourii* (H. Milne-Edwards in d'Archiac, 1850)	Prodelta (marly sandstones)
	Tumidocarcinidae Schweitzer, 2005		*Titanocarcinus decor* Schweitzer, Artal, van Bakel, Jagt & Karasawa, 2007	Prodelta (marly sandstones)
Goneplacoidea MacLay, 1838	Magyarcarcinidae Domínguez & Ossó, 2016		*?Magyarcarcinus* sp.	Prodelta (marly sandstones)
Majoidea Samouelle, 1819	Epialtidae MacLeay, 1838		*Periacanthus ramosus* Artal & Castillo, 2005	Prodelta (marly sandstones)
			Periacanthus tetracornis Ferratges, Ortega, Fernández, Moreno & Maza 2014	Prodelta (marly sandstones)
	Majidae Samouelle, 1819	Micromaiinae Beurlen, 1930	*Micromaia* sp.	Prodelta (marly sandstones)
	Inachidae MacLeay, 1838		Inachidae indet.	Prodelta (marly sandstones)
Pilumnoidea Samouelle, 1819	Pilumnidae Samouelle, 1819		*Galenopsis* sp.	Prodelta reef (reef limestones)
Retroplumoidea Gill, 1894	Retroplumidae Gill, 1894		*Gaudipluma bacamortensis* Artal, Van Bakel, Fraaije & Jagt 2013b	Prodelta (marly sandstones)
			Retropluma gallica Artal, van Bakel & Castillo, 2006	Prodelta (marly sandstones)
Xanthoidea MacLay, 1838	Panopeidae Ortmann, 1893	Eucratopsinae Stimpson, 1871	*Glyphithyreus* sp.	Prodelta (marly sandstones)
	Xanthidae MacLeay, 1838		*Collinscarcinus obliquesulcatus* Artal & van Bakel, 2020	Prodelta reef (reef limestones)
Grapsoidea MacLeay, 1838	Varunidae H. Milne-Edwards, 1853	Asthenognathinae Stimpson, 1858	***Asthenognathus fernandezi* Ferratges, Zamora & Aurell, 2022**	Prodelta (marly sandstones)

Tabla 2. Diversidad de crustáceos decápodos en la Fm Roda (Ypresiense superior). En negrita aparecen las especies descritas en la Presente Tesis Doctoral.

Table 2. Diversity of decapod crustaceans at the Roda Fm (upper Ypresian). The species described in this PhD appear in bold.

6.4.3. Tabla de diversidad del Eoceno inferior de la Cuenca de Tremp-Graus (Formación Morillo)

Superfamily	**Family**	**Subfamily**	**Taxon**	**Area**
Callianassoidea Dana, 1852	Callianassidae Dana, 1852		Callianassidae indet.	Carbonate platform
Raninoidea de Haan, 1839	Raninidae De Haan, 1839	Rogueinae Karasawa, Schweitzer, Feldmann & Luque, 2014	*Pseudorogueus sp.*	Carbonate platform
Carpilioidea Ortmann, 1893	Carpiliidae Ortmann, 1893		*Carpilius* sp.	Carbonate platform
Hexapodoidea Miers, 1886	Hexapodidae Miers, 1886		*Eohexapus* sp.	Carbonate platform
Portunoidea Rafinesque, 1815	Portunidae Rafinesque, 1815		*Archaeoportunus isabenensis* Artal, Ossó & Domínguez 2013a	Carbonate platform
	Carcinidae MacLeay, 1838		*Boschetia* sp.	Carbonate platform
Xanthoidea MacLay, 1838	Panopeidae Ortmann, 1893		*Carinocarcinus sp.*	Carbonate platform

Tabla 3. Diversidad de crustáceos decápodos en las calizas bioclásticas nodulares de la Fm Morillo (Ypresiense-Luteciense inferior?).

Table 3. Diversity of decapod crustaceans at the nodular bioclastic limestones of the Morillo Fm (Ypresian-lower Lutetian?).

6.4.4. Tabla de diversidad del Eoceno medio de la Cuenca de Ainsa (Formaciones Grustán y San Vicente)

Superfamily	**Family**	**Subfamily**	**Taxon**	**Area**
Callianassoidea Dana, 1852	Callianassidae Dana, 1852		Callianassidae indet. 1	Prodelta (sandstones)
			Callianassidae indet. 2	Reef slope
Astacidae Latreille, 1802			? Astacidae indet. 1	Reef slope
Paguroidea Latreille, 1802	Diogenidae Ortmann, 1892		? Diogenidae indet.	
	Annuntidiogenidae Fraaije, 2014		*Paguristes* sp.	Prodelta (sandstones)
			Paguridae indet.	Reef slope
Dromioidea De Haan, 1833			Dromidae indet. 1	Reef slope
			Dromidae indet. 2	Reef slope
Raninoidea de Haan, 1839	Raninidae De Haan, 1839		*Lophoranina* sp.	Prodelta (sandstones)
Calappoidea H. Milne Edwards, 1837	Matutidae De Haan, 1841		*"Peltarion" pirenaicus* Aguilar & Castillo, 2017 (*Eomatutta* sp.)	Prodelta (sandstones)
Carpilioidea Ortmann, 1893	Carpiliidae Ortmann, 1893		Carpiliidae indet.	Reef slope
	Zanthopsidae Via, 1959		*Harpactoxanthopsis quadrilobata* (Desmarest 1822)	Prodelta (sandstones)
Goneplacoidea MacLay, 1838	Magyarcarcinidae Domínguez & Ossó, 2016		? *Magyarcarcinus* sp.?	Prodelta (sandstones)
Pilumnoidea Samouelle, 1819	Pilumnidae Samouelle, 1819		*Galenopsis* sp.	Prodelta (sandstones)

Tabla 4. Diversidad de crustáceos decápodos en las Formaciones Grustán y San Vicente (Luteciense).

Table 4. Diversity of decapod crustaceans at the Grustán and San Vicente Formations (Lutetian).

6.4.5. Tabla de diversidad del Eoceno medio y superior de la Cuenca de Jaca (Formaciones Arguis y Pamplona)

Superfamily	**Family**	**Subfamily**	**Taxon**	**Area**
Callianassoidea Dana, 1852	Callianassidae Dana, 1852		?*Vecticallichirus* sp.	Siliciclastic (Arguis-Fanlillo)
			Callianassidae indet.	Patch reef
	Ctenochelidae Manning & Felder, 1991	Ctenochelinae Manning & Felder, 1991	*Ctenocheles* sp.	Siliciclastic (Arguis area)
Astacidae Latreille, 1802			*Enoploclytia* sp. 1	Bryozoan beds
			Enoploclytia sp. 2	Coral Buildups
Achelata Scholtz & Richter, 1995	Scyllaridae Latreille, 1825	Scyllarinae Latreille, 1825	Scyllarinae indet.	Siliciclastic (Fanlillo)
Galatheoidea Samouelle, 1819	Galatheidae Samouelle, 1819		Galatheidae indet.	Patch reef
Paguroidea Latreille, 1802	Diogenidae Ortmann, 1892		***Diogenes augustinus* Ferratges, Zamora & Aurell, 2020**	Siliciclastic (Arguis area)
			Petrochirus sp.	Coral Buildups
	Calcinidae Fraaije, Van Bakel & Jagt, 2017		***Eocalcinus gerardbretoni* Ferratges, Artal & Zamora, 2021**	Siliciclastic (Arguis)
			Eocalcinus cf. *cavus* Beschin, Busulini, De Angeli & Tessier, 2002	Siliciclastic (Fanlillo)
	Paguridae?		Paguridae indet.	Siliciclastic (Arguis)
			Paguridae indet.	Patch reef
Cyclodorippoidea Ortmann, 1892			*?Tymolus*	Siliciclastic (Fanlillo)
Dromioidea De Haan, 1833	Dromiidae De Haan, 1833	Dromiinae De Haan, 1833	Dromidae indet.	Siliciclastic (Arguis)
			Basadromia longifrons Artal, van Bakel, Domínguez & Gómez, 2016	Siliciclastic (Fanlillo)
		Sphaerodromiinae Guinot & Tavares, 2003	*Dromilites* sp.	Siliciclastic (Fanlillo)
	Dynomenidae Ortmann, 1892	Dynomeninae Ortmann, 1892	***Dynomene collinsi* Ossó, Domínguez, De Angeli & Ferratges, 2020**	Siliciclastic (Fanlillo)
		Insertae sedis	***Gemmellarocarcinus riglosensis* Ferratges, Zamora & Aurell, 2020**	Reef (Yeste)
Raninoidea de Haan, 1839	Raninidae De Haan, 1839		*Lophoranina* sp.	Siliciclastic/ glauconitic (Arguis)
			Notopus sp.	Siliciclastic/ glauconitic (Arguis)
			Quasilaeviranina sp.	Siliciclastic (Arguis)
			Raninoides sp .	Siliciclastic (Arguis)
		Rogueinae Karasawa,	*?Pseudorogueus rangiferus* Fraaye, 1995	Siliciclastic (Fanlillo)

		Schweitzer, Feldmann & Luque, 2014		
Aethroidea Dana, 1851a			*Hepatiscus* sp.	Siliciclastic (Arguis)
			Hepatiscus poverelli Via, 1959	Siliciclastic (Fanlillo)
			Aethridae indet. (in study)	Siliciclastic (Fanlillo)
Calappoidea H. Milne Edwards, 1837			*Calappilia* sp.	Siliciclastic/ glauconitic (Arguis)
			Calappilia cf. *scopuli*	Siliciclastic (Fanlillo)
			Calappilia dacica Bittner, 1893	Siliciclastic (Fanlillo)
			Tavernolesia calasanctii (Via, 1959)	Siliciclastic (Fanlillo)
			Bittnerilia sp.	Siliciclastic (Arguis)
Carpilioidea Ortmann, 1893	Carpiliidae Ortmann, 1893		*Liopsalis* cf. *anodon* (Bittner, 1875)	Reef (Yeste)
			Carpilius sp. "*Menippe almerai*"	Siliciclastic (Arguis)
			Carpiliidae (reef)	Reef (Yeste)
			Carpiliidae indet.	Reef (Yeste)
			Ocalina sp.	Reef (Yeste)
	Zanthopsidae Via, 1959		*Harpactocarcinus punctulatus* A. Milne-Edwards, 1862	Siliciclastic (Arguis)
Chasmocarcinidae Serène, 1964			*Chasmocarcinus* cf. *guerini*	Siliciclastic (Fanlillo)
Dairidea Serène, 1965	Dairidae Serène, 1965		***Daira corallina*** **Ferratges, Zamora y Aurell, 2020**	Reef (Yeste)
Dorippoidea MacLeay, 1838	Dorippidae MacLeay, 1838		Dorippiid indet.	Siliciclastic (Fanlillo)
	Ethusidae Guinot, 1977		*Ethusa* sp.	Siliciclastic (Fanlillo)
Eriphioidea MacLeay, 1838	Eriphiidae MacLeay, 1838		?*Eriphia*	Siliciclastic (Arguis)
			Eriphidae indet.	Patch reef
Goneplacoidea MacLay, 1838	Magyarcarcinidae Domínguez & Ossó, 2016		*Magyarcarcinus yebraenisis* Domínguez & Ossó, 2016	Siliciclastic (Arguis)
			?Goneplacoid indet.	Siliciclastic (Fanlillo)
	Vultocinidae Ng & Manuel-Santos, 2007		*Pyreneplax basaensis* Ossó, Domínguez & Artal, 2014	Siliciclastic (Fanlillo y Arguis)
? Hexapodoidea Miers, 1886			Hexapodid indet.	Siliciclastic (Fanlillo)
Leucosioidea Samouelle, 1819	Leucosiidae Samouelle, 1819		Leucosiidae indet.	Siliciclastic (Arguis)
Majoidea Samouelle, 1819	Epialtidae MacLeay, 1838		*Periacanthus horridus* Bittner, 1875	Siliciclastic (Arguis)
		Pisinae Griffin, 1986	?*Paranaxia* sp. (in study)	Siliciclastic (Fanlillo)
			Planobranchia sp. (in study)	Siliciclastic (Fanlillo)
	Macrocheiridae Dana, 1851b		?*Macrocheira* sp. (in study)	Siliciclastic (Fanlillo)
	Majidae Samouelle, 1819		?*Cromimaia* sp. (in study)	Siliciclastic (Fanlillo)
		?Micromaiinae Beurlen, 1930	*Micromaia priabonensis* (Oppenheim, 1901)	Siliciclastic (Fanlillo)

			Spnirostrimaia cfr. *margaritata* (Fabiani, 1910)	Siliciclastic (Fanlillo)
Montezumelloidea Ossó & Domínguez 2019	Montezumellidae Ossó & Domínguez, 2013		*Montezumella* sp.	Siliciclastic (Arguis)
Palicoidea Bouvier, 1898	Palicidae Bouvier, 1898		*Eopalicus squamosus* Beschin, Busulini, De Angeli & Tessier 1996	Siliciclastic (Fanlillo)
Parthenopoidea MacLeay, 1838	Dairoididae Števčić, 2005		***Phrynolambrus sagittalis*** (in review)	Siliciclastic (Fanlillo)
Pilumnoidea Samouelle, 1819	Pilumnidae Samouelle, 1819		*Galenopsis crassifrons* A. Milne-Edwards, 1865	Reef (Yeste)
			Eopilumnus checchii Beschin, Busulini, De angeli & Tessier, 2002	Siliciclastic (Fanlillo)
			***Lobogalenopsis joei* Ferratges, Zamora & Aurell, 2020**	Reef (Yeste)
Portunoidea Rafinesque, 1815	Portunidae Rafinesque, 1815	Portuninae Rafinesque, 1815	*Portunus catalaunicus* (Via, 1941)	Siliciclastic (Arguis-Fanlillo)
			Portunus sp.	Siliciclastic (Arguis)
	Carcinidae Macleay, 1838	?Polybiinae Paul'son, 1875	Carcinidae indet. (in study)	Siliciclastic (Fanlillo)
Retroplumoidea Gill, 1894	Retroplumidae Gill, 1894		*Retrocypoda almelai* Via, 1959	Siliciclastic (Arguis-Fanlillo)
			Retropluma eocenica Via, 1959	Siliciclastic (Arguis-Fanlillo)
			Serrablopluma diminuta Artal, van Bakel, Fraaije & Jagt, 2013b	Siliciclastic (Fanlillo)
?Trapezioidea Miers, 1886	?Trapeziidae Miers, 1886		Trapeziidae indet.	Reef (Yeste)
Xanthoidea MacLay, 1838	Panopeidae Ortmann, 1893		*Scultoplax oscensis* (Ossó & Domínguez, 2017)	Siliciclastic (Fanlillo)
	Xanthidae MacLeay, 1838		Xanthidae indet.	Siliciclastic (Arguis)
		Actaeinae Alcock, 1898	*Actaeites* sp.	Siliciclastic (Fanlillo)
			Phlyctenodes sp.	Patch reef
		Liomerinae Sakai, 1976	?*Liomera* sp.	Patch reef
Grapsoidea MacLeay, 1838	Grapsidae MacLeay, 1838		*Daragrapsus trispinosus* Müller & Collins, 1991	Siliciclastic (Fanlillo)
? Pinnotheroidea De Haan, 1833	? Pinnotheridae De Haan, 1833		Indet.	Siliciclastic (Fanlillo)

Tabla 5: Diversidad de crustáceos decápodos en las margas de la Fm Arguis y Fm Pamplona (Bartoniense-Priaboniense). La información de Fanlillo (Fm Pamplona) se ha complementado con los datos de Domínguez y Ossó, 2016 (poster). En negrita aparecen las especies descritas en la Presente Tesis Doctoral.

Table 5: Diversity of decapod crustaceans in the Pamplona Fm and Arguis Fm (Bartonian-Priabonian). The information from Fanlillo (Fm Pamplona Marls) has been complemented with data from Domínguez and Ossó, 2016 (poster comunication). The species described in this PhD appear in bold.

7. DISCUSIÓN DE LOS RESULTADOS

Este capítulo incluye una discusión de los resultados obtenidos en los diferentes artículos que componen esta Tesis.

- **7.1 Interpretación filogenética**: Donde se discuten las cuestiones sistemáticas más relevantes centradas en la filogenia de la superfamilia Parthenopoidea y se relacionan diferentes grupos actuales y fósiles.
- **7.2 Distribución de los taxones**: Donde se incluye la discusión relacionada con las publicaciones acerca de la distribución de los diferentes taxones en el Eoceno inferior, medio y superior de las cuencas Surpirenaicas.
- **7.3 Cambios de diversidad**: Donde se discuten los factores que dieron lugar a los cambios de diversidad y la relación entre facies carbonatadas y siliciclásticas. En este apartado se incluye una tabla para cada formación muestreada, con todos los taxones estudiados y reconocidos en las diferentes áreas estudiadas, resaltando (en negrita) los taxones eocenos que se han descrito a lo largo de la presente tesis. En estas tablas se hace hincapié en el tipo de ambiente. Finalmente se incluye una gráfica donde se representa el número de especies en los diferentes ambientes muestreados.

7.1. Interpretación filogenética.

Hasta la fecha, no existían estudios detallados que explorasen las relaciones filogenéticas entre los miembros de Parthenopoidea (Tan y Ng, 2007; Ferratges *et al*., 2019), especialmente considerando taxones extintos, a pesar de su riqueza de caracteres anatómicos (Schweitzer *et al*., 2006). Los Parthenopoideos más antiguos conocidos son del Eoceno (Ferratges *et al*., 2019 y referencias) y muestran que este grupo era relativamente diverso ya en dicho periodo (ver Ferratges *et al*., 2019; Schweitzer *et al*., 2020).

Durante el Eoceno, este grupo supuestamente está representado por 20 especies repartidas en 14 géneros, aunque algunos de ellos necesitan ser revisados, ya que los resultados filogenéticos obtenidos revelan que algunos de estos géneros tienen poca afinidad con Parthenopoidea (p. ej., *Mesolambrus* y *Eogarthambrus* en Fig. 42). Por otra parte, la familia Dairoididae, un grupo raro y controvertido (ver detalles en Ferratges *et al*., en revisión), muestra una clara afinidad con los Parthenopideos y en particular con *Phrynolambrus* (Fig. 42).

Recientemente, algunos autores (Lai *et al*., 2014), sugieren que puede haber una base filogenética para la relación entre Dairoididae y Parthenopidae, ya que *Dairoides* es un grupo hermano de *Daldorfia* moderadamente bien sustentado. Los resultados obtenidos apoyan las conclusiones de Lai *et al*. (2014), en el que sugieren que *Dairoides* es un grupo hermano de *Daldorfia*. Por lo tanto, se ha considerado tanto a *Dairoides* como a *Phrynolambrus* miembros de la Superfamilia Parthenopoidea, pero formando un clado diferente de Parthenopidae y, por lo tanto, de las subfamilias Parthenopinae y Daldorfinae. Así, *Phrynolambrus* se considera aquí como miembro fósil de la Familia Dairodidae Števčić, 2005, y a su vez parte de la superfamilia Parthenopoidea.

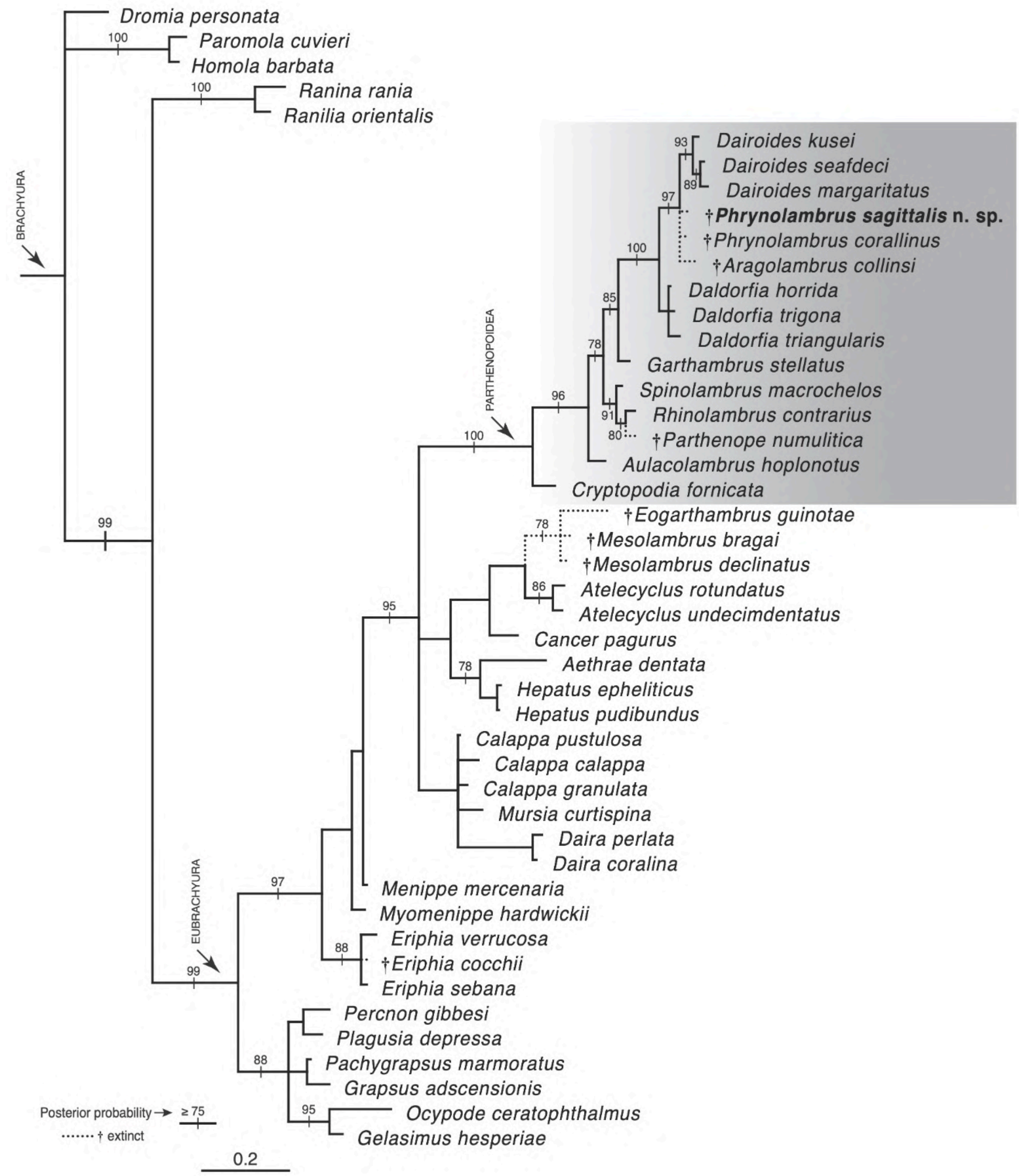


Figura 42: Topología de consenso de la regla de la mayoría bayesiana de la muestra de árboles después de la quema para familias de braquiuros fósiles y actuales seleccionadas, incluido *Phrynolambrus sagittalis*. Valores de soporte de probabilidad posterior indicados encima de las ramas. Las ramas con soporte de probabilidad con valor < 75% se colapsan. Los taxones terminales indicados por una daga (†) están extintos. El recuadro gris indica la familia monofilética Parthenopoidea.

Figure 42: Bayesian majority-rule consensus topology of the post-burnin sample of trees for selected fossil and extant brachyuran families, including *Phrynolambrus sagittalis*. Posterior probability support values indicated above branches. Branches with posterior probability support < 75% are collapsed. Terminal taxa indicated by a dagger (†) are extinct. Grey box indicates the monophyletic family Parthenopoidea.

7.2 Distribución de los taxones

7.2.1. Comparación entre sistemas arrecifales del Eoceno inferior

La distribución faunística de los decápodos en Ramals muestra diferencias importantes tanto en términos de abundancia relativa como de diversidad en cada una de las facies diferenciadas. El análisis sedimentológico sugiere que la mayoría de los especímenes del arrecife fueron transportados a la facies del frente arrecifal (*inner fore-reef*) por eventos de tormenta (como se indica con flechas en la Fig. 38). Para mejorar la comprensión de esta distribución, los datos sobre la localización de los diferentes taxones se han calculado por diversos métodos estadísticos.

Para explorar si existía una relación entre la distribución de las especies en cada facies, se realizó un Análisis de Componentes Principales (PCA). Para simplificar los cálculos, los diferentes taxones reconocidos se agruparon en superfamilias (ver Ferratges *et al*., 2021c). Tomando estos grupos como variables, se pudo inferir qué grupos tenían preferencias por un entorno específico. Al reducir la dimensionalidad de las variables usando PCA, se muestra que ciertos taxones tienen una fuerte afinidad por entornos particulares, mostrando valores mucho más positivos hacia PC1, PC2 o PC3 en comparación a otros grupos (ver detalles en Ferratges *et al*., 2021c).

Algunos grupos muestran una mayor dispersión hacia la facies del frente arrecifal distal (por ejemplo, Aethroidea, Xanthoidea y Axiidea). Esto puede deberse a que son los taxones más abundantes y, por lo tanto, más fáciles de recolectar, pero no se puede descartar que estos grupos estuvieran más extendidos en diferentes facies. En contraste, el único taxón que muestra especímenes completos y articulados en la facies de frente arrecifal distal es *L. macrodactyla*, lo que sugiere un entierro rápido por eventos sedimentarios episódicamente altos. Este taxón probablemente vivió en esta área.

Para demostrar que algunas áreas contenían más especímenes de ciertos grupos que otros, se normalizó el número de especímenes en cada grupo y se calcularon sus densidades. El número de especímenes se dividió por el área total de las diferentes zonas de muestreo. Siguiendo esta normalización, se pueden determinar áreas de mayor abundancia de unos grupos que de otros. Los valores obtenidos para la densidad de crustáceos decápodos en cada sector del afloramiento varían en uno o dos órdenes de magnitud, lo que apoya la idea de que algunos grupos estaban fuertemente vinculados al tipo de facies (ver detalles en Ferratges *et al*., 2021c).

Aunque el análisis de rarefacción indica que el muestreo no se ha estabilizado, las curvas de las tres zonas dejaron de crecer exponencialmente, indicando un punto de estabilización diferente en cada zona (ver Ferratges *et al*., 2021c). Con base al muestreo realizado y el índice de Shannon, los datos obtenidos sugieren que la mayor diversidad se concentra en facies arrecifales. En conjunto, estas evidencias podrían explicar por qué algunos taxones están representados por un pequeño número de individuos (ver detalles en Ferratges *et al*., 2021c).

El índice Chao1, que estima las abundancias, es más alto en el frente arrecifal (*inner fore-reef*). Sin embargo, el hecho de que varios taxones estén representados por un bajo número de especímenes sugiere que estos taxones han sido transportados desde el arrecife propiamente dicho. Por otro lado, las facies adyacentes al frente arrecifal (*inner fore-reef*) contenían el mayor número de especies. Por lo tanto, con base en una variedad de medidas de diversidad, se planteó la hipótesis de que las facies las facies adyacentes al frente arrecifal (*inner fore-reef*) preservaron el conjunto más abundante; aunque algunas especies preservadas en dicha zona fueron transportadas desde el núcleo del arrecife.

Sin embargo, para el Índice de Diversidad de Simpson y el Índice de Shannon-Wiener, las facies de frente arrecifal ocuparon la tercera y segunda posición respectivamente. Estos índices son más altos para la facies arrecifal. El índice de Shannon mide la biodiversidad específica, y los resultados obtenidos indican valores decrecientes desde el arrecife (reefal facies) a las zonas distales (*outer fore-reef*), mostrando que la zona con la mayor diversidad de taxones corresponde a la facies arrecifal. Para comparar si estas diferencias en el índice de Shannon son significativas, se realizó un test T. Las comparaciones de la facies arrecifal (*reefal facies*) *vs* frente arrecifal (*inner fore-reef*) y la facies arrecifal (*reefal facies*) *vs* a la facies del frente arrecifal externo (*outer fore-reef*) indican diferencias significativas entre las facies. Por otro lado, una comparación del frente arrecifal proximal (*inner fore-reef*) *vs* el frente arrecifal externo (*outer fore-reef*), indica que no son significativas.

7.2.2. Comparación entre sistemas arrecifales del Eoceno medio

Los arrecifes del Luteciense (Eoceno medio), son los que han aportado una menor diversidad. Esto puede estar condicionado por un sesgo en el muestro, pero también por sus características. Estas acumulaciones de coral se sitúan en la Cuenca de Ainsa, entre pliegues y cabalgamientos que complican la interpretación estratigráfica y paleoambiental. Entre estos materiales destacan las rampas inestables de la Fm Grustán, con gran abundancia de grandes formainíferos bentónicos y otros invertebrados (ver detalles en Arbués *et al*., 2011). Se pueden observar montículos de coral similares a lo largo del flanco occidental del anticlinal de Balces en el equivalente temporal de Fm. Guara (ver Barnolas *et al*., 1991; Pomar *et al*., 2017). Sin embargo, han proporcionado material escaso y fragmentario (actualmente en estudio), y ninguno de los taxones de este conjunto (ver Canudo *et al*., 2021) coincide con los del Eoceno inferior, ni el superior. La mayor parte del material aparece en olistolitos de la Fm. Grustán que han sido transportados a niveles profundos de la Fm. San Vicente. Esto obviamente puede haber influido también en las diversidades registradas, aunque los resultados son prliminares y serán corroborados en el futuro.

7.2.3. Comparación entre sistemas arrecifales del Eoceno medio y superior

Por último, el arrecife de La Peña presenta similitudes con otros arrecifes del Eoceno medio y superior de la Península Ibérica (p. ej., Busquets *et al*., 1985; Santisteban y Taberner, 1988; Álvarez *et al*., 1994; Hendry *et al*., 1999; Romero *et al*., 2002; Pomar *et al*., 2017). Estas acumulaciones se desarrollaron durante el enfriamiento progresivo posterior al intervalo MECO (ver Fig. 8) y comparten una serie de analogías: 1) asociaciones coralinas y foraminíferos similares; 2) estructuras similares; 3), corales individuales incrustados en una matriz arcillosa o limosa litificada, lo que sugiere baja energía hidrodinámica; 4) presencia exclusiva de algas rojas como autótrofas *in situ*, indicando un desarrollo en la zona meso-oligofótica; 5) acumulaciones asociadas a sistemas deltaicos, por lo que la zona mesofótica podría tener una profundidad de hasta 10 m (ver Pomar *et al*., 2017). Sin embargo, ninguno de estos ambientes arrecifales ibéricos ha proporcionado crustáceos decápodos hasta el momento, por lo que no se pueden hacer comparaciones a ese respecto. Por otro lado, el conjunto de decápodos del arrecife de Rasal tiene similitudes con el material recolectado en otras localidades arrecifes del Eoceno de Europa como los de Italia (p. ej., Beschin *et al*. 2007, 2015; Tessier *et al*., 2011). Aunque, a diferencia de estos últimos los arrecifes del Pirineo parecen tener una aportación siliciclástica mayor y la conservación de los taxones es diferente. Los arrecifes italianos se caracterizan for ser principalmente de caliza pura sin apenas interestratos de material siliciclástico. Esto puede ser debido a variaciones locales en el aporte de detritos y a la batimetría. Sería necesario hacer un estudio similar al de esta tesis en Italia para poder tener una comparativa adecuada.

Las agrupaciones de los arrecifes del Eoceno superior guardan poca similitud con las estudiadas en el Eoceno inferior de la Cuenca de Graus-Tremp como el arrecife de Ramals, y los observados en Iscles-Col del Vent y Aren-Berganui (ver Fig. 11). Estos últimos están formados por domos arrecifales de menor escala (1 a 10 m de espesor), que aparecen como cuerpos de bajo relieve, sobre calizas bioclásticas de alveolina-algas rojas. Estos domos están formados por corales, algas rojas y foraminíferos incrustantes como *Solenomeris* (ver detalles en Ferratges *et al*., 2021c). La abundancia de matriz bioclástica fangosa, la presencia de *Solenomeris* (un foraminífero de aguas relativamente profundas; Plaziat y Perrin, 1992), y la ausencia de algas verdes y otros componentes de aguas poco profundas indica que se formaron a mayor profundidad (Pomar *et al*., 2017; Ferratges *et al*., 2021c). Esta diferencia en las condiciones parece afectar a la composición de crustáceos decápodos.

7.3. Cambios en la diversidad de los taxones en el Eoceno de la zona surpirenaica central

En este capítulo se discuten los resultados obtenidos referentes a los cambios en la diversidad encontrados en los yacimientos estudiados en el Eoceno inferior (Cuenca de Tremp-Graus) y en el Eoceno medio-superior (Cuenca de Jaca). Estos resultados se analizan a la luz de la distribución y el papel de los crustáceos decápodos en los ecosistemas modernos

En los ecosistemas modernos, es común que los cambios en la fauna bentónica dentro de una misma región sigan el gradiente de profundidad. Otros factores relevantes son el tipo de sedimento y la estabilidad física de los cuerpos de agua locales (Sumida y

Pires-Vanin 1997). Algunos autores (p.ej., Paiva, 1990; Pires, 1992; Pires-Vanin, 1993; Bertini y Fransozo, 2004) sugieren que en las primeras decenas de metros de profundidad (generalmente entre 10 y 40 m, y en ocasiones hasta 100 m) el tipo de sedimento es el factor más relevante en la distribución de la macrofauna bentónica, pero a partir de profundidades cercanas a los 40 m, la temperatura afecta significativamente su distribución. Otros parámetros importantes son las diferencias locales en la hidrodinámica y las altas tasas de sedimentación, que pueden reducir el espacio vital de los decápodos, variando la diversidad y abundancia de especies (ver Morgado y Tanaka, 2001).

7.3.1. Diversidad en el Eoceno inferior de la cuenca de Tremp-Graus

Los datos recopilados en el afloramiento del Eoceno inferior de Ramals indican que los montículos arrecifales que proliferaron en las aguas cálidas relativamente poco profundas (zona mesofótica) sufrieron episodios de acción episódica de oleaje de tormenta. Este escenario proporcionó condiciones favorables para el desarrollo de un abundante y diverso conjunto de decápodos (Tabla 1) y otros invertebrados. Sin embargo, esta alta diversidad desapareció repentinamente tras la colmatación de los montículos arrecifales (deposito del miembro margas de Riguala, ver Fig. 43), permaneciendo una sola especie de decápodo (*Litoricola macrodactyla* (Van Strelen, 1924) var. *pyrenaica* (Artal y Via, 1989) y cambiando todo el conjunto de fauna. La desaparición de esta diversidad se explica por la desaparición de los nichos ecológicos que ofrecía el arrecife debido a la colmatación por sedimentos, perdiendo el medio la capacidad de sostener un ecosistema rico y complejo (Ferratges *et al*., 2021c).

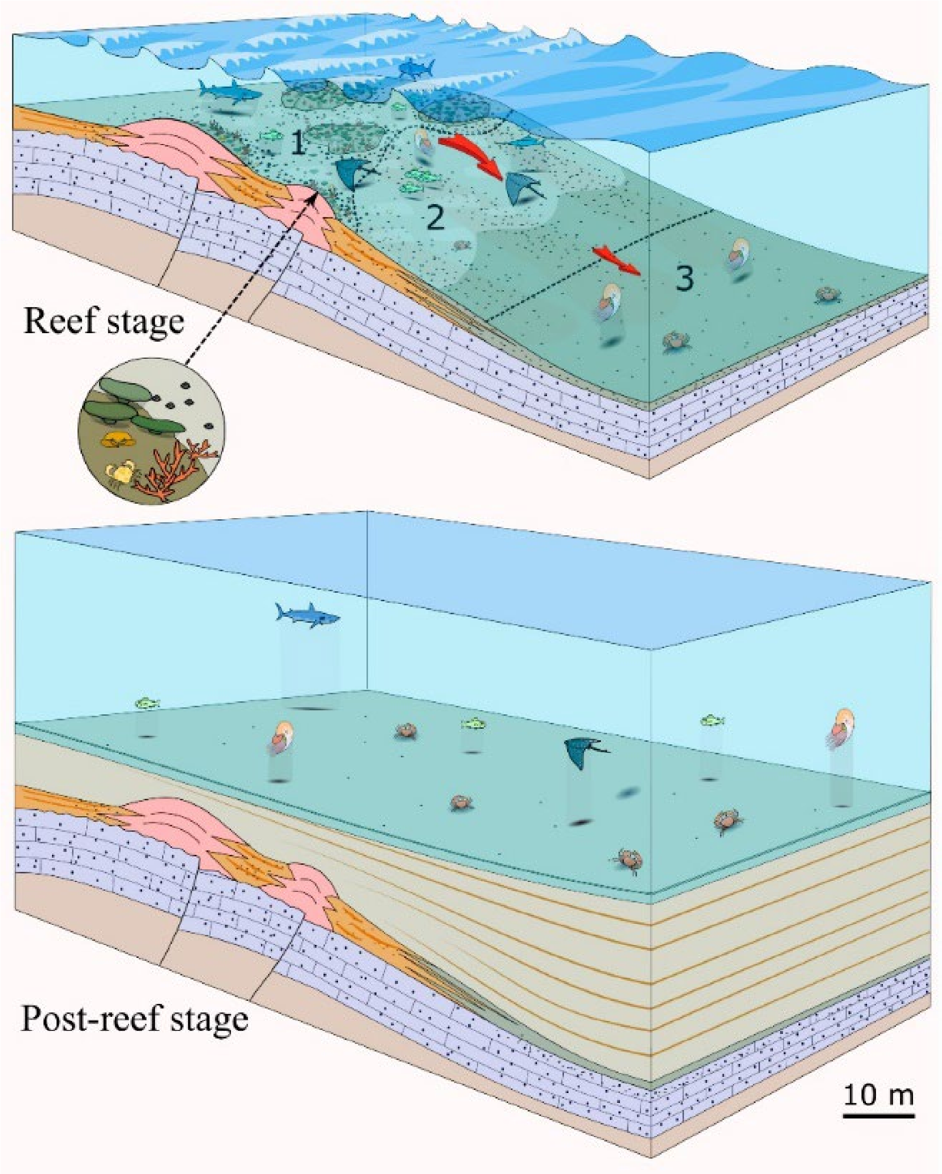


Figura 43: Cambio de las condiciones en la localidad de Ramals. En la segunda etapa (abajo), los arrecifes fueron cubiertos por las margas de Riguala produciéndose una disminución drástica en la diversidad de la fauna bentónica.

Figure 43: Change of conditions in the locality of Ramals. In the second stage (below), the reefs were covered by the Riguala marls, producing a drastic decrease in the diversity of the benthic fauna.

En los materiales de la Fm Roda, correspondientes a margas de prodelta, también se han reconocido diversas especies (Tabla 2) agrupadas en diferentes asociaciones (Fig. 44) que permiten discutir aspectos sobre la diversidad, distribución y características paleoambientales (Figs. 44, 45). Destaca la gran abundancia y amplia distribución de *Zanthopsis dufourii* (H. Milne-Edwards en d'Archiac, 1850) ya mencionada por Via (Via, 1959, 1969; Ferratges *et al.*, 2022b).

Estas agrupaciones con mayor o menor diversidad no han sido estudiadas en su conjunto (Fig. 44) y parecen estar asociadas a intervalos concretos (Fig. 45), por lo que posiblemente su distribución responda a cuestiones paleoambientales que deben ser abordadas en el futuro. Estas asociaciones, que aparecen asociadas a otra diversa fauna bentónica han proporcionado: *Asthenognathus fernandezi* Ferratges, Zamora y Aurell (2022), *Paromola bretoni* Ferratges, Domínguez y Ossó, 2021, *Periacanthus ramosus* Artal y Castillo, 2005, *Eosymethis aragonensis* van Bakel, Guinot, Artal, Fraaije y Jagt, 2012, *Collinscarcinus obliquesulcatus* Artal y van Bakel , 2020, *Titanocarcinus decor* Schweitzer, Artal, van Bakel, Jagt y Karasawa, 2007; *Gaudipluma bacamortensis* Artal, van Bakel, Fraaije y Jagt, 2013 (Artal *et al*., 2013b), *Parapetrochirus robustus* Ferratges, Artal y Zamora, 2021 (Ferratges *et al*., 2021a).

Algunos de los géneros reconocidos en este sector tienen representantes actuales, por lo que se pueden hacer algunas consideraciones. Por ejemplo, *Paromola bretoni* Ferratges, Domínguez y Ossó, 2021b (Fig. 44D-16) presenta la morfología característica de las especies actuales de *Paromola*, cuya distribución está restringida a aguas profundas y fondos blandos, por lo que es esperable unos hábitos similares para la especie fósil.

Por otro lado, tanto el género *Asthenognathus* (en el que se encuentra la especie *Asthenognathus fernandezi* Ferratges, Zamora y Aurell, 2022c (Fig. 44E-22) del Eoceno inferior) como otros géneros muy similares, tiene representantes modernos que se encuentran en ecosistemas de aguas poco profundas a lo largo de los mares templados y tropicales (ver Ferratges *et al*., 2022d y referencias). Estas especies son comúnmente comensales de otros organismos y suelen vivir dentro de la cavidad del manto de moluscos, cnidarios o equinodermos, o asociado a sustratos siliciclásticos móviles y fondos fangosos. La presencia de especímenes delicados y articulados (*Zanthopsis dufourii*, *Glyphithyreus* sp., *Asthenognathus fernandezi*) conjuntamente a otros taxones desarticulados (*Periacanthus ramosus* y *Micromaia* sp.) sugiere la afección episódica de eventos de alta energía que afectan el entorno bentónico, transportan material de áreas cercanas y acumulan tanto especímenes completos como cadáveres desarticulados. El contenido de fauna y las facies presentes indican la presencia de un fondo fangoso emplazado dentro de la zona mesofótica (ver detalles en Ferratges *et al*., 2022c).

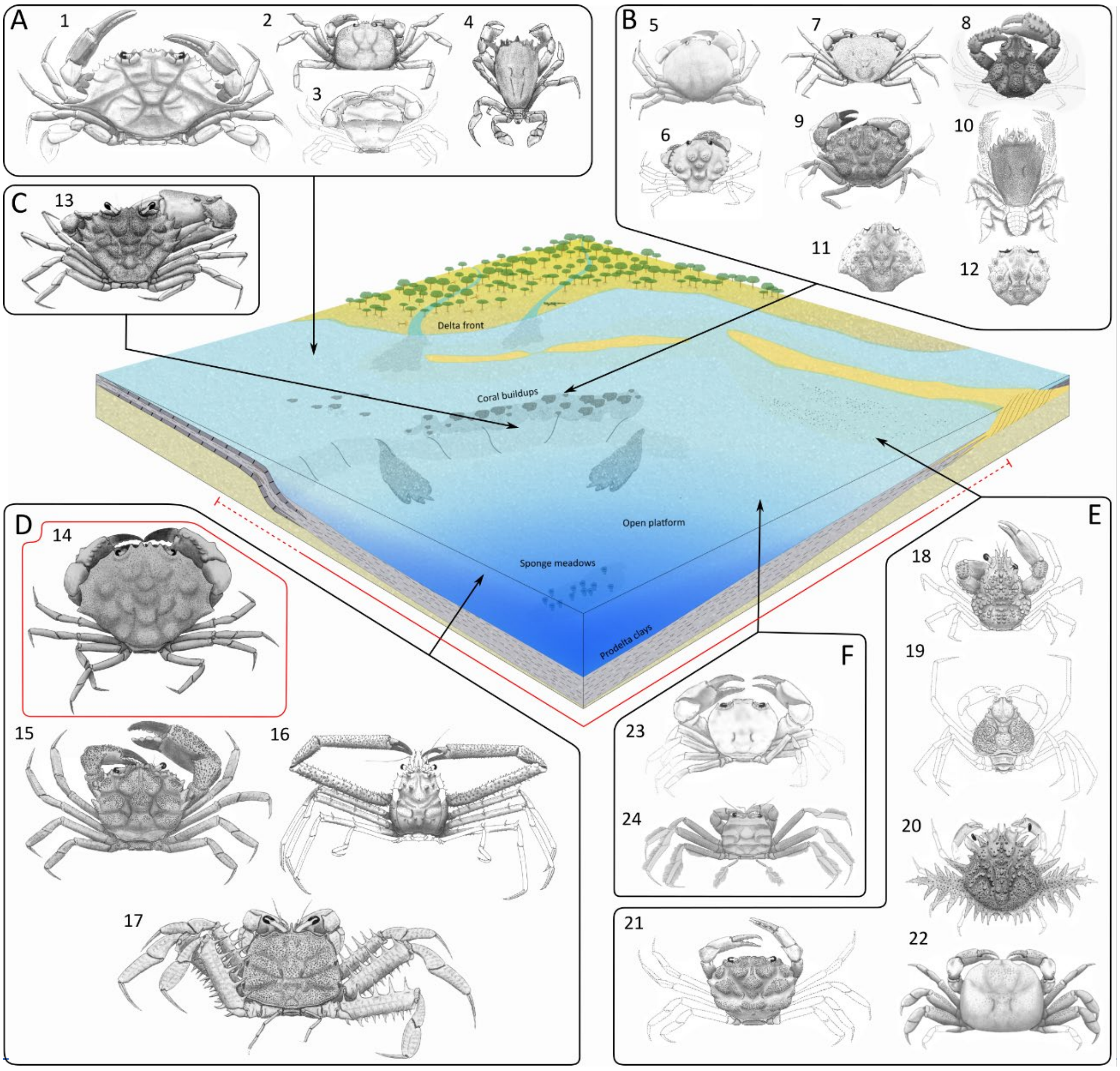


Figura 44: Reconstrucción simplificada del área del Eoceno temprano con la distribución de diferentes facies y los diferentes conjuntos de cangrejos braquiuros encontrados en diferentes ambientes. **A**-**E**: diferentes conjuntos carcínicos del área de estudio. *Zanthopsis dufourii* (D12, enmarcado individualmente) tienen un área de distribución mayor, marcada con una línea discontinua del mismo color que el recuadro donde su registro es fragmentario y disperso, y una línea continua del mismo color donde su registro es menos más homogéneo continuo. Taxones: **1**: *Archaeoportunus isabenensis* Artal, Ossó y Domínguez, 2013a; **2**: Hexapodidae indet.; **3**: *Carinocarcinus* sp.; **4**: *Pseudorogueus* ?*rangiferus* Fraaije, 1995; **5**: Carpilius int.; **6**: *Ilerdapatiscus guardiae*, Artal y Van Bakel, 2018; **7**: *Galenopsis* sp.; **8**: *Aragolambrus collinsi* Ferratges, Zamora y Aurell, 2019; **9**: *Xanthilites* sp.; **10**: *Ranina* sp.; **11**: Calappidae int. (en Ferratges *et al*., 2021c), ¿Cancridae?; **12**: Calappidae int. (en Ferratges *et al*., 2021c), ¿Matutidae?; **13**: *Litoricola macrodactyla* (Van Strelen, 1924) var. *pirenaica* (Artal y Via, 1989); **14**: *Zanthopsis dufourii* (H. Milne-Edwards en d'Archiac, 1850); **15**: decoración *Titanocarcinus* Schweitzer, Artal, van Bakel, Jagt y Karasawa, 2007; **16**: *Paromola bretoni* Ferratges, Domínguez y Ossó, 2021; **17**: *Gaudipluma bacamortensis* Artal, van Bakel, Fraaije y Jagt 2013; **18**: *Micromaia* sp.; **19**: Inachidae int.; **20**: *Periacanthus ramosus* Artal y Castillo, 2005; **21**: *Glyphithyreus* sp.; **22**: *Asthenognathus fernandezi* Ferratges, Zamora y Aurell, 2022; **23**: ?*Magyarcarcinus* sp.; **24**: *Retropluma gallica* Artal, van Bakel y Castillo, 2006. Dibujos A1; B6, 9; C13; D14,15,17; E18, 20, 21; F24 publicados en Ferratges, 2017; D16 Ferratges et al., 2021b; E20 en Ferratges et al., 2022d.

Figure 44: Simplified reconstruction of the early Eocene area with the distribution of different facies and the different assemblages of brachyuran crabs found in different environments. **A-E**: different carcinic

assemblages of the studied area. *Zanthopsis dufourii* (D12, individually framed) have a larger distribution area, marked with a dashed line of the same color as the box where their record is fragmentary and scattered, and a solid line of the same color where their record is less fragmentary and continuous. Taxa: **1**: *Archaeoportunus isabenensis* Artal, Ossó & Domínguez 2013a; **2**: Hexapodidae indet.; **3**: *Carinocarcinus* sp.; **4**: *Pseudorogueus* ?*rangiferus* Fraaije, 1995; **5**: *Carpilius* indet.; **6**: *Ilerdapatiscus guardiae*, Artal & Van Bakel, 2018; **7**: Galenopsis sp.; **8**: *Aragolambrus collinsi* Ferratges, Zamora & Aurell, 2019; **9**: *Xanthilites* sp.; **10**: *Ranina* sp.; **11**: Calappidae indet. (in Ferratges *et al*., 2021c), ¿Cancridae?; **12**: Calappidae indet. (in Ferratges *et al*., 2021c), ¿Matutidae?; **13**: *Litoricola macrodactyla* (Van Strelen, 1924) var. *pyrenaica* (Artal & Via, 1989); **14**: *Zanthopsis dufourii* (H. Milne-Edwards in d'Archiac, 1850); **15**: *Titanocarcinus decor* Schweitzer, Artal, van Bakel, Jagt & Karasawa, 2007; **16**: *Paromola bretoni* Ferratges, Domínguez & Ossó, 2021; **17**: *Gaudipluma bacamortensis* Artal, Van Bakel, Fraaije & Jagt 2013; **18**: *Micromaia* sp.; **19**: Inachidae indet.; **20**: *Periacanthus ramosus* Artal & Castillo, 2005; **21**: *Glyphithyreus* sp.; **22**: *Asthenognathus fernandezi* Ferratges, Zamora & Aurell, 2022; **23**: ?*Magyarcarcinus* sp.; **24**: *Retropluma gallica* Artal, van Bakel & Castillo, 2006. Drawings A1; B6, 9; C13; D14,15,17; E18, 20, 21; F24 taken from Ferratges, 2017; D16 Ferratges *et al*., 2021b; E20 from Ferratges *et al*., 2022d.

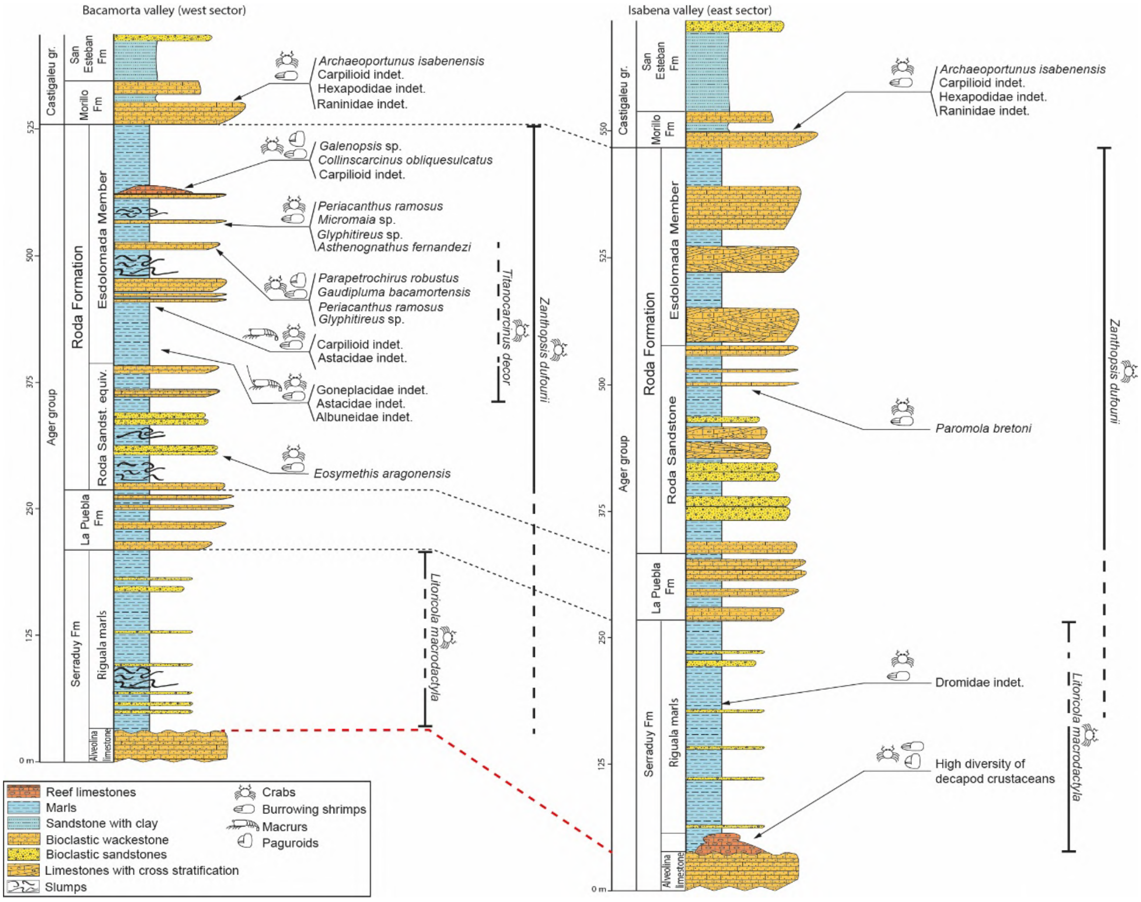


Figura 45: Columnas estratigráficas sintéticas del área Bacamorta-Isabena indicando las principales características litológicas de las formaciones del Ypresiense medio al Luteciense inferior (Eoceno inferior) y los niveles sucesivos con asociaciones de decápodos. Para ver la alta diversidad de crustáceos decápodos al fondo del sector este (intervalo arrecifal de la Formación Serraduy), ver tablas 1 y 2 (tomado de Ferratges *et al*., 2022b).

Figura 45: Synthetic stratigraphic logs of the Bacamorta-Isabena area indicating the main lithological features of the middle Ypresian to lower Lutetian (lower Eocene) formations and the successive levels with recorded decapod associations. To see de high diversity of decapod crustaceans to the bottom of the east sector (reefal interval of the Serraduy Formation), see tables 1 and 2 (from Ferratges *et al*., 2022b).

7.3.2. Diversidad en el Eoceno medio y superior de la cuenca de Jaca

Los materiales del Eoceno medio y superior analizados en la Cuenca de Jaca (Fm Arguis) revelan ciertos cambios de la diversidad de forma más o menos abrupta en un espacio relativamente reducido. Las asociaciones de decápodos estudiadas en las plataformas someras de la Fm Arguis muestran una marcada distribución en función de los diferentes ambientes. El conjunto de decápodos recolectado corresponde a taxones asociados a diferentes ambientes de plataforma siliciclástica (fondos arenosos y blandos) y ambientes carbonatados (sistemas arrecifales y biohermos de algas y esponjas). En particular, se han observado algunas variaciones en la diversidad que podrían estar relacionadas tanto con la paleobatimetría (dominios proximales *vs* distales de la plataforma), como con la mayor o menor influencia terrígena (plataformas carbonatadas *vs* siliciclásticas o mixtas).

La presencia de ciertos modos de preservación, como cangrejos ermitaños articulados fuera de su concha, concuerda con las observaciones de los representantes modernos que sugieren que el abandono de la concha huésped ocurre en el 46 % de los casos, cuando los cangrejos ermitaños quedan sepultados después de una sedimentación episódica repentina (Shives y Dunbar 2010). En este sentido, los pulsos episódicos de alta actividad hidrodinámica asociados con un entorno deltaico aumentan la tasa de sedimentación y pueden enterrar organismos bentónicos vivos (p. ej., Nichols *et al*., 1978; Hinchey *et al*., 2006; Shives y Dunbar 2010) (ver detalles en Ferratges *et al*., 2020b).

De particular interés son las plataformas de Arguis y Belsué, que muestran una marcada diferencia entre las facies proximales poco profundas (sinclinal de Belsué), y las facies distales más profundas (sinclinal de Arguis). Estas facies se desarrollaron desde de la zona afótica a eufótica, desde unas pocas decenas a más de 140 metros de profundidad (Morsilli *et al*., 2012), probablemente con un alto contenido de nutrientes, que favoreció la diversidad de organismos bentónicos. Es interesante notar que la preservación preferencial con especímenes articulados se dio tanto en áreas poco profundas proximales como en áreas profundas relativamente distales. Esto probablemente se correlacione con las condiciones tafonómicas más favorables con tasas de sedimentación más altas en las áreas poco profundas que compensan las altas energías, y menos energía en las áreas profundas para desarticular los restos.

La plataforma carbonatada bioclástica desarrollada a techo de la secuencia II en el sinclinal de Rasal (*Bryozoan beds*) se desarrolló durante una etapa con tasas de sedimentación relativamente bajas (Millán *et al*., 1994). La sedimentación irregular y discontinua pudo haber permitido el establecimiento de una comunidad bentónica diversa, y la proliferación de crustáceos decápodos como señalan Morgado y Tanaka (2001) en los ecosistemas actuales. En general, esta plataforma incluye una comunidad bentónica rica y diversa, con una interesante diversidad de crustáceos decápodos, distribuidos en diferentes áreas (ver Tabla 5). El yacimiento de crustáceos encontrado en los niveles superiores de la platforma ricos en glauconita (Br3) registra un aumento de la diversidad en crustáceos decápodos, pero también son muy abundantes otros restos como equinodermos endobentónicos, crinoideos y restos de vertebrados (especialmente dientes de tiburón). Las bajas tasas de sedimentación en un ambiente relativamente poco profundo y relativamente alejados de la línea de costa, podrían permitir el asentamiento de una comunidad bentónica compleja. Sin embargo, se observa una desaparición dramática y repentina de estas faunas por encima de este nivel debido a la brusca profundización generalizada (drowning unconformity; Millán *et al*., 1994), que da paso al inicio de la sedimentación de la sucesión de margas de la plataforma externa de la Secuencia III suprayacente.

Las plataformas de Arguis y Belsué contienen una gran diversidad de fauna. Estas asociaciones se dividen entre facies menos profundas, con *Portunus*, y facies más profundas, con *Harpactocarcinus*. Las concentraciones de estos taxones pueden ser puntualmente importantes, siendo escasos los restos de otros crustáceos en los niveles de apogeo de estos taxones dominantes. El menor tamaño de los ejemplares de *Harpactocarcinus* encontrados en las zonas distales y profundas (Br1), puede estar relacionado con un menor aporte de nutrientes u otros factores limitantes que controlan su crecimiento, pero siguen siendo dominantes en el ecosistema bentónico.

El muestreo realizado y el índice de Shannon sugieren que la mayor diversidad se concentra en las áreas someras y proximales de las plataformas. El índice Chao1, que estima abundancias, es más alto en la plataforma de Pectínidos (PP, parte alta Secuencia III). Sin embargo, el hecho de que varios taxones estén representados por un bajo número de especímenes, y en general restos muy fragmentados, sugiere que la mayoría de estos taxones han sido transportados desde las áreas someras y proximales. Estos índices son más altos para la plataforma Belsué (BP somero, correspondiente a aguas menos profundas). El índice de Shannon mide la diversidad específica. E área de estudio presenta un índice de Shannon de 1,995 para las áreas someras de la plataforma Belsué (BP somera), pero solo de 0,3443 en las áreas más profundas y distales de la misma facies. Lo mismo ocurre con las zonas proximales de la plataforma de Arguis (AP proximal), con 1,922 en las zonas proximales y 0 en las distales. PP, CB y BB muestran valores intermedios.

Por el contrario, la máxima diversidad, pero con una abundancia relativamente baja se correlaciona con facies de arrecifes (Rasal-La Peña, Secuencia IV) y las capas de briozoos (con biohermos de esponjas, techo de Secuencia II). Esto puede explicar por la mayor cantidad de nichos y refugios ecológicos que ofrecen estos ambientes (ver Ferratges *et al*., 2020 y referencias), que permiten una menor competencia entre especies, pero al mismo tiempo, dan lugar a un bajo potencial de fosilización (Schweitzer y Feldmann, 2015). Sin embargo, el tipo de acumulación puede afectar la diversidad de decápodos y albergar conjuntos muy diferentes (Tabla 5 y Fig. 46).

Por otro lado, el afloramiento del Priaboniense (Eoceno superior) de Fanlillo, en el margen norte de la Cuenca de Jaca, destaca por su alta diversidad asociada a ambientes marinos someros terrígenos (ver Tabla 5). Los datos recopilados para esta localidad sugieren un ambiente de energía relativamente baja dominado por sedimentación arcillosa, con eventuales episodios de alta energía. En concreto, los datos sedimentológicos y paleoecológicos indican un ambiente con fondos blandos y ambientes siliciclásticos con briozoos, colonias pequeñas y aisladas de corales esféricos (*Stylocoeni* sp.) y praderas de fanerógamas marinas, que probablemente se desarrollaron en la zona eufótica, por encima del nivel base de las olas de tormenta, a profundidades que no excedieron los 20-30m. Este tipo de ambientes pudo actuar de forma parecida a ciertos tipos de arrecife durante el Eoceno (ver Silva-Casal, 2017), lo que explicaría esta gran diversidad tanto en crustáceos decápodos como en moluscos.

Hay que notar que algunos de cambios de diversidad parecen estar relacionados con la distribución de ciertos taxones (Fig. 46). Las asociaciones de crustáceos varían drásticamente, destacándose la presencia de ciertos taxones predominantes. Por ejemplo, en los intervalos con mayor abundancia de cangrejos grandes como *Portunus catalaunicus* o *Harpactocarcinus punctulatus*, parece haber una disminución en la diversidad de crustáceos decápodos. La presencia de *P. catalaunicus* está asociada a áreas siliciclásticas someras, relativamente pobres en diversidad de crustáceos decápodos, y los crustáceos asociados son principalmente endobentónicos. Esto puede sugerir hábitos depredadores de este taxón hacia el resto de los organismos bentónicos. En los ecosistemas modernos, los portúnidos son depredadores de muchos invertebrados y pequeños vertebrados (Careddu *et al*., 2017). Esto se puede ver claramente en especies invasoras de forma y tamaño similar a *P. catalanicus*, como el cangrejo azul (*Callinectes sapidus*) en el mar Mediterráneo, y el gran impacto que han causado en poco tiempo en las zonas someras invadidas (p.ej., Prado *et al*., 2021 y referencias). Esto también es consistente con los ecosistemas modernos, donde los braquiuros depredadores son más típicos en hábitats submareales poco profundos porque estas áreas concentran más nutrientes provenientes del continente que conducen a una mayor abundancia y diversidad de presas (p.ej., Careddu *et al*., 2017; Davie, 2021).

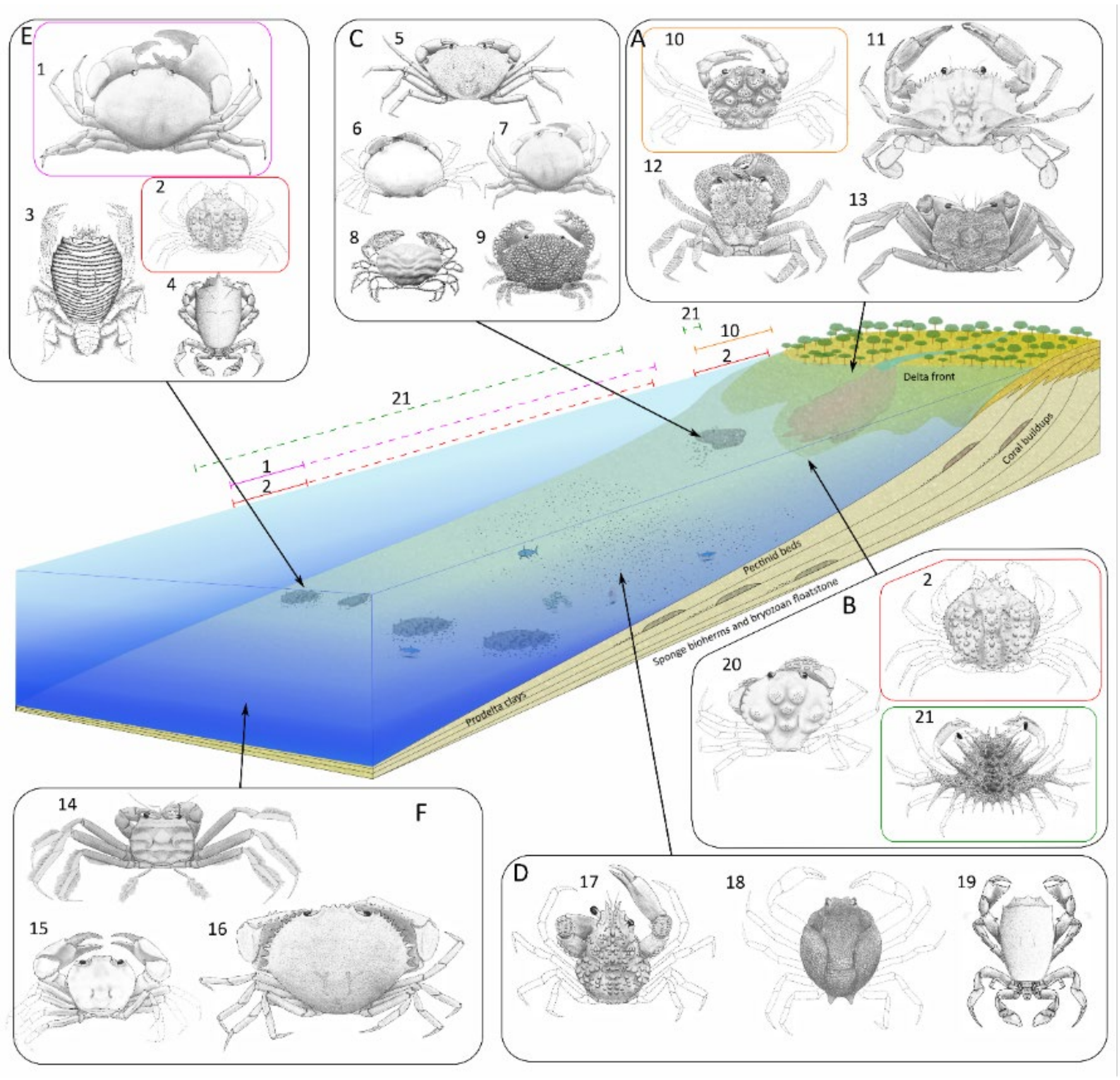


Figura 46: Reconstrucción simplificada del área de estudio con la distribución de las diferentes facies y los diferentes ensambles de cangrejos encontrados en diferentes ambientes. A-F: diferentes asociaciones carcínicas del área de estudio. Las subdivisiones geográficas producidas por los diferentes anticlinales se han omitido para simplificar el esquema. Los taxones enmarcados individualmente tienen áreas de distribución más grandes, marcadas con una línea discontinua del mismo color que cada recuadro donde su registro es fragmentario y disperso, y una línea continua del mismo color donde su registro es menos fragmentario y continuo. Taxones: 1: Carpiliidae indet. 1; 2: *Calappilia* sp.; 3: *Lophoranina* sp.; 4: *Notopus* sp.; 5: *Galenopsis crassifrons*; 6: *Liopsalis anodon*; 7: Carpiliidae indet. 2; 8: *Gemmellarocarcinus riglosensis*; 9: *Daira coralina*; 10: *Pyreneplax* cf. *basaensis*; 11: *Portunus* catalaunicus; 12: *Montezumella* cf. *amenosis*; 13: *Retrocypoda almelai*; 14: *Retropluma eocenica*; 15: *Magyarcarcinus yebraensis*; 16: *Harpactocarcinus punctulatus*; 17: *Micromaia priabonensis*?; 18: Leucosidae int.; 19: *Quasilaeviranina* sp.; 20: *Hepatiscus* sp.; 21: *Periacanthus horridus*.

Figura 46: Simplified reconstruction of the study area with the distribution of different facies and the different assemblages of crabs found in different environments. A-F: different carcinic assemblages of the studied area. The geographical subdivisions produced by the different anticlines have been omitted to simplify the scheme. Individually framed taxa have larger distribution areas, marked with a dashed line of the same colour as each box where their record is fragmentary and scattered, and a solid line of the same colour where their record is less fragmentary and continuous. Taxa: 1: Carpiliidae indet. 1; 2: *Calappilia* sp.; 3: *Lophoranina* sp.; 4: Notopus sp.; 5: *Galenopsis crassifrons*; 6: *Liopsalis anodon*; 7: Carpiliidae indet. 2; 8: *Gemmellarocarcinus riglosensis*; 9: *Daira corallina*; 10: *Pyreneplax* cf. *basaensis*; 11: *Portunus catalaunicus*; 12: *Montezumella* cf. *amenosi*; 13: *Retrocypoda almelai*; 14: *Retropluma* *eocenica*; 15: *Magyarcarcinus yebraensis*; 16: *Harpactocarcinus punctulatus*; 17: *Micromaia priabonensis*?; 18: Leucosidae indet.; 19: *Quasilaeviranina* sp.; 20: *Hepatiscus* sp.; 21: *Periacanthus horridus*.

7.4. Comparación entre las agrupaciones arrecifales y de prodelta

7.4.1. Agrupaciones arrecifales

Los arrecifes del Eoceno inferior estudiados presentan características particulares con una asociación de organismos bioconstructores compuesta tanto por corales como algas y foraminíferos incrustantes (ver detalles en Ferratges *et al*., 2021c) que albergan una elevada diversidad de crustáceos decápodos (ver Tabla 1 y Fig. 47A). Entre estos crustáceos, destaca la presencia de taxones con características basales de ciertos grupos (*Aragolambrus*, *Ilerdapatiscus*, y otros actualmente en estudio) que parecen estar emparentados con diferentes grupos modernos (p. ej., Ferratges *et al*., 2019, Ferratges *et al*., en revisión), sugiriendo una posición cercana al momento de divergencia. Esto sugiere que este tipo de nichos tuvo un papel importante en su diversificación (p. ej., Saint Martin y Müller, 1988; Müller y Collins, 1991; Krobicki y Zatoń, 2008; Klompmaker, 2013; Klompmaker *et al*., 2013a).

Estas formas basales convivieron con los representantes más antiguos conocidos de algunos géneros modernos (p. ej., *Carpilius* sp., *Ranina* sp., *Paromola* sp.) y los primeros representantes de varios géneros de cangrejos ermitaños modernos (ver Ferratges *et al*., 2022a). Este conjunto de datos apoya la suposición de que el Eoceno, y especialmente los arrecifes del Eoceno inferior actuaron no solo como puntos calientes de biodiversidad, sino que además pudieron albergar diversidades a las actuales. Además, el muestreo exhaustivo ha permitido señalar que no solo el arrecife en sí alberga una rica fauna de decápodos, si no que las facies adyacentes presentan sus propias asociaciones, vinculadas de forma secundaria a los biohermos.

Los arrecifes del Eoceno superior, como el de La Peña, están formados principalmente por corales coloniales de morfologías diversas (ver Morsilli *et al*., 2012). En cuanto a la composición del conjunto de decápodos reconocidos, destacan especies con formas más derivadas y especializadas, parecidas a las que existen actualmente (p. ej., *Daira*, *Carpilius*). La diversidad de este tipo de arrecifes es inferior a la del Eoceno inferior (Fig. 47C), sin embargo, la excelente exposición ha permitido situar estadísticamente las preferencias de algunas de estas especies. Los datos obtenidos muestran que ya en el Eoceno superior, las especies adaptadas a los arrecifes de coral estaban adaptadas a uno u otro tipo de coral (ver detalles en Ferratges *et al*., 2020a), y respaldan la suposición de que los arrecifes del pasado tenían características similares a los actuales, siendo puntos calientes de biodiversidad (p. ej., Förster, 1985; Müller *et al*., 2000; Krobicki y Zatoń, 2008; Klompmaker, 2013; Klompmaker *et al*., 2013a, b).

Por otro lado, otros sistemas carbonatados como las praderas de Briozoos (bryozoan beds) del Eoceno medio-superior de la zona de Arguis contienen biohermos de esponjas y praderas de esponjas, que permitieron el desarrollo de una relativamente diversa comunidad bentónica con una gran diversidad de equinodermos y de moluscos. En cuanto a los crustáceos muestra una diversidad relativamente alta (ver Fig.46) con carpiliidos indeterminados, calappidos (*Calappilia* sp., *Bitnerilia* sp.), raninidos (*Lophoranina* sp.; ?*Notopus* sp.) y májidos (*Periacanthus*).

7.4.2. Agrupaciones de prodelta

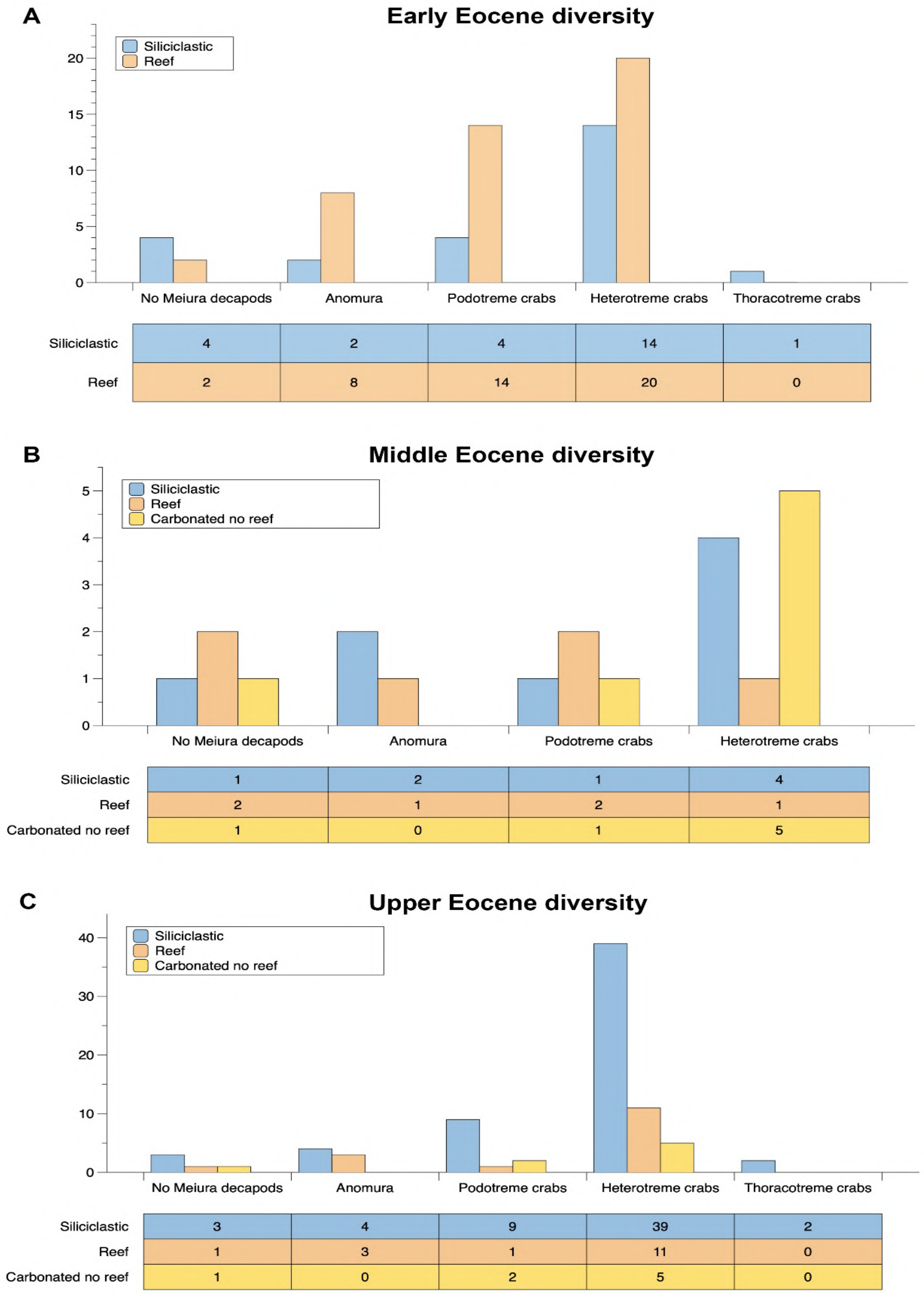
La zona de prodelta de la Cuenca de Graus-Tremp (Eoceno inferior), preserva diversas asociaciones, que al ser estudiadas en detalle muestran una distribución particular, asociadas a ambientes concretos con una distribución específica (ver Figs. 44, 45 y 47A). Algunos de estos géneros se han encontrado en otras cuencas del Eoceno inferior de Europa (ver Tabla 1), como la Cuenca de Hampshire (*Periacanthus*, *Zanthopsis*), Bélgica (*Glyphithyreus*) Italia (*Boschetia*, *Carinocarcinus*, *Galenopsis*, *Micromaia*, *Titanocarcinus*), Francia (*Glyphithyreus*, *Litoricola*, *Titanocarcinus*) o Hungría (*Titanocarcinus*). Sin embargo, algunos de los géneros encontrados no se conocen en ninguna otra parte (ver Tablas 2, 3), por lo que podrían ser endemismos (p. ej., *Archaeoportunus*, *Gaudipluma*, *Torodromia* y *Sierradromia*).

Las formaciones Grustán y San Vicente (Tabla 4) correspondientes al Luteciense (Eoceno medio) han mostrado una de las diversidades más bajas en todos los ambientes (Fig. 47B). Esta baja diversidad en el Luteciense aragonés contrasta con las grandes diversidades reconocidas en cuencas cercanas como las de Cataluña (Via, 1959; 1969 y observación personal). Esta diferencia de diversidad probablemente esté justificada por los diferentes ambientes de estas dos regiones. Por otra parte, el retroceso de los arrecifes de coral como resultado del optimo climático (EECO) (ver Pomar *et al*., 2017 y referencias) podría estar relacionado con la disminución en la diversidad de crustáceos decápodos en ambientes arrecifales.

Este conjunto de faunas presenta tanto taxones bien conocidos como formas enigmáticas (ver Canudo *et al*., 2021) actualmente en estudio. Algunos de los géneros reconocidos en este área se han encontrado en otras cuencas de Europa como las de Hungría, Eslovenia e Italia (*Harpactoxanthopsis*, *Lophoranina* y ?*Eomatuta* [referido como "*Peltarion pirenaicum*" por Aguilar y Castillo, 2017]) y del noroeste (López-Horgue y Bodego, 2017) y sureste (Via, 1959; Solé y Via, 1988) de la Península Ibérica.

En el conjunto de facies de prodelta del Eoceno superior (Bartoniense medio-Priaboniense inferior) presenta una diversidad muy alta (ver Tabla 5 y Fig. 47C). Concretamente, en el sector de Arguis se han encontrado diversos taxones que se encuentran en varias cuencas europeas situadas al Este de la zona surpirenaica central (Cataluña, Italia, Hungría, Eslovenia e incluso Irán e India), pero no al norte, como sucede en el Eoceno inferior (con la excepción de *Harpactocarcinus punctulatus* (ver van Bakel *et al*., 2006). Entre estas especies destacan *Harpactocarcinus punctulatus* (Cataluña, Hungría, Eslovenia, Italia), *Portunus catalaunicus* (Cataluña), *Montezumella* cf. *amenosi* (Cataluña, Italia?), *Galenopsis crassifrons* (Hungría, Italia), *Liopsalis* cf. *anodon* (Cataluña, Italia, India), *Retrocypoda almelai* (Cataluña, Italia, Irán), *Retropluma eocénica* (Cataluña, Italia).

Algunos de estos grupos tienen un origen claramente anterior al Eoceno, como es el caso de los retroplumidos, cuyo registro más antiguo se conoce en el Cretácico de México (ver Khodaverdi Hassan-vand *et al*., 2016). Sin embargo, durante el Eoceno, su registro se concentra en Europa, presentando la mayor diversidad en las cuencas Surpirenaicas (con al menos 4 de las 5 especies conocidas).



	No Meiura decapods	Anomura	Podotreme crabs	Heterotreme crabs	Thoracotreme crabs
Siliciclastic	4	2	4	14	1
Reef	2	8	14	20	0

	No Meiura decapods	Anomura	Podotreme crabs	Heterotreme crabs
Siliciclastic	1	2	1	4
Reef	2	1	2	1
Carbonated no reef	1	0	1	5

	No Meiura decapods	Anomura	Podotreme crabs	Heterotreme crabs	Thoracotreme crabs
Siliciclastic	3	4	9	39	2
Reef	1	3	1	11	0
Carbonated no reef	1	0	2	5	0

Figura 47: Número de especies para las diferentes facies del Eoceno en la zona surpirenaica central: **A**: Eoceno inferior (Ypresiense); **B**: Eoceno medio (Luteciense) y; **C**: Eoceno superior (Bartoniense medio-Priaboniense inferior).

Figure 47: Number of species for the different Eocene facies in the central southern Pyrenees: **A**: early Eocene (Ypresian); **B**: middle Eocene (Lutecian) and; **C**: upper Eocene (middle Bartonian-lower Priabonian).

8. CONCLUSIONES y PERSPECTIVAS FUTURAS

Esta Tesis Doctoral presenta los resultados obtenidos de combinar la estratigrafía y sedimentología, con el estudio sistemático y filogenético de crustáceos decápodos en el Eoceno de las cuencas de la zona central surpirenaica. El conjunto de trabajos realizados durante cuatro años de investigación ha puesto de relieve la importancia de este grupo de invertebrados durante el Eoceno. La prospección activa y estudio sistemático de los yacimientos ha demostrado contener una gran e inédita diversidad de crustáceos decápodos asociados a diferentes facies. El examen del nuevo material fósil aumenta notablemente (casi cuatriplicando) la diversidad previamente conocida en el área estudiada e incrementa notablemente la diversidad de crustáceos decápodos del Eoceno de toda la Península Ibérica. Esto hace posible uno de los estudios sistemáticos más completos de los decápodos del Eoceno Surpirenaico, dejando claro que las cuencas Surpirenaicas fueron un punto caliente de diversidad, con un total de al menos 163 especies de decápodos reconocidos hasta la fecha (66 para el Ypresiense, 21 en el Luteciense, y 76 para el Bartoniense y Priaboniense inferior).

Por otro lado, los datos obtenidos durante la investigación son útiles para inferir cómo se han diversificado los crustáceos decápodos durante el Cenozoico, así como aportar datos para la calibración de relojes moleculares y para explorar la relación entre su diversidad y el desarrollo de diferentes ambientes (diferentes tipos de zonas arrecifales y áreas de prodelta), y el impacto que los cambios ambientales han tenido sobre este tipo de organismos en el pasado. De este modo, el trabajo realizado representa uno de los pocos estudios de crustáceos decápodos fósiles en los que se relaciona su diversidad y distribución en diferentes ambientes sedimentarios.

Para alcanzar estos resultados se han empleado métodos avanzados, tanto en el campo de la estadística, usando programas especializados, como en el procesado digital de modelos 3D a partir de Microtomografía Computarizada empleando fósiles de preservación excepcional. Gracias a estos métodos se han podido analizar tanto aspectos de la distribución de multitud de taxones en diferentes sectores de las cuencas Surpirenaicas, como aspectos filogenéticos basados en la posición y estructura de los elementos morfológicos (en algunos casos no visibles a simple vista).

A continuación, se resumen los puntos específicos importantes de las conclusiones y las perspectivas de futuro que se abordarán en cada una de ellas.

Conclusiones sistemáticas

A lo largo de este trabajo se han descrito un total de 6 géneros y 22 especies nuevas. En concreto, 1 género y 9 especies de cangrejos ermitaños (Paguroidea) que corresponden a los siguientes taxones: *Anisopagurus primigenius*, *Clibanarius isabenaensis*, *Dardanus balaitus*, *Diogenes augustinus*, *Eocalcinus veteris*, *Eocalcinus gerardbretoni*, *Parapetrochirus* robustus, *Parapetrochirus serratus*, *Paguristes perlatus*. Por otro lado, entre el nuevo material descrito, se encuentran los 5 géneros y 13 especies de cangrejos verdaderos que se nombran a continuación: *Basidromilites glaessneri*, *Dynomene collinsi*, *Gemmellarocarcinus riglosensis*, *Kromtitis isabenensis*, *Mclaynotopus longispinosus*, *Sierradromia gladiator*, *Torodromia elongata*, (Dromioidea), *Paromola bretoni* (Homoloidea), *Aragolambrus collinsi*, *Phrynolambrus sagittalis* (Parthenopoidea), *Daira corallina* (Dairidea), *Lobogalenopsis joei* (Pilumnoidea), *Asthenognathus fernandezi* (Grapsoidea).

Entre estos nuevos taxones se encuentran los representantes más antiguos de los géneros *Anisopagurus*, *Asthenognathus*, *Basidromilites*, *Mclaynotopus* y *Parapetrochirus*, y el registro más antiguo y moderno del género *Eocalcinus*, además de numerosos taxones actualmente en estudio que probablemente corresponden a especies o géneros nuevos, o son la primera cita en la Península Ibérica

Por otro lado, algunos de los nuevos taxones descritos corresponden a la primera cita en la Península Ibérica de varios géneros ya conocidos ampliando su distribución estratigráfica y paleobiogeográfica (*Daira*, *Dynomene*, *Galenopsis*, *Gemmellarocarcinus*, *Liopsalis*, *Lobogalenopsis*, *Paromola*, *Phrynolambrus* y *Scultoplax*). Varios de los nuevos taxones muestran características anatómicas que incluyen elementos diagnósticos importantes, ampliando nuestra comprensión de sus orígenes, diversidad anatómica y afinidades sistemáticas. Todos estos datos aportan información fundamental que pueden mejorar la calibración de relojes moleculares, abren la puerta a diversos estudios filogenéticos y estudios paleoambientales. Además, algunos de estos taxones dejan entrever tendencias evolutivas de algunos grupos. Por ejemplo, cangrejos ermitaños como *Eocalcinus* hacia formas más especializadas (pinzas operculares); evolución en los Pathenopoideos hacia formas especializadas con cutículas complejas; o géneros como *Asthenognathus* mostrando una adaptación temprana a la vida en el interior de cavidades.

Finalmente, estas agrupaciones contienen la mayor asociación de dromioideos del Eoceno inferior, y una de las mayores diversidades de cangrejos ermitaños del Eoceno de todo el mundo. Todos estos datos ponen de manifiesto que el Eoceno corresponde a una época de rápida evolución para los crustáceos decápodos y arroja luz sobre los orígenes tempranos, la diversidad anatómica y las afinidades sistemáticas de ciertos grupos.

Conclusiones filogenéticas

Comprender la diversidad o disparidad anatómica de los eubraquiuros del Paleógeno es fundamental para desentrañar las relaciones sistemáticas entre varias de las principales familias modernas e investigar los patrones espaciotemporales que conducen a la evolución de las faunas modernas.

Los resultados obtenidos sugieren que *Phrynolambrus* está estrechamente relacionado con el género moderno *Dairoides*, y que ambos grupos quedan incluidos en Parthenopoidea, filogenéticamente distantes de formas convergentes, como las observadas entre algunos miembros de Eriphioidea. Este descubrimiento plantea un orígen para los Dairoideos 40 millones de años antes de lo que se pensaba, al menos durante el Eoceno superior, y proporciona un punto de calibración fiable de esta familia para estudios filogenéticos moleculares. Los resultados obtenidos, además indican que algunos géneros asignados a Parthenopoidea deben ser revisados, pues el análisis de los caracteres morfológicos no apoya la sistemática tradicional.

Conclusiones sobre la distribución de los crustáceos decápodos

La distribución de los decápodos durante el Eoceno no es aleatoria y muestra claros patrones, que pueden quedar enmascarados por procesos tafonómicos posteriores.

Aunque todavía existen muchas incertidumbres en nuestra comprensión de los patrones de zonificación de diferentes especies dentro de facies arrecifales, de prodelta y de plataformas carbonatadas, el material descrito, asociado con información sedimentológica proporcionará datos importantes para futuros estudios paleoecológicos.

Distribución en el Eoceno inferior

El afloramiento de Ramals (**Eoceno inferior,** Ypresiense, Cuenca Graus-Tremp) expone un cinturón de facies arrecifales que incluye montículos estrechamente espaciados de hasta cinco metros de altura, y facies interarrecifes y ante-arrecifes asociadas. La estructura del arrecife consta de biohermos de coral (coral framestones) con matriz bioclástica de wackestone a packstone, con corales coloniales (*Stylocoenia, Astrocoenia, Astreopora, Agaricia, Actinacis, Cyathoseris, Colpophyllia* y *Caulastraea*), corales solitarios (*Placosmilopsis, Leptophyllia*), algas rojas incrustantes, foraminíferos incrustantes (*Solenomeris*) y briozoos. Los montículos arrecifales y las facies asociadas se desarrollaron dentro de la zona eufótica a mesofótica (algunas decenas de metros de profundidad), con cierto contenido de nutrientes para mantener la diversidad de organismos bentónicos asociados. La acción episódica de olas y corrientes inducidas por tormentas implica la presencia de abundantes fragmentos de coral (*coral rubble*) dentro del propio arrecife, y en los niveles bioclásticos gruesos acumulados en los dominios interarrecifes y de frente arrecifal. Estos niveles están dominados por moluscos, foraminíferos, corales, briozoos, crustáceos decápodos, equinodermos y fragmentos de vertebrados. La presencia de epibiontes en algunos restos óseos y en invertebrados (moluscos, decápodos y equinodermos), indica largos periodos de exposición en el fondo marino.

Los montículos arrecifales que prosperaron en aguas cálidas relativamente poco profundas (zona mesofótica) proporcionaron condiciones favorables para el desarrollo de una comunidad de crustáceos decápodos diversa y abundante. Se ha podido definir una rica asociación de decápodos en Ramals, compuesta por 42 especies. Esta gran diversidad de fauna disminuyó repentinamente después de que los montículos arrecifales fueran cubiertos por sedimentos fangosos de plataforma externa (las margas de Riguala). Después de este evento de profundización y alta tasa de sedimentación solo permanece una especie de cangrejo perteneciente al género *Litoricola macrodactyla*. En definitiva, la pérdida de la capacidad del medio para sostener un ecosistema rico y complejo se explica por la desaparición de los nichos ecológicos que ofrecía el arrecife debido a la obstrucción por sedimentos.

En su mayoría los restos de crustáceos decápodos se conservan como fragmentos de dedos o caparazones aislados, aunque se ha observado poca abrasión o rotura. El análisis de componentes principales (PCA) sugiere que las superfamilias se distribuyeron en diferentes facies. Así, en las zonas arrecifales e interarrecifes, los grupos más representativos son: Carpilioideos, pilumnoideos, xanthoideos, *Ilerdapatiscus* y paguroideos; la zona interna del frente arrecifal (*inner fore-reef*) está dominado por Axiidae, dromioideos, parthenopoideos, calappoideos y raninoideos; en la zona externa del frente arrecifal (*outer fore-reef*), el taxón más representativo es *Litoricola macrodactila*. Este últimos es el único decápodo que quedó en las margas post-arrecifales. Esta distribución ha podido ser corroborada mediante análisis estadísticos de diversidad. Estos análisis también fortalecen la hipótesis de que la mayor diversidad se encontró en el cinturón de facies arrecifales y que una parte importante de los restos generados en dicha área fueron transportados a las facies de frente arrecifal.

Por otro lado, los ambientes siliciclásticos de frente deltaico y las plataformas carbonatadas del Eoceno inferior han aportado una diversidad menor, pero agrupada en diferentes asociaciones y en diferentes ambientes que proporcionan información sobre las características de la cuenca. Los datos sistemáticos tomados de forma individual aportan escasa información a este respecto, pero en su conjunto, estas asociaciones reflejan la presencia de diferentes comunidades bentónicas asociadas a ambientes particulares, aportando una visión más completa del área y de la evolución ambiental de la cuenca.

Distribución en el Eoceno medio y superior

En el **Eoceno medio y superior de la cuenca de Jaca**, los resultados obtenidos en los muestreos han dado lugar a la descripción o primera mención de al menos 47 taxones en el área estudiada, asociados a diversos ambientes. Este conjunto de resultados muestra importantes picos en la diversidad que parecen correlacionados con condiciones tafonómicas muy específicas en ambientes de prodelta proximales. Las facies someras y proximales muestran grandes diversidades y abundancias, y esto puede ser controlado tanto por factores biológicos como tafonómicos (mayor producción biológica y mayor tasa de sedimentación). Estas asociaciones se dividen entre facies menos profundas, con predominio de *Portunus*, y facies más profundas, con *Harpactocarcinus*. Las concentraciones de estos taxones pueden ser puntualmente importantes, siendo escasos los restos de otros crustáceos en los niveles de apogeo de estos taxones dominantes.

Gran parte del material se ha conservado como fragmentos de pinzas o caparazones aislados, con diferente grado de abrasión y rotura. Los resultados sugieren que la distribución de los decápodos en la cuenca de Jaca estuvo influenciada por la profundidad y la exposición al oleaje y las corrientes (estrés hídrico causado por el flujo hidrodinámico). La distribución faunística de los decápodos muestra diferencias importantes tanto en términos de abundancia relativa como de diversidad en cada una de las facies diferenciadas. La composición de la comunidad estudiada sugiere una estructura compleja, que comprende especies de diferentes superfamilias que explotan diferentes nichos. Con base en una variedad de medidas de diversidad, la hipótesis que parece más acertada es que las áreas poco profundas albergaron el conjunto más abundante y diverso. Las áreas profundas y distales contienen, con mucho, la diversidad más baja, y algunas especies preservadas en ellas fueron transportadas desde áreas menos profundas.

Los análisis estadísticos realizados apoyan los datos adquiridos por la observación de campo y los análisis sedimentológicos, reforzando la hipótesis de que la mayor diversidad se encuentra en áreas con bioconstrucciones como biohermos de esponjas, briozoos y arrecifes de coral, y probablemente ambientes de pradera marina. Además, la excelente exposición de estos afloramientos ha permitido concretar diferentes asociaciones dentro de un mismo arrecife en función de la posición respecto al arrecife o el dominio de un tipo concreto de coral (ramificados, tabulares o masivos).

En los arrecifes del Eoceno superior estudiados en La Peña-Rasal, se ha demostrado la fuerte correlación estadística entre ciertos decápodos y facies coralinas específicas. En este arrecife en concreto, las facies de corales ramificados presenta la mayor diversidad y abundancia de crustáceos decápodos con predominio de taxones pequeños. Esto probablemente esté relacionado en las condiciones de energía más baja dentro del arrecife, y también con abundantes cavidades que este entorno proporcionaba dando refugio, alimento y otras interacciones. La facies de corales tabulares contiene principalmente *Galenopsis crassifrons*, y los domos de coral masivo muestran la menor abundancia, con los carpiliidos como el grupo más abundante. Este último probablemente esté controlado tanto por condiciones tafonómicas (cantidad de sedimento entre colonias) como biológicas (espacio limitado para refugio).

En el caso de las áreas proximales de la plataforma, expuesta en el entorno de Bentué, las altas tasas de sedimentación probablemente contribuyeron a mantener intactos algunos especímenes, siendo transportados y enterrados rápidamente. Los datos proporcionados refuerzan la idea previamente documentada de que un aumento en la tasa de sedimentación, eventos sedimentarios repentinos y ausencia de carroñeros favorecen la preservación de los cangrejos ermitaños articulados.

Conclusiones sobre la diversidad de los crustáceos decápodos

Aunque los arrecifes muestran en general un bajo potencial de fosilización para los crustáceos decápodos debido a las bajas tasas sedimentarias y los entornos de alta energía, el sedimento interno preservado en los arrecifes fósiles puede proporcionar asociaciones diversas de este grupo. Los datos obtenidos en el conjunto de trabajos realizados respaldan la suposición ampliamente aceptada de que los arrecifes del pasado actuaron como puntos calientes de biodiversidad. La gran diversidad de crustáceos decápodos probablemente esté relacionada con su ubicación en sistemas arrecifales, con las colonias de corales. Como se ha visto, desde el punto de vista geológico parece existir una correlación entre el desarrollo de arrecifes y la diversificación de los decápodos, donde se alcanzan las mayores diversidades del Eoceno inferior, lo que sugiere que este tipo de nichos tuvo un papel fundamental en su diversificación. No obstante, durante el Eoceno medio y superior esta tendencia parece no mantenerse, mostrando un conjunto de faunas más diversas en los ambientes siliciclásticos de prodelta.

Sin embargo, hay que puntualizar que los ambientes arrecifales muestreados corresponden a un área menor que los ambientes siliciclásticos, y aun así concentran una diversidad y abundancia elevada en comparación a las áreas circundantes, con la excepción de un afloramiento con una diversidad por encima de lo normal (Fanlillo). La alta diversidad de este afloramiento se está estudiando actualmente, pero los datos recopilados hasta el momento parecen indicar que esta alta diversidad concentrada en una localidad puntual se debe a la presencia de praderas de fanerógamas marinas que pudieron actuar a modo de "arrecife". En cualquier caso, los resultados obtenidos indican que los cambios faunísticos se deben (por lo menos en parte) a cambios paleoecológicos.

En resumen, las cuencas de la zona central surpirenaica registran horizontes de alta diversidad que apoyan la idea de que se trata de un *hot-spot* de paleodiversidad durante el Eoceno, de forma parecida a lo que se ve hoy en día en regiones tropicales. Con todos estos datos se amplía significativamente el conocimiento sobre la diversidad y disparidad anatómica de Meiura (braquiuros y anomuros) del Eoceno, lo cual es fundamental para entender los patrones espacio-temporales que han dado lugar a la gran diversidad actual.

En conclusión, aunque los estudios realizados se han centrado en el Eoceno, estudios similares en otras áreas y periodos podrían proporcionar datos ecológicos importantes sobre la distribución de estos crustáceos en ambientes marinos antiguos, ayudando a dar respuesta a cuestiones de actualidad, como mejorar la comprensión de la diversidad actual o como afectan los cambios climáticos y ambientales a este grupo. Sin duda, el trabajo en esta línea ofrecerá muchos más hallazgos novedosos que ayudarán a aportar luz a cuestiones biológicas, evolutivas y paleoclimáticas/paleoambientales.

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10. APÉNDICES/ANNEX

APÉNDICE 1: Factor de impacto, cuartil y Área temática de las revistas en las que se han publicado los trabajos principales.

Revista	Factor de impacto	Cuartil en la categoría	Área temática
Palaeogeography, Palaeoclimatology, Palaeoecology	3.318	Q1	Paleontology - SCIE
Acta Palaeontologica Polonica	2.061	Q2	Paleontology
Journal of Crustacean Biology	1.254	Q2/Q3	Zoology/Biology
Journal of Paleontology	1.471	Q3	Paleontology - SCIE
Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen	0.95	Q4	Paleontology
Boletín de la Sociedad Geológica Mexicana	0.81	Q4	Paleontology

APÉNDICE 2: Justificación de la contribución del doctorando.

Artículo I. Ferratges, F.A., Zamora, S., Aurell, M. (2019). A new genus and species of Parthenopidae MacLeay, 1838 (Decapoda: Brachyura) from the lower Eocene of Spain. *Journal of Crustacean Biology*, 39(3), 303–311

La contribución del doctorando Fernando A. Ferratges fue la colaboración en el planteamiento inicial y posterior, recolección y preparación del material (actual y fósil), colaboración en la redacción del artículo, colaboración en las correcciones requeridas por los revisores de la revista y presentación y discusión de los resultados.

Artículo II. Ferratges, F.A., Zamora, S., Aurell, M. (2020). Systematics and distribution of decapod crustaceans associated with late Eocene coral buildups from the southern Pyrenees (Spain). *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, 79–100.

La contribución del doctorando fue la colaboración en el planteamiento, recolección y preparación del material, colaboración en la redacción del artículo, realización de cálculos estadísticos mediante programas específicos, colaboración en las correcciones requeridas por los revisores de la revista y presentación y discusión de los resultados.

Artículo III. Ferratges, F.A., Zamora, S., Aurell, M. (2020). A new hermit crab out of its shell from the Eocene Arguis Formation, Huesca, Spain. *Acta Palaeontologica Polonica*, 65(4), 787–792.

La contribución del doctorando en este trabajo fue la colaboración en el planteamiento y preparación del material, colaboración en la redacción del artículo, colaboración en las correcciones requeridas por los revisores de la revista y presentación y discusión de los resultados.

Artículo IV. Ossó, À., Domínguez, J.L., De Angeli, A., Ferratges, F.A. (2020). First record of *Dynomene* (Brachyura, Dromioidea) from the Eocene of the Iberian Peninsula and remarks on the generic placement of *Eoacantholobulus oscensis* (Brachyura, Xanthoidea). *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, VIII, 185–192.

La contribución del doctorando en este trabajo fue la colaboración en la comparativa sistemática de los taxones estudiados y su comparación con otras especies, así como las discusiones e implicaciones paleogeográficas y paleoambientales.

Artículo V. Ferratges, F.A., Zamora, S., Aurell, M. (2021). Unravelling the distribution of decapod crustaceans in the Lower Eocene coral reef mounds of NE Spain (Tremp-Graus Basin, southern Pyrenees). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 575, 110439.

La contribución del doctorando en este trabajo fue la colaboración en el planteamiento, recolección y preparación del material, colaboración en la redacción del artículo, realización de cálculos estadísticos mediante programas específicos, colaboración en las correcciones requeridas por los revisores de la revista y presentación y discusión de los resultados.

Artículo VI. Ferratges, F.A., Domínguez J.L, Ossó, À. (2021). First record of a homolid crab (Crustacea: Decapoda: Homoloidea) from the early Eocene of the Iberian Peninsula. *Boletín de la Sociedad Geológica Mexicana*, 73(3), A311220.

La contribución del doctorando en este trabajo fue la colaboración en el planteamiento, preparación del material, colaboración en la redacción del artículo, colaboración en las correcciones requeridas por los revisores de la revista y presentación y discusión de los resultados.

Artículo VII. Ferratges, F.A., Artal, P., Zamora, S. (2021). New hermit crabs (Paguroidea, Anomura) from the Eocene of Huesca, Spain. *Boletín de la Sociedad Geológica Mexicana*, 73 (3) /A070121.

La contribución del doctorando en este trabajo fue la colaboración en el planteamiento, recolección y preparación del material, colaboración en la redacción del artículo, colaboración en las correcciones requeridas por los revisores de la revista y presentación y discusión de los resultados.

Artículo VIII. Artal, P., Ferratges, F.A., van Bakel, B.W.M., Zamora, S. (2022). A highly diverse dromioid crab assemblage (Decapoda, Brachyura) associated with pinnacle reefs in the lower Eocene of Spain. *Journal of Paleontology*. 1–20.

La contribución del doctorando en este trabajo fue la colaboración en el planteamiento, recolección y preparación del material, colaboración en la redacción del artículo, colaboración en las correcciones requeridas por los revisores de la revista y presentación y discusión de los resultados.

Artículo IX. Ferratges, F.A., Zamora, S., Aurell, M. (2022). Systematics and palaeoecology of a new species of Varunidae H. Milne Edwards, 1853 (Decapoda: Brachyura) from the lower Eocene of Spain. *Journal of Crustacean Biology*. 42(2), 1–9.

La contribución del doctorando en este trabajo fue la colaboración en el planteamiento, recolección y preparación del material, colaboración en la redacción del artículo, colaboración en las correcciones requeridas por los revisores de la revista y presentación y discusión de los resultados.

Artículo X. Ferratges, F.A., Artal, P., van Bakel, B.W.M., Zamora, S. (2022). Filling the early Eocene gap of paguroids (Decapoda, Anomura): A new highly diversified fauna from the Spanish Pyrenees (Serraduy Formation, Graus-Tremp Basin). *Journal of Paleontology*. 1–17.

La contribución del doctorando en este trabajo fue la colaboración en el planteamiento, recolección y preparación del material, colaboración en la redacción del artículo, colaboración en las correcciones requeridas por los revisores de la revista y presentación y discusión de los resultados.

Artículo XI. Ferratges, F.A., Zamora, S., Klompmaker, A.A., Aurell, M. (en preparación). Spatio-temporal variations in decapod crustaceans diversity during the middle-upper Eocene in the Jaca-Pamplona Basin (South-central Pyrenees, Spain).

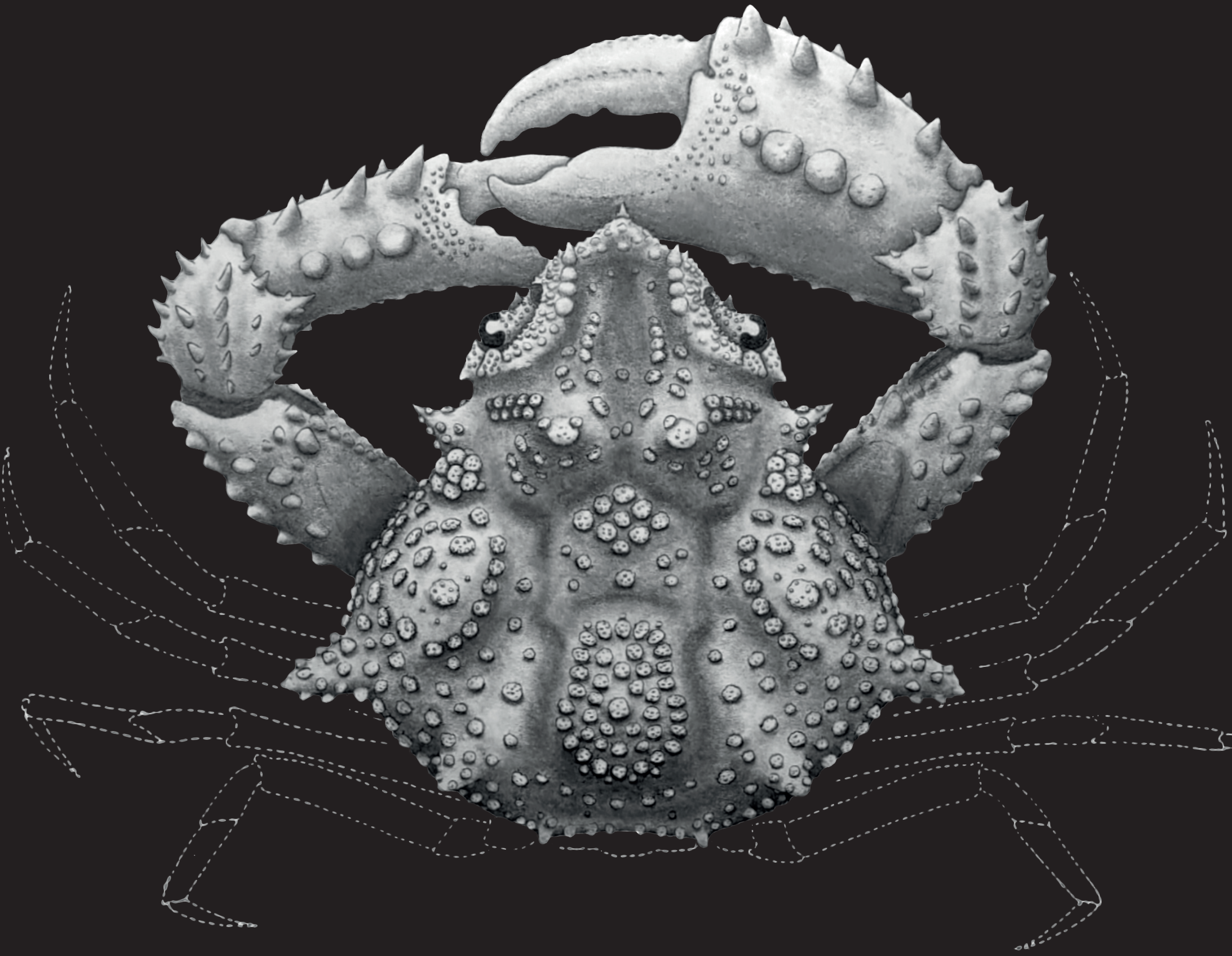
La contribución del doctorando en este trabajo fue la colaboración en el planteamiento, recolección y preparación del material, colaboración en la redacción del artículo, realización de cálculos estadísticos mediante programas específicos, colaboración en las correcciones requeridas por los revisores de la revista.

Artículo XII. Ferratges, F.A., Luque, J., Ossó, À., Domínguez, J.L., Aurell, M., Zamora, S. (en revisión). The oldest dairoidid crab (Decapoda: Brachyura: Parthenopoidea) from the Eocene of Spain.

La contribución del doctorando en este trabajo fue la colaboración en el planteamiento inicial y posterior, recolección y preparación del material (actual y fósil), procesamiento de las tomografías computarizadas, colaboró con el diseño del análisis filogenético, elaboración de las matrices de datos en base a taxones actuales y fósiles, colaboración en la redacción del artículo y las correcciones requeridas por los evaluadores de la revista.

Artículo XVIII. Ferratges, F.A., García-Penas, Á., Aurell, M., Zamora, S. (2022). Distribution of Decapod communities from the early Eocene of the South-Pyrenean Central Unit (Tremp-Graus Basin, Spanish Pyrenees) En: S. Zamora, F.A. Ferratges, A. García-Penas, y M. Aurell, (Eds.). 8th Symposium on Fossil Decapod Crustaceans. Field Guidebook. Palaeontological Publications, 1, 113–136.

La contribución del doctorando en este trabajo fue la colaboración en el planteamiento inicial y posterior, colaboración en la redacción del artículo, diseño de las figuras.



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