

8th Symposium on Fossil Decapod Crustaceans



**Abstracts Book
Field Guidebook**

**Zaragoza (Spain)
June 2022**



Zamora, S., Ferratges, F.A., García-Penas, A., Aurell, M. (Eds.)



8th Symposium on Fossil Decapod Crustaceans



Zaragoza (Spain)

June 2022

**Abstracts Book
Field Guidebook**

Zamora, S., Ferratges, F.A., García-Penas, A., Aurell, M. (Eds.)

Published by:



SOCIEDAD ESPAÑOLA DE PALEONTOLOGÍA

Series: Palaeontological Publications Nº 1

8th Symposium on Fossil Decapod Crustaceans. Abstracts Book - Field Guidebook. Zamora, S., Ferratges, F.A., García-Penas, A., Aurell, M. (Eds.). Zaragoza, Spain, 2022.

165pp, 17x24cm

978-84-09-41246-4

1. Paleontology - 2. Symposium - 3. Decapods - I. Zamora, Samuel, ed. - II. Ferratges, Fernando Ari, ed. III. García-Penas, Álvaro, ed. - IV. Aurell, Marcos, ed. V. Sociedad Española de Paleontología, ed.

All rights reserved. No part of this publication may be reproduced or transmitted in any form or by any means, electronic or mechanical, including photocopy, recording, or any information storage and retrieval system now known or to be invented, without permission in writing from the publisher.

It is suggested that either of the following alternatives should be used for future bibliographic references to the whole or part of this volume:

Zamora, S., Ferratges, F.A., García-Penas, A., Aurell, M. (Eds.) 2022. 8th Symposium on Fossil Decapod Crustaceans. Zaragoza, Spain. Abstracts Book - Field Guidebook. Palaeontological publications, 1, 165 pp.

López-Horgue, M.A., Klompmaker A.A. and Fraaije, R.H.B. 2022. Decapod crustacean diversity and habitats in the Upper Albian deposits of Navarre (western Pyrenees, Spain): The Koskobillo quarry limestones and their coeval deposits. In: Zamora, S., Ferratges, F.A., García-Penas, A., Aurell, M. (Eds.), 8th Symposium on Fossil Decapod Crustaceans. Zaragoza, Spain. Abstracts Book - Field Guidebook. Palaeontological publications, 1, 137-162.

Cover:

Harpactoxanthopsis quadrilobata (Desmarest, 1822) from the Eocene of Huesca. Photo: Isabel Pérez Urresti

Back cover:

Valley of the Isábena river with the Sierra de Sis in the background. Panoramic view from Roda de Isábena. Photo: Samuel Zamora

© SOCIEDAD ESPAÑOLA DE PALEONTOLOGÍA

editor@sepaleontologia.es

ISBN: 978-84-09-41246-4

Design and layout: Isabel Pérez-Urresti

Printing: Gráficas Vela. C/ Aneto, 15. P.I. Valdeconejo. 50410 Cuarte de Huerva (Zaragoza)



ORGANIZATION

Chairs

- » Samuel Zamora (Spanish Geological Survey, IGME-CSIC, Zaragoza, Spain)
- » Fernando A. Ferratges (University of Zaragoza, Zaragoza, Spain)

Secretary and web manager

- » Alvaro García Penas (University of Zaragoza, Zaragoza, Spain)

Organizers

- » Marcos Aurell (University of Zaragoza, Zaragoza, Spain)
- » José Ignacio Canudo (University of Zaragoza, Zaragoza, Spain)
- » Juan Carlos García Pimienta (Diputación General de Aragón, Spain)
- » Mikel López-Horgue (University of the Basque Country)
- » Adiël Klompmaker (University of Alabama)
- » Zain Belaustegui (University of Barcelona)

Scientific Committee

- » Barry Van Bakel (Oertijdmuseum Boxtel, Netherlands)
- » Matúš Hyžný (Comenius University, Slovakia)
- » Javier Luque (University of Harvard, USA)
- » Joachim T. Haug (Ludwig-Maximilians-University of Munich, Germany)
- » John Jagt (Natuurhistorisch Museum Maastricht, Netherlands)
- » Peter Castro (California State Polytechnic University, USA)
- » Rodney M. Feldmann (Kent State University, USA)
- » Sylvain Charbonnier (Muséum National d'Histoire Naturelle, France)

Sponsors & Collaborators

- » University of Zaragoza
- » Gobierno de Aragón
- » Instituto Geológico y Minero de España, IGME-CSIC
- » Instituto Universitario de Investigación en Ciencias Ambientales de Aragón, IUCA
- » Sociedad Española de Paleontología
- » Sociedad de amigos del Museo de Ciencias Naturales de la Universidad de Zaragoza, SAMPUZ
- » Museo de Ciencias Naturales de la Universidad de Zaragoza
- » The Crustacean Society
- » University of the Basque Country
- » Ayuntamiento de Olazti





INDEX

PREFACE	7
PLENARY TALKS	
Hyžný, M. Fossil burrowing shrimps: an overview	11
Luque, J., Bracken-Grissom, H.D., Briggs, D.E.G., Jenkins, K.M., Lindgren, J., Ortega-Hernandez, J., Palmer, A.R., Porter, M.L. and Wolfe, J.M. The evolution of compound eyes across extant and fossil crabs	21
ABSTRACTS	
Ando, Y., Hachiya, K., Mizuno, Y., Makiguchi, T., Yamaoka, M., Hayashi, T. and Oji, T. New information on <i>Megaceradocus</i> (Amphipoda) from the Lower Miocene Morozaki Group, Central Japan, with notes of <i>Callianopsis</i> (Decapoda) <i>in situ</i> in burrows	27
Andrada, A.M., Luci, L., Lazo, D.G. and Aguirre-Urreta, M.B. Taphonomy of Mecochirid lobsters from the Lower Cretaceous of West-Central Argentina	29
Audo, D., Kawai, T., O'Flynn, R., Devillez, J. and Huang, D. Crayfishes from the Jehol Biota	32
Audo, D., Kawai, T., Charbonnier, S., Jauvion, C. and Huang, D. Taphonomy of the stomach in three mesozoic decapods	34
Belaústegui, Z. and Muñiz, F. Decapod crustacean ichnology: A state of the art	36
Braig, F. and Haug, J.T. Changes in shield morphology of Carcinidae - A geometric morphometrics perspective on ontogeny and evolution	40
Busulini, A., Beschin, C. and Tessier, G. Eocene patch reefs in the Lessini Mountains (NE Italy): an ancient biodiversity hotspot	42
Charbonnier, S. and Garassino, A. Fossil decapod crustacea in the historical collections of the Paris Museum (1750-1880)	45
Ferratges, F.A., Luque, J., Domínguez, J.L., Ossó, A., Aurell, M. and Zamora, S. The origin of Dairoid crabs (Decapoda, Brachyura, Parthenopoidea)	47
Fraaije, R.H.B., Jagt, J.W.M., van Bakel, B.W.M. and Wallaard, J.J.W. Novel data on hermit crabs and further phylogenetic refinements for the Paguroidea (Crustacea, Anomura)	49
Fraaije, R.H.B., Wallaard, J.J.W., Jagt, J.W.M., van Bakel, B.W.M. and Krobicki, M. Preliminary notes on Mesozoic and Cenozoic hermit crabs (Crustacea, Anomura, Paguroidea) from Europe and the United States	51
García-Penas, A., Ferratges, F.A., Zamora, S. and Aurell, M. Decapod-bearing carbonate concretions from a lower Aptian siliciclastic platform (E Spain)	53
Gašparič, R., Jovanović, G., Čosović, V., Vrabac, S. and Glamuzina, G. Preliminary report on decapod crustacean fossil record from south-eastern european countries	56
Heteš, A. and Hyžný, M. Taxonomy of Late Jurassic (Oxfordian) decapod crustaceans from Kraków-Wieluń Upland (Southern Poland)	59
Hof, C.H.J., Fraaije, R.H.B., van Bakel, B.W.M. and Jagt, J.W.M. Early "spearing" stomatopod claws from the Maastrichtian type area	61
Hyžný, M., Veselská, M.K., Jagt, J.W.M. and Tshudy, D.M. <i>Oncopareia</i> : a convoluted story of an extinct lobster with pectinate claws	63



Klomp maker, A.A., Brezina, J., Nyborg, T., Kloess, P.A., Ando, Y. and Landman, N. The fossil record of crustaceans in methane seep deposits with a focus on decapods from the western interior seaway, USA	66
Laville, T., Forel, M.B. and Charbonnier, S. Resolving the tagmatization and the phylogenetic affinities of Thylacocephala: input from 3D data	68
Laville, T., Hitij, T., Gašparič, R., Žalohar, J., Forel, M.B. and Charbonnier, S. The Triassic Thylacocephalans from Slovenia: implications for their evolution and diversification	70
Méndez, J.M., Ossó, A., Vila, B., Sellés, A. and Gaete, R. Brachyuran (Decapoda) remains associated to dinosaurs in fluvial deposits of the Tremp Group (Catalonia)	72
Ossó, A., Arasa, A. and Pastó, Q. First report of the freshwater crab <i>Potamon</i> (Decapoda: Brachyura: Potamidae) in the Pliocene of the Iberian Peninsula	75
Ossó, A., van Bakel, B.W.M., Artal, P. and Moreno-Bedmar, J.A. "The vineyard crabs", the Aptian decapods assemblage of Cal Cassanyes (Garraf Massif, Alt Penedès, Catalonia, NE Iberian Peninsula)	79
Ossó, A., Abelló, P. and Díaz Medina, G.. An early tourist: when <i>Cancer pagurus</i> visited Andalusia. First record in the Mediterranean Pliocene	82
Pérez-Pueyo, M., Ferratges, F.A., Núñez-Lahuerta, C., Galán, J., Puértolas-Pascual, E., Bádenas, B. and Canudo, J.I. An unusual accumulation of decapod crustacean fingers from the latest Maastrichtian of the Southern Pyrenees (NE Spain)	86
Robins, C.M., Klomp maker, A.A., Jakobsen, S.L. and Sheldon, E. Expanding the fossil squat lobster record in North America and Europe	89
Tessier, G., Beschin, C., Busulini, A., Zorzini, R. Enrico Nicolis' specimens in Alexander Bittner's studies	90
van Bakel, B.W.M., Simpson, M.I., Ossó, A., Jagt, J.W.M. and Fraaije, R.H.B. Palaeoenvironment and faunal composition of Early to Late Aptian Brachyuran faunules from the Isle of Wight, UK ...	91
Wallaard, J.J.W., Fraaije, R.H.B., Jagt, J.W.M. and van Bakel, B.W.M. New insights into reef-associated decapod crustacean faunules from the Miocene Pakhna Formation of Cyprus	93

FIELD TRIPS

Day 1: June 22nd, 2022

García-Penas, A., Ferratges, F.A., Aurell, M. and Zamora, S. Barremian-Aptian shallow-marine decapod communities from the Oliete subbasin (Maestrazgo basin, E Spain)	99
--	-----------

Day 2: June 23rd, 2022

Ferratges, F.A., García-Penas, A., Aurell, M. and Zamora, S. Distribution of decapod communities from the Early Eocene of the south-Pyrenean central unit (Tremp-Graus basin, Spanish Pyrenees)	113
--	------------

Day 3: June 24th, 2022

López-Horgue, M.A., Klomp maker, A.A. and Fraaije, R.H.B. Decapod crustacean diversity and habitats in the Upper Albian deposits of Navarre (Western Pyrenees, Spain): The Koskobillo quarry limestones and their coeval deposits	137
--	------------

AUTHOR INDEX	165
---------------------------	------------



PREFACE

Decapod crustaceans are diverse animals in modern ecosystems and have a rich fossil record. This book publishes a series of proceedings and abstracts from the 8th Symposium on Fossil Decapod Crustaceans which has been developed 19-24 June 2022 in Zaragoza (Spain). This is the first time that this meeting is celebrated in Spain supported by the Spanish Geological Survey (IGME-CSIC) and the University of Zaragoza. The book also contains three chapters that summarize the field trip of the meeting, that cover important areas for the understanding of fossil decapod crustaceans in Spain. Penás *et al.* (this book) introduces the classic localities of decapod crustaceans from the Aptian Oliete subbasin, that where first mentioned by Juan Vilanova at the end of the nineteen century. The second chapter by Ferratges *et al.* (this book) focuses on Eocene decapod crustaceans from the Graus-Tremp basin (Southern Pyrenees). The third chapter by López-Horgue *et al.* (this book) focuses on the spectacular Albian reefs around Olatzi (Foral Community of Navarre), where a set of pinnacle hosts the highest decapod diversity for the Albian.

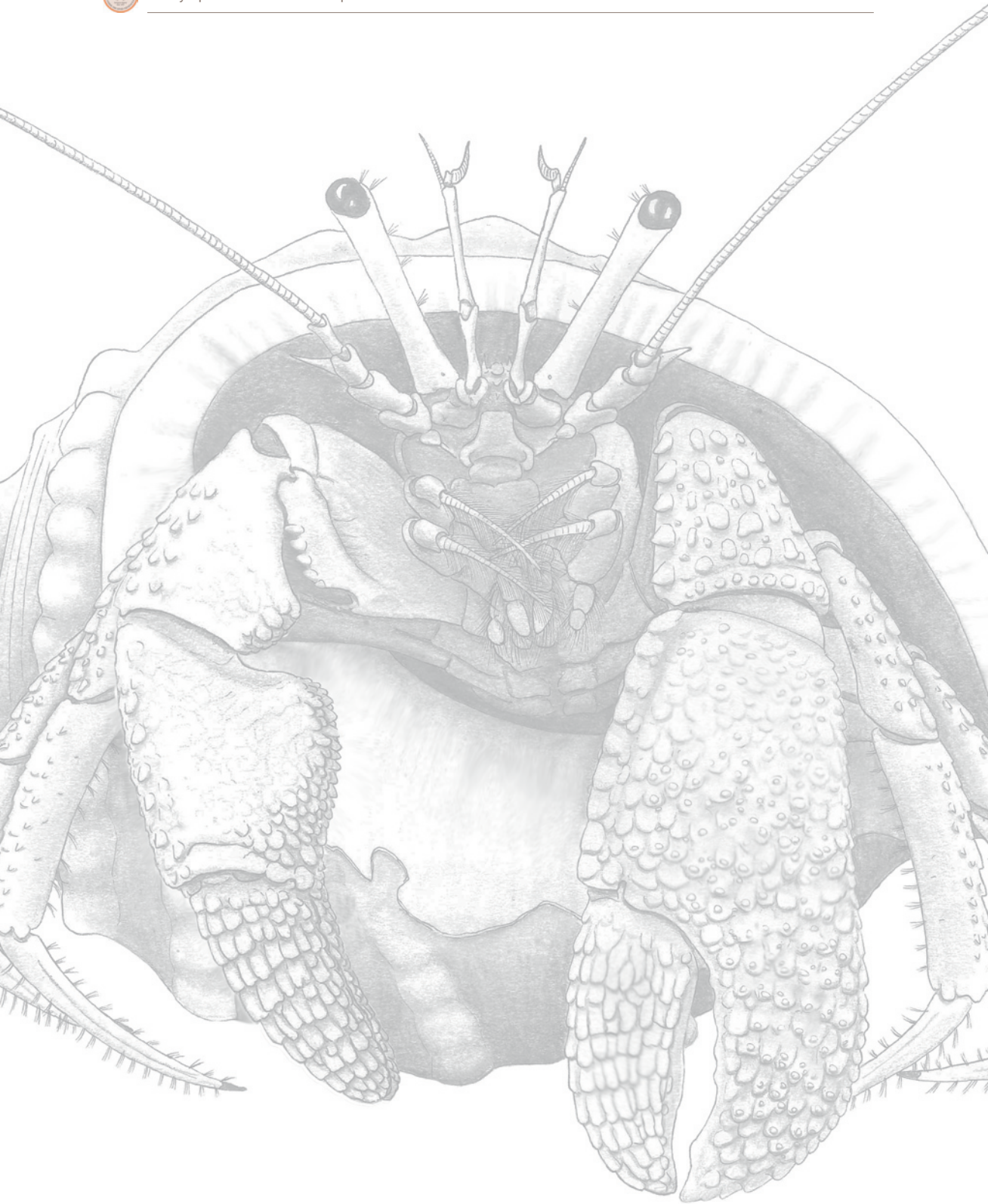
The Spanish Society of Palaeontology is honored to be part of this meeting based on such important group of fossils, with the publication of the first number of a new series that I have the pleasure to present as "Palaeontological Publications". We hope that most palaeontological meetings organized by our society and related bodies can be published in the subsequent numbers of this series of monographs.

Lastly, we would like to acknowledge all the participants and supporters to this meeting, including the organizing and scientific committees, as well as the Government of Aragón, University of the Basque Country, IUCA, SAMPUZ, Natural History Museum of the University of Zaragoza, Río Martín, and City Council of Olatzi.

Isabel Rábano

President

Sociedad Española de Paleontología





PLENARY TALKS







FOSSIL BURROWING SHRIMPS: AN OVERVIEW

Matúš Hyžný¹

¹ Department of Geology and Palaeontology, Faculty of Natural Sciences, Comenius University, Ilkovičova 6, 842 15 Bratislava, Slovakia. hyzny.matus@gmail.com

Keywords: Decapoda, Axiidea, Gebiidea, taxonomy, taphonomy, fossil record

INTRODUCTION

Many representatives of decapod crustaceans excavate (semi)permanent burrows. However, there are two distinctly separate groups, i.e., Gebiidea and Axiidea that have converged morphologically and ecologically as fully burrowing forms. Nowadays they belong to major bioturbators (Rowden and Jones, 1993; Ziebis *et al.*, 1996) and ecosystem engineers (Berkenbusch and Rowden, 2003; Kneer *et al.*, 2013). An impressive record of trace fossils attributed to fossorial activities of these animals suggests that they have been an important part of marine ecosystems at least since the Mesozoic times.

Because of broadly similar habitus of all burrowing shrimps and a similar degree of calcification of cuticular surfaces, the fossilization potential is comparable within representatives of Axiidea and Gebiidea (Bishop and Williams, 2005; Hyžný and Klompmaker, 2015). In general, taxonomically important characters for these animals as recognized by neontologists (Dworschak *et al.*, 2012; Poore *et al.*, 2019) are not preserved in the fossil record in most cases. Dworschak *et al.*, (2012: 110) stated that: “the sparse fossil record for this groups is essentially a series of major chelae, especially for the callianassids, and possible trace fossils of burrows, as well as some coprolites”. This is an overly simplified statement not taking into account well-preserved near-complete individuals from Lagerstätten (Garassino and Schweigert, 2006; Charbonnier *et al.*, 2017), nevertheless, major chelae indeed have greatest fossilization potential (Hyžný and Klompmaker, 2015) and in some strata they are virtually ubiquitous. In some cases, chelipeds can be successfully used for reliable taxonomic evaluation of the fossil remains of burrowing shrimps as discussed in many contributions cited further below. The situation with the proxy characters on chelipeds is paralleled with a similar situation in brachyuran crabs when proxy characters on a dorsal carapace are being evaluated (e.g., Schweitzer, 2003).

GHOST SHRIMPS, MUD SHRIMPS, AND ALLIES

Representatives of Axiidea and Gebiidea were treated together as (infraorder) Thalassinidea (e.g., Martin and Davis, 2001), or even as a distinct group within (infraorder) Anomura (e.g., Glaesner, 1969), but advances in phylogenetic research have demonstrated that the two groups represent separate lineages (Robles *et al.*, 2009; Bracken *et al.*, 2010; Wolfe *et al.*, 2019). This is reflected in the most updated published classification of decapod crustaceans (De Grave *et al.*, 2009) as well as in WoRMS database (<https://marinespecies.org>). Thus, the usage of (infraorder) Thalassinidea is obsolete and should be abandoned. Similarly, usage of “*Callianassa*” sensu lato to accommodate any fossil remain with a mainstream burrowing shrimp morphology is not recommended.

(infraorder) Gebiidea de Saint Laurent, 1979	(infraorder) Axiidea de Saint Laurent, 1979
(family) Axianassidae Schmitt, 1924	(family) Anacalliidae Manning and Felder, 1991
(family) Laomediidae Borradaile, 1903	(family) Axiidae Huxley, 1879
(family) Thalassinidae Latreille, 1831	(family) Callianassidae Dana, 1852
(family) Upogebiidae Borradaile, 1903	(family) Callianideidae Kossman, 1880
	(family) Callianopsidae Manning and Felder, 1991
	(family) Callichiridae Manning and Felder, 1991
	(family) Ctenochelidae Manning and Felder, 1991
	(family) Eucalliidae Manning and Felder, 1991
	(family) Micheleidae K. Sakai, 1992
	(family) Paracalliidae K. Sakai, 2005
	(family) Strahlaxiidae Poore, 1994

Higher classification of burrowing shrimps
(WoRMS 2022)

FOSSIL RECORD OF GEBIIDEA

Axianassidae, Laomeiidae and Thalassinidae comprise 17, 24 and 11 extant species, respectively. Their fossil record is scarce. As for Axianassidae, from the Miocene–Pliocene of Chile, Feldmann *et al.* (2010) described *Axianassa? chilensis*, based on three specimens. From the Eocene of Italy, Beschin *et al.* (2018) described *Axianassa petrea*, based on two isolated cheliped meri. Whereas the Chilean material clearly is assignable to a burrowing shrimp, the Italian occurrence is considered doubtful herein. From five extant genera of Laomeiidae, three (*Jaxea* Nardo, 1847; *Laomedia* De Haan, 1841; *Saintlaurentiella* Paiva, Tavares and Silva-Neto, 2010) have been identified in the fossil record (Karasawa, 1993; Hyžný, 2011; Gašparič and Hyžný, 2018). There is no pre-Miocene record of the family known to date. Putative representative of Laomeiidae, *Reschia barbarae* Schweigert, 2009 from the Tithonian of Germany was removed from the family by Hyžný (2011). The diagnosis and reconstruction presented by Schweigert (2009) shows an animal with pereopods 1–3 being chelate. If this is correct, then *Reschia* Schweigert, 2009 cannot be accommodated within Gebiidea or Axiidea.

A single genus of Thalassinidae, *Thalassina* Latreille, 1806, is known from a number of fossil occurrences, largely coming from the Miocene to Pleistocene of the Indo-West Pacific region (Collins *et al.*, 2003; Ando *et al.*, 2016). Nevertheless, the oldest confirmed fossil record of *Thalassina* is that from the Oligocene of Italy (Hyžný and De Angeli, 2022). The record of *Thalassina* from the Lower Cretaceous of France (Robineau Desvoidy, 1849) was already disputed by A. Milne-Edwards (1860); this opinion was followed also by Ando *et al.* (2016) and Hyžný and De Angeli (2022).

The most speciose gebiidean group is Upogebiidae with nearly 200 extant species classified within 12 genera. Only two of them (*Upogebia* Leach, 1814; *Gebiakantha* Ngoc-Ho, 1989) were identified in the fossil record (Fraaije *et al.*, 2006; Garassino *et al.*, 2012; Hyžný and Gross, 2016), with the oldest known record coming from the Santonian–Campanian of Poland (Glaessner, 1930). Interestingly, some isolated carapaces from Jurassic strata were ascribed to upogebioid mud shrimps (Moericke, 1897; Carter, 1898); later, however, they were reassigned to axiid shrimps (Patrulus, 1959; Förster, 1977).

FOSSIL RECORD OF AXIIDAE AND STRAHLAXIIDAE

Axiidae comprises 221 species classified within 52 valid extant genera. Extant genera with known fossil record include *Acanthaxius* Sakai and de Saint Laurent, 1989; *Axiopsis* Borradaile, 1903; *Axius* Leach, 1816; and *Paraxiopsis* de Man, 1905; with oldest occurrences from the Albian (Kensley and Williams, 1990; Fraaije *et al.*, 2011; Frantescu, 2014; Hyžný *et al.*, 2017). As many as 12 genera exclusively known as fossils were described, nearly all of them coming from Upper Jurassic and Cretaceous strata (Fritsch and Kafka, 1887; Secretan, 1964; Förster, 1977; Bravi and Garassino, 1998; Schweigert, 2003, 2009; Garassino and Schweigert, 2006; Charbonnier *et al.*, 2012, 2017; Karasawa *et al.*, 2019; Ferratges *et al.*, 2021; Andrada *et al.*, 2022). These genera include *Aperiopyxis* Schweigert, 2009; *Aptaxiopsis* Ferratges, Hyžný and Zamora, 2021; *Cretaxiopsis* Charbonnier, Audo, Garassino and Hyžný, 2017; *Etallonia* Oppel, 1861; *Hinecaris* Karasawa, Kishimoto, Ohara and Ando, 2019; *Huxleycaris* Bravi and Garassino, 1998; *Libanoaxius* Charbonnier, Audo, Garassino and Hyžný, 2017; *Magila* von Münster, 1839; *Megachela* Schweigert, 2003; *Protaxius* Beurlen, 1930; and *Schlueteria* Fritsch and Kafka, 1887. The oldest occurrence of Axiidae, that of *Devonoaxius garlandi* Feldmann and Schweitzer, 2019, from the Devonian of Ohio (Feldmann and Schweitzer, 2019) is simultaneously the oldest record of Axiidea. No fossils of Axiidae are known from the Carboniferous, Permian, or Triassic strata. Strahlaxiidae have not been recognized in the fossil record thus far.

FOSSIL RECORD OF CALLIANIDEIDAE AND MICHELEIDAE

Callianideidae and Micheleidae comprise 18 and 34 extant species, respectively. From Callianideidae, only two species of *Crosniera* Kensley and Heard, 1991 were described as fossils, originating from the Miocene of Slovakia (Hyžný and Schlögl 2011) and the Aptian of Spain (Ferratges *et al.*, 2021). The fossil record of Micheleidae is spanning back to Cretaceous, with the oldest occurrence classified within its own genus, *Amatukamius* Karasawa and Ohara, 2019, originating from the Barremian of Japan (Karasawa and Ohara, 2019). Yet another exclusively fossil genus is *Paki* Karasawa and Hayakawa 2000 from the Campanian of Japan (Karasawa and Hayakawa, 2000). From extant micheleid genera, only *Meticonaxius* de Man, 1905 is known as fossils, with occurrences from the Aptian of Spain (Ferratges *et al.*, 2021) and Cenomanian of Texas (Frantescu, 2014).

FOSSIL RECORD OF "CALLIANASSOID" GHOST SHRIMPS

Hyžný and Klompmaker (2015) presented an overview of state of knowledge of the fossil record of ghost shrimps, i.e., representatives of the families Callianassidae and Ctenochelidae ("callianassoids" sensu Poore *et al.*, 2019) as recognized at that time, including the list of all pertinent fossil taxa described to date. The higher-level classification of these families, however, changed with a number of newly introduced families and genera (Poore *et al.*, 2019; Robles *et al.*, 2020). Also, many novel fossil occurrences including new taxa have been published since the synopsis of Hyžný and Klompmaker (2015). Thus, the emphasis here is put on the updates since the respective work.

Anacalliidae comprise one extant (*Anacalliax* de Saint Laurent, 1973) and two extinct genera (*Aptanacalliax* Ferratges, Hyžný and Zamora, 2021; *Turbiocheir* Schweitzer, Feldmann, Casadío and Rodríguez Raising, 2012). Fossil occurrences include those from the Aptian of Spain (Ferratges *et al.*, 2021) and Eocene to Oligocene of South America (Hyžný *et al.*, 2021; Schweitzer *et al.*, 2021).

Callianassidae include more than 100 extant species classified in 26 genera. Four of these genera (*Callianassa* Leach, 1814; *Gilvossius* Manning and Felder, 1992; *Neotrypaea* Manning and Felder, 1991; *Trypaea* Dana, 1852) are known also as fossils, not older than Miocene (Karasawa, 1993; Portell and Agnew, 2004; Fraaije *et al.*, 2010; Hyžný and Dulai, 2021), although future research will likely confirm also some Eocene occurrences (Hyžný and Klompmaker, 2015).

Callianopsidae comprise 6 extant species in three genera. Two of them (*Callianopsis* de Saint Laurent, 1973; *Bathycalliax* Sakai and Türkay, 1999). The fossil record of *Callianopsis* is well studied, with occurrences spanning from Eocene to Miocene (Schweitzer Hopkins and Feldmann, 1997; East 2006; Hyžný and Schlögl, 2011), although some of them were disputed (Pasini *et al.*, 2020). The fossil record of *Bathycalliax* comprises occurrences from the Eocene of Japan (Ando *et al.*, 2019) and the Pleistocene of Italy (Baldanza *et al.*, 2013; Pasini *et al.*, 2014). From the Cenomanian of Lebanon, *Cretacalliax levantina* Pasini, Poore and Garassino, 2020, was described.

Callichiridae consists of nearly 100 extant species classified in 17 genera, half of them having a relatively well documented fossil record spanning back into the Cenomanian (Portell and Agnew, 2004; Hyžný and Müller, 2010, 2012; Hyžný and Klompmaker, 2015; Hyžný, 2016; Hyžný, *et al.* 2016; Charbonnier *et al.*, 2017; Komai *et al.*, 2019). Exclusively fossil genera include *Eoglypturus* Beschin, De Angeli, Checchi and Zarantonello, 2005 from the Eocene of Italy (Beschin *et al.*, 2005), and *Vecticallichirus* Quayle and Collins, 2012 from the Eocene of Isle of Wight (Quayle and Collins, 2012; Hyžný, 2020) and Japan (Ando, 2020).

Ctenochelidae comprise 30 extant species in 7 genera; three of them, *Ctenocheles* Kishinouye, 1926, *Dawsonius* Manning and Felder, 1991, and *Gourretia* de Saint Laurent, 1973 are known also as fossils spanning back into the Albian (Hyžný and Klompmaker, 2015). Exclusively fossil genus includes *Ahazianassa* Karasawa, Kishimoto, Ohara and Ando, 2019 from the Maastichtian of Japan (Karasawa *et al.*, 2019).

Eucalliicidae comprise 26 extant species in 7 genera; four of them, *Calliax* de Saint Laurent, 1973, *Calliaxina* Ngoc-Ho, 2003, *Eucalliix* Manning and Felder, 1991, and *Eucalliixiopsis* Sakai, 2011 are known also as fossils (Hyžný and Klompmaker, 2015; Ando *et al.*, 2020; Kiel *et al.*, 2020; Hyžný and Dulai, 2021). The stratigraphically oldest record is that of *Calliaxina* from the Cenomanian of Lebanon (Charbonnier *et al.*, 2017). Pasini *et al.* (2019) reassigned *Protaxius eocenicus* Secrétan, 1975 from the Eocene of Italy into a genus on its own, *Bolcacalliix* Hyžný in Pasini *et al.*, 2019.

Paracalliicidae comprise a single extant monotypic genus *Paracalliix* de Saint Laurent, 1979, which is without any fossil occurrences. Two extinct genera are known, *Pleuronassa* Ossó-Morales, Garassino, Vega and Artal, 2011 from the Campanian of Morocco (Ossó-Morales *et al.* 2011) and *Rathbunassa* Hyžný in Bermúdez *et al.*, 2013 from the Albian of Colombia and Turonian of Texas and Mexico (Bermúdez *et al.*, 2013).

GHOST SHRIMPS IN TAXONOMIC LIMBO

There is a number of exclusively fossil "callianassoid" genera not assigned to any axiidean group (family). When being erected, they were classified within Callianassidae, however, since the recent reassessment of the higher classification of the group (Poore *et al.*, 2019) and recognition of a number of distinct clades (Robles *et al.*, 2020) where there was once only one (Callianassidae) or two (Callianassidae + Ctenochelidae), these genera remained in a taxonomic limbo, pending their revision in respect to new classification scheme. These genera include *Comoxianassa* Schweitzer, Feldmann, Čosović, Ross and Waugh, 2009 and *Cowichianassa* Schweitzer, Feldmann, Čosović, Ross and Waugh, 2009, both from the Campanian of Canada (Schweitzer *et al.*, 2009); *Melipal* Schweitzer, Feldmann, Encinas and Suárez, 2006 from the Eocene of Chile (Schweitzer *et al.*, 2006); *Psammionassa* Schweitzer, Feldmann, Kues and Bridge, 2017 from the Turonian of New Mexico (Schweitzer *et al.*, 2017); and *Vegarthron* Schweitzer and Feldmann, 2002 from the Eocene of Southern California (Schweitzer and Feldmann, 2002). Additionally, there are two genera, *Mesostylus* Bronn and Roemer, 1852 and *Protocallianassa* Beurlen, 1930, known nearly entirely from Cretaceous strata (Swen *et al.*, 2001; Mourik *et al.*, 2005; Schweitzer and Feldmann, 2012; Hyžný and Sumesberger, 2019). While Beurlen (1930) erected a higher taxon Protocallianassinae for species currently assigned to these two genera, its usage (as a distinct clade/family) is considered preliminary here. In this respect, Hyžný and Summesberger (2019) advised for a re-evaluation of all species treated as *Protocallianassa* at a time before some implications for higher taxonomy can be made.

Acknowledgements

The research was supported by VEGA 02/0136/15 and the Slovak Research and Development Agency under contracts no. APVV-17-0555 and APVV-20-0079.

REFERENCES

- Ando, Y. 2020. Additional record of *Collinsius simplex* (Brachyura, Chasmocarcinidae) from the Upper Eocene to Lower Oligocene strata in Kyushu (Japan), and description of a new species of ghost shrimp (Axiidea, Callichiridae). *Neues Jahrbuch für Geologie und Paläontologie. Abhandlungen*, 296, 9-18.



- Ando, Y., Kishimoto, S. and Kawano, S. 2016. Two new species of *Thalassina* (Decapoda, Thalassinidae) from the Miocene of Japan. *Neues Jahrbuch für Geologie und Paläontologie. Abhandlungen*, 280, 107-117.
- Ando, Y., Kawano, S. and Ugai, H. 2019. Two new species of Decapoda from the Eocene Sakasagawa Formation in Amakusa Islands, Kyushu, Japan. *Neues Jahrbuch für Geologie und Paläontologie. Abhandlungen*, 293, 57-66.
- Ando, Y., Kawano, S., Muramiya, Y., Niiyama, S., Kameyama, S. and Shimoyama, S. 2020. Fossil decapods from the Upper Quaternary in Shinjima Island in Kagoshima, Kyushu, Japan, and description of a new species of ghost shrimp (Axiidea, Eucalliidae). *Zootaxa*, 4878, 523-541.
- Andrada, A.M., Lazo, D.G., Bressan, G.S. and Aguirre-Urreta, M.B. 2022. Revision of the genus *Protaxius* (Decapoda, Axiidea, Axiidae), with description of a new species from the Lower Cretaceous of west-central Argentina. *Cretaceous Research*, 130, 105053.
- Baldanza, A., Bizzarri, R., Famiani, F., Garassino, A., Hyžný, M. and Pasini, G. 2013. The bathyal decapod crustacean community from the Poggio i Sodi quarries (Siena Basin, Tuscany, Italy). *Boletín de la Sociedad Geológica Mexicana*, 65, 335-353.
- Berkenbusch, K. and Rowden, A.A. 2003. Ecosystem engineering - moving away from 'just-so' stories. *New Zealand Journal of Ecology*, 27, 67-73.
- Bermúdez, H.D., Gómez-Cruz, A. de J., Hyžný, M., Moreno-Bedmar, J.A., Barragán, R., Moreno Sánchez, M. and Vega, F.J. 2013. Decapod Crustacea from the Cretaceous San Gil Group (Aptian-Albian) at Villa de Leyva section, central Colombia. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 267, 255-272.
- Beschin, C., De Angeli, A., Checchi, A. and Zarantonello, G. 2005. Crostacei eocenici di Grola presso spagnago (Vicenza, Italia Settentrionale). *Studi e Ricerche – Associazione Amici del Museo – Museo Civico „G. Zannato“, Montecchio Maggiore (Vicenza)*, 12, 5-35.
- Beschin, C., Busulini, A., Fornaciari, E., Papazzoni, C.A. and Tessier, G. 2018. La fauna di crostacei associate a coralli dell'Eocene superior di Campolongo di Val Liona (Monti Berici, Vicenza, Italia nordorientale). *Bollettino del Museo di Storia Naturale di Venezia*, 69, 129-215.
- Bishop, G.A. and Williams, A.B. 2005. Taphonomy and preservation of burrowing thalassinidean shrimps. *Proceedings of the Biological Society of Washington*, 118, 218-236.
- Bracken, H.D., De Grave, S., Toon, A., Felder, D.L. and Crandall, K.A. 2010. Phylogenetic position, systematic status, and divergence time of the Procarididea (Crustacea: Decapoda). *Zoologica Scripta*, 39, 198-212.
- Bravi, S. and Garassino, A. 1998. New biostratigraphic and palaeoecologic observations on the "Plattenkalk" of the Lower Cretaceous (Albian) of Pietraroia (Benevento, S Italy), and its decapod crustacean assemblage. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, 138, 119-171.
- Carter, J. 1898. A contribution to the palaeontology of the decapod Crustacea of England. *The Quarterly Journal of the Geological Society of London*, 54, 15-44.
- Charbonnier, S., Garassino, A. and Pasini, G. 2012. Revision of Mesozoic decapod crustaceans from Madagascar. *Geodiversitas*, 34, 313-357.
- Charbonnier, S., Audouin, D., Garassino, A. & Hyžný, M. 2017. *Fossil Crustacea of Lebanon*. Mémoires du Muséum national d'Histoire naturelle, Tome 210, 1-252.
- Collins, J.S.H., Lee, C. and Noad, J. 2003. Miocene and Pleistocene crabs (Crustacea, Decapoda) from Sabah and Sarawak. *Journal of Systematic Palaeontology*, 1, 187-226.



- De Grave, S., Pentcheff, N.D., Ahyong, S.T., Chan, T.-Y., Crandall, K.A., Dworschak, P.C., Felder, D.L., Feldmann, R.M., Fransen, C.H.J.M., Goulding, L.Y.D., Lemaitre, R., Low, M.E.Y., Martin, J.W., Ng, P.K.L., Schweitzer, C.E., Tan, S.H., Tshudy, D. and Wetzer, R. 2009. A classification of living and fossil genera of decapod crustaceans. *The Raffles Bulletin of Zoology Supplements*, 21, 1-109.
- Dworschak, P.C., Felder, D.L. and Tudge, C.C. 2012. Infraorders Axiidea de Saint Laurent, 1979 and Gebiidea de Saint Laurent, 1979 (formerly known collectively as Thalassinidea). In Schram, F.R., Vaupel Klein, J.C. von, Charmantier-Daures, M. and Forest, J. (eds.), *Treatise on Zoology – Anatomy, Taxonomy, Biology – The Crustacea, Decapoda, Volume 9 Part B Decapoda: Astacidea P.P. (Enoplometopoidea, Nephropoidea), Glypheidea, Axiidea, Gebiidea, and Anomura*. Vol. 9B. Brill, Leiden, 109–219.
- East, E.H. 2006. Reconstruction of the fossil mud shrimp *Callianopsis clallamensis*. *Journal of Crustacean Biology*, 26, 168-175.
- Feldmann, R.M. and Schweitzer, C.E. 2019. The oldest fossil axiid (Decapoda: Pleocyemata: Axiidea), from the Late Devonian (Famennian) Chagrin Shale Member of the Ohio Shale, USA. *Journal of Crustacean Biology*, 39, 724-728.
- Feldmann, R.M., Schweitzer, C.E. and Encinas, A. 2010. Neogene decapod Crustacea from southern Chile. *Annals of Carnegie Museum*, 78, 337-366.
- Ferratges, F.A., Hyžný, M. and Zamora, S. 2021. Taphonomy and systematics of decapod crustaceans from the Aptian (Lower Cretaceous) in the Oliete Sub-basin (Teruel, Spain). *Cretaceous Research*, 122, 104767.
- Förster, R. 1977. Untersuchungen an jurassischen Thalassinidea (Crustacea, Decapoda). *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie*, 17, 137-156.
- Fraaije, R.H.B., van Bakel, B.W.M., Jagt, J.W.M. and Coole, Y. 2006. Two new Paleogene species of mud shrimp (Crustacea, Decapoda, Upogebiidae) from Europe and North America. *Bulletin of the Mizunami Fossil Museum*, 33, 77-85.
- Fraaije, R.H.B., Menkveld-Gfeller, U.E., van Bakel, B.W.M. and Jagt, J.W.M. 2010. Decapod crustaceans from the type area of the Helvetian Stage (lower Miocene) in the Bern area, Switzerland. *Bulletin of the Mizunami Fossil Museum*, 36, 1-11.
- Fraaije, R.H.B., van Bakel, B.W.M., Jagt, J.W.M. & Mollen, F.H. 2011. A new axiid (Crustacea: Decapoda: Axiidea) from the Neogene of Belgium and the Netherlands. *Neues Jahrbuch für Geologie und Paläontologie. Abhandlungen*, 260, 157-163.
- Frañescu, O.D. 2014. Fossil mudshrimps (Decapoda: Axiidea) from the Pawpaw Formation (Cretaceous: Albian), northeast Texas, USA. *Bulletin of the Mizunami Fossil Museum*, 40, 13-22.
- Fritsch, A. and Kafka, J. 1887. *Die Crustaceen der böhmischen Kreideformation*. F. Řivnáč, Prague.
- Garassino, A. and Schweigert, G. 2006. The Upper Jurassic Solnhofen decapod crustacean fauna: review of the types from old descriptions. Part I. Infraorders Astacidea, Thalassinidea, and Palinura. *Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, 34, 1, 1-64.
- Garassino, A., Pasini, G., De Angeli, A., Charbonnier, S., Famiani, F., Baldanza, A. and Bizzarri, R. 2012. The decapod community from the Early Pliocene (Zanclean) of “La Serra” quarry (San Minato, Pisa, Toscana, central Italy): sedimentology, systematics, and palaeoenvironmental implications. *Annales de Paléontologie*, 98, 1-61.



- Gašparič, R. and Hyžný, M. 2018. *Jaxea kuemeli* Bachmayer, 1954 (Malacostraca, Gebiidea, Laomediidae) from the Middle Miocene of Tunjice Hills (central Slovenia). *Geologija*, 61, 111-119.
- Glaessner, M.F. 1930. Neue Krebsreste aus der Kreide. *Jahrbuch der Preussischen Geologischen Landesanstalt zu Berlin*, 51, 1-7.
- Glaessner, M.F. 1969. Decapoda. In: Moore, R.C. (ed.), *Treatise on Invertebrate Paleontology, Part R. Arthropoda 4 (2)*. Geological Society of America, Boulder, and University of Kansas Press, Lawrence, R399-R533
- Hyžný, M. 2011. Revision of *Jaxea kuemeli* Bachmayer, 1954 (Decapoda: Gebiidea: Laomediidae) from the Miocene of Europe, with remarks on the palaeobiogeography of the genus *Jaxea* Nardo, 1847. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 260, 173-184.
- Hyžný, M. 2016. *Balsscallichirus* Sakai, 2011 (Decapoda: Axiidea: Callianassidae) in the fossil record: systematics and palaeobiogeography. *Annalen des Naturhistorischen Museums in Wien, Serie A*, 118, 39-63.
- Hyžný, M. 2020. *Vecticallichirus batei* (Woodward, 1869) n. comb. – a remarkable Paleogene ghost shrimp (Decapoda, Axiidea, Callichiridae) from the Isle of Wight, southern England. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 296, 119-128.
- Hyžný, M. and De Angeli, A. 2022. Mud lobster *Thalassina* Latreille, 1806 (Decapoda: Gebiidea: Thalassinidae), its Cenozoic occurrences in Italy and palaeobiogeography. *Geodiversitas*, 44(13), 417-425.
- Hyžný, M. and Dulai, A. 2021. *Badenian decapods of Hungary*. GeoLittera Publishing House, Institute of Geosciences, University of Szeged, Hungary.
- Hyžný, M. and Gross, M. 2016. From the palaeontological collection of the Universalmuseum Joanneum – The Cenozoic Decapod Crustaceans (Crustacea: Malacostraca: Decapoda). *Joannea Geologie und Paläontologie*, 12, 73-127.
- Hyžný, M. and Klompmaker, A.A. 2015. Systematics, phylogeny, and taphonomy of ghost shrimps (Decapoda): a perspective from the fossil record. *Arthropod Systematics & Phylogeny*, 73, 401-437.
- Hyžný, M. and Müller, P.M. 2010. The first fossil record of the genus *Callichirus* (Decapoda, Axiidea, Callianassidae) from the middle Miocene of Hungary, with description of a new species. *Bulletin of the Mizunami Fossil Museum*, 36, 37-43.
- Hyžný, M. and Müller, P.M. 2012. The fossil record of *Glypturus* Stimpson, 1866 (Crustacea, Decapoda, Axiidea, Callianassidae) revisited, with notes on palaeoecology and palaeobiogeography. *Palaeontology*, 55, 967-993.
- Hyžný, M. and Schlögl, J. 2011. An early Miocene deep-water decapod crustacean faunule from the Vienna Basin (Western Carpathians, Slovakia). *Palaeontology*, 54, 323-349.
- Hyžný, M. and Summesberger, H. 2019. A new species of *Mesostylus* (Decapoda, Axiidea, Callianassidae) – a peep into the private life of a Late Cretaceous burrowing shrimp. *Cretaceous Research*, 101, 108-123.
- Hyžný, M., Charbonnier, S., Merle, D., Ahmed Lashari, R., Bartolini, A. and Métais, G. 2016. New Early Cenozoic ghost shrimps (Decapoda, Axiidea, Callianassidae) from Pakistan and their palaeobiogeographic implications. *Geodiversitas*, 38, 341-353.
- Hyžný, M., Jakobsen, S.L. and Fraaije, R.H.B. 2017. Reappraisal of the burrowing lobster *Axius* (Malacostraca: Decapoda: Axiidea) in the fossil record with notes on palaeobiogeography



- and description of a new species. *Bulletin de la Société géologique de France*, thematic issue 188, 12.
- Hyžný, M., Zambrano, P., Muñiz, F. and Aragón, J.C. 2021. Ghost shrimp genus *Turbiocheir* from the Palaeogene of Argentina and Chile revisited: the first fossil record of *Anacalliax* (Decapoda: Anacalliidae). *Historical Biology*, 33, 2639-2645.
- Karasawa, H. 1993. Cenozoic decapod Crustacea from southwest Japan. *Bulletin of the Mizunami Fossil Museum*, 20, 1-92, 24 pls.
- Karasawa, H. and Hayakawa, H. 2000. Additions to Cretaceous decapod crustaceans from Hokkaido, Japan – Part I. Nephropidae, Micheleidae and Galatheididae. *Paleontological Research*, 4, 139-145.
- Karasawa, H. and Ohara, M. 2019. Establishment of a new genus for *Callianassa* (s.l.) *sakakuraorum* Karasawa, 2000 (Decapoda: Axiidea). *Bulletin of the Mizunami Fossil Museum*, 45, 33-42.
- Karasawa, H., Kishimoto, S., Ohara, M. and Ando, Y. 2019. Late Cretaceous Decapoda from the Izumi Group of Japan, with descriptions of two new genera and one new species of Axiidea and one new family of Brachyura. *Bulletin of the Mizunami Fossil Museum*, 45, 43-85.
- Kensley, B. and Williams, A.B. 1990. Axiopsis eximia, a new thalassinidean shrimp (Crustacea, Decapoda, Axiidae) from the Middle Eocene of South Carolina. *Journal of Paleontology*, 64, 798-802.
- Kiel, S., Hybertsen, F., Hyžný, M. and Klompmaker, A.A. 2020. Mollusks and a crustacean from early Oligocene methane-seep deposits in the Talara Basin, northern Peru. *Acta Palaeontologica Polonica*, 65, 109-138.
- Kneer, D., Asmus, H. and Jompa, J. 2013. Do burrowing callianassid shrimp control the lower boundary of tropical seagrass beds? *Journal of Experimental Marine Biology and Ecology*, 446, 262-272.
- Komai, T., Yokooka, H., Henmi, Y. and Itani, G. 2019. A new genus for "*Neocallichirus*" *grandis* Karasawa and Goda, 1996, a ghost shrimp species (Decapoda: Axiidea: Callianassidae) heretofore known only by fossil materials. *Zootaxa*, 4604, 461-481.
- Martin, J.W. and Davis, G.E. 2001. An updated classification of the Recent Crustacea. *Natural History Museum of Los Angeles County, Science Series*, 39, 1-124.
- Milne-Edwards, A. 1860. Histoire des Crustacés podophthalmiques fossiles et monographie des Décapodes macroures de la famille des Thalassiens fossiles. *Annales des Sciences Naturelles, (Zoologie)*(4), 14, 129-293, pls. 1-10.
- Moericke, W. 1897. Die Crustaceen der Stramberger Schichten. *Palaeontographica, Supplement II, Sechste Abtheilung*, 43-72, pl. 6.
- Mourik, A.A., Fraaije, R.H.B., Van der Zwaan, G.J. and Scheer, U. 2005. The burrowing shrimp, *Procallianassa faujasi* (Crustacea, Decapoda, Thalassinoidea), from the Lower Campanian at Dülmen, Germany. *Bulletin of the Mizunami Fossil Museum*, 32, 1-12.
- Ossó-Morales, À., Garassino, A., Vega, F.J. and Artal, P. 2011. *Pleuronassa timerchidouensis* n. gen., n. sp. (Axiidea, Callianassidae) from the Calcaires à slumps de Taghit Fm., Late Campanian of the Moyenne Moulouya, NE Morocco. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, 152, 165-175.
- Pasini, G., Garassino, A., Hyžný, M., Baldanza, A., Bizzarri, R. and Famiani, F. 2014. The bathyal decapod crustacean community from the early Pleistocene of Volterra (Pisa, Tuscany, central Italy). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 271, 243-259.



- Pasini, G., Garassino, A., De Angeli, A., Hyžný, M., Giusberti, L. and Zorzin, R. 2019. Eocene decapod faunas from the Konservat-Lagerstätten laminites of "Pesciara" (Bolca, Verona) and Monte Postale (Altissimo, Vicenza) in northeast Italy: a review and update. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 293, 233-270.
- Pasini, G., Poore, G.C.B. and Garassino, A. 2020. A new ghost shrimp (Axiidea, Callianopsidae) from the Late Cretaceous (Cenomanian) of Hadjoula, Lebanon. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 297, 217-225.
- Patrullius, D. 1959. Contributions à la systématique des décapodes néojurassiques. *Revue de Géologie et Géographie*, 3(2), 249-257.
- Poore, G.C.B., Dworschak, P.C.D., Robles, R., Mantelatto, F.L. and Felder, D.L. 2019. A new classification of Callianassidae and related families (Crustacea: Decapoda: Axiidea) derived from a molecular phylogeny with morphological support. *Memoirs of Museum Victoria*, 78, 73-146.
- Portell, R.W. and Agnew, J.G. 2004. Pliocene and Pleistocene decapod crustaceans. *Florida Fossil Invertebrates*, 4, 1-29.
- Quayle, W.J. and Collins, J.S.H. 2012. A review of the decapod crustaceans from the Tertiary of the Isle of Wight, Hampshire, U.K., with description of three new species. *Bulletin of the Mizunami Fossil Museum*, 38, 33-51.
- Robineau-Desvoidy, J.B. 1849. Mémoire sur les Crustacés du terrain néocomien de St. Sauveur-en-Puisaye. *Annales de la Société Entomologique de France*, (2)7, 95-141, pls. 4, 5.
- Robles, R., Tudge, C.C., Dworschak, P.C., Poore, G.C.B. and Felder, D.L. 2009. Molecular phylogeny of the Thalassinidea based on nuclear and mitochondrial genes. In: Martin, J.W., Crandall, K.A. and Felder, D.L. (eds.), *Decapod Crustacean Phylogenetics*. Taylor & Francis/CRC Press, Boca Raton, 309-326.
- Robles, R., Dworschak, P.C., Felder, D.L., Poore, G.C.B. and Mantelatto, F.L. 2020. A molecular phylogeny of Callianassidae and related families (Crustacea: Decapoda: Axiidea) with morphological support. *Invertebrate Systematics*, 34, 113-132.
- Rowden, A.A. and Jones, M.B. 1993. Critical evaluation of sediment turnover estimates for Callianassidae (Decapoda: Thalassinidea). *Journal of Experimental Marine Biology and Ecology*, 446, 262-272.
- Schweigert, G. 2003. Megachela frickhingeri n. g. n. sp. (Crustacea: Decapoda: Thalassinidea: Axiidae) aus dem Solnhofener Plattenkalk (Ober-Jura, Bayern). *Stuttgarter Beiträge zur Naturkunde*, (B), 333, 1-12.
- Schweigert, G. 2009. New genera and species of "thalassinideans" (Crustacea: Decapoda: Axiidea, Gebiidea) from the Upper Jurassic of Eichstätt and Brunn (S Germany). *Archaeopteryx*, 27, 21-30.
- Schweitzer, C.E. 2003. Utility of proxy characters for classification of fossils: an example from the fossil Xanthoidea (Crustacea: Decapoda: Brachyura). *Journal of Paleontology*, 77, 1107-1128.
- Schweitzer, C.E. and Feldmann, R.M. 2002. New Eocene decapods (Thalassinidea and Brachyura) from Southern California. *Journal of Crustacean Biology*, 22, 938-967.
- Schweitzer, C.E. and Feldmann, R.M. 2012. Revision of Decapoda deposited in the Muséum national d'Histoire naturelle, Paris. *Bulletin of the Mizunami Fossil Museum*, 38, 15-27.
- Schweitzer, C.E., Feldmann, R.M., Encinas, A. and Suárez, M. 2006. New Cretaceous and Eocene Callianassoidea (Thalassinidea, Decapoda) from Algarrobo, Chile. *Journal of Crustacean Biology*, 26, 73-81.



- Schweitzer, C.E., Feldmann, R.M., Čosović, V., Ross, R.L.M. and Waugh, D. 2009. New Cretaceous and Eocene Decapoda (Astacidea: Thalassinidea: Brachyura) from British Columbia, Canada. *Annals of Carnegie Museum*, 77, 403-423.
- Schweitzer, C.E., Feldmann, R.M., Kues, B.S. and Bridge, E.K. 2017. New Decapoda (Axiidea, Anomura, Brachyura) from the Turonian of New Mexico, USA. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 284, 89-115.
- Schweitzer, C.E., Hyžný, M. and Feldmann, R.M. 2021. New Paleogene and Neogene decapod crustaceans (Axiidea, Brachyura) from Venezuela. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 300, 245-266.
- Schweitzer Hopkins, C. and Feldmann, R.M. 1997. Sexual dimorphism in fossil and extant species of *Callianopsis* de Saint Laurent. *Journal of Crustacean Biology*, 17, 236-252.
- Secretan, S. 1964. Les crustacés décapodes du Jurassique Supérieur et du Crétacé de Madagascar. *Mémoires du Muséum national d'Histoire naturelle. Nouvelle Série. Série A, Zoologie*, 19, 1-223.
- Swen, K., Fraaije, R.H.B. and Van der Zwaan, G.J. 2001. Polymorphy and extinction of the Late Cretaceous burrowing shrimp *Protocallianassa faujasi* and first record of the genera *Corallianassa* and *Calliax* (Crustacea, Decapoda, Thalassinidea) from the Cretaceous. *Contributions to Zoology*, 70, 85-98.
- Wolfe, J.M., Breinholt, J.W., Crandall, K.A., Lemmon, A.R., Moriarty Lemmon, E., Timm, L.E., Sidall, M.E. and Bracken-Grissom, H.D. 2019. A phylogenomic framework, evolutionary timeline and genomic resources for comparative studies of decapod crustaceans. *Proceedings of the Royal Society B*, 286, 20190079.
- Ziebis, W., Forster, S., Huettel, M. and Jørgensen, B.B. 1996. Complex burrows of the mud shrimp *Callianassa truncata* and their geochemical impact in the sea bed. *Nature*, 382, 619-622.



THE EVOLUTION OF COMPOUND EYES ACROSS EXTANT AND FOSSIL CRABS

Javier Luque^{1,2*}, Heather D. Bracken-Grissom², Derek E.G. Briggs³,
Kelsey M. Jenkins³, Johan Lindgren⁴, Javier Ortega-Hernandez¹, A.
Richard Palmer⁵, Megan L. Porter⁶ and Joanna M. Wolfe¹

¹ Museum of Comparative Zoology and Department of Organismal and Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA. jluque@fas.harvard.edu

² Department of Biological Sciences, Florida International University-Biscayne Bay Campus, North Miami, FL 33181, USA.

³ Department of Earth and Planetary Sciences, Yale University, New Haven, CT 06520-8109, USA.

⁴ Department of Geology, Lund University, Lund, Sweden.

⁵ Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada.

⁶ Department of Biology, University of Hawaii at Manoa, Honolulu, HI 96822, USA.

Keywords: Apposition, Brachyura, Cretaceous, Phylogeny, Superposition

Image-forming compound eyes are such a valuable sensory adaptation that similar visual systems have evolved independently multiple times across panarthropods. However, the origin and evolution of different compound eye types remain poorly constrained, and the eyes of most extant families additionally are understudied. Moreover, fossils preserving compound eyes—especially internal neural tissues—generally are rare, and information about visual systems is seldom placed in a broader phylogenetic and evolutionary context.

True crabs, or Brachyura, are ideal study organisms to explore the evolution of compound eyes because they are one of few groups of arthropods that display all four of the known compound eye types (i.e., apposition, parabolic, refractive, and reflective superposition eyes; Gaten, 1998; Luque *et al.*, 2019a). In addition, due to their rich fossil record, details of the eye structures can be compared across extant and fossil groups to infer the visual ecology of extinct species (e.g., Jenkins *et al.*, 2022). Although preserved eyes of fossil crabs were once considered rare, we show that they are more common than previously assumed but often overlooked, discarded, or inadvertently destroyed during the process of mechanical preparation.

We investigated the utility of crab eye structures and ommatidia morphology for assessing the ecology and resolving phylogenetic relationships by integrating new data from both fossil and extant taxa across the brachyuran tree of life. We applied geometric morphometric techniques to our morphological dataset, demarcating two distinct ommatidial morphologies: (i) square facets and packing typical of reflecting superposition ('mirror') eyes; and (ii) hexagonal facets and packing typical of larval and postlarval apposition eyes. Our findings suggest that the plesiomorphic 'mirror' eyes present in most adult decapod crustaceans is also present in the phylogenetically least inclusive brachyuran groups (e.g., homolodromioids, dromioids, homoloids) (Fig. 1A–F). On the contrary, 'mirror' eyes have been lost in the most recent common ancestor of the more inclusive podotremes (e.g., etyoids, cenomanocarcinids, raninoids and cyclodorippoids) and eubrachiurans (Fig. 1G–T). This supports a growing number of morphological, molecular, and phylogenomic studies that consistently recover a paraphyletic grade of podotreme crabs, where the more phylogenetically inclusive podotremes, such as raninoids and cyclodorippoids, may form a monophyletic group with eubrachiurans (e.g., Ah Yong *et al.*, 2007; Tsang *et al.*, 2014; Tang *et al.*, 2018; Chen *et al.*, 2019; Luque *et al.*, 2019b; Luque *et al.*, 2021; Wolfe *et al.*, 2021; Ballou *et al.*, 2022).

The exceptional preservation of compound eyes in several Cretaceous and Cenozoic crabs from different families and ontogenetic stages (Luque *et al.*, 2019a; Jenkins *et al.*, 2022), highlights the advantage of mapping optical characters in a phylogenetic context at different taxonomic and time scales to investigate the origins of visual systems. The preservation of external corneal eye lenses together with soft neural tissues (e.g., retinotopic neuropils) is rare among fossil arthropods and largely restricted to a few Cambrian taxa. The exceptional preservation of

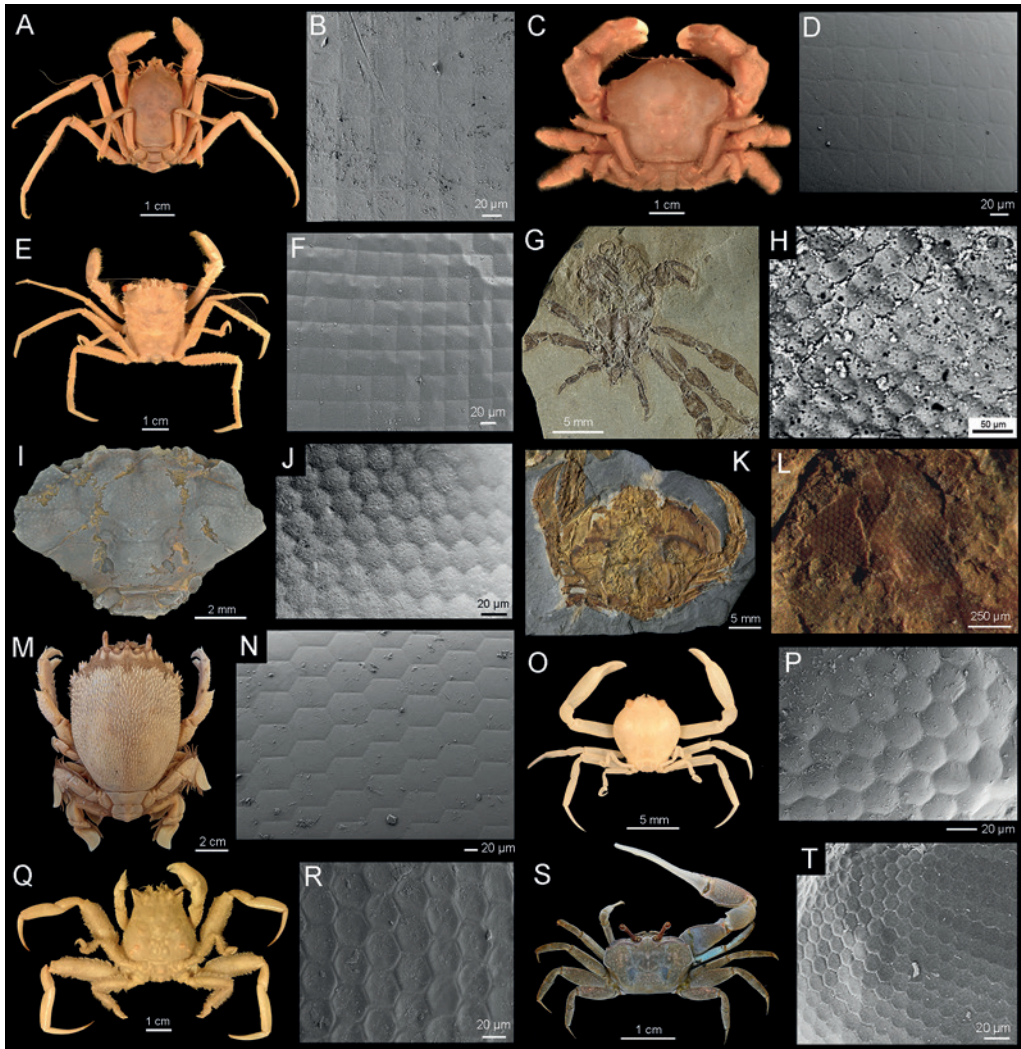


Figure 1. Examples of compound eyes across selected fossil and extant brachyuran superfamilies. A–F. Crabs with eyes bearing square facets in orthogonal packing, typical of reflecting superposition (=‘mirror’) eyes. A–B. Homolodromioidea: Homolodromiidae: *Dicranodromia felderi*, USNM 252207. C–D. Dromioidea: Dromiidae; C. *Moreiradromia saraburei*, USNM 1277453; D. *Dromia personata*, USNM 1277452. E–F. Homoloidea: Homolidae: *Homola minima*, USNM 1185786. G–T. crabs with eyes bearing hexagonal facets in hexagonal packing, typical of apposition eyes and parabolic and refracting superposition eyes. G–H. Callichimaeroidea: Callichimaeridae: *Callichimaera perplexa*; G. MUNSTRI 27044–02; H. IGM p881220. I–J. Etyoidea: Etyidae: *Xanthosia* sp., USNM PAL 706416 (1), upper Lower Cretaceous (Albian, ~105 Ma), Texas, USA. K–L. Necrocarcinoidae: Cenomanocarcinidae: *Cenomanocarcinus* sp. 32006-073, lower Upper Cretaceous (Turonian, ~90 Ma), Colombia. M–N. Raninidae: Ranininae: *Ranina ranina*; M. USNM 239219; N. USNM 265062. O–P. Cyclodorippoidea: Cyclodorippidae: *Clythrocerus nitidus*, USNM 77380. Q–T. Eubrachyura; Q–R. Dorippoidea: Dorippidae: Dorippoidea: Dorippidae; A–C. *Dorippe frascione*, QMW 1304. S–T. Ocypodoidea: Ocypodidae: *Leptuca oerstedii*. All photos by Javier Luque, modified from Luque et al. (2019a) <https://doi.org/786010.781101/786087>.

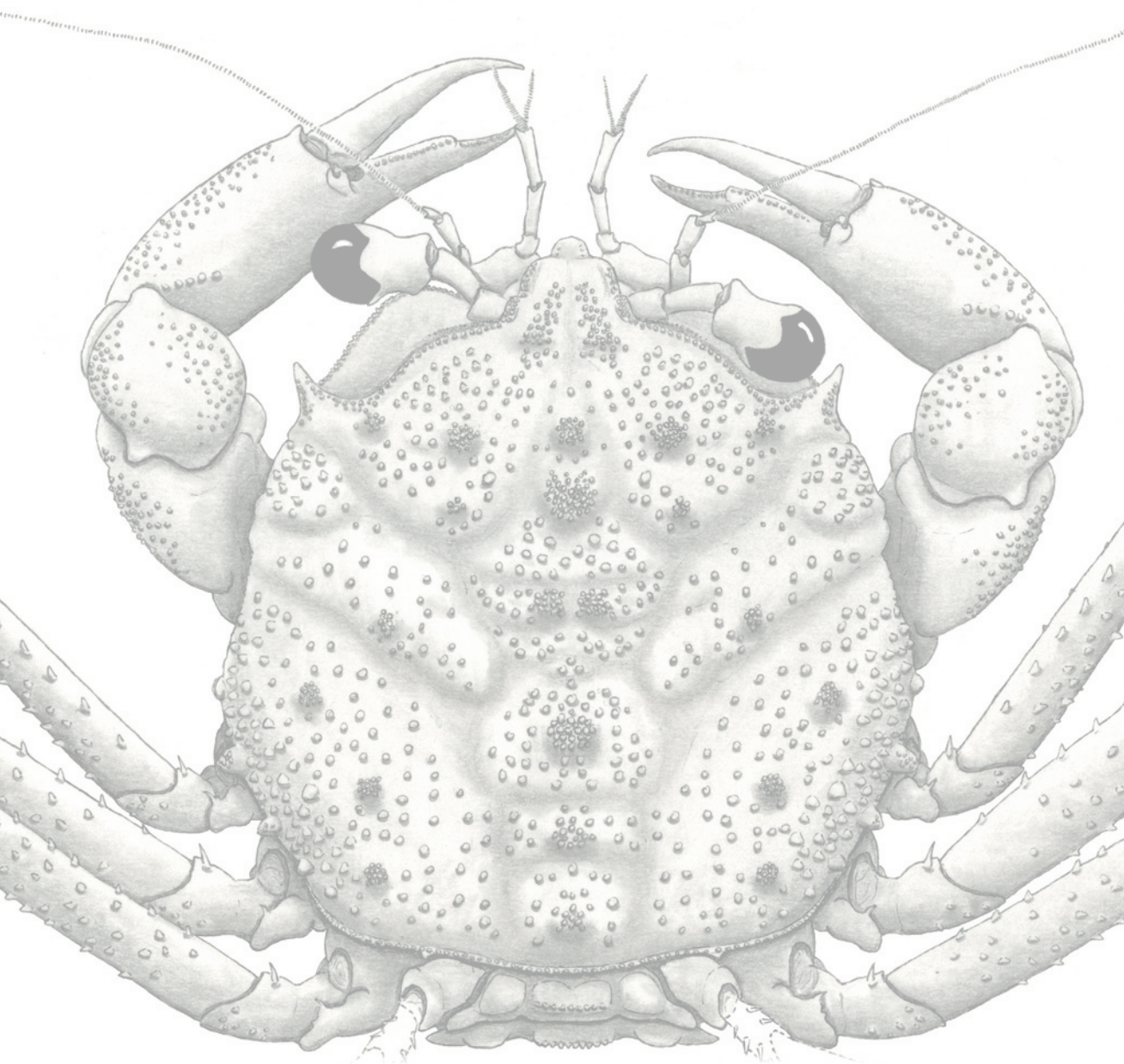
delicate corneal lenses together with corneagenous cells and retinotopic neuropils in the Cretaceous *Callichimaera perplexa* (Luque *et al.*, 2019b) is the first example of such combination of preservational styles discovered in a post-Paleozoic marine arthropod (Jenkins *et al.*, 2022), and illuminates the roles of development and ecology as important drivers of the evolution of visual systems among higher taxa. Ongoing work aims at shedding light on whether particular selection pressures account for convergent origins and/or losses of different eye types among true crabs and other decapod crustaceans through deep time.

Acknowledgements

The lead author was supported by a Natural Science and Engineering Research Council of Canada Graduate Scholarship (NSERC CGS-D), an NSERC Postdoctoral Fellowship (NSERC PDF), the Yale Institute for Biospheric Studies (YIBS), and the National Science Foundation (NSF), DEB grant #1856679 (USA). A.R.P. was supported by NSERC Discovery Grant RGPIN 04863 (Canada), and J.O.-H. and J.M.W. by the NSF-DEB grant #1856679 (USA).

REFERENCES

- Ahyong, S.T., Lai, J.C.Y., Sharkey, D., Colgan, D.J. and Ng, P.K.L. 2007. Phylogenetics of the brachyuran crabs (Crustacea: Decapoda): The status of Podotremata based on small subunit nuclear ribosomal RNA. *Molecular Phylogenetics and Evolution*, 45(2), 576–586.
- Ballou, L., Wolfe, J.M., Luque, J., Watson-Zink, V. and Bracken-Grissom, H.D. 2022. Using an integrative approach to assess habitat transitions and phylogenetic relationships within Brachyura. *The Crustacean Society Congress (TCS) and The Brazilian Society of Carcinology (SBC) Joint Meeting*, Brazil. June 06–09.
- Chen, J., Xing, Y., Yao, W., Xu, X., Zhang, C., Zhang, Z. and Liu, Q. 2019. Phylomitogenomics confirm the phylogenetic position of the genus *Metaplex* inferred from the two grapsid crabs (Decapoda: Brachyura: Grapsoidea). *PLoS One*, 14(1), e0210763.
- Gaten, E. 1998. Optics and phylogeny: is there an insight? The evolution of superposition eyes in the Decapoda (Crustacea). *Contributions to Zoology*, 67(4), 223–236.
- Jenkins, K.M., Briggs, D.E.G. and Luque, J. 2022. The remarkable visual system of a Cretaceous crab. *iScience*, 25(1), 103579.
- Luque, J., Allison, W.T., Bracken-Grissom, H.D., Jenkins, K.M., Palmer, A.R., Porter, M.L. and Wolfe, J.M. 2019a. Evolution of crab eye structures and the utility of ommatidia morphology in resolving phylogeny. *bioRxiv preprint*: 786087. <https://doi.org/10.781101/786087>.
- Luque, J., Feldmann, R.M., Vernygora, O., Schweitzer, C.E., Cameron, C.B., Kerr, K.A., Vega, F.J., Duque, A., Strange, M., Palmer, A.R. and Jaramillo, C. 2019b. Exceptional preservation of mid-Cretaceous marine arthropods and the evolution of novel forms via heterochrony. *Science Advances*, 5, eaav3875.
- Luque, J., Xing, L., Briggs, D.E.G., Clark, E.G., Duque, A., Hui, J., Mai, H. and McKellar, R.C. 2021. Crab in amber reveals an early colonization of non-marine environments during the Cretaceous. *Science Advances*, 7, eabj5689.
- Tang, B.P., Liu, Y., Xin, Z.Z., Zhang, D.Z., Wang, Z.F., Zhu, X.Y. and Liu, Q.N. 2018. Characterisation of the complete mitochondrial genome of *Helice wuana* (Grapsoidea: Varunidae) and comparison with other Brachyuran crabs. *Genomics*, 110(4), 221–230.
- Tsang, L.M., Schubart, C.D., Ahyong, S.T., Lai, J.C.Y., Au, E.Y.C., Chan, T.-Y., Ng, P.K.L. and Chu, K.H. 2014. Evolutionary history of true crabs (Crustacea: Decapoda: Brachyura) and the origin of freshwater crabs. *Molecular Biology and Evolution*, 31(5), 1173–1187.
- Wolfe, J., Luque, J. and Bracken-Grissom, H. 2021. How to become a crab: Phenotypic constraints on a recurring body plan. *Bioessays*, 43(5), 1–14.





ABSTRACTS







NEW INFORMATION OF *MEGACERADOCUS* (AMPHIPODA) FROM THE LOWER MIOCENE MOROZAKI GROUP, CENTRAL JAPAN, WITH NOTES OF *CALLIANOPSIS* (DECAPODA) *IN SITU* IN BURROWS

Yusuke Ando¹, Kiichiro Hachiya², Yoshiaki Mizuno², Takahisa Makiguchi²,
Masatoshi Yamaoka², Tsuneki Hayashi² and Tatsuo Oji³

¹ Mizunami Fossil Museum, 1-47 Yamanouchi, Akeyo-cho, Mizunami, Gifu 509-6132, Japan. tyyu-destiny53@hotmail.co.jp

² Tokai Fossil Society, 9-21 Atsuta, Nagoya, Aichi 456-0006, Japan.

³ University Museum, Nagoya University, Furo-cho, Nagoya, Aichi 464-8601, Japan.

Keywords: Crustacea, early Miocene, *Megaceradocus*, *Thalassinoides*, deep-sea fossils, fossil lagerstätten

Morozaki Group is one of the “fossil lagerstätten” and occurrence of deep-sea fossils were reported (e.g., Muramiya *et al.*, 2020). During the 21th to 24th October 2021, a large-scale paleontological excavation was conducted at a locality in Iwaya, Minamichita-cho, Aichi Prefecture, central Japan (Fig. 1A). This excavation led to the discovery of a variety of deep-sea faunas, such as deep-sea fish, echinoids, ophiuroids, molluscs and amphipods, from the lower Miocene Yamami Formation of Morozaki Group (18 Ma).

This group is divided into the Himaka, Toyohama, Yamami and Utsumi formations (Fig. 1B) in upward sequence and is considered to have deposited mainly in upper bathyal depths (e.g., Muramiya *et al.*, 2020). Many decapods and a few amphipods were already described from this group (e.g., Karasawa *et al.*, 2017).

Megaceradocus sp., an amphipod was collected during the large excavation at Iwaya (two specimens) and at Umenoki quarry (one specimen) (Fig. 1 I–K). The Iwaya specimens were collected from highly tuffaceous siltstone associated with deep-sea fish such as *Diaphus* sp. (Fig. 1K). The Umenoki specimen was collected from siltstone. Moreover, we reexamined the specimen which was already collected from the Yamami Formation and was described as *Megaceradocus* cf. *gigas* by Mukai and Takeda (1987) (Fig. 1C–G), as well as (Fig. 1H). They are similar to extant *M. gigas*, but clearly differ in having the well-convex posterior margin of the ischium of the pereopods 5 to 7. Additionally, length of peduncular article 2 of antenna 2 of the fossil specimens are 1.3 times longer than the extant species. Therefore, the fossil specimens are distinguishable from extant *M. gigas*.

Beside this excavation, *Callianopsis titaensis* preserved *in situ* were collected from burrows at a different locality of Toyohama Formation. This is an abundant decapod species from the Morozaki Group (e.g., Muramiya *et al.*, 2020). Two *C. titaensis* were collected from the Toyohama Formation and they were preserved *in situ* in burrows (Fig. 1L, M). The present burrows have some junctions, some rounded rooms and U-shape turn. Therefore, they seem to be identified with ichnogenus *Thalassinoides* and were possibly created by *C. titaensis*.

REFERENCES

- Karasawa, H., Mizuno, Y., Hachiya, K. and Ando, Y. 2017. Reappraisal of anomuran and brachyuran decapods from the lower Miocene Morozaki Group, Japan, collected by the Tokai Fossil Society. *Bulletin of the Mizunami Fossil Museum*, 43, 47–69.
- Mukai, H. and Takeda, M. 1987. A Giant Amphipod Crustacea from the Miocene Morozaki Group in the Chita Peninsula, Central Japan. *Bulletin of the National Science Museum, Series C*, 13, 35–39.

Muramiya, Y., Ujihara, A., Oji, T. and Yoshida, E. 2020. Spherical carbonate concretions and deep-sea fossils in the Morozaki Group, Chita Peninsula, central Japan. *The Journal of the Geological Society of Japan*, 126 (7), 355–363.

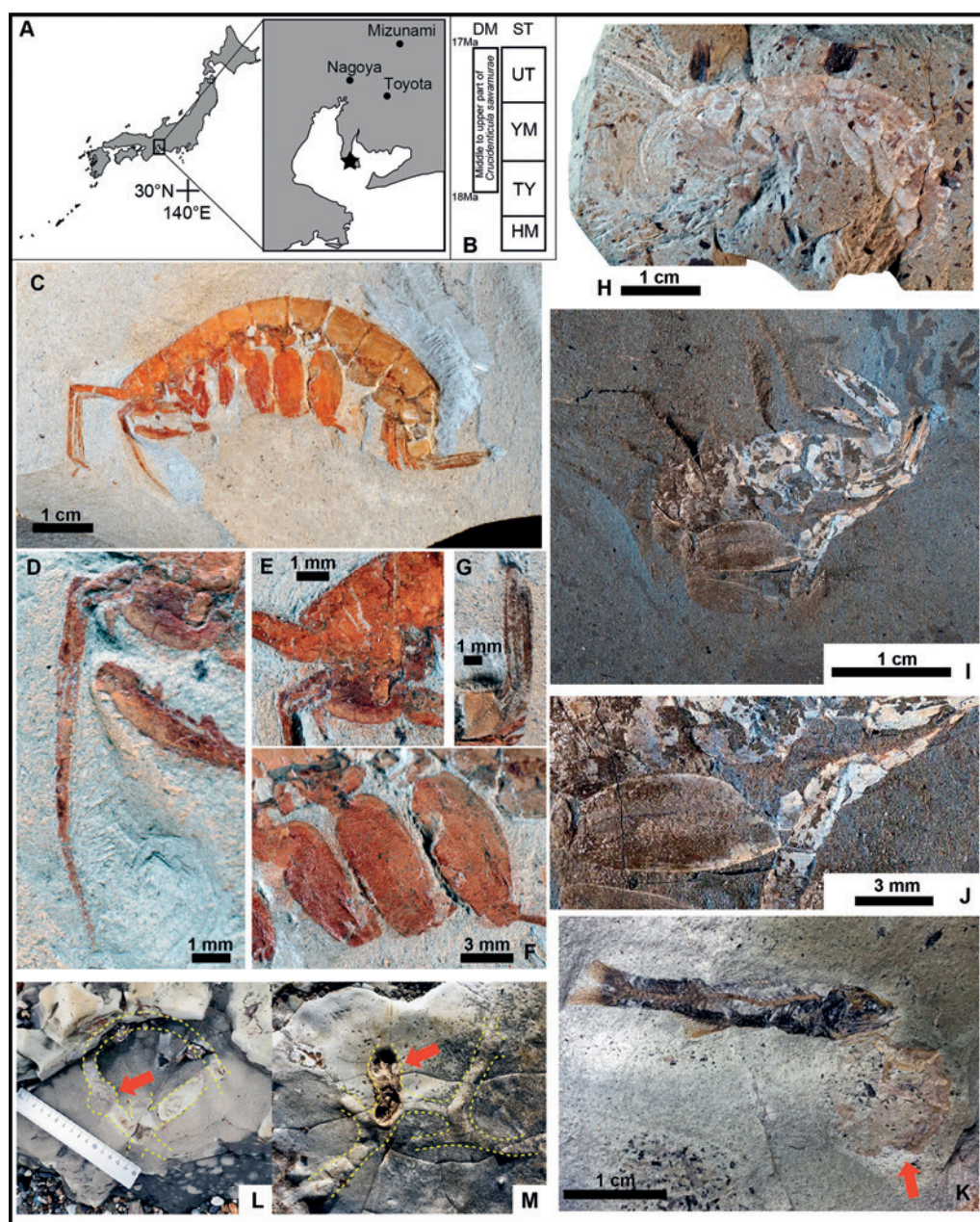


Figure 1. A. locality map (star). B. Stratigraphy and diatom zone of the Morozaki Group. DM: diatom zone; ST: stratigraphy; HM: Himaka; TY: Toyohama; YM: Yamami; UT: Utsumi. C–G. *Megaceradocus cf. gigas* described by Mukai & Takeda (1987). H–K. *Megaceradocus sp.* H. collected from Yamami; I, J. Umenoki specimen; K. Iwaya specimen (red arrow). L, M. burrows associated with *Callianopsis titaensis* (red arrows).

TAPHONOMY OF MECOCHIRID LOBSTERS FROM THE LOWER CRETACEOUS OF WEST-CENTRAL ARGENTINA

Alejandra Mariel Andrada¹, Leticia Luci^{1,2}, Darío Gustavo Lazo^{1,2} and María Beatriz Aguirre-Urreta^{1,2}

¹ Instituto de Estudios Andinos "Don Pablo Groeber", Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Pabellón II, Ciudad Universitaria, C1428EGA, Ciudad Autónoma de Buenos Aires, Argentina. andradam@gl.fcen.uba.ar

² CONICET, Consejo Nacional de Investigaciones Científicas y Técnicas, Godoy Cruz 2290, C1425FQB, Ciudad Autónoma de Buenos Aires, Argentina. leticialuci@gl.fcen.uba.ar, dlazo@gl.fcen.uba.ar, aguirre@gl.fcen.uba.ar

Keywords: *Atherfieldastacus rapax*, Valanginian, skeletal concentration, encrustation

INTRODUCTION

Lobsters of the genus *Atherfieldastacus* are widely distributed in the Lower Cretaceous and are usually preserved in 3D within *Thalassinoides* burrows or inside nodules and as laterally compressed specimens. They are commonly abundant in the outcrops where they occurred (e.g. Neto de Carvalho, 2016, Ferratges *et al.*, 2021). At Cerro La Parva locality in the Neuquén province, west-central Argentina, thin skeletal concentrations composed mainly by glypheidean lobsters were reported by Regairaz (1944) and Aguirre-Urreta (1989, 1998, 2003) in two levels belonging to the *Karakaschiceras attenuatum* Subzone of early/late Valanginian age. Two additional decapod-bearing levels were registered in recent exploration at this locality. Studied lobsters are represented by two different species of glypheideans: abundant *Atherfieldastacus rapax* (Harbort) (family Mecochiridae) and only four specimens of *Rectaglyphea* cf. *R. howardae* (family Glypheiidae). The aim of this work is to present the preliminary results of a taphonomic analysis of the skeletal concentrations of *A. rapax* including an interpretation of their genetic mechanisms and their paleobiological implications.

GEOLOGICAL SETTING

The studied skeletal concentrations of lobsters at Cerro La Parva are recorded in a thick interval of greenish and grayish siliciclastic shales that has been identified either as the upper member of the Mulichinco Formation or the lower member of the Agrio Formation (see alternative interpretations in Aguirre-Urreta, 1998, and Schwarz *et al.*, 2011). Aguirre-Urreta (1998) reported the presence of *A. rapax* in a nodular bed associated with the ammonoid *Karakaschiceras attenuatum* and the bivalve *Panopea* sp., within a 0.15 m level of hard silty shales (level P11), and a 0.8 m level consisting in a coquina with small oysters and nodules with *A. rapax* (level P15). Additionally, other two levels of shales with small calcareous nodules (P12, P14) were recently found that contained scarce, isolated, *in-situ* decapod-bearing nodules. Levels P11 and P15 correspond to skeletal concentrations that show evidence of reworking of the lobster-bearing nodules, and level P11 has an erosive base. Levels P12 and P14 are thin nodular beds immersed in shales with scattered disposition of lobsters along strike.

MATERIALS AND METHODS

Study materials include those previously known from levels P11 and P15 and those collected from the two new decapod-bearing levels. They were invariably preserved in incomplete calcareous nodules. A total of 112 nodules with *A. rapax* were recovered in the field from these four levels (P11: n=67; P12: n=11; P14: n=10; P15: n=24) plus additional material (n= 136) previously collected from the same locality but without precision of the level of collection. Taphonomic analysis included the scoring of the following attributes: completeness of the lobsters (nearly complete exoskeletons, disassociation units –*sensu* Hyžný and Klompmaker, 2015– or isolated carapaces), encrustation (presence, absence; type of encruster; encrusted region), and disposition

of the elements (anatomical connection or not, displacement of the pleon in relation with the carapace and of the pereopods in relation with the carapace).

RESULTS

Specimens of *A. rapax* are abundant and occurred in the four studied levels. Only one specimen occurs in each nodule. They are generally preserved as articulated carapaces, pleon and different elements of the pereopods, including from complete body fossils (32%) to disassociation units (51%) and a few isolated elements (17%). Many specimens show a connection between the carapace and pleon (53%, Fig. 1A) or these elements are found near each other (23%), while others have their carapaces raised and separated from the pleon (23%).

Nodules and lobsters are encrusted by small cementing oysters, serpulid tubes and bryozoans. Oysters and serpulids are externally attached to the exoskeletons and on the external surface of nodules at the same time in several specimens (Fig. 1B). Bryozoans were represented by multiserial encrusting colonies assigned to the cheilostome *Charixa burdonaria* (see Taylor *et al.*, 2009), and were found only on the mesial surface of a mold of the meri of two specimens (Fig. 1C). Colonies are single-layered, though in different paleoenvironmental settings they have been reported to have conformed multilayered masses (Taylor *et al.*, 2009).



Figure 1. A. Specimen of *A. rapax* showing connection between the carapace and the pleon, interpreted as a corpse (MOZ Pi 12034). B. Oyster (O) and serpulid tube (S) encrusting a carapace (C) (CPBA 18320). Note that the serpulid tube is encrusting part of the nodule also. C. Molds of bryozoan *Charixa burdonaria* encrusting the mesial surface of a merus (CPBA 18318). Specimen MOZ Pi 12034 was coated with ammonium chloride prior to photography. Scale bars: A-B: 10 mm, C: 200 μ m.

DISCUSSION

The connection between carapace and pleon in more than half of the specimens of which this relation could be seen is indicative that these samples represent corpses, but a minor portion of the specimens (23%) could be interpreted as exuviae because of the displacement of the pleon (and sometimes the pereopods). Association of parts that are not anatomically connected in the latter and lack of disarticulation in the former suggest that there was not any reworking and that the lobsters were rapidly entombed and protected from scavengers. They might have been preserved within their own burrows. Carbonate cement precipitated rapidly around the remains during a pause in sedimentation in the early diagenetic stage. This cementation was interrupted originating the incomplete nodules with exposed elements of the lobsters. Then, the nodules were reworked and exposed on the surface, possibly by erosion caused by transgression, allowing for the encrustation by serpulids and oysters. Finally, the encrusted incomplete nodules were buried. The presence of bryozoans on the mesial surface of two meri indicates that they were probably attached in-vivo. This is because cheilostomes were not found encrusting the nodules, and because they were locally restricted to specific parts of the lobsters. In addition, their posi-

tioning close to the breathing currents of their host could be reflecting a symbiotic relationship among them, possibly a commensal one since bryozoans could have benefitted from the inhaling currents of lobsters (placed between their pereopods), while causing no harm to the hosts. Being single-layered colonies, the cheilostomes likely added little relief to the lobster's exoskeletons thus causing minimum to no discomfort for the hosts. The presence of these cheilostomes suggests good water circulation and stenohaline waters.

Acknowledgements

We are grateful M. Tanuz (UBA) and B. Boilini (Museo Olsacher) for the access to the collections in their care. We thank L.J. Pazo and A. Moreno (Fundación Félix de Azara) for the mechanical preparation of the material, and M. Pianetti (Laboratorio de Microscopía Electrónica, INTI-Mecánica) for the SEM photos of the bryozoans. We are also grateful to C. Cataldo and A. Toscano for their help during the field work. This is contribution C-188 of the Instituto de Estudios Andinos "Don Pablo Groeber" (UBA-CONICET).

REFERENCES

- Aguirre-Urreta, M.B. 1989. The Cretaceous decapod crustacea of Argentina and the Antarctic Peninsula. *Palaeontology*, 32(3), 499-552.
- Aguirre-Urreta, M.B. 1998. The ammonites *Karakaschiceras* and *Neohoploceras* (Valanginian Neocomitidae) from the Neuquén Basin, west-central Argentina. *Journal of Paleontology*, 72 (1), 39-59.
- Aguirre-Urreta, M.B. 2003. Early Cretaceous decapod Crustacea from the Neuquén Basin, west-central Argentina. *Contributions to Zoology*, 72 (2-3), 79-81.
- Hyžný, M. and Klompmaker, A.A. 2015. Systematics, phylogeny, and taphonomy of ghost shrimps (Decapoda): a perspective from the fossil record. *Arthropod Systematics and Phylogeny*, 73 (3), 401-437.
- Ferratges, F.A., Hyžný, M. and Zamora, S. 2021. Taphonomy and systematics of decapod crustaceans from the Aptian (Lower Cretaceous) in the Oliete Sub-basin (Teruel, Spain). *Cretaceous Research*, 122, 104767.
- Neto de Carvalho, C. 2016. The massive death of lobsters smothered within their *Thalassinoides* burrows: the example of the lower Barremian from Lusitanian Basin (Portugal). *Comunicações Geológicas*, 103, 143-152.
- Regairaz, A.C. 1944 Estudio estratigráfico y tectónico del Cerro de La Parva y sus alrededores, Neuquén. Universidad Nacional de La Plata, Tesis, 164 pp. [Unpublished]
- Schwarz, E., Spalletti, L.A. and Veiga, G.D. 2011. La Formación Mulichinco (Cretácico Temprano) en la Cuenca Neuquina. In Leanza, H.A., Arregui, C., Carbone E., Danieli J.C. and Vallés J. (Eds.), *Geología y Recursos Naturales de la Provincia del Neuquén*. Asociación Geológica Argentina, Buenos Aires, 131-144.
- Taylor, P.D., Lazo, D.E. and Aguirre-Urreta, M.B. 2009. Lower Cretaceous bryozoans from Argentina: a 'by catch' fauna from the Agrio Formation (Neuquén Basin). *Cretaceous Research*, 30, 193-203.



CRAYFISHES FROM THE JEHOI BIOTA

Denis Audo¹, Tadashi Kawai², Robert O'Flynn^{3,4}, Julien Devillez¹ and Diying Huang⁴

¹ Centre de Recherche en Paléontologie – Paris (CR2P, UMR 7207), CNRS, MNHN, Sorbonne Université, Muséum national d'Histoire naturelle, CP 38, 57 rue Cuvier, F-75005, Paris, France. denis.audo@mnhn.fr

² Hokkaido Research Organization, Central Fisheries Research Institute, 238 Hamanaka, Yoichi, 045-8555 Hokkaido, Japan. tadashikawai8@gmail.com

³ Yunnan Key Laboratory for Palaeobiology, Institute of Palaeontology, Yunnan University, 650500 Kunming, China and School of Geography, Geology and the Environment, University of Leicester, LE1 7RH, UK.

⁴ MEC International Joint Laboratory for Palaeobiology and Palaeoenvironment, Yunnan University, 650091 Kunming, China. liangwangshani@126.com

⁵ State Key Laboratory of Palaeobiology and Stratigraphy, Center for Excellence in Life and Paleoenvironment, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China. dyhuang@nigpas.ac.cn

Keywords: Astacoidea, biogeography, *Cambaroides*, Cretaceous, freshwater, pleopods

Freshwater crayfishes (Astacoidea and Parastacoidea) are among the largest freshwater invertebrates, they are diverse, with in excess of 660 described species (Crandall and De Grave, 2017), and have an interesting biogeographical distribution tied to the fragmentation of Pangea. In contrast to their important extant biodiversity, fossil species are rare; only 13 fossil species have been described so far (Feldmann *et al.*, 2011). As such, most of what we know about the evolution of crayfishes derives from the study of extant species and palaeogeography (see, e.g., Đuriš and Petrusek, 2015). Besides, most fossil crayfishes have not been reviewed since their first descriptions.

Our current project aims at reviewing and assessing the significance of all freshwater crayfishes. A review of the literature shows that crayfishes once had a wider geographical distribution, and that many taxonomic assignments need to be reviewed. Our review of *Astacus edwardsi* Van Straelen, 1928 from the Thanetian of France (O'Flynn *et al.*, 2021, Fig. 1A) showed it should be assigned to a new genus. Our review of *Astacus multicavatus* Bell, 1863 (Fig. 1B) from the Hauterivian of the United Kingdom (Devillez *et al.*, 2021), for instance, showed that this species is not a crayfish but an erymid lobster. Incidentally, this species had been used as a calibration point for the divergence of crayfishes. Recently, our review of crayfishes from the Jehol biota (Audo *et al.* in progress, Fig. 1C) has shown that it was not possible to differentiate the three species described in this Lagerstätte. In addition, the extinct family Cricoidoscelosidae appears supported by taphonomic biases and characters frequent for northern hemisphere crayfishes, leading us to question its validity.

These first results show there is much to learn from fossil crayfishes, and that fossils may provide crucial insights on the evolutionary history of this group and help understand its present repartition.

Acknowledgments

We are grateful to Claire Mellish (NHMUK, London, UK), Stéphane Jouve (Sorbonne University, Paris, France) and Daojun Yuan (NIGPAS, Nanjing, China) for access to specimens and Kevin Webb (NHMUK) for the photograph of *E. multicavatus*.

REFERENCES

- Crandall, K.A. and De Grave, S. 2017. An updated classification of the freshwater crayfishes (Decapoda: Astacidea) of the world, with a complete species list. *Journal of Crustacean Biology*, 37, 615–653.
- Devillez, J., Kawai, T. and Audo, D. 2021. *Astacus multicavatus* Bell, 1863 is a marine lobster, not a freshwater crayfish. *Journal of Crustacean Biology*, 41 (2), 1–7.

- Đuriš, Z. and Petrušek, A. 2015. Evolution and historical biogeography of crayfishes. In P. Kozák, Z. Đuriš, M. Buřič, L. Horká, A. Kouba, E. Kozubíková-Balcarová & T. Polícar (eds), *Crayfish biology and culture*. Faculty of Fisheries and Protection of Waters, University of South Bohemia, Vodňany, Czech Republic, 39–58.
- Feldmann, R.M, Schweitzer, C.E. and Leahy, J. 2011. New Eocene crayfish from the McAbee beds in British Columbia: first record of Parastacoidea in the Northern Hemisphere. *Journal of Crustacean Biology*, 31, 320–331.
- O'Flynn, R.J., Audo, D. and Kawai, T. 2021. Systematic revision and palaeobiology of *Emplastron edwardsi* (Van Straelen, 1928) gen. et. comb. nov. (Crustacea, Decapoda, Astacidae) entombed within travertine, from Sézanne, France. *Paleontological Research*, 25 (4), 379–388.



Figure 1. Two crayfishes and an erymid lobster. A. *Emplastron edwardsi* (Van Straelen, 1928) from the Thanetian of Sézanne, France. B. *Eryma multicavatum* (Bell, 1863), formerly interpreted as a crayfish, from the Hauterivian of United Kingdom. C. *Palaeocambarus licenti* (Van Straelen, 1928) from the Lower Cretaceous of north-eastern China. Scale bars: 10 mm (1, 2) and 20 mm (3). Photograph: D. Audo (1, 3) and K. Webb (2).

TAPHONOMY OF THE STOMACH IN THREE MESOZOIC DECAPODS

Denis Audo¹, Tadashi Kawai², Sylvain Charbonnier¹, Clément Jauvion¹ and Diying Huang³

¹ Centre de Recherche en Paléontologie – Paris (CR2P, UMR 7207), CNRS, MNHN, Sorbonne Université, Muséum national d'Histoire naturelle, CP 38, 57 rue Cuvier, F-75005, Paris, France. denis.audo@mnhn.fr

² Hokkaido Research Organization, Central Fisheries Research Institute, 238 Hamanaka, Yoichi, 045-8555 Hokkaido, Japan. tadashikawai8@gmail.com

³ State Key Laboratory of Palaeobiology and Stratigraphy, Center for Excellence in Life and Palaeoenvironment, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China. dyhuang@nigpas.ac.cn

Keywords: crayfish, exceptional preservation, gastrolith, Polychelida, putrefaction, stomach

Lobster-like crustaceans are quite rare in the fossil record, as they usually require special taphonomical conditions to be preserved (Bishop, 1986; Klompmaker *et al.*, 2017). In the present presentation, we present three interesting cases of fossil showing the action of decay in the gastric region prior to fossilization: 1) a polychelidan lobster from La Voulte-sur-Rhône, Callovian of France; 2) a fossil crayfish from the Jehol biota, Early Cretaceous of China; 3) a fossil nephropoid lobster from Hakel, Cenomanian of Lebanon.

A few polychelidan from La Voulte-sur-Rhône shows how partial decay led first to the collapse of the gastric area, and that despite this early decay, organs located in the posterior half of the cephalothorax are still preserved.

Several crayfishes from the Jehol biota show corpses, identified by the presence of gastroliths, may superficially resemble exuvia.

In our geologically youngest example, we show how sediment infilling as partially preserved the original volume of the stomach, in an otherwise flattened fossil.

Together, these different fossils illustrate the importance of decomposition in the fossilization process.

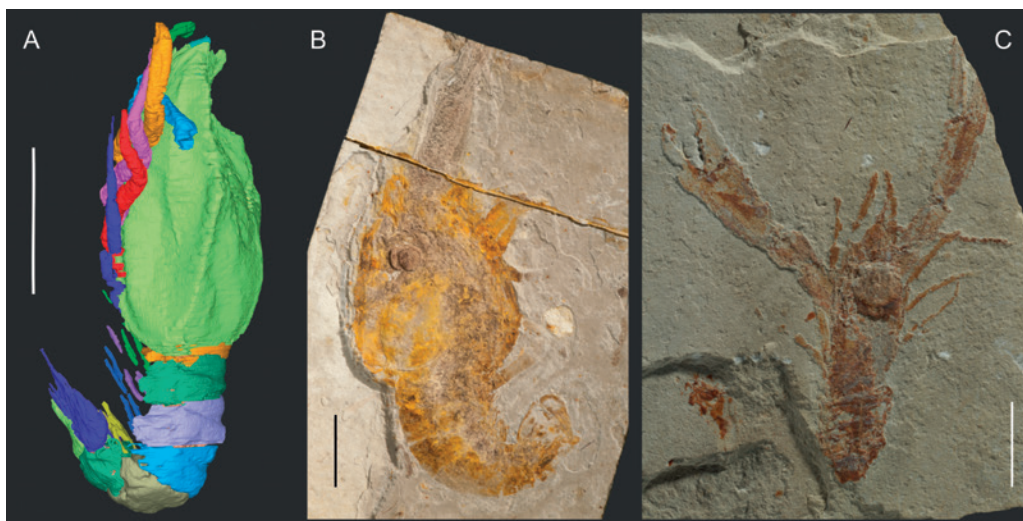


Figure 1. Three fossil decapod crustaceans with noteworthy taphonomy of the stomach. A. *Helerochelis falloti* (Van Straelen, 1923) from the Callovian of La Voulte-sur-Rhône. B. *Palaeocambarus licenti* (Van Straelen, 1928) from the Early Cretaceous of north-eastern China. C. *Notahomarus hakelensis* (Fraas, 1878) from the Cenomanian of Lebanon. Scale bars: 2 mm (1) and 20 mm (2, 3).



Acknowledgments

We are grateful to Miguel Garcia Sanz (formerly MNHN, Paris) who operated the CT-scan and Florent Goussard (MNHN, Paris) for teaching the first author how to use 3D segmentation softwares.

REFERENCES

- Bishop G.A. 1986. Taphonomy of the North American Decapods. *Journal of Crustacean Biology*, 6 (3), 326–355.
- Klompmaaker A.A., Portell R.W. and Frick M.G. 2017. Comparative experimental taphonomy of eight marine arthropods indicates distinct differences in preservation potential. *Palaeontology*, 60 (6), 773–794.



DECAPOD CRUSTACEAN ICHNOLOGY: A STATE OF THE ART

Zain Belaústegui¹ and Fernando Muñiz²

¹ Departament de Dinàmica de la Terra i de l'Oceà, Facultat de Ciències de la Terra, Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona (UB), 08024 Barcelona, Spain. zbelaustegui@ub.edu

² Departamento de Cristalografía, Mineralogía y Química Agrícola, Universidad de Sevilla, 41012 Sevilla, Spain. fmuniz@us.es

Keywords: Decapoda, Ichnology, Bioturbation, Bioerosion, Biodeposition

INTRODUCTION

Decapod crustaceans are one of the groups of organisms that exhibit a more significant bioturbation activity, both today as in the past (in particular during the Mesozoic and Cenozoic; see Carmona *et al.*, 2004). At the moment, their burrowing behavior is probably the best known; many groups of modern decapods [e.g. gebiidean, axiidean or caridean shrimps, astacideans (lobsters and crayfish) and brachyuran crabs] excavate burrows in different environments (mainly marine but also in terrestrial ones), and some of the resulting traces are well known in the fossil record. By contrast, bioerosion structures related or attributed to decapods are rarer and less common; nevertheless, it is known that some groups are (or were) able to bioerode on lithic, skeletal (i.e. shells and bones) and xylic substrates. Finally, several biodeposition structures produced by decapods have been described both in modern settings as in the fossil record; they are mainly represented by feeding, constructional and fecal pellets (e.g. Ekdale *et al.*, 1984; Gibert *et al.*, 2013).

It should be noted that although this contribution does not intend to be an exhaustive review, it does attempt to compile the main aspects related to the ichnology of decapod crustaceans.

TRACE FOSSIL RECORD

Bioturbation structures

Thalassinoides, *Ophiomorpha* and *Spongeliomorpha* are very likely the most common and representative trace fossils attributed to the burrowing activity of decapod crustaceans. These ichnogenera correspond to vertical and mostly horizontal burrows that constitute more or less complex systems, in which Y- or T-shaped branching points are very common; in fact, they are only differentiated by wall features (Gibert and Ekdale, 2010). While *Ophiomorpha* burrows exhibit a characteristic pelleted lining, *Spongeliomorpha* and *Thalassinoides* never possess pellets in their walls. In turn, whereas *Spongeliomorpha* is characterized by the presence of bioglyphs covering the walls of their tunnels, such bioglyphs are absent in *Thalassinoides*. Although examples of these three ichnotaxa have been recorded since the Paleozoic, those clearly linked to the burrowing activity of decapods correspond to Mesozoic and Cenozoic occurrences which are mainly associated to shallow marine settings (although they have also been recorded linked to deeper marine and even continental environments) (Buatois *et al.*, 2016). Commonly, axiidean and gebiidean shrimps are proposed as their more likely tracemakers; in particular, conducting dwelling or feeding behaviors.

Psilonichnus, *Macanopsis* and *Parmaichnus* consists of vertical-to-oblique, cylindrical, unlined, J-, Y- or U-shaped burrows, mainly attributed to the burrowing activity of upogebiid shrimps and/or ocypodid crabs (e.g. Frey *et al.*, 1984). Despite some Mesozoic occurrences, these ichnotaxa are common in Cenozoic outcrops related to shallow marine environments (near-shore to backshore) and even in transitional areas to continental settings (Buatois *et al.*, 2016).

Gyrolithes and *Lapispira* correspond to more or less complex, helical burrows with or without a pelleted lining. Both ichnogenera have been described in association with other 'decapod' ichnotaxa such as *Thalassinoides* or *Ophiomorpha* in Cenozoic outcrops (e.g. Gibert *et al.*, 2012;

Muñiz and Belaústegui, 2019). In particular and associated to tidal flat settings, the modern species *Axianassa australis* are able to excavate vertical helical galleries identical to the ichnogenus *Gyrolithes* (Dworschak and Rodrigues, 1997).

Other ichnotaxa such as *Sinusichnus*, *Lepeichnus* or *Pholeus*, less frequent in the fossil record, consist of more or less complex dwelling burrows that have also been interpreted as the result of different kind of burrowing decapods mainly associated to marine depositional settings (e.g. Belaústegui *et al.*, 2014, 2016; Knaust, 2002). It is remarkable that, at the moment, the ichnogenus *Lepeichnus* constitutes the most complete ichnogenetic sequence of a trace fossil (see Belaústegui *et al.*, 2016).

In relation to Mesozoic and Cenozoic continental depositional settings (e.g. marshes, swamps, lakes, wetlands or fluvial systems), the ichnogenera *Camborygma*, *Loloichnus*, *Lunulichnus*, *Katbergia* or *Egbellichnus* have been also attributed to decapod tracemakers, mainly to burrows of crayfishes (see Genise *et al.*, 2016) but also of ghost shrimps (Hyžný *et al.*, 2015).

Breeding traces or brood structures (calichnia) associated to decapod crustaceans have also been identified in Mesozoic and Cenozoic sedimentary rocks; in particular, the ichnogenera *Dagnichnus* and *Celliclichnus* for terrestrial crayfishes (Genise *et al.*, 2016), and *Maikarichnus* for marine callinassid shrimps (Verde and Martínez, 2004).

Resting and moulting traces (cubichnia and ecdysichnia, respectively) linked to decapods have also been identified in the trace fossil record (mainly in Mesozoic examples). For example, the ichnogenus *Tripartichnus* or even *Rusophycus*-like structures would correspond to resting traces and the ichnogenus *Harpichnus* would be the result of a moulting process (see Vallon *et al.*, 2015).

Finally, trackways, trails or bilobate structures attributed to decapod locomotion (i.e. repichnia) are also common; several ichnogenera such as *Diplichnites*, *Foersterichnus*, *Coenobichnus* or even *Cruziana*-like structures are good examples; they occurred in different depositional settings and ages (Buatois *et al.*, 2016).

Bioerosion structures

Contrary to bioturbation, the diversity of bioerosion structures produced or attributed to decapod crustaceans is much lower. Those more frequently preserved in the fossil record correspond to the scars that other invertebrates (mainly bivalves and gastropods) exhibit in their shells; commonly, these scars are the result of unsuccessful attacks conduct by durophagous crabs (for example, genera *Calappa* or *Necora*) (Ekdale *et al.*, 1984).

Bioerosion structures produced on bones of shallow- and deep-sea whale-falls, and attributed to the feeding behavior of osteophagous crabs (Oregoniidae), have also been described in the fossil record (Belaústegui *et al.* 2017).

Biodeposition structures

The fossil record of biodeposition structures produced by decapod crustaceans mainly consist of fecal pellets, in particular those included within the ichnofamily Favreinidae (see Knaust, 2020). Ichnogenera belonging to this ichnofamily (e.g. *Favreina*, *Parafavreina*, *Palaxius* or *Thoronetia*) mainly consist of sub-cylindrical coprolites with smooth or ornamented surface and various internal canals. By comparison with modern analogues, anomurans (decapod crustaceans, including hermit crabs) have been proposed as the most likely producers (see Knaust, 2020).

NEOICHOLOGY

Neoichnological studies have proven to be a very useful and fundamental tool for understanding and interpreting the paleoichnological record. From them, it is possible to obtain a huge

amount of information about bioturbation, bioerosion and biodeposition processes (or structures) conducted (or produced) by modern organisms. In that sense and focusing on the aim of this contribution, there are many neoichnological studies focused on decapod crustaceans (both marine and terrestrial) and based on different kinds of techniques (e.g. Dworschak and Rodrigues, 1997; Melchor *et al.*, 2010; Gibert *et al.*, 2013; Seike and Curran, 2014).

Acknowledgements

FM has been supported by the Research Group RNM-293 "Geomorfología Ambiental y Recursos Hídricos" of the University of Huelva.

REFERENCES

- Belaústegui, Z., Gibert, J.M. de, López-Blanco, M. and Bajo, I. 2014. Recurrent constructional pattern of the crustacean burrow *Sinusichnus sinuosus* from the Paleogene and Neogene of Spain. *Acta Palaeontologica Polonica*, 59, 461–474.
- Belaústegui, Z., Muñiz, F., Mángano, M.G., Buatois, L.A., Domènech, R. and Martinell, J. 2016. *Lepeichnus giberti* igen. nov. isp. nov. from the upper Miocene of Lepe (Huelva, SW Spain): Evidence for its origin and development with proposal of a new concept, ichnogeny. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 452, 80–89.
- Belaústegui, Z., Muñiz, F., Domènech, R. and Martinell, J. 2017. Ichnogenia, nuevos ejemplos a partir de estructuras de bioerosión. In O'Dogherty, L. (coord.), *33 Jornadas de Paleontología*. Sociedad Española de Paleontología, 28–31.
- Buatois, L.A., Carmona, N.B., Curran, H.A., Netto, R.G., Mángano, M.G. and Wetzel, A. 2016. The Mesozoic Marine Revolution. In M.G. Mángano and Buatois, L.A. (eds.), *The trace-fossil record of major evolutionary events*. Springer. Topics in Geobiology, 40, 19–134.
- Carmona, N.B., Buatois, L.A. and Mángano, M.G. 2004. The trace fossil record of burrowing decapods crustaceans: evaluating evolutionary radiations and behavioural convergence. In B.D. Webby, M.G. Mángano and L.A. Buatois (eds.), *Trace Fossils in Evolutionary Palaeoecology. Fossils and Strata*, 51, 141–153.
- Dworschak, P.C. and Rodrigues, S. de A. 1997. A modern analogue for the trace fossil *Gyrolithes*: burrows of the thalassinidean shrimp *Axianassa australis*. *Lethaia*, 30, 41–52.
- Ekdale, A.A., Bromley, R.G. and Pemberton, S.G. 1984. *Ichnology, Trace Fossils in Sedimentology and Stratigraphy*. Society for Sedimentary Geology Short Course Notes, 15, 316 pp.
- Frey R.W., Curran, H.A. and Pemberton, S.G. 1984. Tracemaking activities of crabs and their environmental significance: the ichnogenus *Psilonichnus*. *Journal of Paleontology*, 58(2), 333–350.
- Genise, J.F., Bedatou, E., Bellosi, E.S., Sarzetti, L.C., Sánchez, M.V. and Krause, J.M. 2016. The Phanerozoic four revolutions and evolution of paleosol ichnofacies. In M.G. Mángano and Buatois, L.A. (eds.), *The trace-fossil record of major evolutionary events*. Springer. Topics in Geobiology, 40, 301–370.
- Gibert, J.M. de and Ekdale, A.A. 2010. Paleobiology of the crustacean trace fossil *Spongeliomorpha iberica* in the Miocene of southeastern Spain. *Acta Palaeontologica Polonica*, 55, 733–740.
- Gibert, J.M. de, Mas, G. and Ekdale, A.A. 2012. Architectural complexity of marine crustacean burrows: unusual helical trace fossils from the Miocene of Mallorca, Spain. *Lethaia*, 45, 574–585.



- Gibert, J.M. de, Muñiz, F., Belaústegui, Z. and Hyžný, M. 2013. Fossil and modern fiddler crabs (*Uca tangeri*: Ocypodidae) and their burrows from SW Spain: ichnologic and biogeographic implications. *Journal of Crustacean Biology*, 33(4), 537–551.
- Hyžný, M., Šimo, V. and Starek, D. 2015. Ghost shrimps (Decapoda: Axiidea: Callianassidae) as producers of an Upper Miocene trace fossil association from sublittoral deposits of Lake Pannon (Vienna Basin, Slovakia). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 425, 50–66.
- Knaust, D. 2002. Ichnogenus *Pholeus* Fiege, 1944, revisited. *Journal of Paleontology*, 76(5), 882–891.
- Knaust, D. 2020. Invertebrate coprolites and cololites revised. *Papers in Palaeontology*, 6(3), 385–423.
- Melchor, R.N., Genise, J.F., Farina, J.L., Sánchez, M.V., Sarzetti, L. and Visconti, G. 2010. Large striated burrows from fluvial deposits of the Neogene Vinchina Formation, La Rioja, Argentina: A crab origin suggested by neoichnology and sedimentology. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 291, 400–418.
- Muñiz, F. and Belaústegui, Z. 2019. Helical crustacean burrows: *Gyrolithes* ichnofabrics from the Pliocene of Lepe (Huelva, SW Spain). *Palaios*, 34, 1–14.
- Seike, K. and Curran, H.A. 2014. Burrow morphology of the land crab *Gecarcinus lateralis* and the ghost crab *Ocypode quadrata* on San Salvador Island, The Bahamas: comparisons and palaeoenvironmental implications. *Spanish Journal of Palaeontology*, 29(1), 61–70.
- Vallon, L.H., Schweigert, G., Bromley, R.G., Röper, M. and Ebert, M. 2015. Ecdysichnia – a new ethological category for trace fossils produced by moulting. *Annales Societatis Geologorum Poloniae*, 85, 433–444.
- Verde, M. and Martínez, S. 2004. A new ichnogenus for crustacean trace fossils from the late Miocene Camacho Formation of Uruguay. *Palaeontology*, 47, 39–49.

CHANGES IN SHIELD MORPHOLOGY OF CARCINIDAE – A GEOMETRIC MORPHOMETRICS PERSPECTIVE ON ONTOGENY AND EVOLUTION

Florian Braig¹ and Joachim T. Haug^{2,3}

¹ Faculty of Biology, LMU Munich, Biocenter, Großhaderner Str. 2, 82152 Planegg-Martinsried, Germany. braig@bio.lmu.de

² Faculty of Biology, LMU Munich, Biocenter, Großhaderner Str. 2, 82152 Planegg-Martinsried, Germany. joachim.haug@palaeo-evo-devo.info

³ GeoBio-Center of the LMU Munich, Richard-Wagner-Str. 10, 80333 Munich, Germany.

Keywords: Ancestral state reconstruction, Development, Morphological diversity, Disparity, Megalopa

INTRODUCTION

Carcinidae is an ingroup of Eubrachyura, with globally abundant species, such as the invasive European shore crab (*Carcinus maenas*; Young and Elliott, 2020). As an ingroup of Portunoidea, the group Carcinidae underwent several phylogenetic reorganizations during the last decades. With the last molecular phylogenetic analysis, the number of species of Carcinidae increased significantly (Evans, 2018). This also expanded the number of fossil specimens included into the group, which provide additional data for reconstructing the evolutionary history of the group. We compare the morphology of the shield of representatives of Carcinidae through their ontogeny and phylogeny and investigate how shield morphology changed during the course of their evolution.

MATERIAL AND METHODS

We used elliptic Fourier transformation on the shield outlines of 191 extant and fossil Carcinidae, using the R-statistics environment (ver. 4.1.0; R Core Team, 2021). Our data set contains developmental stages starting with the megalopa stage. We used principal component analysis to create morphospaces of the shields. Furthermore, we used a combination of current morphological and molecular character matrices to create a combined phylogeny, which we use for a reconstruction of ancestral states of the shield shape. Thereby, we can describe the evolutionary path of the shield morphology during the evolution of Carcinidae.

RESULTS

Our results show that although our data set contains high phylogenetic variability with at least 53 species, the ontogenetic signal has the strongest influence on the morphospace of the group (Fig. 1). The largest difference is created by broad shields of the adults, partially with strong anterior-lateral protruding areas, on one side of the morphospace, and the slim shields of the megalopa with elongated rostrums on the other side.

DISCUSSION

Shield outlines of Carcinidae can be used to distinguish developmental stages, specifically between megalopae and adults, and to some degree also early crab stages. This provides a frame for identifying fossil representatives to distinct developmental stages. Currently estimating the developmental stages, in fossils is still challenging (Gerber, 2011). The ancestral state reconstruction indicates a plesiomorphic shape of shields with anterior-lateral slightly protruded regions (shield shape depicting negative PC2 values; Fig. 1).

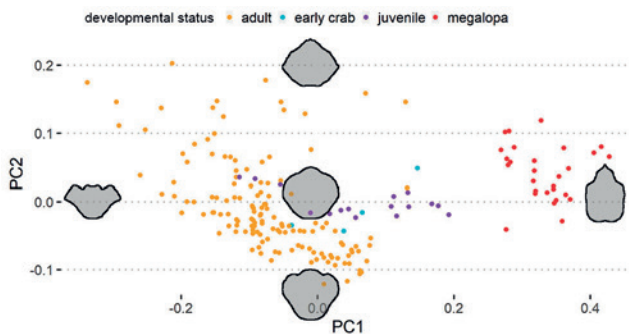


Figure 1. Principal component analysis of elliptic Fourier analyses on the shield outlines of Carcinidae. First and second principal component of the analyses plotted against each other, depicting 46.8% and 23.3% percent of variation respectively. Grey shapes depict graphical component loadings of the principal components.

Acknowledgments

We thank all providers of free software and Open-Access tools. We would like to thank Prof. J. M. Starck (LMU, Munich) for long-standing support. This study was funded by the German Research Foundation under DFG Ha 6300/3-3 and by the Volkswagen Foundation in the frame of a Lichtenberg professorship.

REFERENCES

- Evans, N. 2018. Molecular phylogenetics of swimming crabs (Portunoidea Rafinesque, 1815) supports a revised family-level classification and suggests a single derived origin of symbiotic taxa. *PeerJ*, 6, e4260.
- Gerber, S. 2011. Comparing the differential filling of morphospace and allometric space through time: the morphological and developmental dynamics of Early Jurassic ammonoids. *Palaeobiology*, 37 (3), 369-382.
- R Core Team 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Young, A.M. and Elliott, J.A. 2020. Life history and population dynamics of green crabs (*Carcinus maenas*). *Fishes*, 5 (1), 4.

EOCENE PATCH REEFS IN THE LESSINI MOUNTAINS (NE ITALY): AN ANCIENT BIODIVERSITY HOTSPOT

Alessandra Busulini¹, Claudio Beschin² and Giuliano Tessier¹

¹ Società Veneziana di Scienze Naturali, c/o Museo di Storia Naturale di Venezia Giancarlo Ligabue, Santa Croce 1730, 30135 Venezia, Italy. busulini@tin.it, giultess@virgilio.it

² Museo Civico "G. Zannato", Piazza Marconi 15, 36075 Montebelluna Maggiore (Vicenza), Italy. beschin.cl@libero.it

Keywords. Decapoda, Eocene, NE Italy, Patch reefs, Biodiversity

The first report on coral-associated crustaceans from Eocene rocks in Venetia (NE Italy) goes back to 2000 after the discovery of some non-stratified and strongly recrystallized limestone domes in the quarry at contrada Gecchelina (Monte di Malo - Vicenza) (Beschín *et al.*, 2000, 2007).

Until then the fossil crustaceans found in the same area had been preserved in rocks of different origin, above all laminated nummulitic or marly limestones and volcanoclastic sandstones.

The new fauna from contrada Gecchelina had shown immediately some peculiar features:

- » High paleodiversity.
- » Abundance of specimens of small size.
- » Abundance of species, many of which new, related with modern crustaceans specialized for living in coral reefs, first of all the Trapezioidea.
- » Few decapods conspecific with already known species in Eocene stratified rocks.

The existence of possible bioherms heterotopic with Ypresian strata had been previously reported only by De Zanche (1965) for the Chiampo valley between Mussolino and Zovo di Castelvecchio (Vicenza). After these first findings dating in the first decade of the XXI century, which can be considered fortuitous, the search of heterotopic bioconstructions within Eocene stratified layers became methodical and fruitful in the numerous quarries opened in the area but also in other outcrops. As a result, in the last twenty years of study authors have analyzed about 4500 specimens of fossil crustaceans found in Eocene organogenous builtups widespread in several sites in the Vicenza and Verona territories and more than 300 taxa have been recognized.

The Ypresian remains are particularly abundant and several bioconstructions have been found in places in the Alpone and in the Chiampo valleys (Bolca, Vestenanova, Altissimo, San Pietro Mussolino), in the Agno valley (Cornedo Vicentino, Valdagno), and in the area around Monte di Malo (Figs. 1A, B). About 3500 specimens have been found representing more than 200 species (Beschín *et al.*, 2016, 2017, 2021, 2022 in press). Evidences suggest a large shallow lagoon with widespread patch reefs as the most plausible palaeoenvironmental interpretation; there, amongst corals and together with crustaceans, also mollusks and echinoids, all of small size, have been found. Compared with the today lagoon of Belize, small domes of coral-algal origin had grown with a few dozen meters long diameter at a depth of few meters. The environment was relatively calm and sheltered by a true coral reef (Papazzoni *et al.*, 2014). The territory where Ypresian biohermal mounds have been found has an area of about 100 km².

Such a large number of specimens and taxa allow identifying an ancient biodiversity hotspot. This hypothesis is confirmed by the continuous findings of new species and the high value of the total Shannon-Weaver biodiversity index ($H' = 3.9$). There, decapods referred to five infraorders have been found: Caridea, Axiidea, Gebiidea, and above all Anomura and Brachyura. 40 species of Anomura within seven families have been recognized (the Galatheididae and the Diogenidae are the richest of species). The families within Brachyura are 39 (Fig. 1C).

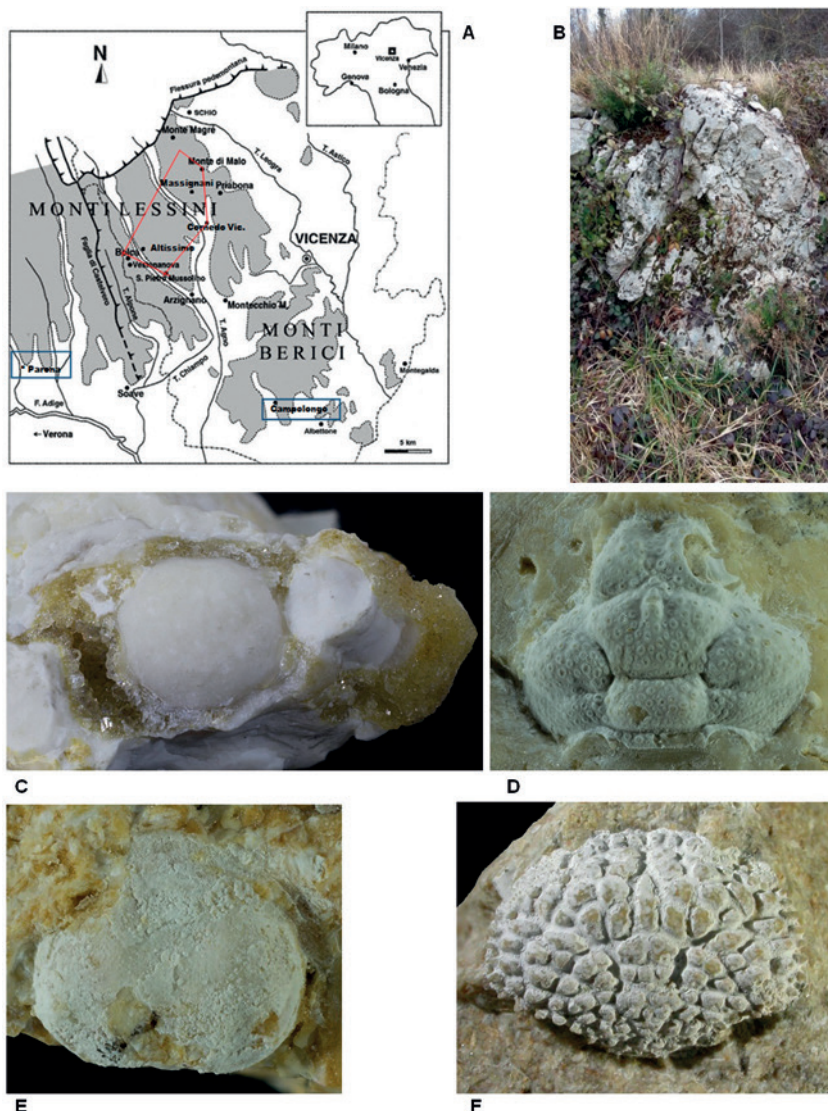


Figure 1. A. Map of the sites of the studied crustacean-bearing bioconstructions (the red perimeter bounds the Ypresian patch reef area). B. A coral-algal dome cropping out at Contrada Zerbatì (Altissimo - Vicenza). C. *Vicetitrapeziaex altissimo*, Ypresian, Altissimo (Vicenza); D. *Nachioides tuberculatus*, Priabonian, Parona (Verona). E. *?Polyonyx* sp., Priabonian, Parona (Verona); F. *Daira pseudovulgaris*, Priabonian, Campolongo di Val Lione (Vicenza).

More recently, similar structures but Priabonian in age have been discovered in the southern part of this territory and precisely at Parona (Verona) and at Campolongo di Val Lione (Berici Mountains – Vicenza) (Beschinet *et al.*, 2018, 2019) (Fig. 1A). The distance between these two sites is about 42.5 km and it testifies to the existence of a large lagoon during the Late Eocene, too. The specimens here found are fewer than one thousand with about 150 species. The Anomura are represented by 37 species within 7 families and the Brachyura by 33 families (Fig. 1D-F). The biodiversity index is even higher ($H' = 4.2$).



REFERENCES

- Beschin, C., Busulini, A., De Angeli, A., Tessier, G. and Ungaro, S. 2000. The fauna of the Gecchelina quarry at Monte di Malo (Vicenza - Northern Italy): a preliminary study. "1st Workshop on Mesozoic and Tertiary decapod crustaceans", *Studi e ricerche - Associazione Amici del Museo - Museo civico "G. Zannato", Montecchio Maggiore (Vicenza)*, 7-10.
- Beschin, C., Busulini, A., De Angeli, A. and Tessier, G. 2007. *I decapodi dell'Eocene inferiore di Contrada Gecchelina (Vicenza - Italia settentrionale) (Anomura e Brachyura)*. Museo di Archeologia e Scienze naturali "G. Zannato", Montecchio Maggiore (Vicenza), 76 pp.
- Beschin, C., Busulini, A., Tessier, G. and Zorzin, R. 2016. I crostacei associati a coralli nell'Eocene inferiore dell'area di Bolca (Verona e Vicenza, Italia nordorientale). *Memorie del Museo Civico di Storia Naturale di Verona - 2. serie. Sezione Scienze della Terra*, 9, 189 pp.
- Beschin, C., Busulini, A., Calvagno, M., Tessier, G. and Zorzin, R. 2017. Ypresian Decapod Crustacean faunas from the coral-algal environments in the Eastern Lessini Mountains (Vicenza and Verona territory - NE Italy): a comparative analysis. *Bulletin de la Société géologique de France*, 188, 13.
- Beschin C., Busulini A., Fornaciari, E., Papazzoni, C.A. and Tessier, G. 2018. La fauna di crostacei associati a coralli dell'Eocene superiore di Campolongo di Val Lione (Monti Berici, Vicenza, Italia nordorientale). *Bollettino del Museo di Storia Naturale di Venezia*, 69, 129-215.
- Beschin, C., Busulini, A., Tessier, G. and Zorzin, R. 2019. La fauna di crostacei dell'Eocene superiore di Parona di Verona (Italia nordorientale): nuovi ritrovamenti. *Bollettino del Museo di Storia Naturale di Venezia*, 70, 71-142.
- Beschin, C., Busulini, A. and Tessier, G. 2021. La fauna di crostacei associati a coralli nell'Eocene inferiore dell'Alta Valle del Chiampo (Altissimo - Vicenza - Italia nordorientale). *Lavori Società veneziana di Scienze naturali*, 46, 67-128.
- Beschin, C., Busulini, A. and Tessier, G. 2022. Decapodi associati a coralli dell'Eocene inferiore della Valle dell'Agno (Vicenza - Italia nordorientale) presenti nelle collezioni del Museo "G. Zannato" di Montecchio Maggiore (Vicenza). *Studi e Ricerche - Associazione Amici del Museo - Museo civico "G. Zannato", Montecchio Maggiore (Vicenza)*, (in press).
- De Zanche, V. 1965. Le microfacies eoceniche nella Valle del Chiampo tra Arzignano e Mussolino (Lessini orientali). *Rivista Italiana di Paleontologia e Stratigrafia*, 71, 925-948.
- Papazzoni, C.A., Vescogni, A., Bosellini, F., Giusberti, L., Roghi, G. and Dominici, S. 2014. First evidence of coral bioconstruction in the Monte Postale succession (Lower Eocene of Lessini Mts., Veneto, northern Italy). *Rendiconti Online della Società Geologica Italiana*, 31, 163-164.

FOSSIL DECAPOD CRUSTACEA IN THE HISTORICAL COLLECTIONS OF THE PARIS MUSEUM (1750-1880)

Sylvain Charbonnier¹ and Alessandro Garassino²

¹ Centre de Recherche en Paléontologie – Paris (CR2P, UMR 7207), CNRS, MNHN, Sorbonne Université, Muséum national d'Histoire naturelle, CP 38, 57 rue Cuvier, F-75005, Paris, France. sylvain.charbonnier@mnhn.fr

² Department of Earth and Biological Sciences, Loma Linda University, Loma Linda, CA 92350 and Department of Paleontology, North Carolina Museum of Natural Sciences, Raleigh, NC 27601, USA. alearassino@gmail.com

Keywords: Arthropoda, Crustacea, systematic palaeontology, type series, collections

Fossil crustaceans housed in the palaeontological collections at the Muséum national d'Histoire naturelle (MNHN, Paris, France) played a major role in the rise of a new discipline at the very beginning of the nineteenth century, namely palaeocarcinology. The undisputed pioneer of this discipline was Anselme-Gaëtan Desmarest (1784-1838), whose contributions were invaluable. He was followed by a considerable number of naturalists, who used and amplified his methods of describing and classifying extinct crustaceans. Among them, Alphonse Milne-Edwards (1835-1900) probably ranks amongst the most influential specialists in palaeocarcinology worldwide. The present contribution revises all the MNHN historical specimens that formed the basis of early palaeocarcinology and its subsequent development during the nineteenth century. In spite of their convoluted histories, some of these fossils are still extant. These are specimens that were collected between 1750 and 1880, a period encompassing the end of Enlightenment, the French Revolution, the First Empire and numerous political upheavals during the nineteenth century (Bourbon Restoration, July Monarchy, Second Republic, Second Empire and Third Republic). Thus, these specimens also saw the transition from the King's Cabinet to the new National Museum of Natural History, which was founded in 1793.

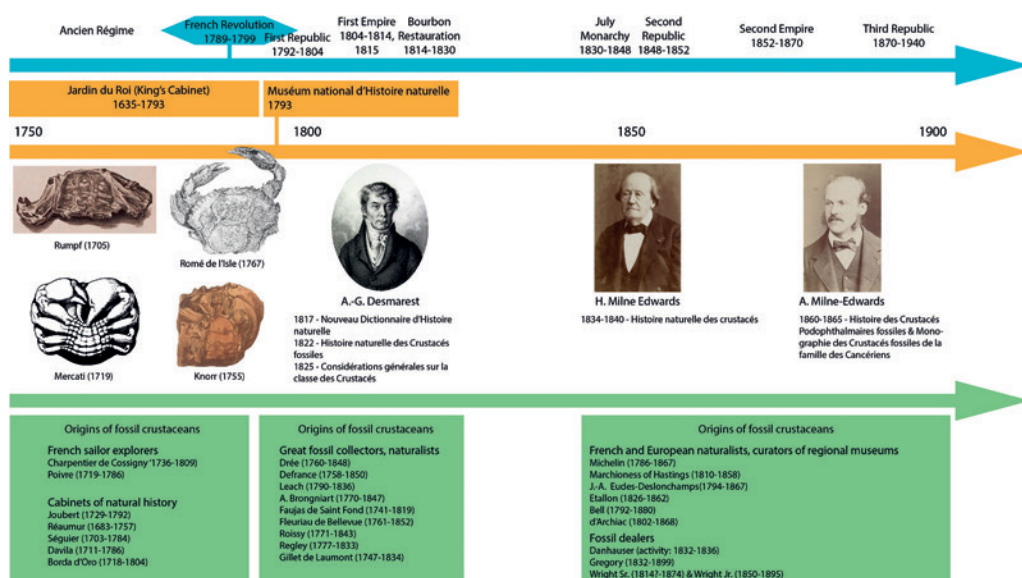


Figure 1. Timeline of the origin of the MNHN collections of fossil crustaceans and of the birth of palaeocarcinology in France.



Between 1817 and 1880, A.-G. Desmarest, H. Milne Edwards and A. Milne-Edwards formed and studied a collection of about 800 specimens of fossil crustaceans. Desmarest based his descriptions on specimens inherited from the Enlightenment and housed in the King's Cabinet, as well as on material in private cabinets of natural history. The oldest specimens were collected in the 1750s by explorers in eastern Asia, as well as in France by regional naturalists. In the 1860s, Alphonse Milne-Edwards considerably increased the collections, revised the taxa erected by Desmarest and proposed numerous new genera and species with an updated classification.

Here we present the main results of a monograph in press about the general review of 776 historical specimens that are included in the suborder Dendrobranchiata Rafinesque, 1815 (1 species), the infraorders Astacidea Latreille, 1802 (5 species), Glypheidea Winkler, 1881 (9 species, including a new one), Achelata Scholtz and Richter, 1995 (3 species), Anomura MacLeay, 1838 (7 species) and Brachyura Linnaeus, 1758 (69 species). Our main purpose is to describe and figure all of the surviving type specimens at MNHN (Paris). Therefore, the present study updates the old literature and revises 94 species that were described by A.-G. Desmarest, A. Milne-Edwards and their respective contemporaries. Moreover, it encompasses historical specimens collected by A. Milne-Edwards during his travels and those sent to him or to his father Henri Milne Edwards by different European palaeontologists and naturalists. Whenever possible, a historical review of the origin of the type material is also given, which enables a detailed account and understanding of the context of the original description. Our talk will also focus on extraordinary stories about some fossil crustaceans stored at MNHN, Paris.

THE ORIGIN OF DAIROIDID CRABS (DECAPODA, BRACHYURA, PARTHENOPOIDEA)

Fernando A. Ferratges¹, Javier Luque^{2,3}, José L. Domínguez⁴,
Àlex Ossó⁵, Marcos Aurell¹ and Samuel Zamora^{1,6}

¹ Departamento de Ciencias de la Tierra-IUCA, Universidad de Zaragoza, E-50009 Zaragoza, Spain. ferratges@unizar.es

² Museum of Comparative Zoology and Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, MA 02138, USA.

³ Department of Biological Sciences, Florida International University-Biscayne Bay Campus, North Miami, FL 33181, USA.

⁴ Padre Manjón, 12, 50010 Zaragoza, Spain.

⁵ Llorenç de Villalonga, 17B, 1r 1^a, 43007 Catalonia, Spain.

⁶ Instituto Geológico y Minero de España (IGME-CSIC), C/Manuel Lasala, 44, 9B, Zaragoza E-50006, Spain.

Keywords: fossil crabs, phylogeny, Eocene, Pyrenees, Iberian Peninsula

The origin of modern families of true crabs (Brachyura) and how they relate to each other is matter of ongoing discussion. Phylogenetic analyses based on molecular and morphological data offer a good opportunity to understand the relationships between different extant groups beyond the alpha taxonomy (Tsang *et al.*, 2008; Wolfe *et al.*, 2016; 2019; Luque *et al.*, 2019, 2021), while reliable fossils are crucial to calibrate molecular trees. However, there are few works that combine fossils and extant taxa in a phylogenetic context using different optimality criteria (Luque *et al.*, 2019, 2021).

Although brachyurans have a rich fossil record extending back into the early Jurassic, is during the Eocene that the oldest representatives of most extant families are first known (e.g. Schweitzer and 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. Nevertheless, many species, genera, and even families, are known only from isolated carapaces, and rarely with chelipeds associated with the body or ventral carapace (e.g., epistome, pterygostome, sternum and pleon). New material of *Phrynombrus* Bittner, 1893, found in the upper Eocene (Priabonian) of Huesca (Northern Spain), shows detailed anatomical

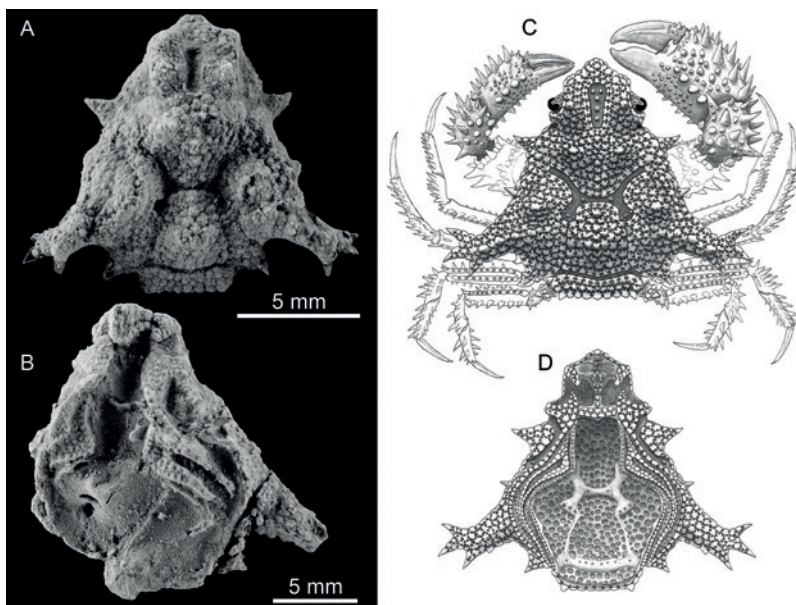


Figure 1. *Phrynombrus* sp. A. Specimen MPZ 2022/203 in dorsal view. B. Specimen MPZ 2022/204 in ventral view. C-D. Idealized reconstruction of *Phrynombrus* sp. based on the new material in dorsal (A) and ventral views (B) from the upper Eocene of Fanlillo (Huesca, Spain).

features including the dorsal regions, the orbits and rostrum, the ventral carapace, cuticular ornamentation, and chelipeds (Fig. 1). We assessed the anatomy of a well-preserved specimen of *Phrynoslambrus* via mechanical preparation and a CT-scan, which allowed the recognition of several diagnostic features useful for taxonomic and phylogenetic comparative purposes. This is the first record of this genus in the Iberian Peninsula, and the second report of Eocene Parthenopidae from Spain, expanding the palaeogeobiographic distribution of Paleogene parthenopids and our understanding of their early origins, anatomical diversity, and systematic affinities.

To clarify the systematic position of this enigmatic genus and its relationships with other true crabs, we performed phylogenetic analyses including 46 taxa from 13 brachyuran families and 113 morphological characters. Preliminary data suggest that *Phrynoslambrus* 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.

Acknowledgements

The present work has been supported by CGL2017-85038-P, funded by the Spanish Ministry of Science and Innovation, the European Regional Development Fund and Project E18 Aragossaurus: Recursos Geológicos y Paleoambientes of the government of Aragón-FEDER. The research of Fernando A. Ferratges is funded by an FPU Grant (FPU17/03623, of Spanish Ministry of Science and Innovation). Isabel Pérez provided photographic assistance.

REFERENCES

- Bittner, A. 1893. Decapoden des pannonischen Tertiärs. *Sitzungsberichte der kaiserlichen Akademie der Wissenschaften in Wien*, 102, 10–37.
- Luque, J., Feldmann, R. M., Vernygora, O., Schweitzer, C. E., Cameron, C. B., Kerr, K. A., Vega, F. J., Duque, A., Strange, M., Palmer, A. R. and Jaramillo, C. 2019. Exceptional preservation of mid-Cretaceous marine arthropods and the evolution of novel forms via heterochrony. *Science Advances*, v. 5(4), eaav3875.
- Luque, J., Schweitzer, C. E., Santana, W., Portell, R. W., Vega, F. J., and Klompmaker, A. A. 2017. Checklist of fossil decapod crustaceans from tropical America. Part I: Anomura and Brachyura. *Nauplius*, 25, e2017025.
- Luque, J., Xing L., Briggs, D.E., Clark, E.G., Duque A., Hui, J., Mai H. and McKellar R.C. 2021. Crab in amber reveals an early colonization of nonmarine environments during the Cretaceous, *Science Advances*, v. 7(43), eabj5689.
- Schweitzer, C.E. and Feldmann, R. M. 2015. Faunal turnover and niche stability in marine Decapoda in the Phanerozoic. *Journal of Crustacean Biology*, 35(5), 633–649.
- Stebbing, T. R. R. 1920. XXIII. The Malacostraca of Durban Bay. *Durban Museum Novitates*, 2(6), 263–278.
- Tsang, L. M., Schubart, C. D., Ahyong, S. T., Lai, J. C. Y., Au, E. Y. C., Chan, T.-Y., Ng, P. K. L. and Chu, K. H. 2014. Evolutionary history of true crabs (Crustacea: Decapoda: Brachyura) and the origin of freshwater crabs. *Molecular Biology and Evolution*, 31, 1173–1187.
- Wolfe, J. M., Breinholt, J. W., Crandall, K. A., Lemmon, A. R., Lemmon, E. M., Timm, L. E., Siddall, M.E. and Bracken-Grissom, H. D. 2019. A phylogenomic framework, evolutionary timeline and genomic resources for comparative studies of decapod crustaceans. *Proceedings of the Royal Society B*, 286(1901), 20190079.
- Wolfe, J. M., Daley, A. C., Legg, D. A. and Edgecombe, G. D. 2016. Fossil calibrations for the arthropod Tree of Life. *Earth-Science Reviews*, 160, 43–110.

NOVEL DATA ON HERMIT CRABS AND FURTHER PHYLOGENETIC REFINEMENTS FOR THE PAGUROIDEA (CRUSTACEA, ANOMURA)

René H.B. Fraaije¹, John W.M. Jagt², Barry W.M. van Bakel¹ and Jonathan J.W. Wallaard¹

¹ Oertijdmuseum, Bosscheweg 80, 5283 WB Boxtel, the Netherlands. info@oertijdmuseum.nl, curator@oertijdmuseum.nl, barryvanbakel@gmail.com

² Natuurhistorisch Museum Maastricht, De Bosquetplein 6-7, 6211 KJ Maastricht, the Netherlands. john.jagt@maastricht.nl

Keywords: Paguroidea, phylogeny, carapace morphology, isochely, heterochely

During the last two decades, fairly large numbers of carapaces or shields of extinct hermit crabs have become available for study and description (e.g., Fraaije *et al.*, 2019, 2020). Morphological features of these carapaces and shields, not previously used by neontologists, form the basis for phylogenetic refinements for paguroids in order to unravel patterns of their evolution through geological time.

In our ongoing studies of both extinct and extant hermit crabs (Paguroidea Latreille, 1802), we have noted a number of morphological changes that have occurred between the Early Jurassic (c. 185 million years ago) and the present day. For instance, there was a predominance of paguroids with cylindrical carapaces in reef-related settings during the Late Jurassic (Oxfordian, Kimmeridgian), but these were gradually replaced by taxa with non-cylindrical carapaces. The most basal paguroids possess a branchial groove, but subsequently branchial condensation

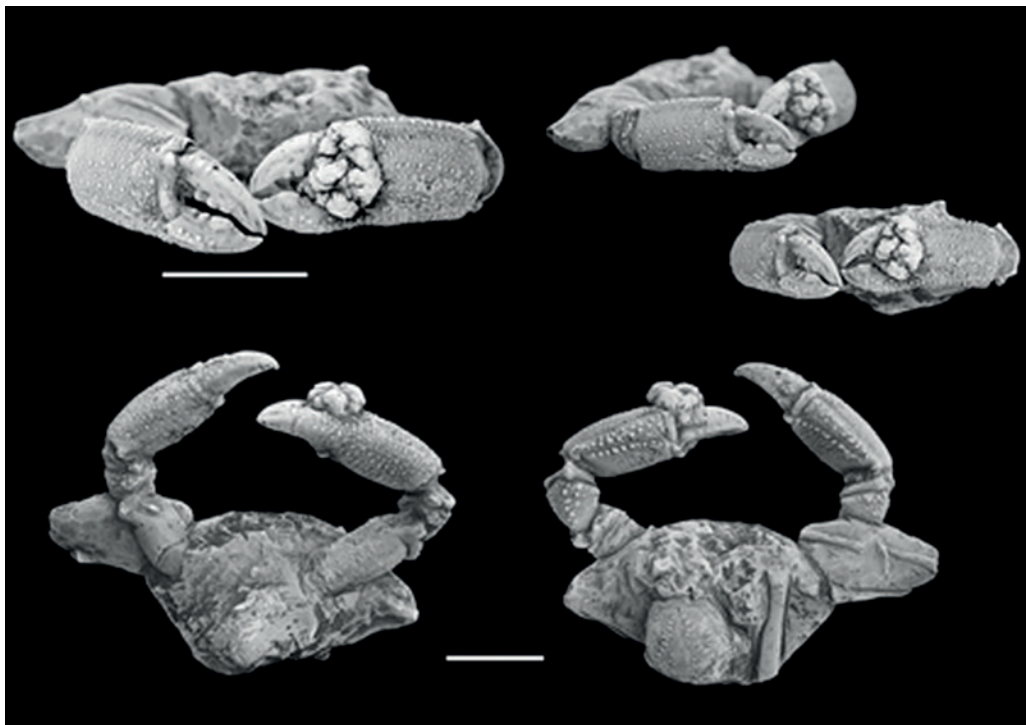


Figure 1. Isochelous chelipeds in *Schobertella simonsenetlangi* Schweigert, Fraaije, Havlik and Nützel, 2013 (SMNS 70555, Staatliches Museum für Naturkunde, Stuttgart, Germany), from the Lower Jurassic (upper Pliensbachian) Amaltheenton Formation of Iggingen near Aalen, southwest Germany (Schweigert *et al.*, 2013). Scale bars equal 10 mm.

towards a single (i.e., cervical) groove took place early in their evolutionary history. In several extant genera, remnants of a branchial groove, in combination with several other basal features, may be observed. These taxa are here considered to constitute the most primitive members amongst extant hermit crabs.

All Early and Middle Jurassic pairs (i.e., right and left) of paguroid chelipeds known to date – one from the Lower Jurassic (Pliensbachian) of Germany, two from the Middle Jurassic (Callovian) of France and a single coeval specimen from Romania) appear to be isochelous (see Fig. 1). The earliest known example of clearly heterochelous chelipeds in the fossil record of hermit crabs originates from upper Kimmeridgian/Tithonian (Upper Jurassic) strata of the Boulonnais region in northwest France. The occurrence of isochelous chelipeds in Lower and Middle Jurassic deposits, combined with the abundance of symmetrical calcified tergites (sixth abdominal tergites) in late Jurassic paguroid faunas (Fraaije *et al.*, 2012, 2013, 2014), provides strong support for a symmetrical ancestry of the Paguroidea.

A phylogenetic scheme of marine hermit crabs, as based on morphological data of paguroid carapaces and shields, is here presented for fourteen families. It is our hope that our current palaeontology-based reconstruction of paguroid phylogeny may prove beneficial to future biological studies of this group of decapod crustaceans. We think that our data may well form the basis for additional studies, in combination with both genetic and molecular techniques.

Acknowledgements

We thank Guenter Schweigert, Staatliches Museum für Naturkunde Stuttgart, Germany for making the figured paguroid specimen below available for study.

REFERENCES

- Fraaije, R.H.B., Krzemiński, W., Van Bakel, B.W.M., Krzemińska, E. and Jagt, J.W.M., 2012. The sixth abdominal tergites of paguroid anomurans – a newly recognized crustacean macrofossil type. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 266, 115–122.
- Fraaije, R.H.B., Artal, P., Van Bakel, B.W.M., Jagt, J.W.M. and Klompmaier, A.A., 2013. An array of sixth abdominal tergite types of paguroid anomurans (Crustacea) from the mid-Cretaceous of Navarra, northern Spain. In: Mulder, E.W.A., Jagt, J.W.M. and Schulp, A.S. (eds). *The Sunday's child of Dutch earth sciences – a tribute to Bert Boekschoten on the occasion of his 80th birthday. Netherlands Journal of Geosciences*, 92 (2/3), 109–117.
- Fraaije, R.H.B., Krzemiński, W., Van Bakel, B.W.M., Krzemińska, E. and Jagt, J.W.M., 2014. A new type of pylochelid sixth abdominal tergite (Anomura, Paguroidea) from the Upper Jurassic of Poland. In: Fraaije, R.H.B., Hyžný, M., Jagt, J.W.M., Krobicki, M. and Van Bakel, B.W.M. (eds), *Proceedings of the 5th Symposium on Mesozoic and Cenozoic decapod crustaceans, Krakow [sic], Poland, 2013: a tribute to Pál Mihály Müller. Scripta Geologica*, 147, 21–25.
- Fraaije, R.H.B., Robins, C., Van Bakel, B.W.M., Jagt, J.W.M. and Bachmayer, F., 2019. Paguroid anomurans from the Tithonian Ernstbrunn Limestone, Austria – the most diverse extinct paguroid assemblage on record. *Annalen des Naturhistorischen Museums Wien*, 121, 257–289.
- Fraaije, R.H.B., Van Bakel, B.W.M., Jagt, J.W.M. and Skupien, P., 2020. Paguroid anomurans from the upper Tithonian-lower Berriasian of Štramperk, Moravia (Czech Republic). *Geologija*, 63 (1), 7–16.
- Schweigert, G., Fraaije, R.H.B., Havlik, P. and Nützel, A., 2013. New Early Jurassic hermit crabs from Germany and France. *Journal of Crustacean Biology*, 33, 802–817.

PRELIMINARY NOTES ON MESOZOIC AND CENOZOIC HERMIT CRABS (CRUSTACEA, ANOMURA, PAGUROIDEA) FROM EUROPE AND THE UNITED STATES

René H.B. Fraaije¹, Jonathan J.W. Wallaard¹, John W.M. Jagt²,
Barry W.M. van Bakel¹ and Michał Krobicki³

¹ Oertijdmuseum, Bosscheweg 80, 5283 WB Boxtel, the Netherlands. info@oertijdmuseum.nl, curator@oertijdmuseum.nl, barryvanbakel@gmail.com

² Natuurhistorisch Museum Maastricht, de Bosquetplein 6-7, 6211 KJ Maastricht, the Netherlands. john.jagt@maastricht.nl

³ Department of General Geology and Geotourism; Faculty of Geology, Geophysics and Environmental Protection, AGH University of Science and Technology, Mickiewicza 30, 30-059 Kraków, Poland. krobicki@agh.edu.pl

Keywords: Paguroidea, carapaces, tergites, *in-situ* preservation, taxonomy, Oxfordian, Miocene

In recent years, a new paguroid assemblage has been recovered from Oxfordian (Upper Jurassic) strata at a small, disused quarry in the forested valley close to the village of Szklary, close to the motorway from Kraków to Katowice in southern Poland (Fig. 1). Deposits sampled here are part of the Late Jurassic sponge buildups of the peri-Tethyan epicontinental sea, documenting the so-called sponge megafacies across Europe, extending from Portugal in the west to Romania in the east. These deposits have been interpreted as sponge-bearing (cyanobacteria/sponge) buildups or reefs that formed as inter- and/or peri-biohermal structures on a deep-neritic sea floor (Krobicki, 1994, 2014; Krobicki and Zatoń, 2008).

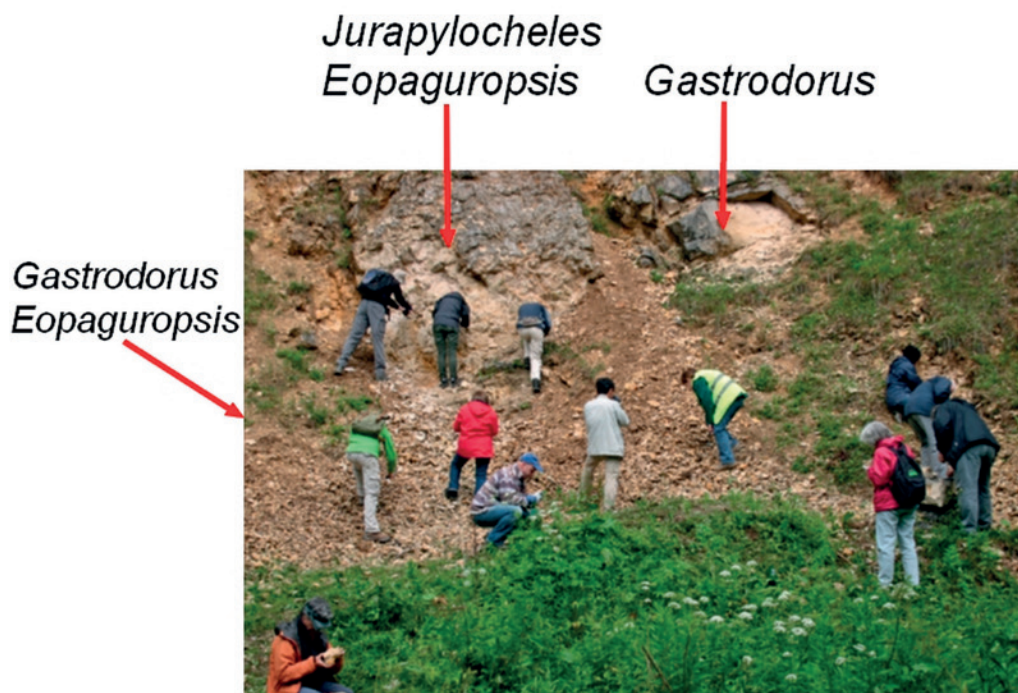


Figure 1. A small, disused quarry in the forested valley close to the village of Szklary, southern Poland. Photograph taken during a fieldtrip (June 26, 2013) of the 5th Symposium on Mesozoic and Cenozoic decapod crustaceans at Kraków, Poland. This locality has provided the oldest most diverse paguroid fauna known to date (Fraaije *et al.*, in prep.).

The Szklarka assemblage comprises carapaces of representatives of the families Gastrodoridae, Paguropsidae, Parapylochelidae, Pylochelidae and Schobertellidae. The presence of a new species of *Daciapagurus* extends the known stratigraphical and palaeogeographical ranges of this genus considerably. In addition, a novel, markedly ornamented symmetrical paguroid tergite confirms the abundance of pylochelids during the early evolutionary stages of the Paguroidea. With eight carapace-based genera present, the Szklarka faunule constitutes the oldest, most diverse paguroid assemblage from the fossil record to date (Fraaije *et al.*, in prep.).

In a parallel study, two newly collected hermit crabs, preserved inside their gastropod host shells, from Maryland (Atlantic Coast, USA), are examined. A new species of *Pagurus* is recorded from the lower to middle Miocene Calvert Formation; this is preserved within a shell of the gastropod *Buccinofusus parilis* Conrad, 1932 (see Vokes *et al.*, 2000). In addition, we have a new species of *Paguristes* preserved within the shell of the gastropod *Siphonalia* sp., from the upper Miocene St. Marys Formation. Both taxa are morphologically close to extant species and are welcome additions to the limited number of fossil hermit crabs that are preserved within their molluscan host shells (Wallaard *et al.*, in prep.).

These new faunules furnish important new data to our understanding of paguroid evolution and palaeogeography on both sides of the Atlantic Ocean.

Acknowledgements

We thank Dr Adiël A. Klompmaker (Curator of Paleontology, University of Alabama, USA) for making important paguroid specimens from Szklarka available for study.

REFERENCES

- Fraaije, R.H.B., Krzemiński, W., Van Bakel, B.W.M., Krzemińska, E. and Jagt, J.W.M., 2012. The sixth abdominal tergites of paguroid anomurans – a newly recognized crustacean macrofossil type. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 266, 115–122.
- Krobicki, M., 1994. Decapod Crustacea in the Oxfordian limestones in the vicinity of Cracow. In: *3rd International Meeting of IGCP N° 43, Excursion Guidebook*, 52.
- Krobicki, M., 2014. The 5th Symposium on Mesozoic and Cenozoic decapod crustaceans, Kraków/Poland, 24–27 June 2013; a brief report. In: Fraaije, R.H.B., Hyžný, M., Jagt, J.W.M., Krobicki, M. and Van Bakel, B.W.M. (eds). *Proceedings of the 5th Symposium on Mesozoic and Cenozoic decapod crustaceans, Krakow [sic], Poland, 2013: a tribute to Pál Mihály Müller. Scripta Geologica*, 147, 5–8.
- Krobicki, M. and Zatoń, M., 2008. Middle and Late Jurassic roots of brachyuran crabs: palaeoenvironmental distribution during their early evolution. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 263, 30–43.
- Vokes, H.E., Glaser, J.D. and Conkwright, R.D., 2000. Miocene fossils of Maryland (2nd Edition). *Maryland Geological Survey Bulletin*, 20, 1–80.

DECAPOD-BEARING CARBONATE CONCRETIONS FROM A LOWER APTIAN SILICICLASTIC PLATFORM (E SPAIN)

Álvaro García-Penas¹, Fernando A. Ferratges¹, Samuel Zamora² and Marcos Aurell¹

¹ Departamento de Ciencias de la Tierra-IUCA, Universidad de Zaragoza, 50009 Zaragoza, Spain.

² Instituto Geológico y Minero de España (IGME-CSIC), C/Manuel Lasala, 44, 9B, Zaragoza E-50006, Spain.

Keywords: fossorial, diagenesis, concretions, Iberian Peninsula

INTRODUCTION

The glypheid lobster *Atherfieldastacus magnus* is the dominant decapod taxon in the lower Aptian Forcall Formation of the Oliete subbasin (Maestrazgo Basin, E Spain) with individuals commonly occurring isolated or inside calcareous nodules and, occasionally, associated to burrows. A locality with an exceptionally high concentration of lobster-bearing nodules, reported originally in Ferratges *et al.* (2021), has been resampled (Fig. 1A, B). Carbonate nodules recovered from two different levels contain individuals of *Atherfieldastacus magnus* in varying states of preservation. The aim of this study is to offer a preliminary taphonomic interpretation of these decapod-bearing nodules, with special focus on assessing the possible association between nodules and non-preserved burrow systems.

GEOLOGICAL SETTING

The Forcall Formation is a decametric terrigenous unit dominated by silts and marls with frequent sandstone and sandy limestone intercalations, which contain ammonites of the early Aptian *Deshayesites forbesi* biozone. It forms an asymmetric transgressive-regressive cycle, with a short transgressive interval, and a long regressive stage representing the gradual transition from a relatively distal siliciclastic platform to lower shoreface environments. The studied material has been recovered from two red-stained silty mudstone levels containing abundant calcareous nodules (Fig.1B). The predominance of thick marl and silt intervals around the sampled levels, and the presence of other scarce thin levels of silty mudstones and wackestones without evidence of wave or current action, suggests deposition in relatively distal and deep platform domains located below storm-wave base level.

MATERIAL AND METHODS

Sixty four nodules have been recovered from the studied location, of which only 31 contain lobsters. Isolated non-fossiliferous gallery fragments have been recovered from the same levels. The preservation status of the fossil material has been assessed following the classification of Hyžný and Klompmaker (2015). The possibility of association between nodules and non-preserved burrow systems has been evaluated following the criteria compiled in Andrada *et al.* (2020).

RESULTS

Non-fossiliferous nodules are irregular to subspherical with occasional small protuberances. They present an undifferentiated mudstone texture, with occasional concentric color banding. Fossiliferous nodules (n=31) are predominantly oblate and kidney-shaped, with a smooth surface. They present a smooth interior with no textural variation, but occasional concentric color banding. The recovered gallery fragments exhibit the same internal homogeneous micritic composition and structure as the nodules.

Most fossiliferous nodules (n=30) contain a single lobster specimen (whole or fragmented), and only one nodule containing two individuals was found. Most specimens (48%) are isolated carapaces with varying preservation of the pereopods. 29% of specimens are well-preserved,

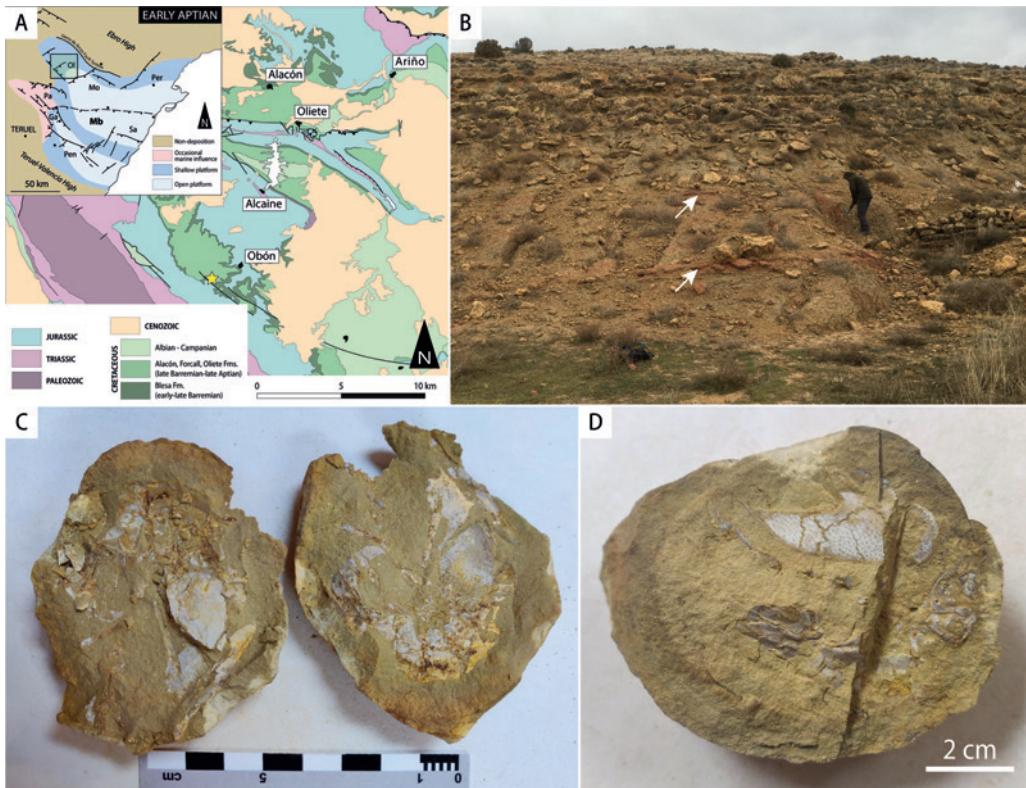


Figure 1. A. Location of the Oliete subbasin (Ob) in the Maestrazgo Basin (Mb). The present eastern coastline of the Iberian Peninsula is represented for reference. A green square indicates the area represented in the detailed geological map. A yellow star indicates the location of the studied outcrop. B. Outcrop of the upper Forcall Formation, showing the two reddish levels sampled for this study (white arrows). C. Completely articulated specimen of *Atherfieldastacus magnus*, interpreted as a corpse. D. Specimen showing disarticulation of the cephalothorax and pleon, interpreted as an exuvia.

with complete articulation of the cephalothorax and pleon (Fig. 1C), and preserving most pereiopods. 23% of specimens, presenting the cephalothorax disarticulated and laterally displaced from the pleon, have been interpreted as exuviae (Fig. 1D). Isolated pleon and cephalothorax fragments represent 6,5% of the total specimens.

Most specimens (77%) appear near the center of concretions and only some (23%) appear in a marginal position. None of the nodules are directly associated with galleries. 4 of the fossiliferous nodules (13%) are incomplete, exposing elements of the lobsters.

DISCUSSION

Although some nodules present protuberances, which some authors interpret as connections with branching non-preserved galleries, most of them are subspherical to oblate, which is regarded as negative evidence of connection with gallery networks. Furthermore, most of the lobster individuals appear in the center of nodules, and there appears to be no correlation between types of preservation, nodule shape and position of the individuals. Thus, it is unclear if there is any association between lobster-bearing nodules, the recovered gallery fragments, and other speculative, non-preserved, gallery networks.

The genesis of organism-bearing nodules has been widely discussed in scientific literature, and is commonly attributed to biological or early diagenetic precipitation of minerals around decaying carcasses (e.g. Feldmann *et al.*, 2013; Plet *et al.*, 2016). In the case of the decapod-bearing concretions of the Forcall Formation, further geochemical analysis would be required to shed light on the processes driving nodulization, as no inferences can be made from direct or microscopic observation due to textural and compositional homogeneity. However, 52% of individuals are preserved whole (including whole lobsters and exuviae), and another 48% are isolated carapaces preserving articulated pereopods. These features imply little to no postmortem transport, followed by rapid burial and possibly early diagenetic nodulization, which preserved the remains before scavenging organisms could disarticulate them. Incomplete nodules with exposed body parts may indicate episodes of disturbance (e.g. exhumation).

REFERENCES

- Andrada, A.M., Bressan, G.S. and Lazo, D. G. 2020. Taphonomy of decapod-bearing concretions and their associated trace fossils from the Agrio Formation (Lower Cretaceous, Neuquén basin), with paleobiological implications for axiid shrimps. *Revista de La Asociacion Geologica Argentina*, 77(3), 366–383.
- Feldmann, R.M., Frantescu, A., Frantescu, O.D., Klompmaker, A.A., Logan, G., Robins, C.M., Schweitzer, C.E. and Waugh, D. A. 2013. Formation of lobster-bearing concretions in the Late Cretaceous Bearpaw shale, Montana, United States, in a complex geochemical environment. *Palaios*, 27(12), 842–856. <https://doi.org/10.2110/palo.2012.p12-035r>
- Ferratges, F.A., Hyžný, M., and Zamora, S. 2021. Taphonomy and systematics of decapod crustaceans from the Aptian (Lower Cretaceous) in the Oliete Sub-basin (Teruel , Spain). *Cretaceous Research*, 122. <https://doi.org/10.1016/j.cretres.2021.104767>
- Hyžný, M. and Klompmaker, A.A. 2015. Systematics, phylogeny, and taphonomy of ghost shrimps (Decapoda): A perspective from the fossil record. *Arthropod Systematics and Phylogeny*, 73(3), 401–437.
- Plet, C., Grice, K., Pagès, A., Ruebsam, W., Coolen, M.J.L. and Schwark, L. 2016. Microbially-mediated fossil-bearing carbonate concretions and their significance for palaeoenvironmental reconstructions: A multi-proxy organic and inorganic geochemical appraisal. *Chemical Geology*, 426, 95–108. <https://doi.org/10.1016/j.chemgeo.2016.01.026>

PRELIMINARY REPORT ON DECAPOD CRUSTACEAN FOSSIL RECORD FROM SOUTH-EASTERN EUROPEAN COUNTRIES

Rok Gašparič¹, Gordana Jovanović², Vlasta Čosović³, Sejfidin Vrabac⁴ and Goran Glamuzina⁵

¹ Oertijdmuseum De Groene Poort, Bosscheweg 80, NL-5283 WB Boxtel, Netherlands. rok.gasparic@gmail.com

² Natural History Museum, Njegoševa 51, SRB-11000 Belgrade, Serbia. gordana.j@nhmbeo.rs

³ Faculty of Science, Department of Geology, Horvatovac 102a, HR-10000 Zagreb, Croatia. vcosovic@geol.pmf.hr

⁴ Faculty of Mining, Geology and Civil Engineering, Univerzitetska 2, BA-75000 Tuzla, Bosnia and Herzegovina. sejfidin.vrabac@untz.ba

⁵ Herag P.I., Blidinjska 1, BA-88240 Posušje, Bosnia and Herzegovina. glam_goran@yahoo.com

Keywords: Croatia, Bosnia and Herzegovina, Serbia, Decapoda, palaeobiodiversity

Even though crustaceans play an important role in all marine ecosystems, the fossil record of decapod crabs is modest. Fossil remains of decapods received less attention within the paleontological sciences due to their lower biostratigraphic significance compared to other crustaceans like ostracods, or several other invertebrate groups. However, from the 1970s onwards, there is an increased interest in this group, and the remarkable rise in palaeontological activities in the study of decapod fossils has now been ongoing since the 1990s. Taxonomic revisions of individual fossil taxa in recent years have been followed by new interpretations regarding their evolution and phylogeny.

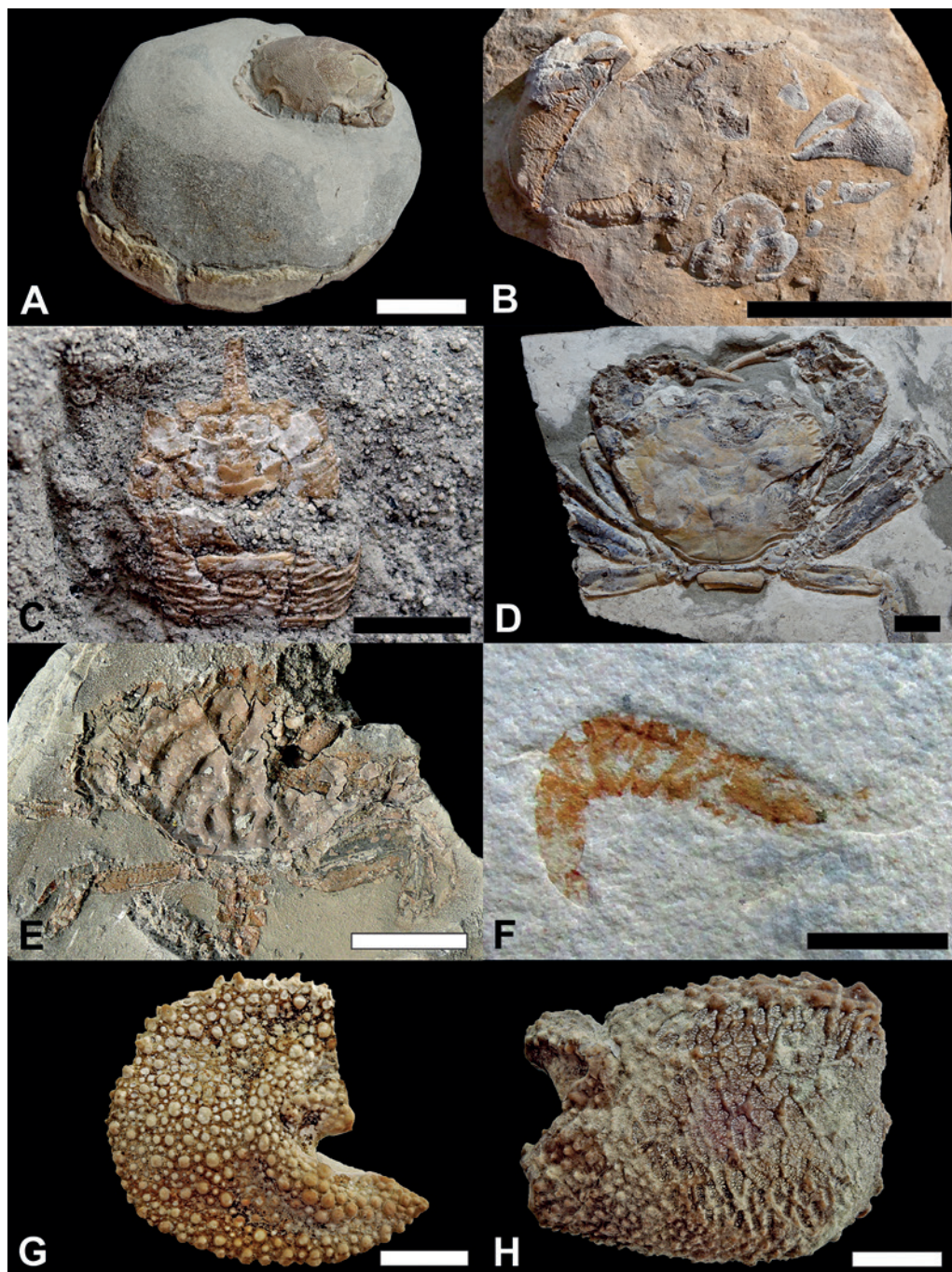
Looking at the decapod fossil record in Europe, it is clear that research has been focused on western European countries with a long history in natural sciences and palaeontology, a larger number of institutional repositories, and established decapod specialists among their palaeontologists (e.g., in France, Spain, Italy, Germany, Austria, Hungary). Work on fossil decapod crustaceans from several Eastern European countries (e.g., Poland, the Czech Republic, Romania) has intensified in the beginning of the 21st century, but the fossil record from South-Eastern Europe (SEE) and the Balkans (mostly countries from former Yugoslavia, i.e. Slovenia, Croatia, Bosnia and Herzegovina, Serbia, North Macedonia, and Montenegro) remains poorly understood.

As was demonstrated for Slovenia (Gašparič *et al.*, 2019a), it is likely that the decapod fossil record from these SEE countries is severely underestimated. A systematic overview of repositories and intensive fieldwork in the past decade has significantly expanded our knowledge of fossil decapod crustaceans from Slovenia. Here, on top of the 96 specimens belonging to 17 different species recorded previously, as much as 1,507 specimens were newly collected, and an additional 64 new taxa of fossil decapods were identified. Additionally, 15 new species, three new genera, and one new family of fossil crabs were newly erected in scientific papers. The palaeobiodiversity of decapods in Slovenia was thus proved to be on a similar level to countries like Austria and Hungary, i.e. countries with a continuity of research in fossil decapods.

Fossil remains of decapods in SEE countries are often overlooked and have not received sufficient scientific attention in the past. Only in the past decade several papers have dealt with specimens of fossil decapods from Croatia (Mikuž, 2002, 2003, 2010a, 2010b, 2011, 2015; Schweitzer *et al.*, 2005; Gašparič *et al.*, 2015, 2016) and Bosnia and Herzegovina (Hyzny, 2019; Gašparič *et al.*, 2019b), however, the bulk of scientific work on the material from this region is still waiting to

Figure 1. Representative decapod crustaceans from SEE countries. A. *Harpactoxanthopsis quadrilobatus* within a test of *Conoclypus conoideus*, Middle Eocene, Roč, Croatia. B. *Harpactoxanthopsis quadrilobatus*, Eocene, Mostar, Bosnia and Herzegovina. C. *Munidopsis salinaria*, Middle Miocene, Tuzla, Bosnia and Herzegovina. D. *Potamon* sp., Middle Miocene, Gračanica, Bosnia and Herzegovina. E. Cancridae gen. et sp. indet., Middle Miocene, Višnjica, Serbia. F. Penaeidae gen. et sp. indet., Late Cretaceous, Neum, Bosnia and Herzegovina. G. *Lessinipagurus vasjamikuzi*, Eocene, Gračišće, Croatia. H. Paguroidea gen. et sp. indet., Eocene, Krk, Croatia. Scale bar in A and B is 50 mm, in C and G is 5 mm, and scale bar in others is 10 mm.

be analysed. As we recognized in Slovenia, it is easier to collect fossil decapods than to invest the time necessary to describe them. Crustaceans represent interesting and sought-after fossil specimens, therefore museums and private collections are likely housing a lot of material that remains unpublished. An additional barrier is also the decline of active taxonomist working on fossil invertebrates, not limited only to specialists in fossil decapods.





The planned work in SEE countries will attempt to provide an overview of the quantity and diversity of Cenozoic and Mesozoic decapod crustaceans from this region by visiting regional institutions, working together with local specialists, and raise awareness of possibilities of decapod fossil record in their countries. The aim is to compile a list of fossil material collected by previous authors and new specimens collected in the past decades, which are kept in institutional as well as private collections. Guest lectures will be used to promote palaeocarcinology and to encourage new taxonomist by introducing them to the latest developments in the field. Hands on presentations work best, as decapods crustaceans are among the most attractive invertebrate fossils.

SEE countries represent an untapped resource for new scientific research on fossil decapod crustaceans. With diverse stratigraphic successions and plenitude of available exposed Cenozoic and Mesozoic strata in Croatia, Bosnia and Herzegovina, Serbia, North Macedonia, and Montenegro we can expect a similar level of diversity of fossil decapod communities there as well.

REFERENCES

- Gašparič, R., Fraaije, R.H.B., Van Bakel, B.W.M., Jagt, J.W.M. and Skupien, P. 2015. Mesozoic Cenozoic crustaceans preserved within echinoid tests and bivalve shells. *Bulletin of Geosciences*, 90(3), 601-611.
- Gašparič, R., Fraaije, R.H.B., Robin, N. and De Angeli, A. 2016. The first record of paguroids from the Eocene of Istria (Croatia) and further phylogenetic refinement of the Paguroidea (Crustacea, Anomura). *Bulletin of Geosciences*, 91(3), 467-480.
- Gašparič, R., Gale, L. and Križnar, M. 2019. Repositories of fossil decapod crustaceans in Slovenia - an overview of institutional and private collections. *7th Symposium on Mesozoic and Cenozoic Decapod Crustaceans*, Book of Abstracts, 57-60, Ljubljana, Slovenia.
- Gašparič, R., Hyžný, M., Jovanović, G., Ćorić, S. and Vrabac, S. 2019. Middle Miocene decapod crustacean assemblage from the Tuzla Basin (Tušanj, Bosnia and Herzegovina), with a description of two new species and comparison with coeval faunas from Slovenia. *Palaeontologia Electronica*, 22(1), 9A 1-21.
- Hyžný, M. 2019. A freshwater crab *Potamon* (Brachyura: Potamidae) from the middle Miocene Lake Bugojno (Gračanica, Bosnia and Herzegovina), with notes on potamid taphonomy. *Palaeobiodiversity and Palaeoenvironments*, 100, 577-583.
- Mikuž, V. 2002. New finding of crab *Harpactoxanthopsis quadrilobata* (Desmarest) in the Eocene flysch at Gračišće near Pazin in Istria (Croatia). *Geologija*, 45, 97-102.
- Mikuž, V. 2003. *Lophoranina marestiana* from Middle Eocene flysch beds at Gračišće in Istria, Croatia. *Geologija*, 47, 23-27.
- Mikuž, V. 2010a. *Lophoranina* from Eocene beds in central Istria, Croatia. *Geologija*, 53, 47-54.
- Mikuž, V. 2010b. *Cyrtorhina globosa* from Middle Eocene beds of Ćopi in Istria, Croatia. *Geologija*, 53 (2), 165-168.
- Mikuž, V. 2011. Eocene crab from Ćopi in central Istria, Croatia. *Folia biologica et geologica*, 52 (3), 23-28.
- Mikuž, V. 2015. Some new finds of Eocene crabs from Ćopi in Istria, Croatia. *Geologija*, 58 (1), 63-70.
- Schweitzer, C.E., Ćosović, V. and Feldmann, R.M. 2005. *Harpactocarcinus* from the Eocene of Istria, Croatia, and the paleoecology of the Zanthopsidae Via, 1959 (Crustacea: Decapoda: Brachyura). *Journal of Paleontology*, 79, 663-669.



TAXONOMY OF LATE JURASSIC (OXFORDIAN) DECAPOD CRUSTACEANS FROM KRAKÓW- WIELUŃ UPLAND (SOUTHERN POLAND)

Adam Heteš¹ and Matuš Hyžný¹

¹ Department of Geology and Palaeontology, Faculty of Natural Sciences, Comenius University, Bratislava, Slovakia. adamhetes@gmail.com, email: hyzny.matus@gmail.com

Keywords: Anomura, Axiidea, Brachyura, sponge megafacies, semiquantitative analysis, dominance

The knowledge of Upper Jurassic decapod crustaceans from southern Poland has increased during the last decade, with published studies focusing on Anomura (Fraaije et al., 2012; 2014; Krzemińska et al., 2015) and Brachyura (Krzemińska, 2021; Starzyk, 2015; 2016). In 2012 the Department of Geology and Palaeontology (Faculty of Natural Sciences, Comenius University, Bratislava) conducted field research in the Kraków-Wieluń Upland (southern Poland; NW of Kraków). A rich collection of decapod crustaceans was acquired from eight localities, including Bobrowniki, Lisowice, Młynka, Niegowonice, Ogrodzieniec, Sobków, Wysoka, and Zawodzie. Oxfordian strata of sponge megafacies are exposed at these localities representing the sediments of the northern margin of the Tethys Ocean (Collins and Wierzbowski, 1985; Matyszkiewicz, 1997). The largest amount of complete or almost complete individuals comes from Lisowice and Ogrodzieniec; the most undeterminable specimens occur in Niegowonice. Additionally the material was collected directly from the strata (which has not been reported previously), thus offering new possibilities of further study.

The studied material consists of more than 350 specimens of decapod crustaceans (Fig.1) of which 47 % represent complete or almost complete dorsal carapaces belonging to 23 species of axiideans (*Magila*), anomurans (*Ammopylocheles*, *Eopaguropsis*, *Gastrodorus*), and brachyurans (*Abyssopthalmus*, *Bucculentum*, *Eodromites*, *Gabriella*, *Goniodromites*, *Planoprosopon*, *Tanidromites*). The rest of the collection consists of isolated cheliped, propodi and undeterminable carapace fragments.

The material was analysed semiquantitatively resulting into an assessment of dominant decapod genera which differ among the studied localities. At Lisowice, the sample of 78 specimens was dominated by *Goniodromites* (n=30) and *Gastrodorus* (n=21); at Niegowonice, the sample of 32 specimens was dominated by *Tanidromites* (n=15) and *Goniodromites* (n=7); at Ogrodzieniec, the sample of 40 specimens was dominated by *Goniodromites* (n=28) and *Tanidromites* (n=8). Localities Bobrowniki, Młynka, Sobków, Wysoka, and Zawodzie yielded much less specimens hindering the assessment of dominant taxa.

Acknowledgements

The research was supported by VEGA 02/0136/15 and the Slovak Research and Development Agency under contracts no. APVV-17-0555 and APVV-20-0079.

REFERENCES

- Collins, J.S.H. and Wierzbowski, A. 1985. Crabs from the Oxfordian sponge megafacies of Poland. *Acta Geologica Polonica*, 35, 73-88.
- Fraaije, R.H.B., Krzemiński, W., van Bakel, B.W.M., Krzemińska, E. and Jagt, J.W.M. 2012. The sixth abdominal tergites of paguroid anomurans – a newly recognized crustacean macrofossil type. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 266 (2), 115-122.

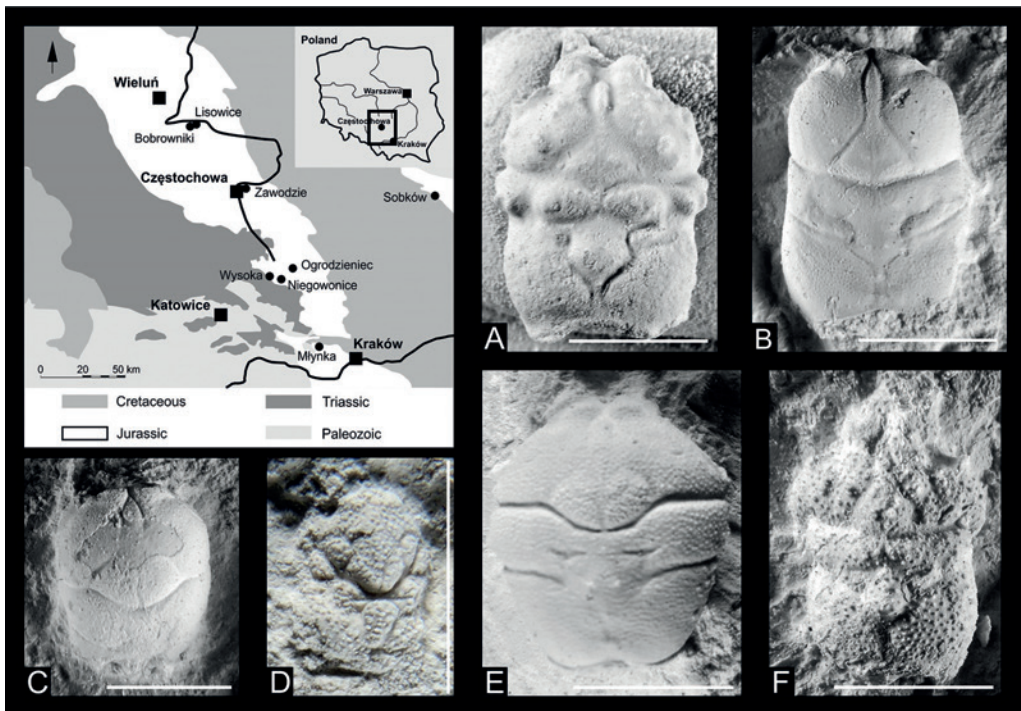


Figure 1. Map of studied localities with representatives of Late Jurassic decapod species. A. *Abyssosphthalmus spinosus* (Lisowice). B. *Gabriella biburgensis* (Lisowice). C. *Tanidromites etaloni* (Niegowonice). D. *Gastrodorus bzowiensis* (Lisowice). E. *Goniidromites serratus* (Lisowice). F. *Bucculentum bucculentum* (Niegowonice). Scale bars: 0.5 mm.

- Fraaije, R.H.B., Krzemiński, W., van Bakel, B.W.M., Krzemińska, E. and Jagt, J.W.M. 2014. New Late Jurassic symmetrical hermit crabs from the southern Polish Uplands and early paguroid diversification. *Acta Paleontologica Polonica*, 59 (3), 681-688.
- Krzemińska, E., Krzemiński, W., Fraaije, R.H.B., van Bakel, B.W.M. and Jagt, J.W.M. 2015. Allometric ontogenetic changes in two Late Jurassic gastrodorid hermit crabs (Crustacea, Decapoda, Anomura) from central Europe. *Journal of Systematic Palaeontology*, 14 (2), 139-148.
- Krzemińska, E., Starzyk, N., Fraaije, R.H.B., Schweigert, G. and Lukeneder, A. 2021. Jurassic brachyurans of the genus *Bucculentum*. *Zootaxa*, 5032 (3), 395-410.
- Matyszkiewicz, J. 1997. Microfacies, sedimentation and some aspects of diagenesis of Upper Jurassic sediments from the elevated part of the Northern peri-Tethyan Shelf: a comparative study on the Lothen area (Schwabische Alb) and the Cracow area (Cracow-Wieluń Upland, Poland). *Berliner Geowissenschaftliche Abhandlungen*, E21, 1-111.
- Starzyk, N. 2015. Reappraisal of the primitive crab *Eodromites*, with description of three new species from European localities (Decapoda: Brachyura: Goniidromitidae). *Palaeontologia Electronica*, 18.3.50A, 1-19.
- Starzyk, N. 2016. Three new species of the genus *Tanidromites* (Decapoda: Brachyura: Tanidromitidae) from the Late Jurassic (Oxfordian) of Poland. *Palaeontologia Electronica*, 19.3.45A, 1-14.

EARLY “SPEARING” STOMATOPOD CLAWS FROM THE MAASTRICHTIAN TYPE AREA

Cees H.J. Hof¹, René H.B. Fraaije², Barry W.M. van Bakel^{2,3} and John W.M. Jagt⁴

¹ Data Archiving and Networked Services, Royal Netherlands Academy of Arts and Sciences, Anna van Saksenlaan 51, 2593 HW The Hague, the Netherlands. cees.hof@dans.knaw.nl

² Oertijdmuseum, Bosscheweg 80, 5283 WB Boxtel, the Netherlands. info@oertijdmuseum.nl

³ Department of Earth Sciences, Faculty of Geosciences, Utrecht University, Budapestlaan 4, 3584 CD Utrecht, the Netherlands. b.w.m.vanbakel@uu.nl

⁴ Natuurhistorisch Museum Maastricht, de Bosquetplein 6-7, 6211 KJ Maastricht, the Netherlands. john.jagt@maastricht.nl

Keywords: Stomatopoda, Crustacea, Maastrichtian, evolution, raptorial appendages, dactyls, functional morphology, cuticular microstructures, LV-SEM

The fossil remains of a stomatopod crustacean are being presented, originating from the Maastrichtian type area in the Netherlands. The fossil find shows the two dactyls of the paired raptorial appendages of a so called “spearing” stomatopod (Patek *et al.* 2016). These toothed claws belong to one of the oldest records of spearing stomatopods, only a few other Mesozoic records of evidently spearing Stomatopoda have been described so far (Haug *et al.* 2016). Closer observations, by camera or using a standard stereomicroscope, show a (faint) pattern of cuticular ridges on the surface of the dactyls. As every detail of these dactyls might reveal information, relevant for our understanding of early stomatopod evolution, the material was also examined using a low vacuum Scanning Electron Microscope (LV-SEM). Because of the small size of the slab in which the dactyls are preserved and the solid preservational condition of the dactyls, LV-SEM examination was a safe way to investigate morphological details. The LV-SEM examination provided a much clearer and detailed image of the grooves and ridges present on the surface of especially the teeth of the dactyls. Other cuticular microstructures, such as serrated edges on the inner side of the spines, were also clearly visualized (Fig. 1).

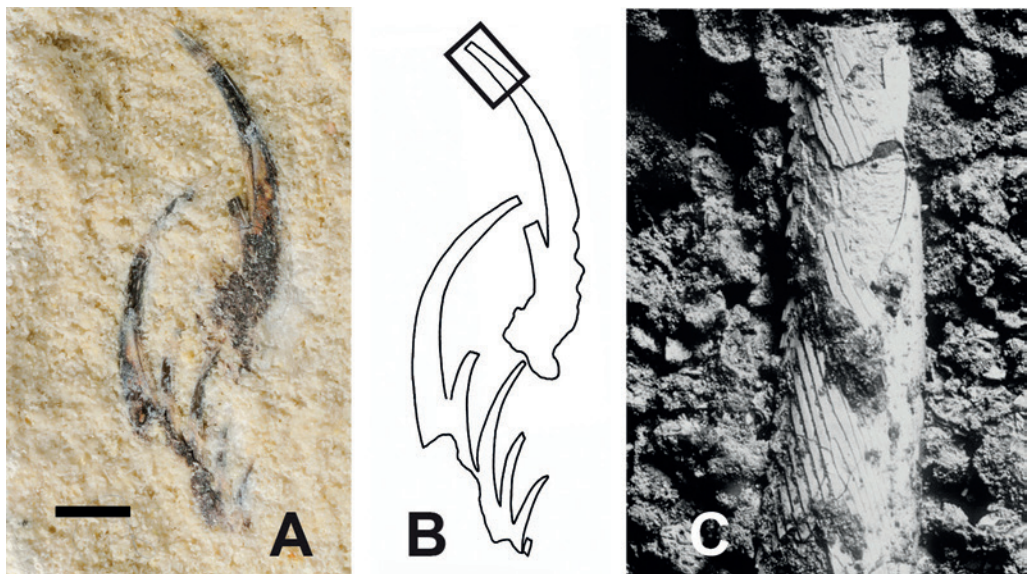


Figure 1. Paired dactyls of the raptorial appendages of a stomatopod from the Maastrichtian type area. A. Dactyls in situ, most likely the left and right dactyl of a single individual. B. Schematic drawing of both dactyls, the rectangle indicates the area visualized in image C. C. Low vacuum Scanning Electron Microscope (LV-SEM) image of the distal area of one of the teeth that has been examined. Parallel ridges on the surface and the serrated inner edge are visible. Scale bar represents 2 mm in A.

Cuticular microstructures such as ridges, grooves, small teeth and crests on the dactyls of stomatopods, are not new to science. These kind of structures can be observed in many published images of Recent as well as fossil specimens and in some publications these structures are even the subject of detailed descriptions (e.g. Fig. 6 in Haug et al. 2013). A very rudimentary survey, based on available collection material from the former Zoological Museum of the University of Amsterdam, indicates that there is quite a variety in patterns of ridges and marginal serrations amongst extant stomatopod taxa. Take for example the serrated wave patterns of the ridges on the dactyls of *Pseudosquilla ciliata* (Fig. 2).



Fig 2. Scanning Electron Microscope (SEM) image of the tip of a dactyl of the extant stomatopod species *Pseudosquilla ciliata*. Scale bar is 0.1 mm.

The overall shape of the dactyls from the Maastrichtian type locality, as well as the observed cuticular microstructures, seem to indicate affinities with the modern Lysiosquilloidea or Squillidae. The exact function of the cuticular microstructures on stomatopod dactyls is not fully understood yet, although (sharp) teeth and serrated edges without doubt bear a relation to the grabbing and holding of soft-bodied preys, spearing stomatopods hunt for. Despite the questions around functional (micro) morphology and despite the fact that stomatopod dactyls have not been structurally examined at a micro morphological level, and within a taxonomic context, the Maastrichtian fossil dactyls do tell an important story. This fossil record clearly proves that at the end of the Mesozoic, specialized spearing stomatopods did occur and already showed a very high level of morphological specialisation.

The presented research demonstrates the importance of studying and analysing microstructures in stomatopod fossil remains to widen the relevance and importance of the sparse stomatopod fossil record when studying their evolutionary history. As the strata where the dactyls were found have been examined in detail, also the palaeoecology of these spearing predators shall be considered.

Acknowledgements

Special thanks to Chris G. Jones, Head of Core Research Laboratories at Natural History Museum, London, for providing the low vacuum SEM facilities and assistance.

REFERENCES

- Haug, C., Haug, J.T., Shannon, K.R. and Vega, F.J. 2016. The oldest modern spearer-type mantis shrimp dactyli – fossils from the Maastrichtian (Cretaceous) of the Peedee Formation, North Carolina, USA. *Neues Jahrbuch für Geologie und Paläontologie*, 282 (3), 251-261.
- Haug, C., Shannon, K.R., Nyborg, T. and Vega, F.J. 2013. Isolated mantis shrimp dactyli from the Pliocene of North Carolina and their bearing on the history of Stomatopoda. *Boletín de la Sociedad Geológica Mexicana*, 65 (2), 273-284.
- Patek, S.N., Rosario, M.V. and Taylor, J.R.A. 2013. Comparative spring mechanics in mantis shrimp. *The Journal of Experimental Biology*, 216, 1317-1329.



ONCOPAREIA: A CONVOLUTED STORY OF AN EXTINCT LOBSTER WITH PECTINATE CLAWS

Matúš Hyžný¹, Martina Kočová Veselská^{2,3}, John W.M. Jagt⁴ and Dale M. Tshudy⁵

¹ Department of Geology and Palaeontology, Faculty of Natural Sciences, Comenius University, Ilkovičova 6, 842 15 Bratislava, Slovakia. hyzny.matus@gmail.com

² Institute of Geology of the Czech Academy of Sciences, v. v. i., Department of Paleobiology and Paleocology, Rozvojová 269, 165 00 Prague 6, Czech Republic

³ Institute of Geology and Palaeontology, Charles University, Albertov 6, 128 43 Prague 2, Czech Republic. veselskamartina@gmail.com

⁴ Natuurhistorisch Museum Maastricht, De Bosquetplein 6-7, 6211 KJ Maastricht, the Netherlands. john.jagt@maastricht.nl

⁵ Department of Geosciences, Edinboro University of Pennsylvania, Edinboro, Pennsylvania 16412, USA. dtshudy@edinboro.edu

Keywords: Decapoda, Astacidea, Nephropidae, acicular dentition, convergent evolution

Oncopareia Bosquet, 1854 is an extinct clawed lobster genus within the clade of thaumastocheliform nephropid lobsters, characterized by short, quadrate pleura on the pleon and a major claw with a bulbous palm and acicular dentition. Extant thaumastocheliform lobsters include *Thaumastocheles* Wood-Mason, 1874; *Thaumastochelopsis* Bruce, 1988; and *Dinorchelus* Ah Yong, Chan and Bouchet, 2010. As a group, their record tells an interesting story, of evolution during the Late Cretaceous, of dwelling at shelf depths during that time interval, of a loss of shelf-dwelling habit in the Paleogene and of a reduction or even complete loss of eyes in extant, deep-water representatives (Tshudy and Saward 2012; Chang *et al.*, 2017). The evolution of this group has recently been assessed by cladistic analysis of morphological, molecular and combined data (Chang *et al.*, 2017). Importantly, thaumastocheliform lobsters are not the only group of decapod crustaceans possessing pectinate claws. These have been developed independently in several lineages (Tshudy and Sorhannus, 2000), including Polychelida (Palaeopentachelidae), Astacidea (Erymidae, Nephropidae, Stenochiridae), Axiidea (Ctenochelidae), and Brachyura (Ipliculidae, Leucosiidae), causing difficulties in taxonomic evaluation of fossil occurrences solely based on isolated claw elements. In fact, a number of extinct taxa have been assigned to *Oncopareia* based merely on isolated cheliped fingers only to be later recognized as representatives of *Ctenocheles* Kishinouye, 1926 (Tshudy, 1993).

Oncopareia is the earliest thaumastocheliform lobster with the oldest record being of early to middle Turonian age. Originally, *Oncopareia* was erected for a single late Maastrichtian species, *O. bredai* Bosquet, 1854 from the Netherlands. The genus has a convoluted taxonomic history that begins with a type species that is an accidental composite of two different lobsters: *Oncopareia bredai* and *Hoploparia beyrichi* Schlüter, 1862. Subsequent to Bosquet's (1854) erection of a composite type species, the taxonomic confusion surrounding lobster-like fossils with pectinate claws with acicular dentition became even more serious. Unintentionally, some workers (Schlüter, 1862; Pelseneer, 1886; Fritsch and Kafka, 1887) erected new genera which later become (partly) synonymous, including *Nymphaeops* Schlüter, 1862; *Ischnodactylus* Pelseneer, 1886; and *Stenocheles* Fritsch, 1887, in Fritsch and Kafka, 1887. Other scholars (Böhm, 1891; Rathbun, 1935) described isolated chelipeds with bulbous palms and slender fingers armed with acicular denticles; most of these were misidentified at the infraordinal level. Mertin (1941) even tried to rectify all of this by bringing all fossil lobsters with pectinate claws into one genus. A recent redescription of the type species, *Oncopareia bredai*, provided a long-needed basis for re-evaluation of all taxa previously attributed to the respective genus (Tshudy *et al.*, in press). Besides the type species, three other *Oncopareia* species were recognized, including *Oncopareia esocina* (Fritsch, in Fritsch and Kafka, 1887), *Oncopareia klintebjergensis* Jakobsen and Collins, 1979, and *Oncopareia lunata* (Fritsch, in Fritsch and Kafka, 1887). Other species previously included within *Oncopareia* were either reassigned to other genera or considered of uncertain affinity (Tshudy *et al.* in press).

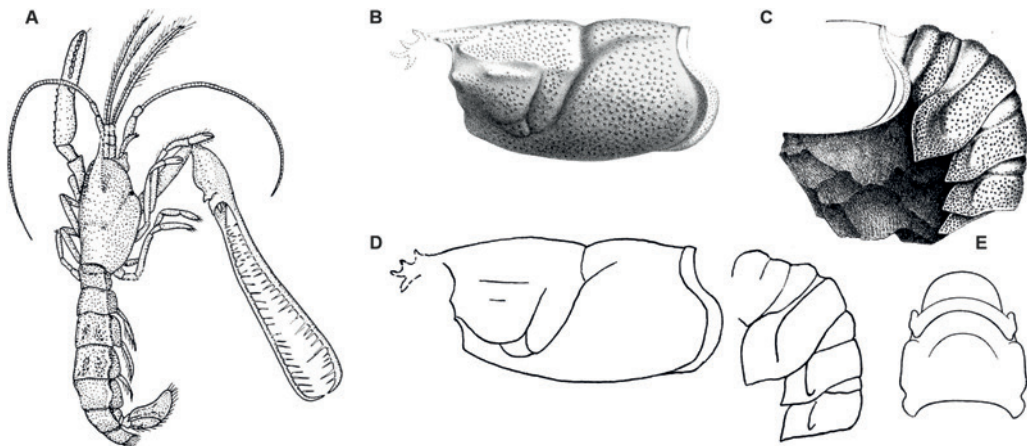


Figure 1. *Oncopareia bredai* (sensu Bosquet, 1854), as a composite species. A. Habitus of thau-mastocheliform lobsters, exemplified by *Thaumastocheles zaleucus* (from Calman, 1911). B. Cephalothorax of *O. bredai* (from Bosquet, 1854, pl. 10, fig. 5). C. Pleon of *Hoploparia beyrichi* Schlüter, 1862 (from Bosquet, 1854, pl. 10, fig. 6). D. Composite drawing from Mertin (1941, text-fig. 9e). E. Pleonal segments 1 and 2 of *O. bredai* (as *Homarus bosqueti* Pelseneer, 1886; from Pelseneer, 1886, fig. 4).

Acknowledgements

The research was supported by VEGA 02/0136/15 and the Slovak Research and Development Agency under contracts no. APVV-17-0555 and APVV-20-0079.

REFERENCES

- Böhm, J. 1891. Die Kreidebildung des Fürbergs und Sulzbergs bei Siegsdorf in Oberbayern. *Palaeontographica*, 38, 1-106.
- Bosquet, J. 1854. Les crustacés fossiles du Terrain Crétacé du Limbourg. *Verhandelingen uitgegeven door de Commissie belast met het Vervaardigen eener geologische Beschrijving en Kaart van Nederland*, 2, 1-127 [10-137]. A.C. Kruseman, Haarlem.
- Chang, S.-C., Tshudy, D., Sorhannus, U., Ah Yong, S.T., and Chan, T.-Y. 2017. Evolution of the thau-mastocheliform lobsters (Crustacea, Decapoda, Nephropidae). *Zoologica Scripta*, 46, 372-387.
- Fritsch, A. and Kafka, J. 1887. *Die Crustaceen der böhmischen Kreideformation*. Prag, Selbstverlag in Commission von F. Rivnáč, 53 pp., pls 1-10.
- Jakobsen, S.L. and Collins, J.S.H. 1979. Decapod Crustacea from the Paleocene of Zealand, Denmark. *Proceedings of the Geologists' Association*, 90, 61-64.
- Mertin, H. 1941. Decapode Krebse aus dem Subhercynen und Braunschweiger Emscher und Untersenon sowie Bemerkungen über einige verwandte Formen in der Oberkreide. *Nova Acta Leopoldina*, 10, 1-264.
- Pelseneer, P. 1886. Notice sur les Crustacés décapodes du Maestrichtien du Limbourg. *Bulletin du Musée royal d'Histoire naturelle de Belgique*, 4(2), 161-175 [1-15].
- Rathbun, M.J. 1935. Fossil Crustacea of the Atlantic and Gulf Coastal Plain. *Geological Society of America, Special Papers*, 2, 1-160.



- Schlüter, C. 1862. Die macruren Decapoden der Senon- und Cenoman-Bildungen Westphalens. *Zeitschrift der deutschen geologischen Gesellschaft*, 14, 702-749.
- Tshudy, D. 1993. Taxonomy and evolution of the clawed lobster families Chilenophoberidae and Nephropidae. Unpublished PhD dissertation, Kent State University, Kent, Ohio.
- Tshudy, D. and Saward, J. 2012. *Dinochelus steeplensis*, a new species of clawed lobster (Nephropidae) from the London Clay (Eocene) of England. *Journal of Crustacean Biology*, 32, 67-79.
- Tshudy, D. and Sorhannus, U. 2000. Pectinate claws in decapod crustaceans: convergence in four lineages. *Journal of Paleontology*, 74, 474-486.
- Tshudy, D.M., Hyžný, M., Kočová Veselská, M. and Jagt, J.W.M. in press. Taxonomic revision of the extinct clawed lobster genus *Oncopareia* Bosquet, 1854 (Decapoda, Astacidea, Nephropidae). *Palaeontologia Electronica*.

THE FOSSIL RECORD OF CRUSTACEANS IN METHANE SEEP DEPOSITS WITH A FOCUS ON DECAPODS FROM THE WESTERN INTERIOR SEAWAY, USA

Adiël A. Klompmaker¹, Jamie Brezina², Torrey Nyborg³, Peter A. Kloess⁴, Yusuke Ando⁵ and Neil Landman⁶

¹ Department of Museum Research and Collections & Alabama Museum of Natural History, University of Alabama, Box 870340, Tuscaloosa, Alabama 35487, USA. adielklompmaker@gmail.com

² South Dakota School of Mines and Technology, Rapid City, SD 57701, USA. rezinagate@hotmail.com

³ Department of Earth and Biological Sciences, Loma Linda University, Loma Linda, CA 92350, USA. tnyborg06g@llu.edu

⁴ Department of Integrative Biology and Museum of Paleontology, University of California, Berkeley, CA, 94720, USA. pakloess@berkeley.edu

⁵ Mizunami Fossil Museum, 1-47, Yamanouchi, Akeyo-cho, Mizunami, Gifu, 509-6132, Japan. tyuu-destiny53@hotmail.co.jp

⁶ Division of Paleontology (Invertebrates), American Museum of Natural History, New York, NY 10024, USA. landman@amnh.org

Keywords: Axiidea, Brachyura, Cirripedia, Decapoda, Ostracoda

Numerous crustaceans such as ostracods, decapod, and some barnacles inhabit modern methane (cold) seep ecosystems, but little is known about their fossil record in these chemosymbiotic-based ecosystems. Consequently, their importance in structuring faunas at these biodiversity hotspots on the sea floor is poorly known, including to what extent seeps acted as refuges from extinction, the timing of occupancy of cold seeps, the degree of endemism, depth preferences, and the longevity of crustacean lineages in seeps. Although many of these questions cannot be answered yet, we provide the first synthesis of crustaceans in ancient seep deposits and show that they have been found at each continent due to a rapid increase in research since the 1990s (Klompmaker *et al.*, in press). Ostracods and barnacles are known from body fossils alone. Conversely, decapods are represented by two types of fossils: body fossils primarily attributed to true crabs and ghost shrimps, and their traces such as coprolites, repair scars, and burrows. The last ~150 million years saw a remarkable rise in the number of localities and occurrences of seep crustaceans, mostly caused by the diversification and spread of decapods into a variety of environments including seeps. Previous papers on seep decapod body fossils include, among others, Bishop and Williams (2000), Schweitzer and Feldmann (2008), and Karasawa and Kano (2021).

In addition to a meta-analysis, we also performed specimen-based research by studying seep decapods from South Dakota and Wyoming, USA, through museum visits and field work (Fig. 1). This has resulted in many additional decapod body fossils found in seep limestones from



Figure 1. One of the seep limestone sites in South Dakota in 2019. Photo: Adiël A. Klompmaker

the Upper Cretaceous (Campanian-Maastrichtian) Pierre Shale, deposited in what was the Western Interior Seaway. Thirty-three body fossils of decapods were found in the American Museum of Natural History, two in the Black Hills Institute, and ~300 specimens were collected in the field, mostly over the last three years. For taxonomic purposes, we also studied specimens from the South Dakota School of Mines and Technology and the Smithsonian Institution. Decapods

from these seep limestones are represented by (1) true crabs (Brachyura) that had a burying, epifaunal, and swimming lifestyle, and (2) burrowing ghost shrimps (Axiidea). All specimens belong to at least seven known species, implying that there is no endemism in these shallow-water seeps. The abundance of decapods can vary substantially among and within seeps, and seep decapod faunas can also differ substantially in terms of composition. Two remarkable specimens were encountered. One specimen with a parasitic swelling in the branchial region was found (ichnotaxon *Kanthylooma crusta* Klompmaker *et al.*, 2014), suggesting that the prevalence of parasitism by epicaridean isopods is low in the Pierre Shale seep faunas. One crab specimen appears to have at least the gills and esophagus preserved.

Using seep specimens from the Pierre Shale of South Dakota in the American Museum of Natural History collection, we found several lines of evidence for predation that may be attributed to crustaceans: (1) repair scars in seven mollusks (six inoceramid bivalves and one gastropod), (2) two specimens of lucinid bivalves with pinch traces, and (3) one inoceramid shell with interconnected, arcuate holes in the shell. Thus, it appears that decapods affected the fauna of these seeps, but more research is needed to quantify to what degree they did.

Although considerable progress was made in the last 30 years, the relatively unexplored fossil record of seep crustaceans provides ample opportunities for further taxonomic, macroevolutionary, and paleoecological research. The study on the South Dakota/Wyoming material herein is one example.

Acknowledgements

For various reasons, we express our gratitude to (in alphabetical order by family name): Denis Audo, Christina Belanger, Gale Bishop, Simone Brandão, Tim-Yam Chan, Erica Clites, Rodney Feldmann, Mark Florence, Katsunori Fujikura, Krzysztof Hryniewicz, Bushra Hussaini, Matus Hyžný, Azusa Ikuta, Andrzej Kaim, Yasumitsu Kanie, Hiroaki Karasawa, Steffen Kiel, Neal Larson, Ryuichi Majima, William Newman, Anastasia Rashkova, Cristina Robins, Michael Sandy, Carrie Schweitzer, Sally Shelton, and Chau-Chang Wang. JB thanks the research crews from the AMNH, Stonybrook College, and Brooklyn College for their work collecting at seeps in the Western Interior Seaway, ranchers for allowing access to private property, and the USDA Forest Service for granting access to forest service and BLM land. This research was supported by an American Museum of Natural History Lerner-Gray grant and a Karl Hirsch Memorial grant to AAK.

REFERENCES

- Bishop, G.A. and Williams, A.B. 2000. Fossil crabs from tepee buttes, submarine seeps of the Late Cretaceous Pierre Shale, South Dakota and Colorado, U.S.A. *Journal of Crustacean Biology*, 20, 286-300.
- Karasawa, H. and Kano, M. 2021. A first notice of the goniodromitid crab from the Cenomanian (Upper Cretaceous) cold seep deposit of Hokkaido, Japan, with the redescription of *Sabelidromites inflata* (Collins and Karasawa, 1993) (Decapoda: Goniodromitidae). *Boletín de la Sociedad Geológica Mexicana*, 73, A020121.
- Klompmaker, A.A., Artal, P., Van Bakel, B.W.M., Fraaije, R.H.B. and Jagt, J.W.M. 2014. Parasites in the fossil record: a Cretaceous fauna with isopod-infested decapod crustaceans, infestation patterns through time, and a new ichnotaxon. *PLoS One*, 9, e92551.
- Klompmaker, A.A., Nyborg, T., Brezina, J. and Ando, Y. In press. Crustaceans in cold seep ecosystems: fossil record, geographic distribution, taxonomic composition, and biology. In: A. Kaim (ed.), *Ancient Methane Seeps and Cognate Communities, Topics in Geobiology*.
- Schweitzer, C.E. and Feldmann, R.M. 2008. New Eocene hydrocarbon seep decapod crustacean (Anomura: Galatheidae: Shinkaiinae) and its paleobiology. *Journal of Paleontology*, 82, 1021-1029.

RESOLVING THE TAGMATISATION AND THE PHYLOGENETIC AFFINITIES OF THYLACOCEPHALA: INPUT FROM 3D DATA

Thomas Laville¹, Marie-Béatrice Forel¹ and Sylvain Charbonnier¹

¹ Centre de Recherche en Paléontologie – Paris (CR2P), Muséum national d'Histoire naturelle, Sorbonne. Université, CNRS UMR 7207, Paris, France. thomas.laville2@mnhn.fr, marie-beatrice.forel@mnhn.fr, sylvain.charbonnier@mnhn.fr

Keywords: X-ray tomography, synchrotron, appendages, La Voulte, Lagerstätte

Known from at least the Silurian (Haug *et al.* 2014) to the Late Cretaceous (e.g. Charbonnier *et al.* 2017), Thylacocephala Pinna, Arduini, Pesarini and Terruzzi 1982 is an enigmatic group of extinct euarthropods characterised by a folded protective shield, hypertrophied compound eyes, three pairs of raptorial appendages, eight pairs of gills and an eight to 22-segmented posterior trunk (Schram, 2014; Fig. 1). Despite this knowledge on their anatomy, many questions remain on their phylogenetic affinities. Since its recognition as a monophyletic group, Thylacocephala has been related to a huge variety of pancrustaceans: thecostracans (Pinna *et al.* 1982), malacostracans (e.g. Secrétan 1985; Vannier *et al.* 2016) or remipeds (Haug *et al.* 2014). This uncertainty on their phylogenetic relationships is due to a lack of knowledge on their tagmatisation. Indeed, the origin of the shield, the exact number of cephalic and posterior trunk segments and appendages as well as the nature of raptorial appendages are still unknown as they are rarely preserved.

In order to resolve the remaining questions on their tagmatisation, modern imaging techniques such as micro-computed X-ray tomography (μ CT) provide important information. Conventional μ CT has proven to be efficient in order to reconstruct the internal anatomy of thylacocephalans (digestive and respiratory systems; Vannier *et al.* 2016). However, it did not provide insight into their various appendages. Thus, we decided to apply Synchrotron Phase Contrast μ CT to *Dollocaris ingens* Van Straelen, 1923 from the La Voulte-sûr-Rhône Lagerstätte, Ardèche, France (Callovian, Middle Jurassic). It enables us to investigate the segmentation of the posterior and anterior trunk. We were also able to study the morphology and nature of cephalic and raptorial appendages as well as the morphology and number of posterior trunk segments.

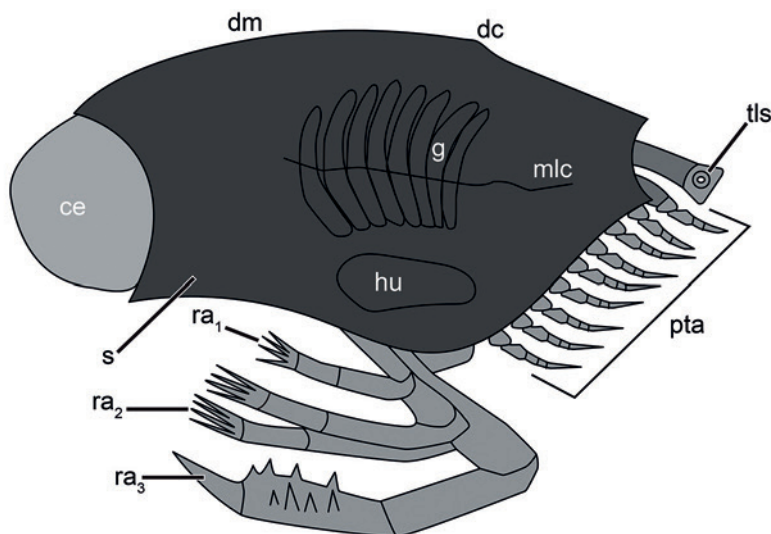


Figure 1. External anatomy of *Dollocaris ingens* Van Straelen, 1923. Abbreviations: ce, compound eyes; dc, dorsal carina; dm, dorsal midline; g, gills; hu, hump; mlc, medio-lateral carina; pta, posterior trunk appendages; ra1-3, raptorial appendages; s, shield; tls, telson.



Based on those findings, two phylogenetic analyses (cladistic and bayesian) were run on two different datasets (Legg *et al.*, 2013; Aria *et al.*, 2021) consisting respectively of 322 taxa and 754 characters, and of 114 taxa and 276 characters. Three thylacocephalan species were included in the analyses: *Dollocaris ingens*, *Thylacares brandonensis* Haug *et al.*, 2014 and *Mayrocaris buculata* Polz, 1994. This allows us to test for the monophyly of Thylacocephala and to resolve the phylogenetic affinities of Thylacocephala.

Acknowledgements

We acknowledge SOLEIL for provision of synchrotron radiation facilities and we would like to thank Andrew King for assistance in using beamline Psiche (project 20210093). We also thank Jean-Michel Pacaud (MNHN) for access to the collections.

REFERENCES

- Aria, C., Zhao, F. and Zhu, M. 2021. Fuxianhuiids are mandibulates and share affinities with total-group Myriapoda. *Journal of the Geological Society*, 178 (5), jgs2020-246.
- Charbonnier, S., Teruzzi, G., Audouin, D., Lasserre, M., Haug, C. and Haug, J.T. 2017. New thylacocephalans from the Cretaceous Lagerstätten of Lebanon. *Bulletin de la Société géologique de France*, 188 (3), 19.
- Haug, C., Briggs, D.E.G., Mikulic, D.G., Kluessendorf, J. and Haug, J.T. 2014. The implications of a Silurian and other thylacocephalan crustaceans for the functional morphology and systematic affinities of the group. *BMC Evolutionary Biology*, 14 (159).
- Legg, D.A., Sutton, M.D. and Edgecombe, G.D. 2013. Arthropod fossil data increase congruence of morphological and molecular phylogenies. *Nature Communications*, 4 (1), 2485.
- Pinna, G., Arduini, P., Pesarini, C. and Teruzzi, G. 1982. Thylacocephala: una nuova classe di crostacei fossili. *Atti della Società italiana di Scienze naturali e del Museo civico di Storia naturale di Milano*, 123 (4), 469–482.
- Schram, F.R. 2014. Family level classification within Thylacocephala, with comments on their evolution and possible relationships. *Crustaceana*, 87 (3), 340–363.
- Secrétan, S. 1985. Conchyliocarida, a class of fossil crustaceans: relationships to Malacostraca and postulated behaviour. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, 76 (2–3), 381–389.
- Vannier, J., Schoenemann, B., Gillot, T., Charbonnier, S. and Clarkson, E. 2016. Exceptional preservation of eye structure in arthropod visual predators from the Middle Jurassic. *Nature Communications*, 7 (1), 10320.

THE TRIASSIC THYLACOCEPHALANS FROM SLOVENIA: IMPLICATIONS FOR THEIR EVOLUTION AND DIVERSIFICATION

Thomas Laville¹, Tomaž Hitij², Rok Gašparič³, Jure Žalohar⁴,
Marie-Béatrice Forel¹ and Sylvain Charbonnier¹

¹ Centre de Recherche en Paléontologie – Paris (CR2P), Muséum national d'Histoire naturelle, Sorbonne Université, CNRS UMR 7207, Paris, France. thomas.laville2@mnhn.fr, marie-beatrice.forel@mnhn.fr, sylvain.charbonnier@mnhn.fr

² Dental School, Faculty of Medicine, University of Ljubljana, Vrazov trg 2, 1000 Ljubljana, Slovenia. tomazhitij@gmail.com

³ Oertijdmuseum, Bosscheweg 80, 5293 WBOxtel, Netherlands. rok.gasparic@gmail.com

⁴ T-TECTO, Kranj, Slovenia. jure.zalohar@guest.arnes.si

Keywords: Anisian, Carnian, geographic distribution, biodiversity

Thylacocephala Pinna, Arduini, Pesarini and Teruzzi, 1982 is an enigmatic fossil euarthropod ingroup, often associated to pancrustaceans. Thylacocephalans are characterised by key anatomical features: a folded shield enveloping most of the body, hypertrophied compound eyes, three pairs of raptorial appendages, a trunk made of eight up to 22 segments bearing appendages and eight pairs of gills. Known from at least the Silurian (Haug *et al.*, 2014) to the Cretaceous (e.g. Charbonnier *et al.*, 2017), thylacocephalans have a patchy fossil record in terms of stratigraphy and of palaeogeography. Despite the few occurrences, it seems that thylacocephalans were the most taxonomically diversified during the Triassic (Laville *et al.*, 2021).

Unknown until recently in the fossil record of Slovenia, many specimens of thylacocephalans were collected from the Middle Triassic (Anisian) beds of the Velika planina Member (Gale *et al.*, 2022) and Strelovec Formation (Križnar and Hitij, 2010) in Kamnik-Savinja Alps, as well as in the Late Triassic beds (Carnian) of the Martuljek Formation in the Julian Alps (Hitij *et al.*, 2019).

A new species of *Atropicaris*, a typical taxon of the Middle and Late Triassic, is described from the Velika planina Member (Fig. 1). In the Strelovec Formation, taxa already known from the Middle and Late Triassic of Austria and Italy (*Microcaris* Pinna, 1974; *Atropicaris* Arduini and Brasca, 1984) have been recorded while two new morphotypes have also been identified. One of the new morphotypes presents typical characters of Jurassic representatives (rounded rostrum, posterior notch and spines). Finally, *Atropicaris* and *Microcaris* specimens were also recovered from the Martuljek Formation in which accumulation of thylacocephalans can be seen. Those accumulations might be the results of mass mortality.

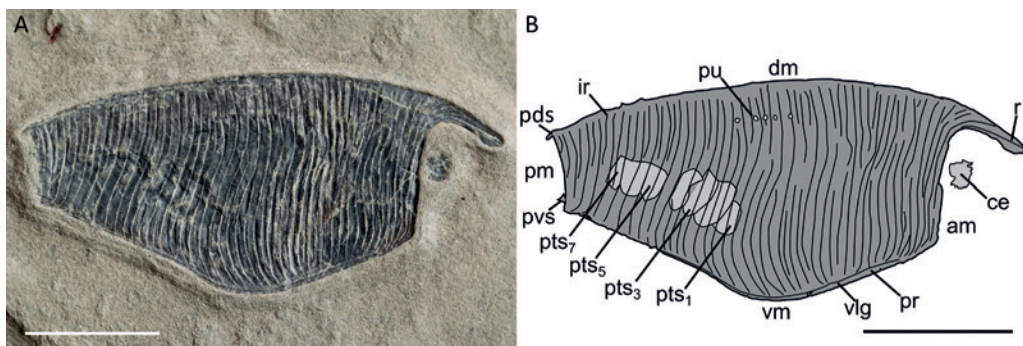


Figure 1. *Atropicaris* sp. nov. from Ilovec, Logarska dolina, Slovenia (Velika planina Member, Anisian, Middle Triassic). A. Lateral view. B. Drawing. Abbreviations: am, anterior margin; ce, compound eyes; dm, dorsal midline; ir, intercalary ridges; pds, postero-dorsal spine; pm, posterior margin; pr, primary ridges; pts₁₋₇, posterior trunk segments 1-7; pu, punctuations; pvs, postero-ventral spine; r, rostrum; vlg, ventro-lateral groove; vm, ventral margin. Scales: 5mm.



Those new findings provide important insight into the diversity and palaeogeographic distribution of thylacocephalans during the Triassic but also into the morphological evolution of this puzzling group.

REFERENCES

- Arduini, P. and Brasca, A. 1984. *Atropicaris*: nuovo genere della classe Thylacocephala. *Atti della Società italiana di Scienze naturali e del Museo civico di Storia naturale di Milano*, 125, 87–93.
- Charbonnier, S., Teruzzi, G., Audouin, D., Lasseron, M., Haug, C. and Haug, J.T. 2017. New thylacocephalans from the Cretaceous Lagerstätten of Lebanon. *Bulletin de la Société géologique de France*, 188 (3), 19.
- Gale, L., Hitij, T., Vičič, B., Križnar, M., Žalohar, J., Celarc, B. and Vrabec, M. 2022. A sedimentological description of the Middle Triassic vertebrate-bearing limestone from Velika planina, the Kamnik-Savinja Alps, Slovenia. *Geologia Croatica*, 75 (1), 14.
- Haug, C., Briggs, D.E.G., Mikulic, D.G., Kluessendorf, J. and Haug, J.T. 2014. The implications of a Silurian and other thylacocephalan crustaceans for the functional morphology and systematic affinities of the group. *BMC Evolutionary Biology*, 14 (159).
- Hitij, T., Gašparič, R., Bogdan, J. and Kolar-Jurkovšek, T. 2019. Paleontološko bogastvo Kozje dnine / Palaeontological treasure of Kozja dnina. *Acta Triglavensia*, 7, 5–42.
- Križnar, M. and Hitij, T. 2010. Nevretenčarji (Invertebrates) Strelovške formacije. *Scopolia Supplement*, 5, 91–107.
- Laville, T., Smith, C.P.A., Forel, M.-B., Brayard, A. and Charbonnier, S. 2021. Review of Early Triassic Thylacocephala. *Rivista Italiana di Paleontologia e Stratigrafia*, 127 (1), 73–101.
- Pinna, G. 1974. I crostacei della fauna triassica di Cene in Val Seriana (Bergamo). *Memorie della Società italiana di scienze naturali in Milano*, 21, 5–34.
- Pinna, G., Arduini, P., Pesarini, C. and Teruzzi, G. 1982. Thylacocephala: una nuova classe di crostacei fossili. *Atti della Società italiana di Scienze naturali e del Museo civico di Storia naturale di Milano*, 123 (4), 469–482.

BRACHYURAN (DECAPODA) REMAINS ASSOCIATED TO DINOSAURS IN FLUVIAL DEPOSITS OF THE TREMP GROUP (CATALONIA)

Josep Manel Méndez¹, Àlex Ossó², Bernat Vila^{1,3}, Albert Sellés^{1,3} and Rodrigo Gaete³

¹ Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Carrer Escola Industrial 23, 08201 Sabadell (Barcelona), Catalonia, Spain. manuel.mendez@icp.cat, bernat.vila@icp.cat, albert.garcia@icp.cat, rgaeteh@yahoo.es

² Llorenç de Villalonga, 17B, 1-1, 43007, Tarragona, Catalonia, Spain. aosso@tinet.cat

³ Museu de la Conca Dellà, Carrer del Museu, 4, 25650, Isona (Lleida), Catalonia, Spain.

Keywords: Decapoda, Brachyura, freshwater crabs, dinosaurs, Upper Cretaceous

The association of brachyuran decapod remains with terrestrial vertebrates such as dinosaurs in land environments is scarce but not uncommon (Robin et al., 2019; Luque et al., 2021, and references therein). In the Uppermost Cretaceous of southern Pyrenees, Marmi et al. (2016, 525, figs. 5D-F) reported and briefly described a dactyl fragment of an indeterminate decapod from the Molí del Baró-1 locality (Pallars Jussà, Catalonia). Although it did not noticed among decapod fossil workers, it was the first formal report of decapods associated to dinosaurs in the Iberian Peninsula.

Herein, we report and describe two remains of eubrachyuran (cf. Robin et al., 2019, 2, 3) crabs recovered in two upper Maastrichtian localities: the aforementioned Molí del Baró-1, and the Obaga de la Collada site (Isona i Conca Dellà, Catalonia). The localities are found in the fluvial deposits of the Tarn Formation or 'Lower red Garumnian' of the Tremp Group and fall within the C29r magnetochron (upper Maastrichtian; Fondévilla et al., 2019). The decapod-bearing strata in both localities correspond to mudstones (representing floodplain deposition) interbedded within thick sandstones (interpreted as meandering rivers). The specimen from the Molí del Baró-1 site was found associated with plants (charophytes, sporomorphs, angiosperm leaves, seeds, and logs), invertebrates (mollusc shells, partial insect exoskeletons and eggs) and vertebrates (mainly teeth, bones, and eggshells of dinosaurs and crocodylomorphs) (Marmi et al., 2016). The dactylus fragment from the Obaga de la Collada site was found associated with indeterminate bone fragments and a dinosaur (hadrosaur) footprint cast.

The Molí del Baró-1 specimen (Fig. 1A-E), appears to be a portion of a relatively long left pollex. It possesses an occlusal margin with four complete serial conical teeth and portions of two more proximally and distally teeth, as well as a slightly convex lower margin. The outer side is slightly convex and the inner side slightly concave. A longitudinal groove and rows of setal pits are present along outer and inner sides. The specimen is similar to some Cenozoic portunids, but proper comparison requires further specimens (cf. Fig. 1F).

The Obaga de la Collada specimen (Fig. 1G-K) is an incomplete right dactylus, relatively long and gently curved forward. The upper margin is rounded and smooth. The occlusal margin presents a proximal flattened molariform tooth, followed by three rounded serial conical teeth. A longitudinal row of spaced setal pits runs along both, inner and outer sides. Taxonomic assignment based on a single finger fragment is difficult. *Eogeryon elegius* Ossó, 2021 (Portunoidea), from the late Cenomanian of the Central Iberian Peninsula presents a very similar gently curved right dactylus, with a proximal flattened molariform tooth followed by rounded serial conical teeth (cf. Fig. 1L, P; Ossó, 2021, fig. 1D). The same occurs with the portunoid *Styracocarcinus meridionalis* (Secrétan, 1961), from the late Campanian of North of Africa (cf. Fig. 1Q; Ossó, 2016, fig. 6B'). The right dactylus of *Dinocarcinus velauciensis* Van Bakel, Hyžný, Valentin and Robin, 2019 in Robin et al., 2019 (Portunoidea s.l.) (Fig. 1M-O), from the late Campanian of France, show how, despite of an apparent similarity such as a proximal flattened molariform tooth, it differs from the Obaga de la Collada specimen in being less curved and having smaller serial teeth that decrease in size

(cf. Robin et al., 2019, fig. 3d). *D. velaucensis* was described from a similar fluvio-lacustrine environment that the specimens reported herein, and also associated with terrestrial dinosaurs, and freshwater fauna (Robin et al., 2019, fig. 4). Given that the greatest similarity of the dactylus of the Obaga de la Collada dactylus is with the dactyli of *E. elegius* and *S. meridionalis*, both placed within Portunoidea (see Ossó, 2021, 145, 147; Luque et al., 2021, fig. 5H), and to lesser extent

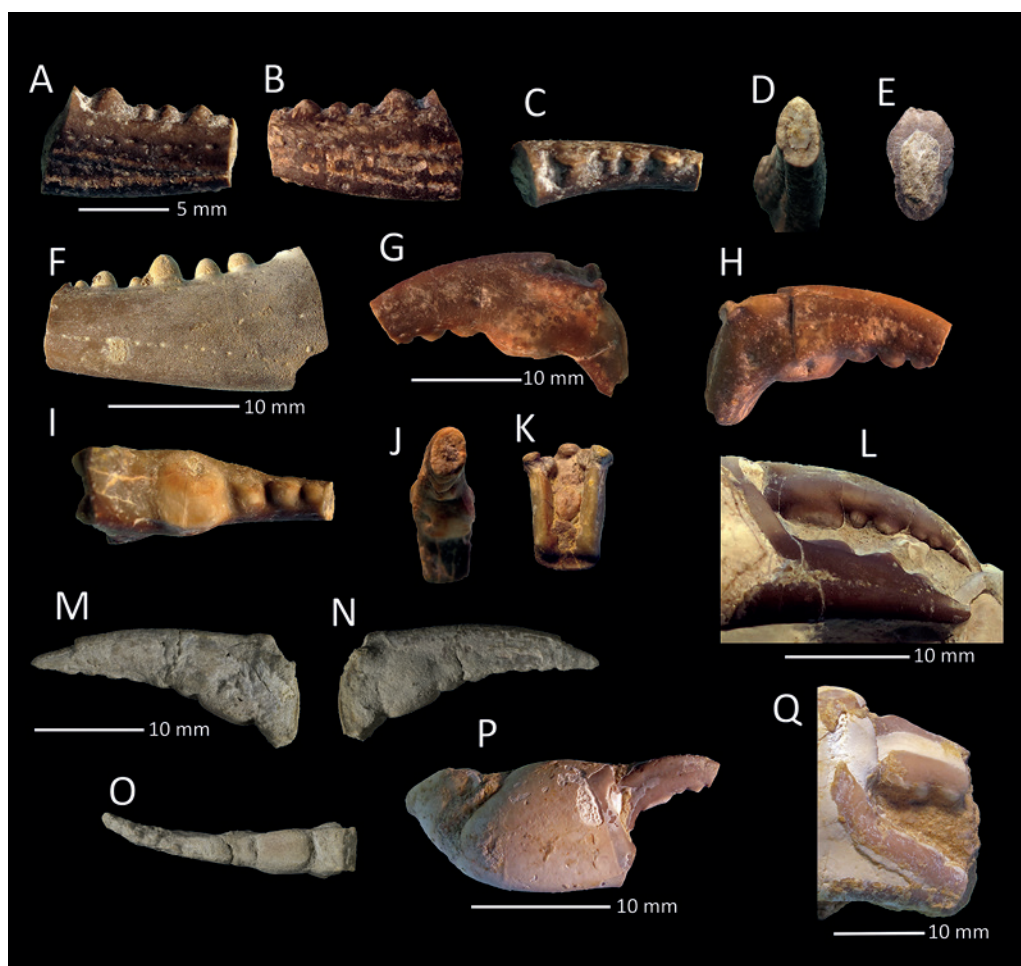


Figure 1. A-E. Molí del Baró-1 specimen, MCD-5538, left pollex. A. Inner side. B. Outer side. C. Occlusal margin. D. Distal view. E. Proximal view. F. *?Necronectes* sp. MHNbX 2021.29.11 from the Oligocene of Gaas (France), left pollex, outer side. G-K. Obaga de la Collada specimen, MCD-340, right dactylus. G. Inner side. H. Outer side. I. Occlusal margin. J. distal view. K. proximal view. L, P. *Eogeryon elegius* Ossó, 2021, Holotype MGB 69151, from the Cenomanian of Condemios de Arriba (Spain), right propodus outer side. M-O. *Dinocarcinus velaucensis* Van Bakel, Hyžný, Valentin and Robin, 2019, MMS/VBN.12.A.00, from the Campanian of Velaux (France), right dactylus. M. Inner side. N. Outer side. O. Occlusal margin. P. *Eogeryon elegius* Ossó, 2021, unnumbered AO col., from the Cenomanian of Condemios de Arriba (Spain), right propodus outer side. Q. *Styrocarcinus meridionalis* (Secréten, 1961), unnumbered AO Col., from the probably Campanian of Merija (Morocco), right propodus outer side. Abbreviations: MCD: Museu de la Conca Dellà (Isona, Catalonia); MHNbX: Muséum d'Histoire naturelle de Bordeaux (France); MGB: Museu de Geologia de Barcelona (Barcelona, Catalonia); MMS/VBN: Musée du Moulin Seigneurial/Velaux-La Bastide Neuve (France).

with *D. velaucensis*, also placed in *Portunoidea s.l.*, this specimen could belong, with doubts, to an unknown member of that superfamily.

The dactyli of the exquisitely preserved in amber *Cretapsara athanata* Luque *in* Luque et al., 2019 (Cretapsaridae), from the lowermost Cenomanian of Myanmar, differs from both specimens described herein in having straighter dactyli with very smaller teeth on the occlusal margin, in addition of the huge difference in size. *C. athanata*, could have lived in a brackish or freshwater setting near to coastal to fluvio-estuarine environment (Luque et al., 2019).

Most probably, both specimens reported herein represent allochthonous remains of marine or coastal decapods, deposited in pools formed at the edge of meandering rivers or in the flood-plain. The finding of coastal decapods in inland sedimentary environments concurs with the widespread occurrence of non-reworked planktonic foraminifera and autogenic glauconite grains documented within the whole Lower Red Unit (Díez-Canseco et al. 2014; Vicente et al., 2015; Ghinassi et al., 2021). Thus, in a similar way, we interpret that the decapod fragments were transported, as a suspended load, on tidal flows from the open sea into meandering channels.

REFERENCES

- Díez-Canseco, D., Arz, J.A., Benito, J.I., Díaz-Molina, M. and Arenillas, I. 2014. Tidal influence in redbeds: A palaeoenvironmental and biostratigraphic reconstruction of the Lower Tresp Formation (South-Central Pyrenees, Spain) around the Cretaceous/Paleogene boundary. *Sedimentary Geology*, 312, 31-49.
- Fondevilla, V., Riera, V., Vila, B., Sellés, A.G., Dinarès-Turell, J., Vicens, E., Gaete, R., Oms, O. and Galobart, A. 2019. Chronostratigraphic synthesis of the latest Cretaceous dinosaur turnover in south-western Europe. *Earth-Science Reviews*, 191, 168-189.
- Ghinassi, M., Oms, O., Cosma, M., Finotello, A. and Giovanni, G. 2021. Reading tidal processes where their signature is cryptic: The Maastrichtian meandering channel deposits of the Tresp Formation (Southern Pyrenees, Spain). *Sedimentology*, 68 (5), 2009-2042.
- Luque, J., Xing, L., Briggs, D.E.G., Clark, E.G., Duque, A., Hui, J., Mai, H. and McKellar, Ryan.C. 2021. Crab in amber reveals an early colonization of nonmarine environments during the Cretaceous. *Science Advances*, 7: eabj5689.
- Marmi, J., Blanco, A., Fondevilla, V., Dalla Vecchia, F.M., Sellés, A.G., Vicente, A., Martín-Closas, C., Oms, O. and Galobart, A. 2016. The Molí del Baró-1 site, a diverse fossil assemblage from the uppermost Maastrichtian of the southern Pyrenees (North-Eastern Iberia). *Cretaceous Research*, 57, 519-539.
- Ossó, À. 2016. *Eogeryon elegius* n. gen. and n. sp. (Decapoda: Eubrachyura: Portunoidea), one of the oldest modern crabs from late Cenomanian of the Iberian Peninsula. *Boletín de la Sociedad Geológica Mexicana*, 68(2), 21-246.
- Ossó, À. 2021. Un cranc nou, *Eogeryon elegius* gen. nov., sp. nov. del Cenomanià tardà de la Península Ibèrica. *Nemus*, 11, 144-158.
- Robin, N., van Bakel, B.W.M., Hyžný, M., Cincotta, A., Garcia, G., Charbonnier, S., Godefroit, P. and Valentin, X. 2019. The oldest freshwater crabs: Claws on dinosaur bones. *Scientific Reports*, 9, 20220.
- Secrétan, S. 1961. Une nouvelle espèce de Xanthidés au Maroc: *Titanocarcinus meridionalis* nov. sp. *Notes de Service Géologique de Maroc*, 20 (152), 39-50.
- Vicente, A., Martín-Closas, C., Arz, J.A., Oms, O. 2015. Maastrichtian-basal Paleocene charophyte biozonation and its calibration to the Global Polarity Time Scale in the southern Pyrenees (Catalonia, Spain). *Cretaceous Research*, 52, 268-285.

FIRST REPORT OF THE FRESHWATER CRAB *POTAMON* (DECAPODA: BRACHYURA: POTAMIDAE) IN THE PLIOCENE OF THE IBERIAN PENINSULA

Àlex Ossó¹, Álvaro Arasa² and Quim Pastó³

¹ Llorenç de Villalonga, 17B, 1-1, 43007 Tarragona, Catalonia, Spain. aosso@tinet.cat

² Grup Ebre Recerca. C/ Rosa Molas 25-A, 2B. 43500 Tortosa, Catalonia, Spain. arasa44@gmail.com

³ Sant Agustí, 21, 43891 Masboquera, Catalonia, Spain. quimpasto@gmail.com

Keywords: Baix Ebre, Brachyura, Decapoda, Freshwater crabs, Pliocene

The westernmost (natural) occurrence of extant primary freshwater crabs in Europe is northern Italy. Also, fossil freshwater crabs were until recently not reported west of northern Italy and the North Alpine Foreland Basin, with exception of a single (juvenile?) specimen reported from the Upper Oligocene-Lower Miocene Izarra Formation in Araba (northern Spain) and attributed to the family Potamidae (López-Horgue and Bodego, 2017).

The discovery of dactyli belonging to Potamidae (Fig. 1) in the Pliocene of Lo Ranxero (Baix Ebre, Catalonia), represents the second record of freshwater crabs in the Iberian Peninsula, and helps to understand the palaeogeobiographic distribution across the circum-Mediterranean area and Europe, and in addition, could fill the existing gap of the fossil record of primary freshwater crabs between the late Miocene and the Pleistocene of Europe (Klaus and Gross, 2009, fig. 1).

The outcrop is located in the lower Ebro river palaeovalley, the so-called Tortosa Graben, incised during the Tortonian-Messinian (late Miocene) between the Catalan Coastal Ranges and its Mediterranean outlet. The flooding of the Mediterranean Sea during the early Pliocene infilled of marine sediments the palaeovalley, subsequently, in late Pliocene and Quaternary, non-marine and alluvial sediments filled the palaeovalley (see Arasa-Tuliesa and Cabrera, 2018, figs. 3, 4C, 5A).

The Cenozoic rocks that crop out in the old clay quarries near Lo Ranxero (also known as Sant Nofre), in the Baix Ebre area, show seven differentiated lithostratigraphic units. The lowermost unit, the 'Pisolitic Clay', is attributed to the Paleocene. The overlying Neogene units such as the Miocene alluvial fan deposits of the 'Conglomerates of the Venta del Ranxero', and the 'Siliceous Conglomerates of Anguera', are attributed to the Tortonian-Messinian (late Miocene) Arasa-Tuliesa and Cabrera, 2018).

The Pliocene sedimentation began with the 'Gravel and Sands with Oysters' unit, considered a transgressive unit, where foreshore and shoreface units can be differentiated. The shallow marine deposits 'Blue Marls of Campredó' unit; within this unit, sandstone was deposited by high and medium storm density flow. The 'Sant Nofre Limestones' unit corresponds to palustrine and lacustrine deposits with expansive and retractive sequences. And the uppermost unit, 'Roca Corba conglomerates', that corresponds to debris flow and braided fluvial deposits that could be attributed to late Pliocene-early Pleistocene (Arasa-Tuliesa, 1990, fig. 2; Arasa-Tuliesa and Cabrera, 2018, fig. 3).

The dactyli presented herein, were recovered associated with freshwater gastropods (*Limnaea* sp.) and remains of indeterminate mammalian, in the lacustrine-palustrine 'Sant Nofre Limestones' levels, that would correspond to the late Pliocene (Agustí et al, 1983; Arasa-Tuliesa, 1990, 280-282, figs. 2, 10; Arasa-Tuliesa and Cabrera, 2018).

In absence of carapace remains, the serial teeth of the dactyli and the grooves and setal pits on their surface, allow – together with the origin from a freshwater facies – to classify the dactyli as of primary freshwater crab origin. We assign them to the genus *Potamon* Savigny, 1816, as

all European (fossil and extant) primary freshwater crabs belong to this genus (Gross and Klaus, 2005).

However, the isolated dactyli of Sant Nofre do not allow an species identification, although they present a remarkable resemblance to those of recent European species, such as *Potamon fluviatile* (Herbst, 1785) (e.g. Pretzmann, 1971, t. 1, fig. 1) and *P. ibericum* (Bieberstein, 1808) (ibid. t. 2, fig. 1), but also with fossil species such as *P. hegauense* Klaus and Gross, 2009 (see Klaus and Gross, 2009, fig. 2B) and *P. quenstedti* (Zittel, 1885) (ibid. fig. 4C). A similar taxonomic approach was taken for isolated dactyli of *Potamon* sp. from the Middle East which were compared with the recent *Potamon potamios* (Olivier, 1804) by Ashkenazi et al. (2005, fig. 4).

Comparisons with the dactyli of the Anatolian specimens of *Potamon* sp. found in the Pleistocene travertine outcrops of the Denizli Basin (SW Turkey) (see Fraaije et al., 2010; Pasini and Garassino, 2011), is not possible, since they are preserved with a thick layer of calcium carbonate that hides the diagnostic details. Anatolian *Potamon* sp. preserved in travertines, could have used thermal springs as local refugia during the Pleistocene glacial times (see Parvizi et al., 2019), according with observations by Klaus and Gross (2009, 15, 16) for Pleistocene *Potamon antiquum* Szombathy, 1916 in Hungary.

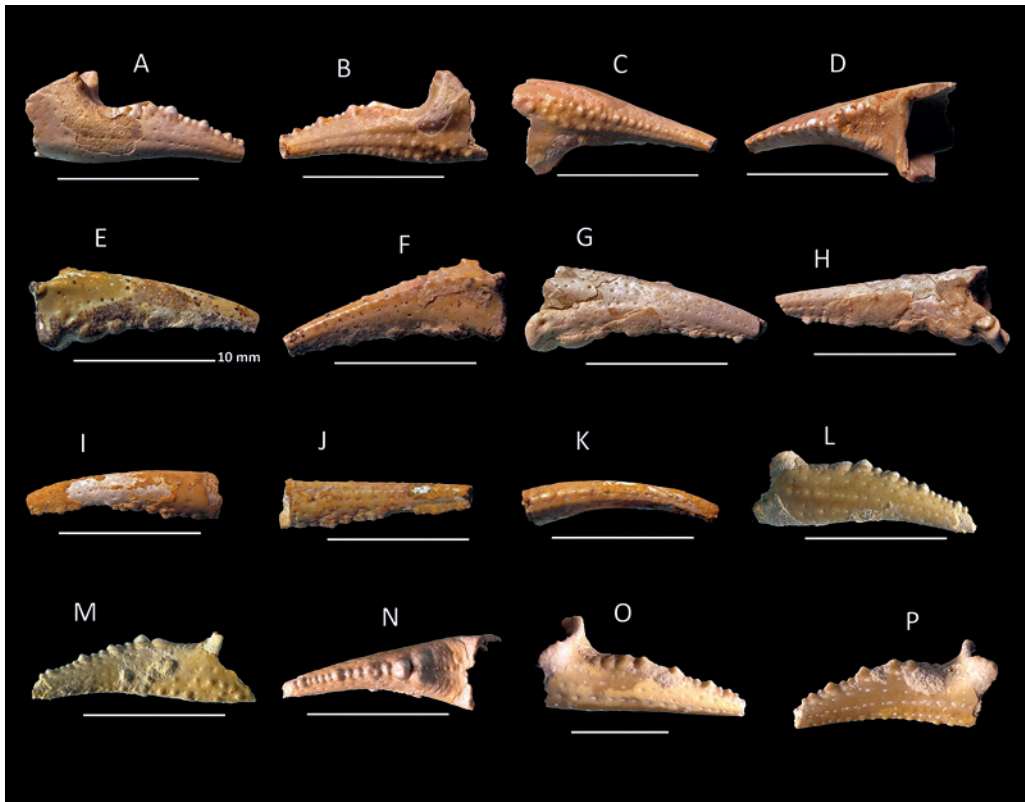


Figure 1. *Potamon* sp. from the Pliocene of Lo Ranxero (Baix Ebre, Catalonia). A-D. MTTE 32434, right pollex, A. outer side; B. inner side; C. lower margin; D. occlusal margin. E-F. MTTE 32462, right dactyl, E. outer side; F. inner side. G-H. MTTE 32912, right dactyl, G. outer side; H. inner side; I-K. MTTE 33015, left dactyl, I. outer side; J. inner side; K. upper margin. L-N. MTTE 34796, right pollex, L. outer side; M. inner side; N. occlusal margin. O-P. MTTE 35271 right pollex, O. outer side; P. inner side. Scale bar equal to 10 mm, except for O and P equal to 5 mm.

In no case, morphological similarities could indicate conspecificity of our specimens, with any of the taxa named above or with any of the other European species compiled by Klaus and Gross (2009), given the restricted taxonomic value of isolated dactyli.

The discovery of dactyli of *Potamon* sp. in the Pliocene of the northeastern of the Iberian Peninsula, expands the occurrence of the genus in Europe further west than the fossil (and extant) record so far indicated. Future work will help to glimpse the palaeogeographic and evolutionary history of the genus *Potamon* during the Cenozoic.

Acknowledgements

We are grateful to Sebastian Klaus for comments on an early version of the manuscript.

REFERENCES

- Agustí, J., Anadón, P. and Julià, R. 1983. Nuevos datos sobre el Plioceno del Baix Ebre. Aportación a la correlación entre las escalas marina y continental. *Acta Geológica Hispánica*, 18 (2), 123-130.
- Arasa-Tuliesa, A. 1990. El Terciario del Baix Ebre: Aportaciones estratigráficas y sedimentológicas. *Acta Geológica Hispánica*, 25 (4), 271-287.
- Arasa-Tuliesa, Á. and Cabrera, L. 2018. Neogene-Quaternary onshore record in the lower Ebro river incised palaeovalley (Ebro margin, Catalan Coastal Range, NE Iberia). *Geologica Acta*, 16, (3), 265-292.
- Ashkenazi, S., Motro, U., Goren-Inbar, N., Biton, R. and Rabinovich, R. 2005. New morphometric parameters for assessment of body size in the fossil freshwater crab assemblage from the Acheulian site of Gesher Benot Ya'akov, Israel. *Journal of Archaeological Science*, 32, 675-689.
- Bieberstein, M. 1808. Notice sur quelques Insectes du Caucase. *Memoires de la Société Impériale des Naturalistes de l'Université Impériale de Moscou*, 2, 3-5.
- Fraaije R.H.B., van Bakel B.W.M. and Jagt J.W.M. 2010. Exceptional preservation of Pleistocene freshwater crabs from southwest Turkey. *4th Symposium on Mesozoic and Cenozoic Decapod Crustaceans*, Eichstatt, 8.
- Gross, M. and Klaus, S. 2005. Upper Miocene freshwater crabs from the North-Western margin of the Styrian Basin (Brachyura, Potamoidea). *Berichte des Institutes für Erdwissenschaften der Karl-Franzens-Universität Graz*, 10, 21-23.
- Herbst, J.F.W. 1782-1804. *Versuch einer Naturgeschichte der Krabben und Krebse nebst einer Systematischen Beschreibung ihrer Verschiedenen Arten*. Gottlieb August Lange, Berlin & Stralsund, Volumes 1-3, 515 pp. + 62 pls.
- Klaus, S. and Gross, M. 2009. Synopsis of the fossil freshwater crabs of Europe (Brachyura: Potamoidea: Potamidae). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 256 (1), 39-59.
- López-Horgue, M.A. and Bodego, A. 2017. Mesozoic and Cenozoic decapod crustaceans from the Basque-Cantabrian Basin (western Pyrenees): new occurrences and faunal turnovers in the context of basin evolution. *Bulletin de la Société géologique de France*, 188 (14), 1-28.
- Olivier, G.A. 1804. Voyage dans l'Empire Ottoman, l'Égypte et la Perse, fait par ordre du gouvernement pendant les six premières années de la république, 4; Paris (Agasse).



- Parvizi, E., Keikhosravi, A., Naderloo, R., Solhjoui-Fard, S., Sheibak, F. and Schubart, C. 2019. Phylogeography of *Potamon ibericum* (Brachyura: Potamidae) identifies Quaternary glacial refugia within the Caucasus biodiversity hot spot. *Ecology and evolution*, 9 (8), 4749-4759.
- Pasini, G. and Garassino, A. 2011. Unusual scaled preservation samples on freshwater decapods (Crustacea, Decapoda) from the Pleistocene (Late Cenozoic) of Turkey and Kazakhstan. *Natural History Sciences*, 152 (1), 13-18.
- Pretzmann, G. 1971. Scheren und Scherenbezeichnung bei *Potamon* (Crustacea: Decapoda). *Annalen des Naturhistorischen Museums Wien*, 75, 489-493.
- Savigny, J.C. 1816. *Mémoires sur les animaux sans vertébrés*. 1. *Description et classification des animaux invertébrés et articulés*, G. Dufour, Paris, 118 pp.
- Szombathy, K. 1916. Die tertiären Formen der Gattung *Potamon* (*Telphusa*) und ihre paläarktischen Nachkommen. *Annales historico-naturales Musei Nationalis Hungarici*, Budapest, 14, 281-472.
- Zittel, K.A. 1885. *Molluska und Arthropoda*. Handbuch der Paläontologie, 2 (2), 679-721. (R. Oldenbourg, Munich).

"THE VINEYARD CRABS", THE APTIAN DECAPOD ASSEMBLAGE OF CAL CASSANYES (GARRAF MASSIF, ALT PENEDEÈS, CATALONIA, NE IBERIAN PENINSULA)

Àlex Ossó¹, Barry.W.M. van Bakel², Pedro Artal³ and Josep Anton Moreno-Bedmar⁴

¹ Llorenç de Villalonga, 17B, 1-1 43007 Tarragona, Catalonia, Spain. aosso@tinet.cat

² Department of Earth Sciences, Faculty of Geosciences, Utrecht University, Budapestlaan 4, 3584 CD Utrecht, the Netherlands, and Oertijdmuseum, Bosscheweg 80, 5283 WB Boxtel, the Netherlands. b.w.m.vanbakel@uu.nl

³ Museu de Geologia del Seminari de Barcelona. Diputació, 231, 08007 Barcelona, Catalonia, Spain. artal.pedro@gmail.com

⁴ Instituto de Geología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Coyoacán, 04510, México, D.F. (Mexico). josepamb@geologia.unam.mx

Keywords: Decapoda, Brachyura, Podotremata, Sponge patch reef, Cretaceous, Iberian Peninsula

A first report of decapods from Cal Cassanyes (Casa Alta) was done by Vía (1951), when he described one chela attributed to *Homarus edwardsi* Robineau-Desvoidy, 1849, and also remains of one carapace and one chela attributed to *Distefania centrosa* Van Straelen, 1940 (= *D. incerta* [Bell, 1863]). It was not until 2008, that Moreno-Bedmar et al. (2008) presented a preliminary note reporting the decapod assemblage. New finds in the outcrop allow to present a more detailed report showing the high decapod diversity of the Cal Cassanyes outcrop.

In the Cal Cassanyes area, Aptian marine strata crops in several vineyards. The vineyard located in the highest topographical position in the northwest, the informally so-called "vineyard above", is the one that yielded the decapod assemblage. In this vineyard the middle part of the Marls of Vallcarca unit crops out, and consists in yellowish to ochre marls, marly limestone and grayish limestones that ranges between the uppermost lower Aptian to the lowermost upper Aptian (*Dufrenoyia furcata* and *Epicheloniceras martini* ammonite Biozones respectively). This stratigraphical interval belongs to the subunit known as 'Porifera marls' due to its extraordinary abundance of sponges (Moreno-Bedmar et al., 2008).

This small outcrop has yielded a large number of mainly siliceous sponges, nautiloids, ammonites, echinoids, bivalves, crinoids, brachiopods and the decapod assemblage reported herein.

The abundance of sponges on this site indicate the presence of nutrients, and even without being a true bioherm, would perform the similar functions as a patch reef serving as a shelter for many invertebrates, including decapods. The decapods are low in number, no more than forty specimens from a small area, ranging from near-complete carapaces to just fragments or isolated chelae, but show a great diversity.

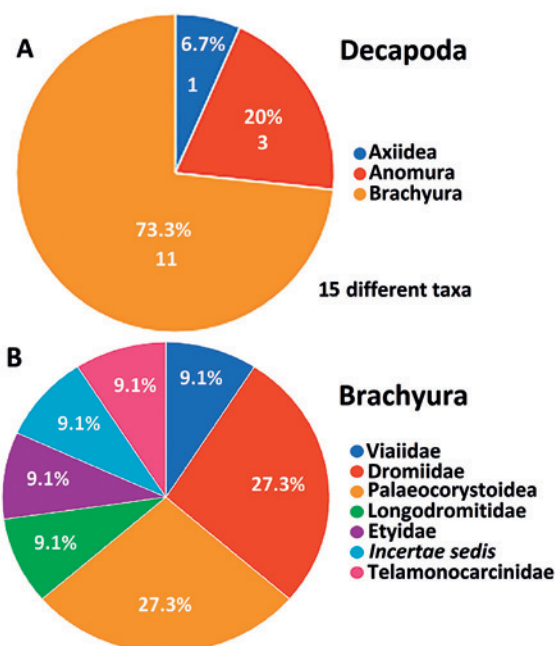


Figure 1. A. Pie chart showing the composition of the Cal Cassanyes decapod assemblage by main groups and number of taxa. B. Pie chart showing the composition of the main group Brachyura at familial or suprafamilial level.

The high diversity of this decapod assemblage is represented by fifteen different taxa including Axiidae, Anomura and Brachyura, with the latest group being the best represented with eleven different taxa. Among them, the dromiids and palaeocorystoids are the best represented, both in number of species and specimens (Fig. 1).

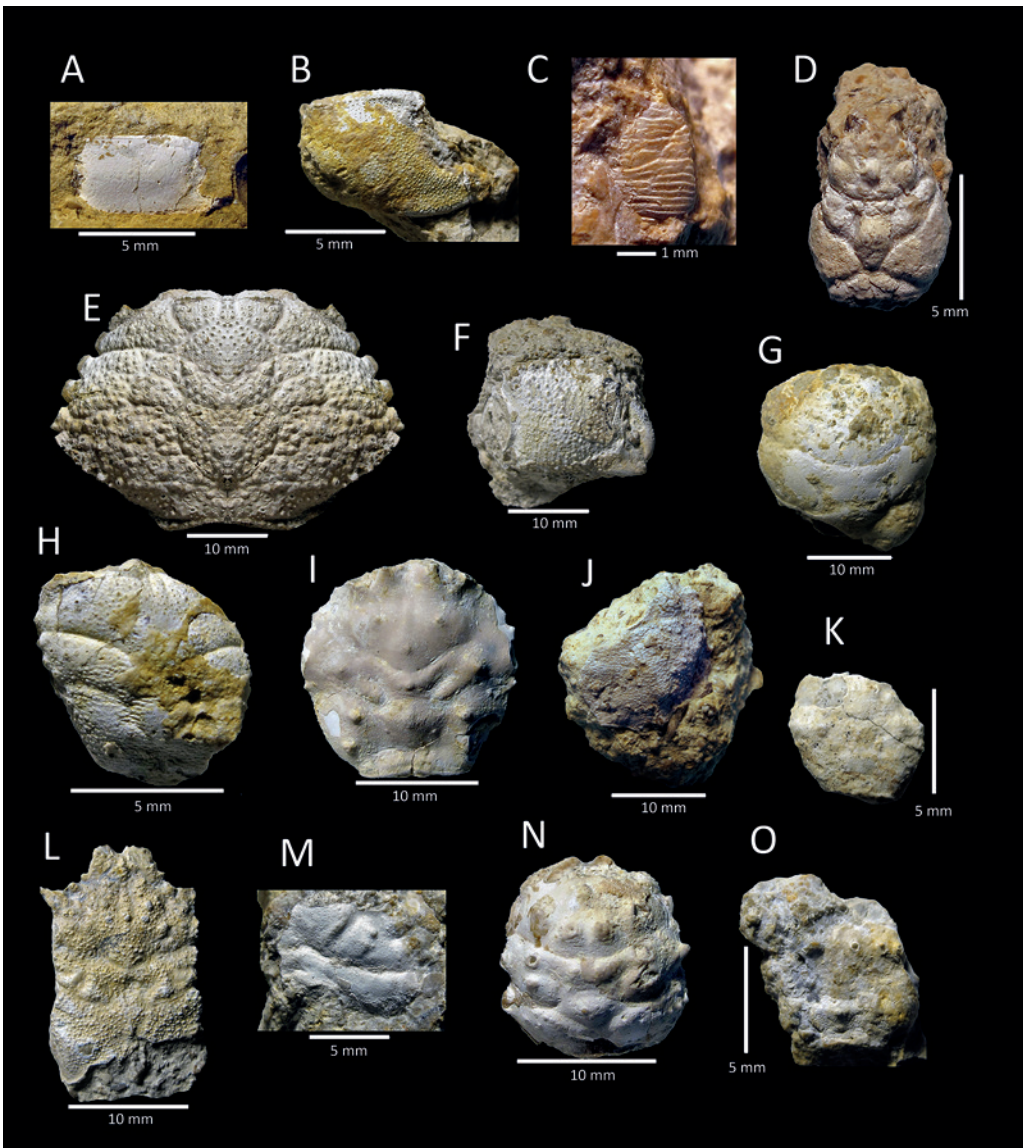


Figure 2. Representatives of the Cal Cassanyes decapod assemblage. A. "*Callianassa*" undetermined MGSB86072a. B. "*Pagurus*" nov. sp. MGSB74530. C. *Eomunidopsis* cf. *navarrensis* (Van Straelen, 1940) MGSB86073a. D. *Vectis* nov. sp. MGSB 86061. E- F. *Distefania incerta* (Bell, 1863). E. MGSB74549c (digital composition). F. MGSB74549a. G. *Eodromites* sp. MGSB74543a. H, *Goniodromites laevis* (Van Straelen, 1940) MGSB86074. I, *Necrocarcinus* nov. sp. MGSB74538. J. ?*Pseudonecrocarcinus* sp. MGSB86075. K. ?*Paranecrocarcinus* sp. MGSB86076. L. "*Glaessnerella*" *angusta* (Wright and Collins, 1972) MGSB86077. M. *Etyxanthosia fossa* (Wright and Collins, 1972) MGSB74550. N. *Mesodromilites* nov. sp. MGSB74540a. O. ?*Withersella* MGSB86078. Abbreviations. MGSB: Museu de Geologia del Seminari de Barcelona.

The different taxa recognized at the site are: "*Callianassa*" sp.; "*Pagurus*" nov. sp.; paguroid ind.; *Eomunidopsis* cf. *navarrensensis* (Van Straelen, 1940); *Vectis* nov. sp.; *Distefania incerta* (Bell, 1863) being by far the most abundant species at the site; *Eodromites* sp.; *Goniodromites laevis* (Van Straelen, 1940); *Necrocarcinus* nov. sp.; ?*Paranecrocarcinus* sp.; ?*Pseudonecrocarcinus* sp.; "*Glaessnerella*" *angusta* (Wright and Collins, 1972) representing potentially a new genus; *Etyxanthosia fossa* (Wright and Collins, 1972), being the oldest record of the species; *Mesodromilites* nov. sp., also being the oldest record of the genus; and the eubrachyuran, ?*Withersella* (Fig. 2).

The Cal Cassanyes decapod assemblage appears as a mix of reef-associated, and non-reef-associated crabs, and shows great similarities, with the lower Aptian fauna of the Isle of Wight (Wright and Collins, 1972) and the late Albian of Navarra (Klomp maker, 2013). Cal Cassanyes has been revealed as the locality with the highest diversity of fossil decapods, especially Brachyura, in the Aptian of the Iberian Peninsula and one of the richest in the world known so far.

REFERENCES

- Bell, T. 1863. *A monograph of the fossil malacostracous Crustacea of Great Britain, Pt. II, Crustacea of the Gault and Greensand*. Palaeontographical Society Monograph, London, 1-40, 11 pls.
- Klomp maker, A. A. 2013. Extreme diversity of decapod crustaceans from the mid-Cretaceous (late Albian) of Spain: Implications for Cretaceous decapod paleoecology. *Cretaceous Research*, 41, 150-185.
- Moreno-Bedmar, J.A., Ferrer, O., Artal, P., Bover-Arnal, T., Company, M., Gallemí, J., Martín-Closas, C., Martínez, R., Ossó, A., Salas, R. and Villalba-Breva, S. 2008. Bioestratigrafía integrada del Aptiense del Macizo del Garraf (Cadenas Costero-Catalanas, NE de España). Datos preliminares. Libro de resúmenes. XXIV Jornadas de la Sociedad Española de Paleontología. Museo del Jurásico de Asturias (MUJA), Colunga, 15-18 de octubre de 2008 (Eds. J.I. Ruiz-Omeñaca, L. Piñuela & J.C. García-Ramos), p. 158-159.
- Robineau-Desvoidy, J.B. 1849. Mémoire sur les Crustacés du terrain néocomien de St. Sauveur-en-Puisaye. *Annales de la Société Entomologique de France*, (2) 7, 95-141, pls. 4, 5.
- Van Straelen, V. 1940. Crustacés décapodes nouveaux du Crétacique de la Navarre. *Bulletin du Musée Royal d'Histoire naturelle de Belgique*, 16, 1-5.
- Vía, L. 1951. Contribución al estudio de los decápodos del secundario en España. *Anales de la Escuela de Peritos Agrícolas y de Especialidades Agropecuarias y de los Servicios Técnicos de Agricultura*, 10, 151-181.
- Wright, C.W. and Collins, J.S.H. 1972. British Cretaceous crabs. *Palaeontographical Society Monographs*, 126 (533), 1-113.

AN EARLY TOURIST: WHEN *CANCER PAGURUS* VISITED ANDALUSIA. FIRST RECORD IN THE MEDITERRANEAN PLIOCENE.

Àlex Ossó^{1*}, Pere Abelló² and Guillermo Díaz Medina³

¹ Llorenç de Villalonga, 17B, 1-1, 43007 Tarragona, Catalonia, Spain. aosso@tinet.cat

² Institut de Ciències del Mar (ICM-CSIC), Passeig Marítim 37-49, 08003 Barcelona, Catalonia, Spain. pabello@icm.csic.es

³ Plaza de las Viñas, 18PC, 18200 Maracena, Granada, Spain. diazmedinaguillermo2@gmail.com

Keywords: brown crab, Cancridae, Edible crab, Iberian Peninsula Piacenzian, Zanclean

The unexpected discovery of a specimen of *Cancer pagurus* Linnaeus, 1758, in the Pliocene strata of the southeastern Iberian Peninsula, in the surroundings of El Ejido (Almería, Spain), reveals a first attempt of incursion of this species in the Mediterranean Sea.

The recovered specimen (Fig. 1) can be attributed to *Cancer pagurus* with confidence. Indeed, its big size (about 125 mm width), the smooth transversely ovate carapace with nine subquadrate teeth, the narrow trifold front and strong chelae with four longitudinal ridges, leave no doubt about its specific attribution.

The oldest records of *Cancer pagurus* are the specimens reported by van Bakel *et al.* (2003, 102, 103, pl. 5, figs. 1-9, and references therein) from the Piacenzian Lillo Formation (late Pliocene) of Antwerp (Belgium).

In the Dalías field, Unit I sediments belong to the Loco formation (Aguirre, 1998). According to Aguirre (1998), the top of Unit I is dated between FO *Globorotalia crassaformis* (i.e., 3.60 mya: Lourens *et al.*, 2004) and top of the Mpl 4 [from 3.31 mya (Lourens *et al.*, 2004); (3.323 mya in Sprovieri *et al.*, 2006) to 3.19 mya (Lourens *et al.*, 2004) (3.211 mya in Sprovieri *et al.*, 2006)].

Aguirre (1995) points out the co-occurrence in the area (Western Coast of Almería) of the planktonic foraminifera *Sphaeroidinellopsis* Banner and Blow, 1959, *Globorotalia crassaformis* Galloway and Wissler, 1927, *G. bononiensis* Dondi, 1962 and *G. puncticulata* Deshayes, 1832 in the green fine sands (which correspond on the top of Unit I). Indeed, FO *Globorotalia crassaformis* is dated to 3.60 mya (Lourens *et al.*, 2004), FO *G. bononiensis* is dated to 3.59 mya (Sprovieri *et al.*, 2006), FO *G. puncticulata* is dated to 4.52 mya (Lourens *et al.*, 2004) and LO *G. puncticulata* is dated to 3.57 mya (Lourens *et al.*, 2004).

These facts permit to constrain the age of the base of the studied series (green fine sands), which conformably underlies the crab-bearing strata, between the FO *Globorotalia bononiensis* and the LO *G. puncticulata*, that is, at the base of the Piacenzian stage (3.59-3.57 mya).

Another cancrroid crab, *Lobocarcinus sismondai* (von Meyer, 1843), was widely spread throughout the western Mediterranean Sea, including the south of the Iberian Peninsula, from the middle-late Miocene to the Pleistocene. This fossil species may probably be the same species known presently as *Cancer bellianus* Johnson, 1861 (see Garassino *et al.* in Baldanza *et al.*, 2013, p. 34). Differing from *C. pagurus*, which is mainly a shallow-water species, *C. bellianus* is a deeper species inhabitant of the continental shelf and upper slope (Zariquiey Álvarez, 1968; González, 1995; d'Udekem d'Acoz, 1999).

The edible crab, also called brown crab, *Cancer pagurus*, is a well-known crab species (Edwards, 1979) that presently inhabits North Atlantic waters from Portugal to Norway (d'Udekem d'Acoz, 1999. Bakke *et al.*, 2018). It has been rarely reported in the Mediterranean Sea (Zibrowius, 1991; d'Udekem d'Acoz, 1999; GBIF, 2021; WORMS, 2021), where it does not constitute viable populations. Presently, *Cancer pagurus* does not establish populations in the Mediterranean, although it has been reported in the Tyrrhenian (late Pleistocene) of Sicilia (Berdar and Guglielmo, 1979).

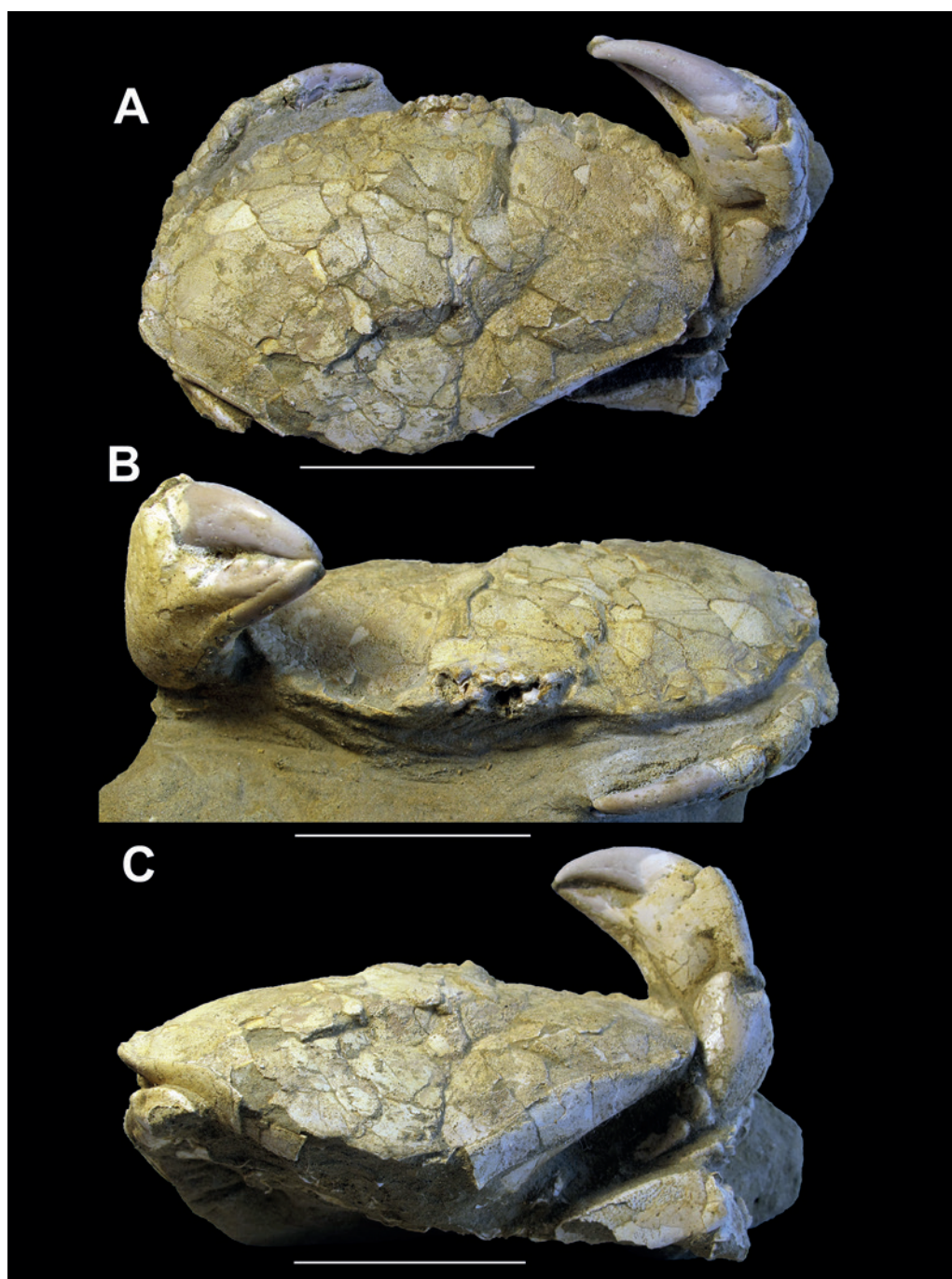


Figure 1. A-C. *Cancer pagurus* Linnaeus, 1758, CECOPAn 512 from the Pliocene of El Ejido (Almería, Spain). A. Dorsal view. B. Frontal view. C. Posterior view. Scale bar = 50 mm.

It is known that *Cancer pagurus* is a stenothermal crab, with a narrow range about 5°-8°, but that it also has high capacity of acclimation (Cuculescu *et al.*, 1998). Thus, its presence in the Mediterranean in apparently subtropical warm waters could be related to the more and more frequent climatic changes, such as in the deterioration at the end of the Zanclean and the cooling-warm trend in the Pleistocene (Taviani, 2002).

Its current presence in the Mediterranean may be due to different incursion attempts over time or to anthropic causes, since crabs of Atlantic origin are often sold alive in Mediterranean markets (personal observations), and that the Pliocene specimen from Almeria was perhaps a stray crab. In any case, it is the southernmost record of this species during the Pliocene and perhaps, if the age of the strata is confirmed, the oldest fossil record of *Cancer pagurus*.

REFERENCES

- Aguirre, J. 1995. *Tafonomía y Evolución Sedimentaria del Plioceno Marino en el Litoral sur de España entre Cádiz y Almería*. Tesis Doctoral, Universidad de Granada, 419 pp.
- Aguirre, J. 1998. El Plioceno del SE de la Península Ibérica (provincia de Almería). Síntesis estratigráfica, sedimentaria, bioestratigráfica y paleogeográfica. *Revista de la Sociedad Geológica de España*, 11 (3-4), 297-316.
- Bagke, S., Larssen, W. E., Woll, A. K., Søvik, G., Gundersen, A. C., Hvingel, C. and Nilssen, E. M. 2018. Size at maturity and molting probability across latitude in female *Cancer pagurus*. *Fisheries Research*, 205, 43–51.
- Baldanza, A., Bizzarri, R., Famiani, F., Garassino, A., Hyžný M. and Pasini, G. 2013. The bathyal decapod crustacean community from the Poggio i Sodi quarries (Siena Basin, Tuscany, Italy). *Boletín de la Sociedad Geológica Mexicana*, 65 (2), 335-353.
- Banner, F.T., and Blow, W.H. 1959. The classification and stratigraphical distribution of the Globigerinaccae, Part 1. *Palaeontology*, 2 (1), 1-27.
- Berdar, A. and Guglielmo, L. 1979. Reperti di *Cancer pagurus* L. nel pleistocene superiore di Poggio Paradiso (Messina). *Memorie di Biologia Marina e di Oceanografia*, 8 (6), 175-184.
- Cuculescu, M., Hyde, D. and Bowler, K 1998. Thermal tolerance of two species of marine crab, *Cancer pagurus* and *Carcinus maenas*. *Journal of Thermal Biology*, 23 (2), 107-110.
- Deshayes, G.P. 1832. *Encyclopedie methodique: Histoire naturelle des vers*. Volume 2 (2), 145-594.
- Dondi, L. 1962. Nota paleontologica stratigrafica sul pedeappennino padano. *Bollettino della Società Geologica Italiana* 81, 113-229.
- d'Udekem d'Acoz, C. 1999. Inventaire et distribution des crustacés décapodes de l'Atlantique nord-oriental, de la Méditerranée et des eaux continentales adjacentes au nord de 25°N. *Patrimoines Naturels* (M.N.H.N./S.P.N.) 40, 1-383.
- Edwards, E. E. 1979. *The edible crab and its fishery in British waters*. Fishing new books Ltd. Farnham, Surrey, England, 1-135 pp.
- Galloway, J.J. and Wissler, S.G. 1927. Pleistocene foraminifera from the Lomita Quarry, Palos Verdes Hills, California. *Journal of Paleontology*, 1, 35-87.
- GBIF 2021. *Cancer pagurus* Linnaeus, 1758 in GBIF Secretariat (2021). GBIF Backbone Taxonomy. Checklist dataset <https://doi.org/10.15468/39omei> accessed via GBIF.org on 2021-12-10.



- González, J. A. 1995. *Catálogo de los Crustáceos Decápodos de las islas Canarias*. Publ. Turquesa, Santa Cruz de Tenerife, 282 pp., Figs 1–190.
- Johnson, J. Y. 1861, Description of a new species of *Cancer* obtained at Madeira: Proceedings of the Scientific Meetings of the Zoological Society of London, 16, 240–242.
- Linnaeus, C. 1758. *Systema Natura per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*. Vol. 1, Holmiae, Laurentii Salvii. iii + 824 pp.
- Lourens, L. J., Antonarakou, A., Hilgen, F. J., Van Hoof, A. A. M., Vergnaud-Grazzini, C., Hilgen, F. J., Shackleton, N. J., Laskar, J. and Wilson, D. 2004. *The Neogene Period*. In Gradstein, F. (Ed.), *A Geologic Time Scale 2004*. 21. Cambridge University Press, 409–440.
- Meyer H. von 1843. Briefwechsel Mittheilungen an der Geheimenrath v. Leonhard gerichtet. *Neues Jahrbuch für Mineralogie, Geologie, und Paläontologie*, 570–590.
- Sprovieri, R., Sprovieri, M., Caruso, A., Pelosi, N., Bonomo, S. and Ferraro, L. 2006. Astronomic forcing on the planktonic foraminifera assemblage in the Piacenzian Punta Piccola section (southern Italy). *Paleoceanography*, 21, PA4204.
- Taviani M. 2002). The Mediterranean benthos from late Miocene up to present: ten million years of dramatic climatic and geologic vicissitudes. *Biologia Marina Mediterranea*, Genova, 9, 445–463.
- van Bakel, B.W.M., Jagt, J.W.M., Fraaije, R.H.B. and Wille, E.R.H. 2003. Piacenzian (Pliocene) decapod crustacean faunules from northwest Belgium. *Bulletin of the Mizunami Fossil Museum*, 30, 97–108.
- WoRMS (2021). *Cancer pagurus* Linnaeus, 1758. Accessed at: <https://www.marinespecies.org/aphia.php?p=taxdetails&id=107276> on 2021-12-10
- Zariquiey Álvarez R. 1968. *Crustáceos decápodos ibéricos*. Inv. Pesq., Barcelona, 32, i-xv + 1–510 pp.
- Zibrowius, H. 1991. Ongoing modification of the Mediterranean marine fauna and flora by the establishment of exotic species. *Mésogée*, 51, 83–107.

AN UNUSAL ACCUMULATION OF DECAPOD CRUSTACEAN FINGERS FROM THE LATEMOST MAASTRICHTIAN OF THE SOUTHERN PYRENEES (NE SPAIN)

Manuel Pérez-Pueyo¹, Fernando Ari Ferratges¹, Carmen Núñez-Lahuerta^{1,2}, Julia Galán^{1,3}, Eduardo Puértolas-Pascual^{1,4}, Beatriz Bádenas¹ and José Ignacio Canudo¹

¹ Grupo Aragosaurus-IUCA, Facultad de Ciencias, Universidad de Zaragoza, C/Pedro Cerbuna, 12, 50009 Zaragoza, Aragón, Spain. manuppueyo@unizar.es

² Institut de Paleoeecologia Humana i Evolució Social (IPHES), Zona Educacional, Campus Sescelades URV (Edifici W3) E3, 43700 Tarragona, Spain. carmennunezlahuerta@gmail.com

³ Departamento de Geología, Facultad de Ciencia y Tecnología, Euskal Herriko Unibertsitatea, UPV/EHU, Barrio Sarriena s/n, 48940, Leioa, Spain.

⁴ GeoBioTec, Departamento de Ciências da Terra, Faculdade de Ciências e Tecnologia, Universidade Nova de Lisboa, Monte da Caparica, Campus FCT, 2829-516 Caparica, Portugal.

Keywords: Brachyuran decapods, dinosaurs, fixed and mobile fingers, digestion, lagoonal environment

INTRODUCTION

Fossil brachyurans associated with dinosaur remains are scarce in the fossil record, and only few occurrences have been documented (e.g., Marmi *et al.*, 2016; Robin *et al.*, 2019; Luque *et al.*, 2021). In this work, we present several remains of decapod crustaceans recovered from the upper Maastrichtian outcrops of the Southern Pyrenees, in the municipality of Beranuy (Huesca, Aragón, NE Spain) that appear associated with dinosaur bones.

The fossils were found in the Veracruz 1 site, located at the lower part of the Tremp Fm, the lithostratigraphic unit encompassing the Maastrichtian and the Paleocene deposits in the South-Pyrenean Basin. The Mesozoic part of the formation in the Beranuy area is dated as uppermost Maastrichtian, within chron C29r, which encompasses the K/Pg boundary (Puértolas-Pascual *et al.*, 2018). This interval is composed by a transitional and a continental subunit: 'Grey Garumnian' and 'Lower Red Garumnian', respectively. Veracruz 1 is located in a thick grey marly mudstone deposit within the upper part of the lagoonal 'Grey Garumnian unit'. The site is rich in fossils, including rizoliths, charcoalified wood, charophytes, foraminifera, bivalves, gastropods, crabs and several groups of vertebrates, including fishes, testudines, crocodylomorphs and dinosaurs (theropods and hadrosaurids) (Pérez-Pueyo *et al.*, 2019). These fossil-rich marly mudstones accumulated in a pond within a partially vegetated fringe of a lagoon, then with both marine and continental influence. Charophyte association (under study) indicates salinity fluctuations between fresh and brackish conditions.

RESULTS

The studied crab fossils correspond to several isolated mobile and fixed fingers of indeterminate brachyurans. These fossils are housed at the Museo de Ciencias Naturales de la Universidad de Zaragoza (abbreviation MPZ). Two morphotypes (A and B) can be recognized in the assemblage. Morphotype A is represented by robust mobile and fixed fingers, dark colored, with several lined setal pits, both in the inner and outer margins (Fig. 1A-D). The fingers show a strong calcification, mottled texture of the cuticle in the upper margin and are slightly curved towards occlusal, more markedly in mobile fingers. However, their most distinctive feature is the molariform teeth of the occlusal margin of the fingers, which may point to a durophagous diet. There are 4-5 molariform teeth per finger, being the most proximal one the most developed. Until now, 15 right mobile fingers and 16 right fixed fingers have been found. The only left element found is a mobile finger. This marked bias towards right side elements could be pointing to an heterochelic condition. The length from the tip to the most proximal molariform ranges between 2.33 to 1.12 cm in mobile fingers and between 2.37 to 0.88 cm in fixed fingers.

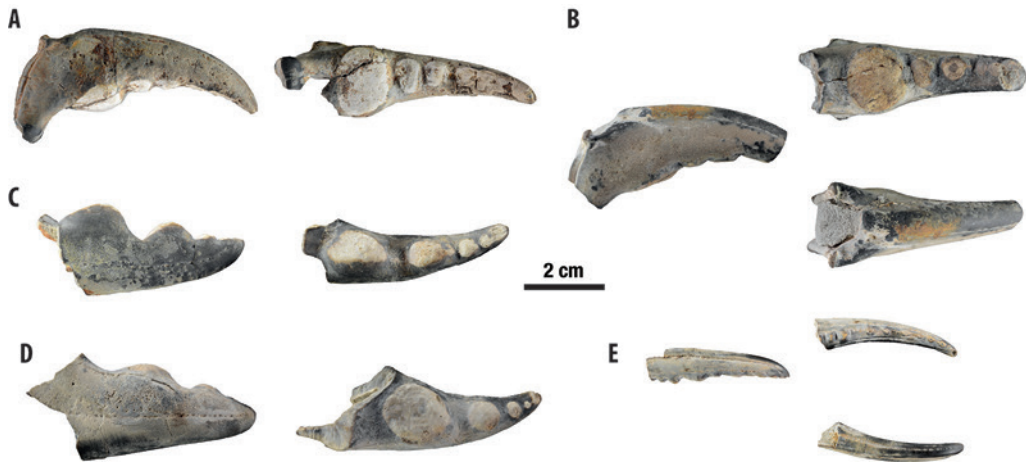


Figure 1. Crustacean decapod fingers from Veracruz 1 site. A. MPZ2022/184, right mobile finger in outer and occlusal views. B. MPZ2022/185, right mobile finger in outer, occlusal and dorsal views. C. MPZ2022/186, right fixed finger in outer and occlusal views. D. MPZ2022/187, right fixed finger in outer and occlusal views. E. MPZ2022/188, right mobile finger in outer, occlusal and dorsal views.

Morphotype B is represented by slender and elongated fingers (Fig. 1E) which, compared to morphotype A, are smaller and lack molariform elements in the occlusal margin. Instead, they have small sharp triangular teeth, which are tightly packed. 3 left and 2 right dactyli, and 1 left and 3 right fixed fingers have been recognized. Both fingers also show the lineation of setal pits in the inner and outer margins, plus an additional one in the dorsal/ventral margin. The length from the tip to the most proximal teeth ranges between 1.77 to 0.31 cm in mobile fingers and between 0.38 to 0.35 cm in fixed fingers.

In overall, the mobile and fixed fingers show good preservation, sometimes even keeping the mottled texture of the cuticle. Some of the dactyli of morphotype A preserve their articular facets, pointing that most of them were separated from the chela by disarticulation or by breakage of the manus. By contrast, in morphotype B the facets are all broken. Dissolution areas and fractures can be observed in some fingers, as well as the loose of the tip of the finger in some few cases. In morphotype A, some molariform elements show wear facets.

DISCUSSION AND CONCLUSIONS

The unusual accumulation of isolated fingers of crustacean decapods at Veracruz 1 site raises certain questions about the genesis of the crab accumulation. This preferential preservation of crab claw elements may be explained by their higher degree of calcification and greater resistance to degradation and weathering (Krause *et al.*, 2011). The lack of other anatomical elements hinders proper taxonomical attribution of the crabs of Veracruz 1, and thus, palaeoecological inferences cannot be proposed with confidence; i.e, there are no criteria to determine if these crabs correspond to allochthonous remains of marine decapods or belong to autochthonous brackish/freshwater living crabs. The general good preservation of the crab fingers, and the presence of both small and big fingers may support, *a priori*, that resedimentation was mild or null.

An alternative hypothesis to explain the studied accumulation of crab fingers relates to predation. Crab dactyli and pollicis are the most common element preserved in gastric pellets of extant birds that predate crabs (e.g., Munilla, 1997), due probably to their higher calcification. Several groups of archosaurs, including some theropod dinosaurs, pterosaurs and crocodylomorphs were known to produce gastric pellets (Myhrvold, 2012; Jiang *et al.*, 2022). Then, the

accumulation of crabs' fingers at Veracruz 1 site may be the result of predation by a medium to big sized archosaur and the posterior vomit of the fingers. Further research is needed to validate this hypothesis, including a better understanding of the digestion and fracture patterns on crabs predated by extant archosaurs (birds, crocodiles). For this purpose, it is necessary to identify the main predation-related features on extant crab elements within gastric pellets and to carry on a proper comparison with the fossil elements.

Acknowledgements

This research was funded by the Spanish Ministry of Science and Innovation, the European Regional Development Fund, the Government of Aragón (Grupo Aragosaurus: Recursos geológicos y Paleoambientes), project CGL2017-85038-P. M.P.P. and F.A.F. are funded FPU grants FPU16/03064 and FPU17/03623, of Spanish Ministry of Science and Innovation. Isabel Pérez photographed the fossils. C.N.-L. is the recipient of a Juan de la Cierva-Formación contract (FJC2020-044561-I) supported by the MCIN cofinanced by the NextGeneration EU/PRTR. J.G. is the recipient of a UPV/EHU contract for PhD research staff specialization 2020 (ESPD0C20/83).

REFERENCES

- Jiang, S., Wang, X., Zheng, X., Cheng, X., Wang, X., Wei, G. and Kellner, A. W. 2022. Two emetolite-pterosaur associations from the Late Jurassic of China: showing the first evidence for antiperistalsis in pterosaurs. *Philosophical Transactions of the Royal Society B*, 377 (1847), 20210043.
- Krause Jr, R. A., Parsons-Hubbard, K. and Walker, S. E. 2011. Experimental taphonomy of a decapod crustacean: Long-term data and their implications. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 312 (3-4), 350-362.
- Luque, J., Xing, L., Briggs, D.E.G., Clark, E.G., Duque, A., Hui, J., Mai, H. and McKellar, R.C. 2021. Crab in amber reveals an early colonization of nonmarine environments during the Cretaceous. *Science Advances*, 7, eabj5689.
- Marmi, J., Blanco, A., Fondevilla, V., Dalla Vecchia, F.M., Sellés, A.G., Vicente, A., Martín-Closas, C., Oms, O. and Galobart, A. 2016. The Molí del Baró-1 site, a diverse fossil assemblage from the uppermost Maastrichtian of the southern Pyrenees (North-Eastern Iberia). *Cretaceous Research*, 57, 519-539.
- Munilla, I. 1997. Henslow's swimming crab (*Polybius henslowii*) as an important food for yellow-legged gulls (*Larus cachinnans*) in NW Spain. *ICES Journal of Marine Science*, 54 (4), 631-634.
- Myhrvold, N. P. 2012. A call to search for fossilised gastric pellets. *Historical Biology*, 24 (5), 505-517.
- Pérez-Pueyo, M., Gilabert, V., Moreno-Azanza, M., Puertolas-Pascual, E., Bádenas, B. and Canudo, J.I. 2019. Late Maastrichtian fossil assemblage of Veracruz 1 site (Beranuy, NE Spain): wildfires and bones in a transitional environment, in: *VIII Jornadas Internacionales Sobre Paleontología de Dinosaurios y Su Entorno*. Salas de Los Infantes (Burgos) Spain. Salas de los Infantes Burgos Spain, pp. 111-113.
- Puértolas-Pascual, E., Arenillas, I., Arz, J.A., Calvín, P., Ezquerro, L., García-Vicente, C., Pérez-Pueyo, M., Sánchez-Moreno, E.M., Villalain, J.J. and Canudo, J.I., 2018. Chronostratigraphy and new vertebrate sites from the upper Maastrichtian of Huesca (Spain), and their relation with the K/Pg boundary. *Cretaceous Research*, 89, 36-59.
- Robin, N., van Bakel, B.W.M., Hyžný, M., Cincotta, A., Garcia, G., Charbonnier, S., Godefroit, P. and Valentin, X. 2019. The oldest freshwater crabs: Claws on dinosaur bones. *Scientific Reports*, 9, 20220.



EXPANDING THE FOSSIL SQUAT LOBSTER RECORD IN NORTH AMERICA AND EUROPE

Cristina M Robins¹, Adiël A Klompmaker¹, Sten L. Jakobsen² and Emma Sheldon³

¹ Department of Museum Research and Collections & Alabama Museum of Natural History, University of Alabama, Box 870340, Tuscaloosa, Alabama 35487, USA. cristina.robins@gmail.com, adielklompmaker@gmail.com

² Geomuseum Faxe, Østsjælland Museum, Rådhusvej 2, 4640 Faxe, Denmark. stenlennart@yahoo.dk

³ Geological Survey of Denmark and Greenland, Øster Voldgade 10, 1350 Copenhagen, Denmark. es@geus.dk

Keywords: Galatheaidea, squat lobster, new taxa

Modern squat lobsters within the Galatheaidea superfamily thrive in all marine ecosystems and are extremely diverse with upwards of 1300 described species. Their fossil record, starting in the Middle Jurassic, is sparse in comparison with only ~200 species described. Additionally, many squat lobsters have been incompletely illustrated or inadequately described, which lends confusion to their overall classification. By examining specimens previously ascribed to known species in the literature and additional specimens in museum collections, we have determined five new species and one new genus of squat lobsters. These new species come from Europe and North America – one from the Kimmeridgian (Late Jurassic) of Germany, two from the Barremian (Early Cretaceous) of Mexico, and two from the Danian (Paleocene) of Denmark. One new genus is erected from the Ypresian (Eocene) of Italy. All new galatheid species were found within coral-associated limestones, consistent with most other known fossil galatheoids. Our work adds to galatheid diversity in deep time by ~2.5%.

ENRICO NICOLIS' SPECIMENS IN ALEXANDER BITTNER'S STUDIES

Giuliano Tessier¹, Claudio Beschin², Alessandra Busulini¹, Roberto Zorzin³

¹ Società Veneziana di Scienze Naturali, c/o Museo di Storia Naturale di Venezia Giancarlo Ligabue, Santa Croce 1730, 30135 Venezia, Italy. busulini@tin.it, giultess@virgilio.it

² Museo Civico "G. Zannato", Piazza Marconi 15, 36075 Montebelluna Maggiore (Vicenza), Italy. beschin.cl@libero.it

³ Museo Civico di Storia Naturale di Verona, Lungadige Porta Vittoria, 9, 37129 Verona, Italia. roberto.zorzin@comune.verona.it

Keywords: Crustaceans, Brachyura, Historical holotypes, Eocene, NE Italy

The rich "Nicolis" geological collection is housed in the Natural History Museum in Verona (Italy). Cavaliere Enrico de Nicolis (1841-1908) (Fig.1.1), Veronese, incorporated beside his commercial activity accurate geological studies. His competence in the latter subject even allowed him in 1882 the development of the 1:75,000 geological map of the province of Verona with its explanatory notes.

His legacy also includes a good number of specimens of fossil crustaceans found in Tertiary rocks from Venetia (NE Italy) that are being reviewed by the authors at the moment.

Nicolis committed some carapaces of its collection to be determined by Alexander Bittner (1850–1902) who had already carried out studies about Eocene crustaceans from Venetia (Bittner, 1875). So, some specimens left from the newborn Kingdom of Italy to Vienna in the Austro-Hungarian Empire: this cooperation resulted in the discovery of some new species (Bittner, 1884, 1886) (Figs 1.2-4).

All the holotypes that are only known by the original drawings in publications have been now located and it would be possible to provide for them a modern scientific work including proper photography.

REFERENCES

Bittner, A. 1875. Die Brachyuren des Vicentinischen Tertiärgebirges. *Denkschriften der kaiserlichen Akademie der Wissenschaften in Wien*, 34, 63-106.

Bittner, A. 1884. Beiträge zur Kenntniss tertiärer Brachyuren-Fauna. *Denkschriften der kaiserlichen Akademie der Wissenschaften in Wien*, 48(2), 15-30.

Bittner, A. 1886. Neue Brachyuren des Eocäns von Verona. *Sitzungsberichten der kaiserlichen Akademie der Wissenschaften in Wien*, 94(1), 44-55.

Nicolis de E. 1882. Carta geologica della Provincia di Verona rilevata da Enrico Nicolis. *Estratto dalle Memorie dell'Accademia di Agricoltura Arti e Commercio di Verona*.



Figure 1. 1. Photograph of Enrico de Nicolis (date unknown). 2. Original label of the holotype of *Dromia veronensis*. 3. *Dromia veronensis* from Bittner (1886, t.1, figs.2). 4. *Dromia veronensis*, holotype (width: 13 mm, length: 16 mm); registration number i.12389; carapace: a. dorsal view, b. frontal view, c. lateral view.

PALAEOENVIRONMENT AND FAUNAL COMPOSITION OF EARLY TO LATE APTIAN BRACHYURAN FAUNULES FROM THE ISLE OF WIGHT, UK

Barry W.M. van Bakel¹, Martin I. Simpson², Álex Ossó³, John W.M. Jagt⁴ and René H.B. Fraaije⁵

¹ Oertijdmuseum, Bosscheweg 80, 5283 WB Boxtel, the Netherlands, and Department of Earth Sciences, Faculty of Geosciences, Utrecht University, Budapestlaan 4, 3584 CD Utrecht, the Netherlands. b.w.m.vanbakel@uu.nl

² Ocean and Earth Science, National Oceanography Centre, University of Southampton, SO14 3ZH, United Kingdom. martinsimpsoniow@hotmail.com

³ Llorenç de Villalonga, 17B, 1-1, 43007 Tarragona, Catalonia, Spain. aosso@tinet.cat

⁴ Natuurhistorisch Museum Maastricht, de Bosquetplein 6-7, 6211 KJ Maastricht, the Netherlands. john.jagt@maastricht.nl

⁵ Oertijdmuseum, Bosscheweg 80, 5283 WB Boxtel, the Netherlands. info@oertijdmuseum.nl

Keywords: Atherfield Clay Formation, Lower Cretaceous, crab, shell accumulations, bioherms

INTRODUCTION

Amongst Aptian crustaceans from the Isle of Wight the best-known taxa are the glypheoid lobster *Atherfieldastacus magnus* (McCoy, 1849) and the homoloid crab *Mithracites vectensis* Gould, 1859. A handful of other brachyurans have been described from these ferruginous sand deposits; for overviews references is here made to Wright and Collins (1972: tables 1, 2) and Klompmaker (2013: table 6, appendix A). Most of these concern isolated records; reliable stratigraphical or palaeoecological data have not yet been published.

Intensive stratigraphical collecting by one of us (M.I. Simpson) over the past 40 years at Atherfield and Shanklin has resulted in the recovery of several hundreds of brachyuran specimens, the vast majority representing *M. vectensis*, but also including over 50 other brachyuran specimens.



Figure 1. Aptian rocks at Atherfield, Isle of Wight, UK.

Fossils were collected *in situ*, mainly from two intervals. The lower Aptian *Deshayesites forbesi* ammonite Zone, both in the 'lower Lobster bed' (clayey deposit) or 'crackers bed' (sandy deposit), appears to have been deposited in a shallow bay to near estuary environment, with soft sedimentary deposits and numerous shell accumulations (Simpson, 1985; see also Robin *et al.*, 2016: fig. 5). Crabs from this level mostly retain ventral elements and appendages, which is indicative of a low-energy setting and high sedimentation rate. The late Aptian faunule originates from the *Parahoplites nutfieldensis* ammonite Zone, known as 'Urchin bed' (*sensu* Casey, 1961). This level, with hardgrounds, distinct shell mounds and small isolated bioherms, was primarily exposed and studied at Shanklin. Crabs from this level are generally preserved as isolated carapaces.

DISCUSSION

Both the early and late Aptian faunules are currently under study, and yield new taxa, plus additional and better-preserved material of several known taxa. In addition, the lower Aptian in particular has produced specimens with associated ventral elements and appendages, of both primitive and derived brachyurans; this is unique for the Lower Cretaceous and provides new insights into an important time interval in brachyuran evolution. Noteworthy, a single small specimen was found preserved inside an articulated, double-valved bivalve shell; in view of the tranquil conditions that prevailed during deposition of this unit, this probably represents a case of inquilinism.

In part, the faunal composition of the two levels differs, which makes it highly interesting to compare the palaeoenvironment of the two beds and analyse what impact environmental conditions had on different clades of brachyurans. In addition, the fauna may be compared with the Aptian brachyuran fauna from Catalonia and Cantabria (Spain) (Artal *et al.* 2010; González-León *et al.* 2016; Ossó *et al.*, work under way).

REFERENCES

- Artal, P., Ossó, À., van Bakel, B.W.M., Fraaije, R.H.B. and Jagt, J.W.M. 2010. A new crab assemblage from the middle Aptian of Barcelona Province (Catalonia, northeast Spain). 4th Symposium on Mesozoic and Cenozoic Decapod Crustaceans, Eichstätt (Germany), poster.
- Casey, R. 1961. The stratigraphical palaeontology of the Lower Greensand. *Palaeontology*, 3, 487-621.
- González-León, O., Ossó, A., Moreno-Bedmar, J.A. and Vega, F. 2016. Brachyura from the Lower Cretaceous (Aptian) of Spain: a new species of *Rathbunopon* (Homolodromioidea, Prosopidae) and the second record of *Mithracites vectensis* (Homoloidea). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 282, 115-124.
- Klompmaier, A.A. 2013. Extreme diversity of decapod crustaceans from the mid-Cretaceous (late Albian) of Spain: Implications for Cretaceous decapod paleoecology. *Cretaceous Research*, 41, 150-185.
- Robin, N., Charbonnier, S., Merle, D., Simpson, M.I., Petit, G. and Fernandez, S. 2016. Bivalves on mecochirid lobsters from the Aptian of the Isle of Wight: Snapshot on an Early Cretaceous palaeosymbiosis. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 453, 10-19.
- Simpson, M.I. 1985. The stratigraphy of the Atherfield Clay Formation (Lower Aptian, Lower Cretaceous) at the type and other localities in southern England. *Proceedings of the Geologists' Association*, 96, 23-45.
- Wright, C.W. and Collins, J.S.H. 1972. *British Cretaceous crabs*. Palaeontographical Society Monographs, 126, 1-113.

NEW INSIGHTS INTO REEF-ASSOCIATED DECAPOD CRUSTACEAN FAUNULES FROM THE MIOCENE PAKHNA FORMATION OF CYPRUS

Jonathan J. W. Wallaard¹, René H. B. Fraaije², John W. M. Jagt³ and Barry W. M. van Bakel⁴

¹ Oertijdmuseum, Bosscheweg 80, 5283 WB Boxtel, the Netherlands. Curator@oertijdmuseum.nl

² Oertijdmuseum, Bosscheweg 80, 5283 WB Boxtel, the Netherlands. info@oertijdmuseum.nl

³ Natuurhistorisch Museum Maastricht, de Bosquetplein 6-7, 6211 KJ Maastricht, the Netherlands. john.jagt@maastricht.nl

⁴ Oertijdmuseum, Bosscheweg 80, 5283 WB Boxtel, the Netherlands. barryvanbakel@gmail.com

Keywords: Anomura, Cenozoic, Miocene, Mediterranean, reefs

Research on the extensive Miocene decapod faunas from Cyprus is still ongoing. During several fieldwork campaigns (between 1991 and 2021), diverse assemblages have been collected at six localities in Cyprus. Few specimens have been already published (Fraaije 2014, Wallaard et al. 2020) while most material still remain for further study.

Reef deposits providing specimens belong to the upper Chattian (Oligocene) to upper Messinian (Miocene) Pakhna Formation, which consists mainly of chalks, with some marls, limestones, gypsum lenses, calcareous sandstones and polymictic conglomerates interspersed (Morse, 1996; personal observations). The Pakhna Formation has a variable thickness between 60 and 500 metres; reef deposits are found both near the base (Terra Limestone Member) and at the top (Koronia Limestone Member) of the unit (Gass et al., 1994; Follows et al., 1996).

Reefs developed locally in two phases, namely during the Aquitanian-Burdigalian (Terra Limestone Member) and during the Tortonian-early Messinian (Koronia Limestone Member) (Follows et al., 1996). Reefs of Langhian and Serravallian (middle Miocene) age are absent, most likely as a result of a rapid sea level rise that drowned the older reefs (Robertson et al., 1991). Reef growth finally came to a halt in connection with the desiccation of the Mediterranean Sea during the Messinian (e.g., Krijgsman et al., 2002).

The Pakhna Formation is overlain by the Kalavassos Formation which consists mainly of evaporites linked to the Messinian salinity crisis. This corresponds with a prominent change in palaeoenvironmental conditions: from open-marine to shallower water (Kouwenhoven et al., 2006).

Of the six localities where decapod crustaceans have been recovered, at three of them the Terra Member is exposed (at Podromi, Kamares and Cap Greco), while the Koronia Member crops out at Tochni, Maroni and Mitsero. At all localities diverse decapod assemblages have been collected, although the highest abundance and diversity has been found in the upper Miocene Koronia Member. At most sites, the concentration of decapod remains proved to be high merely in a few of the blocks resting on the surface, in stark contrast to a near-complete absence from other studied matrix blocks.

This present research focuses on the anomuran fauna (Fig. 1) at these localities; future projects will consider the accompanying brachyuran assemblages. The Terra Member has yielded species of the genera *Galathea* and *Petrolisthes*, while species of *Pagurus*, *Paguristes*, *Galathea*, *Petrolisthes*, *Palmunidopsis* and *Dardanus* are now known from the Koronia Member.

REFERENCES

- Follows, E.J., Robertson, A.H.F. and Scoffin, E.J. 1996. Tectonic controls on Miocene reefs and related carbonate facies in Cyprus. Models for carbonate stratigraphy from Miocene reef complexes of Mediterranean regions. *SEPM Concepts in Sedimentology and Paleontology*, 5, 295-315.

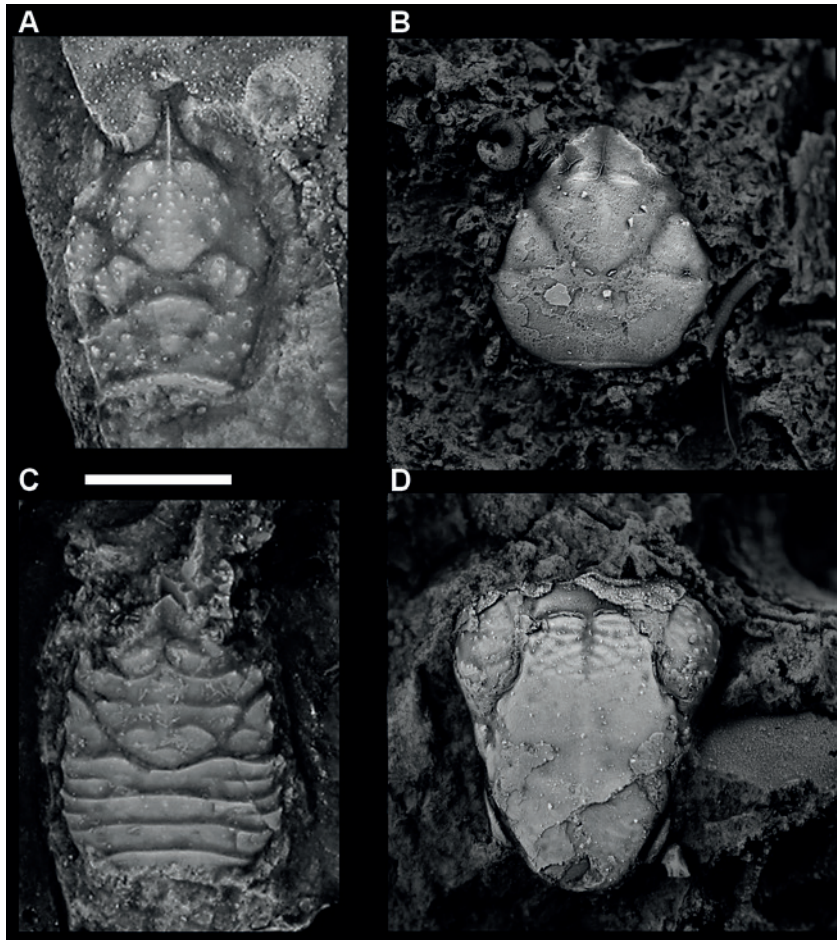


Figure 1. Pictures of several anomurans collected in Cyprus. A. *Palmunidopsis muelleri* (MABk. 3284, holotype) Fraaije, 2014. B. *Petrolisthes haydni* (MABk3501), C. *Galathea weinfurteri* (MABk 3513) and D. *Paguristes joecollinsi* (MAB10456a, Holotype), Wallaard et al. 2020. Scale bar equals 5 mm in A, B and C, and 1.5 mm in D.

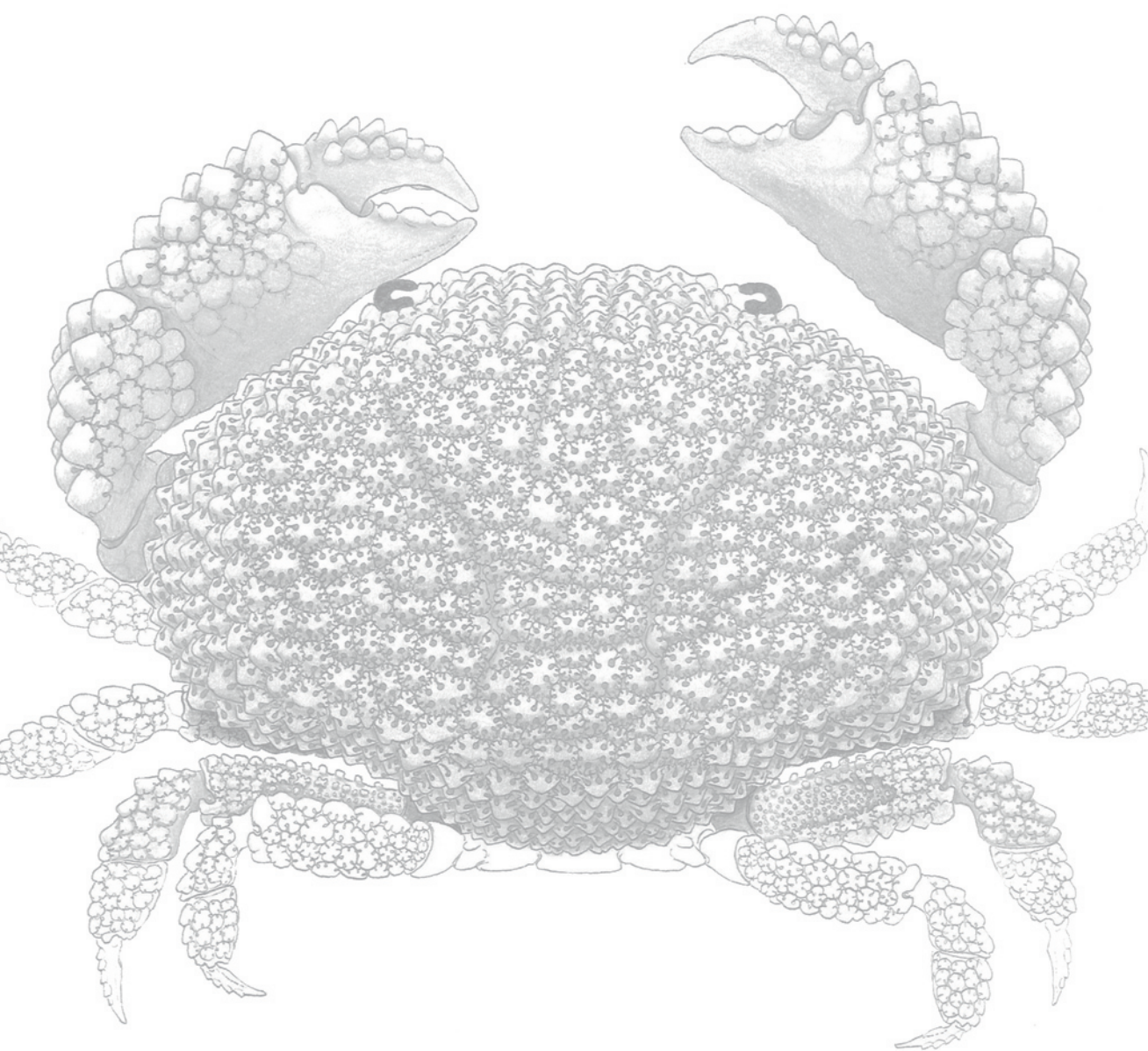
Fraaije, R.H.B. 2014. A new shallow-marine munidopsid (Anomura, Galatheoidea) from the Upper Miocene in the Maroni-Psematismenos Basin of Cyprus. In: Fraaije, R.H.B., Hyžný, M., Jagt, J.W.M., Krobicki, M. and Van Bakel, B.W.M. (eds.). Proceedings of the 5th Symposium on Mesozoic and Cenozoic decapod crustaceans, Krakow [sic], Poland, 2013: a tribute to Pál Mihály Müller. *Scripta Geologica*, 147, 233-239.

Gass, I.G., MacLeod, C.J., Murton, B.J., Panayiotou, A., Simonian, K.O. and Xenophontos, C. 1994. The geology of the southern Troodos Transform Fault Zone. *Cyprus Geological Survey Memoir*, 9, 1-218.

Kouwenhoven, T.J., Morigi, C., Negri, A., Giunta, S., Krijgsman, W. and Rouchy, J.-M. 2006. Palaeoenvironmental evolution of the eastern Mediterranean during the Messinian: constraints from integrated microfossil data of the Pissouri Basin (Cyprus). *Marine Micropaleontology*, 60, 17-44.



- Krijgsman, W., Blanc-Valleron, M.M., Flecker, R., Hilgen, F.J., Kouwenhoven, T.J., Merle, D., Orszag-Sperber, F. and Rouchy, J.-M. 2002. The onset of the Messinian salinity crisis in the eastern Mediterranean (Pissouri Basin, Cyprus). *Earth and Planetary Science Letters*, 194, 299-310.
- Morse, T.J. 1996. *Biostratigraphical constraints (calcareous nannofossils) on the Late Cretaceous to Late Miocene evolution of S.W. Cyprus*. Durham University, E-theses online: <http://etheses.dur.ac.uk/1565/>
- Robertson, A.H.F., Eaton, S., Follows, E.J. and McCallum, J.E. 1991. The role of local tectonics versus global sea-level change in the Neogene evolution of the Cyprus active margin. *Special Publications of the International Association of Sedimentologists*, 12, 331-369.
- Wallaard, J. J.W., Fraaije, R.H.B., Jagt, J.W.M., Klompmaker, A.A. and Van Bakel, B.W.M. 2020. The first record of a paguroid shield (Anomura, Annuntidiogenidae) from the Miocene of Cyprus. *Geologija*, 63, 37-43.





FIELD TRIPS





**DAY 1: JUNE 22nd, 2022****BARREMIAN-APTIAN SHALLOW-MARINE DECAPOD
COMMUNITIES FROM THE OLIETE SUBBASIN
(MAESTRAZGO BASIN, E SPAIN).****Álvaro García-Penas¹, Fernando A. Ferratges¹, Marcos Aurell¹ and Samuel Zamora^{1,2}**¹ Departamento de Ciencias de la Tierra-IUCA, Universidad de Zaragoza, 50009 Zaragoza, Spain. alvarogpenas@gmail.com² Instituto Geológico y Minero de España (IGME-CSIC), C/Manuel Lasala, 44, 9B, Zaragoza E-50006, Spain.**KEYWORDS:** Lower Cretaceous, Callianassidae, glypheid, paleogeography**INTRODUCTION**

The upper Barremian-lower Aptian successions of the Oliete subbasin record the transition from continental to shallow marine proximal environments in a relatively enclosed embayment with unstable environmental conditions, due to relatively poor marine circulation and high riverine inputs. The studied successions preserve interesting decapod faunas, which give a unique glimpse into the evolution and way of life of these animals as they adapted to changing environments.

The Maestrazgo Basin started developing during the Early Cretaceous as a result of extensional tectonics derived from the continued breakup of Pangea and the opening of the Western Tethys and North Atlantic oceans (Salas *et al.*, 2001; Liesa *et al.*, 2019). The Oliete subbasin, located in the northwestern margin of the Maestrazgo Basin (Fig 1A), is a small semi-enclosed subbasin with restricted marine circulation. It started operating during the earliest Barremian (Canérot, 1972; Aurell *et al.*, 2018), with the deposition of the continental to transitional deposits of the Blesa Formation, which preserve abundant vertebrate remains, and continued with the marine Alacón, Forcall and Oliete formations.

This field trip focuses on the upper Barremian to lower Aptian shallow marine carbonates of the Oliete subbasin, represented by the Alacón, Forcall and Oliete formations (Fig. 1B). The Alacón Fm is integrated by bioclastic limestones deposited in a tide-influenced shallow marine embayment which opened progressively to the open seas of the Maestrazgo Basin, located to the southeast (García-Penas *et al.*, 2022). The Forcall Fm is composed of open marine siliciclastic ramp silts and sandstones containing ammonites of the early Aptian *Deshayesites forbesi* biozone (García *et al.*, 2014). The Oliete Fm is a thick mixed carbonate-siliciclastic succession representing a shallow marine ramp environment with exceptional development of oyster biostromes, signaling a significant influence of freshwater inputs. The middle member of this formation has yielded scarce ammonites of the late Aptian *Parahoplites melchioris* and *Acanthoplites nolani* biozones (García *et al.*, 2014). These deposits gradually pass vertically to the transitional and continental deposits of the Albian Escucha and Utrillas formations, which are out of the scope of this field trip.

The field trip consists of four stops (Fig. 1B):

1. **Road to Josa village.** Panoramic view of the Blesa and Alacón formations. A brief explanation of the geological context of the Oliete subbasin will be offered, with an emphasis on carbonate decapod-bearing concretions of the Middle Blesa Formation.
2. **Josa village.** Here, the Alacón Formation is well-exposed and preserves evidences of the activity of infaunal decapod crustaceans.
3. **Tejería de Josa.** An old quarry where local people extracted the silts of the Forcall Fm for making roof-tiles, the Tejería de Josa is a staple outcrop for invertebrate paleontology,

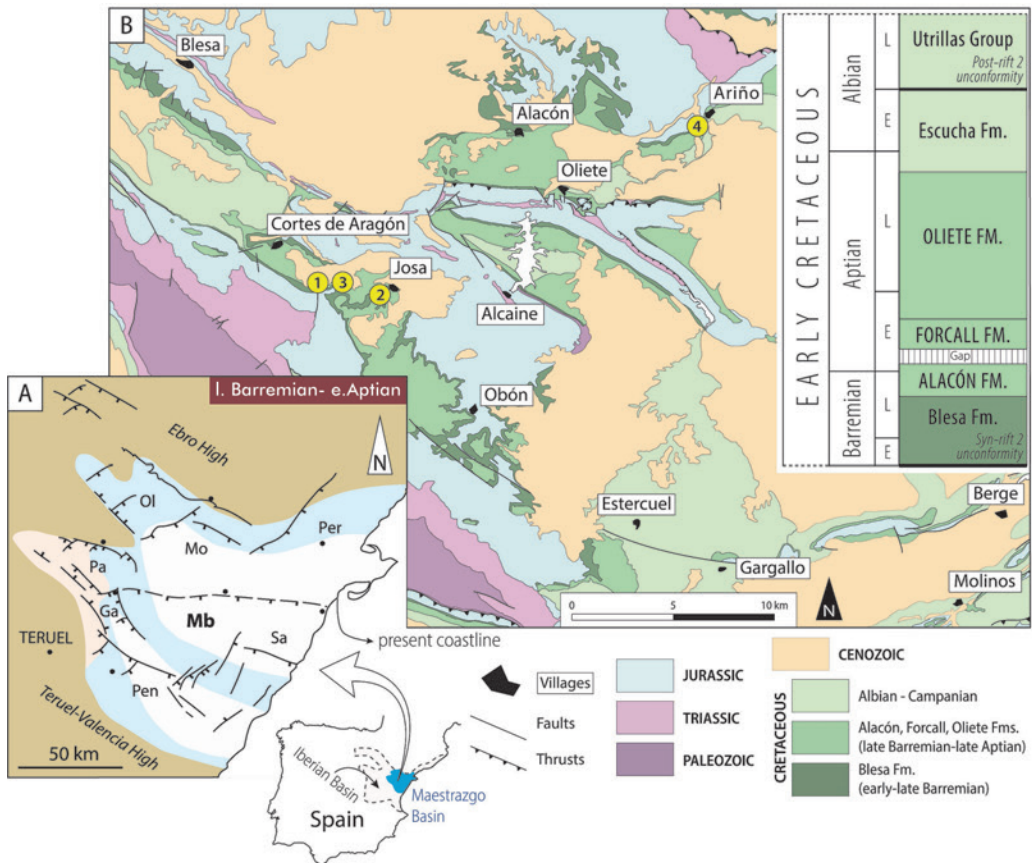


Figure 1. A. Location of the Oliete subbasin in the northern margin of the Maestrazgo Basin and the Iberian Basin Rift System. Environments: light blue: open marine; blue: shallow marine; light brown: occasional marine influence; dark brown: non-deposition/erosion. B. Location of the four planned stops 1–4 and chronostratigraphic chart of the Lower Cretaceous units of the Oliete sub-basin.

and over the years has yielded abundant and diverse ammonite faunas, as well as the highest diversity of Lower Cretaceous fossil decapod crustaceans of Spain (Ferratges et al., 2021).

4. **Oliete Fm in Ariño.** The lowermost levels of the Oliete Fm are well-exposed in the road leading to the village of Ariño. Several beds are cut nearly parallel to bedding, exposing abundant *Thalassinoides* associated with callianassid chelae, and rare *Atherfieldastacus magnus*.

GEODYNAMIC CONTEXT OF THE OLIETE SUBBASIN

The general configuration of the Iberian Basin rift system of the northeast Iberian Plate was a result of two major rifting phases, with localized and intense tectonic subsidence, and their subsequent postrift periods characterized by gentler, widespread, thermal subsidence (Salas et al., 2001). The first rifting stage started in the Early Permian, with deposition of continental facies in very small basins bounded by steep and deep-reaching normal faults. This first extensional stage reached its maximum development during the Triassic (Liesa et al., 2019), with widespread dep-

osition in eastern Iberia of the three Germanic facies (Buntsandstein red sandstones, Muschelkalk dolomites and limestones, and Keuper evaporites), which are found across most of western Europe. After the first rifting stage, a period of thermal subsidence spanning the Late Triassic to the Middle Jurassic allowed the development of extensive shallow carbonate platforms across eastern, northern and southern Iberia (e.g. Vera *et al.*, 2004).

During the Late Jurassic-Early Cretaceous, the motion of the Iberian Plate relative to the surrounding African, European and American plates was conditioned mainly by the opening of the North Central Atlantic Ocean (Liesa *et al.*, 2019), and the Iberian Basin underwent a reactivation. Rekindled extensional stresses caused the demise and breakup of the Jurassic carbonate platforms, and the Iberian Basin was divided into four main depositional domains characterized by localized tectonic subsidence: the Cameros Basin in the north, and the South Iberian, Central Iberian, and Maestrazgo basins in the East.

The Oliete subbasin is a small subdivision of the Maestrazgo Basin. Large scale, NW-SE-trending normal fault systems conditioned the overall geometry of the subbasin, and its internal configuration and depocentral distribution were controlled by sets of smaller normal faults with a NE-SW orientation. Synrift deposition in the Oliete subbasin took place from the early Barremian to the early Albian (Soria *et al.*, 1995; Aurell *et al.*, 2018; García-Penas *et al.*, 2022).

CLIMATE EVOLUTION DURING THE BARREMIAN AND APTIAN

Climate in the Western Tethys was markedly unstable during the Barremian-early Aptian. In Iberia, climatic instability was accentuated by its intermediate geographic position between migrating arid and humid climate belts (Hay and Floegel, 2012).

Alternations between warm and humid periods and dry cold stages with marked seasonality during the early Barremian (e.g. Pucéat *et al.*, 2003; Steuber *et al.*, 2005; Huck *et al.*, 2013; Laita *et al.*, 2020) culminated in the so-called 'mid'-Barremian arid stage (Ruffell and Batten, 1990; Dinis *et al.*, 2020). This event marked the onset of relatively cold and dry conditions, which continued during most of the late Barremian. The existence of limited epicontinental ice caps in higher latitudes during these Early Cretaceous cold, arid stages is considered possible, although no general consensus has been reached on the topic (e.g. Price, 1999; Amiot *et al.*, 2011; Föllmi, 2012).

A generalized shift towards warm and humid conditions took place during the latest Barremian Martelites *sarasini* Zone, followed by a colder and drier period during the early Aptian Deshayesites *oglanlensis* and Deshayesites *forbesi* zones (Föllmi, 2012). Huck and Heimhofer (2021) propose moderate mean annual sea-surface temperatures (22–26 °C) for large parts of the Barremian and Aptian with a major cooling phase at the Barremian–Aptian boundary, followed by a warm pulse during the OAE1a. This proposed latest Barremian-earliest Aptian cooling is coeval with eustatic sea-level drops recognized on the eastern Arabian Plate (van Buchem *et al.*, 2010) and the western Tethys (Pucéat *et al.*, 2003), but is not recognized by other studies, which nevertheless support a late Barremian relatively cool stage (e.g. Bodin *et al.*, 2009; Mutterlose *et al.*, 2009; Malkoć and Mutterlose, 2010).

Climatic instability continued throughout the late Aptian and early Albian. In broad terms, the late Aptian was characterized by short-lived cold stages which disrupted the early Aptian greenhouse, while the earliest Albian was accompanied by a return to relatively warm and humid conditions (Bottini and Erba, 2018; Skelton *et al.*, 2019)

In the western margin of the Maestrazgo Basin, this climatic instability translated into episodic increases in siliciclastic input in the stratigraphic record (e.g. Peropadre, 2011). The palaeogeography of the Oliete subbasin made it especially prone to abrupt palaeoenvironmental changes related to climate oscillations (García-Penas *et al.*, 2022). A step-by-step description of the palaeogeographic evolution of the subbasin during the Barremian and Aptian will be offered below in each stop.

STOP 1. EARLY TO LATE BARREMIAN EVOLUTION OF THE OLIETE SUBBASIN: THE BLESA FORMATION

Location

The stop takes place along the TE-V-1145 road, between the villages of Cortes de Aragón and Josa, at a vantage point offering a panoramic view of the Early Cretaceous succession of the Oliete subbasin.

- » Coordinates: 40° 57' 29"N, 0° 47' 56" W, Elevation: 947m.
- » Geological map of Spain: 1:50000, sheet 493 Oliete (Quintero-Amador et al., 1977).
- » Geological setting: Oliete subbasin, Western Maestrazgo Basin.
- » Lithostratigraphy: Bioclastic limestones, silts and silty marls, fine-to-coarse-grained sandstones.
- » Age: early Barremian to early Aptian.

Aims

- » Showing a panoramic view of the first two formations of the Lower Cretaceous transitional-to-marine succession of the Oliete subbasin: Blesa Fm (mainly continental with occasional development of restricted marine environments) and Alacón Fm (shallow carbonate ramp).
- » Putting the decapod-bearing concretions of the Middle Blesa Sequence into a stratigraphic context.
- » Offering an interpretation of the decapod habitats based on facies interpretation.

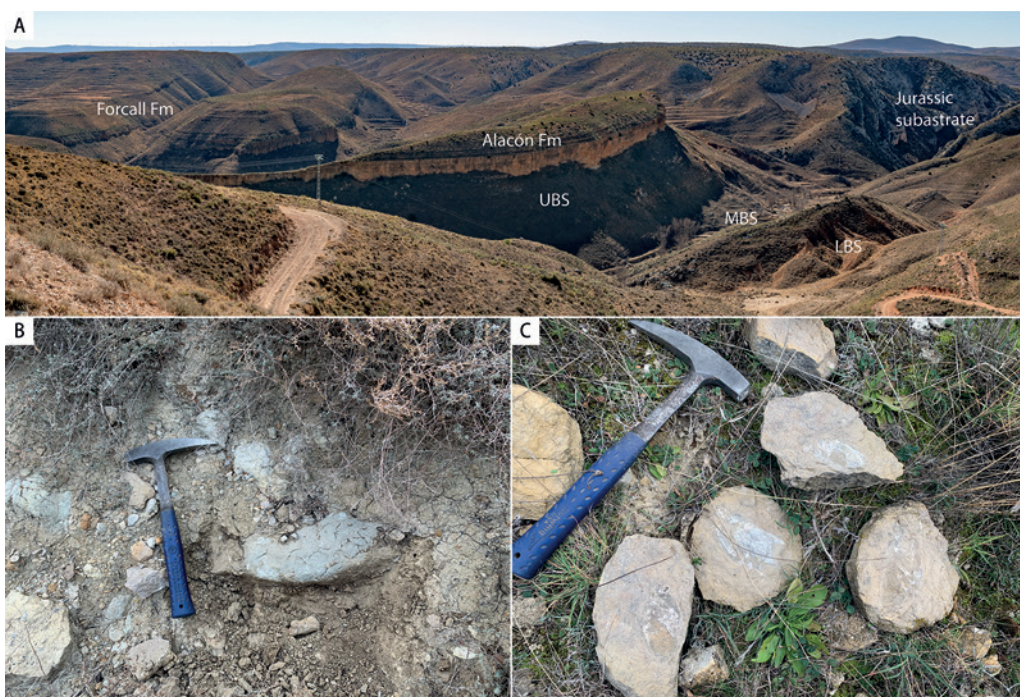


Figure 2. A. Panoramic view of the Blesa (LBS to UBS), Alacón and Oliete formations in Stop 1. B. in-situ nodules in a muddy level of the Middle Blesa Sequence. C. Decapod-bearing nodules of the Middle Blesa Sequence, containing specimens of *Atherfieldastacus rapax*.

Description

At the end of the Jurassic, a major sea-level fall event led to the subaerial exposure of the carbonate platforms that had developed during the first post-rift stage of the Iberian Rift System (IRS). The reactivation of the IRS during the Early Cretaceous led to the tilting and differential erosion of the Jurassic succession, generating an erosive gap that increases towards the southwest (Aurell *et al.*, 2018).

Between the villages of Cortes de Aragón and Josa, this erosive unconformity develops on Middle Jurassic carbonates, and is overlain by the first synrift unit of the Oliete subbasin, the Blesa Formation (Fig. 2A). This unit is integrated by three genetic sequences of mixed climatic and tectonic origin (Aurell *et al.*, 2018), divided by discontinuity surfaces that can be correlated basinwide. The Lower Blesa Sequence is integrated by alluvial and lacustrine-palustrine facies and lateritic soils, developed over the tilted and karstified Jurassic substrate. During the early to late Barremian transition, an intermittent connection was established between the Oliete subbasin and the shallow open seas of the Maestrazgo Basin, resulting in the deposition of restricted marine facies across the subbasin (Middle Blesa Sequence). This sequence is characterized by oyster-bearing marls and limestones deposited in shallow environments of variable salinity.

These environments supported a diverse fauna of chelonians, crocodylomorphs, plesiosaurs and other marine vertebrates (Aurell *et al.*, 2018). Near the village of Obón (Fig. 1B), these facies yield carbonate nodules containing well-preserved glypheid lobsters (Fig. 2B,C). Similar decapod faunas are also found in the coeval shallow marine deposits of the Maestrazgo Basin (González-León *et al.*, 2017).

Episodic marine influence continued throughout deposition of the Upper Blesa Sequence, which is characterized by a variety of continental to shallow marine facies containing isolated remains of terrestrial vertebrates.

STOP 2. LATE BARREMIAN-EARLIEST APTIAN: THE ALACÓN FORMATION

Location

The stop takes place by the village of Josa, in the northern bank of the Sus river.

- » Coordinates: 40° 57' 23"N, 0° 46' 09" W, Elevation: 771m.
- » Geological map of Spain: 1:50000, sheet 493 Oliete (Quintero-Amador *et al.*, 1977).
- » Geological setting: Oliete subbasin, Western Maestrazgo Basin.
- » Lithostratigraphy: Bioclastic limestones, gray marls.
- » Age: late Barremian-earliest Aptian.

Aims

- » Describing the shallow marine deposits of the Alacón Formation.
- » Describing the influence of infaunal decapods on sediment fabric.
- » Documenting the progressive changes in decapod faunas following palaeoenvironmental change.

Description

The striking ochre limestones of the Alacón Formation outcrop near the village of Josa, in the northern bank of the Sus river (Fig. 3A). This formation registers the progressive flooding of the Oliete subbasin during the late Barremian and earliest Aptian. The Alacón Fm is integrated by four genetic sequences bounded by basinwide-correlatable discontinuities (García-Penas *et al.*, 2022).

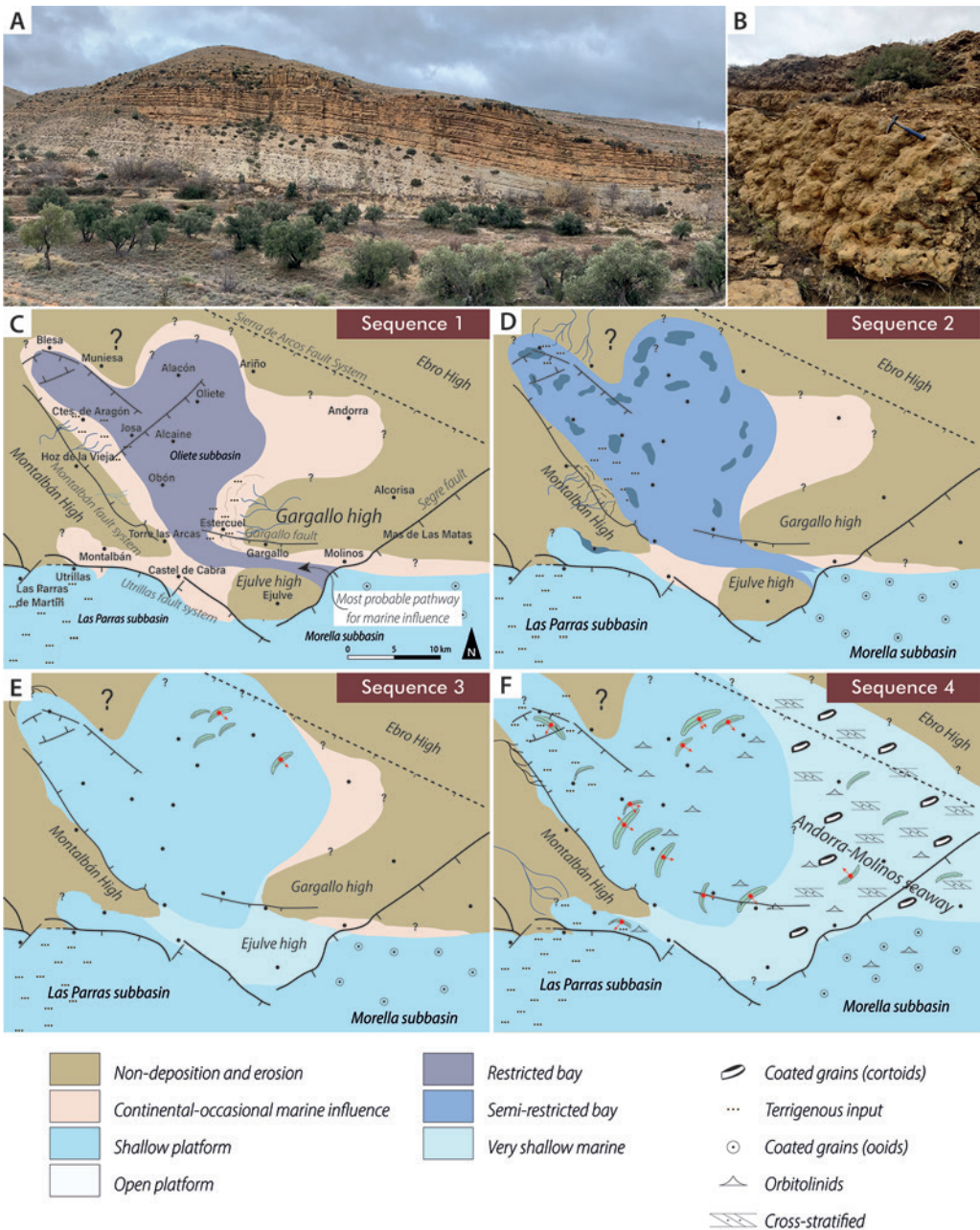


Figure 3. A. Escarpment of the Alacón Fm. near Josa (Stop 2). B. *Thalassinoides*-like burrows on a stratification surface in Sequence 2 of the Alacón Fm. C-F. Palaeogeographic evolution of the Oliete subbasin during deposition of the Alacón Fm.

The first sequence (Fig. 3C) is integrated by whitish lacustrine and restricted marine limestones and marls containing mainly characeans, ostracods, thin-shelled bivalves, oysters and gastropods. During this first stage, the Oliete subbasin was intermittently occupied by a restricted shallow marine bay flanked by palustrine-lacustrine areas, palaeoenvironmentally quite similar to

the lower Barremian Middle Blesa Sequence described in the previous stop. Indeed, these facies have also yielded isolated remains of dinosaurs, chelonians, osteichthyes and other vertebrates, yet to be studied. At this stage, the Oliete subbasin was intermittently connected to the open marine areas located in the southeast through an inferred narrow seaway located in the southern regions of the subbasin.

A sharp flooding surface bounds sequences 1 and 2. Sequence 2 (Fig. 3D) is integrated by well-cemented ochre bioclastic packstones containing restricted marine faunal associations dominated by the grypheid oyster *Ceratostreon*. During this stage, the connection of the Oliete bay to the Maestrazgo Basin must have been wider and more stable, allowing for a generalized increase in salinity. However, this shallow bay is thought to have experienced frequent salinity variations, as evidenced by the coexistence in the same levels (due to time averaging) of euhaline and brachyhaline organisms.

Sequence 3 (Fig. 3E) is characterized by the appearance of thick-shelled infaunal trigoniid and pholadomyid bivalves, brachiopods and dasycladaceans, indicating a stabilization of normal marine salinity levels in the Oliete bay. This was possible due to a widening of the southern seaway, which also implied the onset of a relatively strong tidal regime, as evidenced by the occurrence of cross-bedded deposits interpreted as subaqueous tidal dunes. A sea-level fall of possible eustatic origin generated the iron-stained and burrowed discontinuity surface separating sequences 3 and 4.

Sequence 4 (Fig. 3F) is characterized by the deepening of the depositional setting and expansion of the sedimentary area, caused by a marked transgressive event. The drowning of large areas in the western part of the subbasin generated a wide strait allowing full connection to the shallow seas of the Maestrazgo Basin. In the uppermost part of the Alacón Formation, a significant regressive event is evidenced by the basinwide appearance of cross-stratified deposits interpreted as a large-scale tidal dune field occupying most of the sedimentary area of the subbasin. These dune deposits are crowned by a prominent bored and karstified hardground evidencing the emersion of the subbasin, which separates the Alacón Fm from the overlying Forcall Fm. It has been interpreted that this large-scale sea-level drop coincides with an early Aptian eustatic event recognizable worldwide.

A remarkable palaeoecological aspect of the shallow-marine Alacón Fm is the high abundance of callianassids (used *sensu lato* referring broadly to burrowing shrimps) remains. Thalassinid shrimp chelae are common skeletal components, especially in sequences 2 to 4, with remains occasionally appearing associated to burrowing. *Thalassinoides* sp. traces are another common feature in these sequences (Fig. 3B), being especially abundant at sequence boundaries, where they are commonly preserved as epirreliefs or three-dimensional burrow systems. This is interpreted as resulting from the colonization of firmgrounds during sediment-starved flooding events at the start of each sequence (Sharafi *et al.*, 2012).

Callianassids appeared during the Hauterivian and diversified during the Early Cretaceous (Hyžný and Klompmaker, 2015), eventually becoming one of the most important sediment burrowers up until the present time. Their activity can exert profound changes on the sedimentology (e.g. Tedesco and Wanless, 1991), geochemistry (e.g. Van de Velde and Meysman, 2016) and taphonomy (e.g. Meldahl, 1987) of sediments, obscuring their original depositional features. In the Alacón Fm, overprinting of successive burrow generations during regressive stages with low deposition rates produces very high trace densities that can completely disturb bedding, producing a massive appearance (Gingras *et al.*, 2015).

The large abundance of burrowing shrimp remains in the Alacón Fm is attributed to its particular depositional setting. During sequences 1 to 3, the Oliete subbasin was a semi-enclosed bay subjected to frequent salinity oscillations and communicated with the open seas of the Morella and Las Parras subbasins by a relatively narrow southern seaway, which partly inhibited marine circulation. This bay received episodic freshwater inputs, which were laden with dissolved

organic matter (Raymond and Bauer, 2001). Euryhaline callianassids are known to thrive in similarly stressed environments with high nutrient availability (Dworschak, 2005; Hyžný *et al.*, 2015). *Thalassinoides* traces become significantly larger in Sequence 4. This sequence has been interpreted as equivalent to the basal transgressive intervals of the Forcall Fm in depocentral areas of the Maestrazgo Basin. It is possible that this change in *Thalassinoides* trace size reflects the progressive diversification of producers, as the environmental conditions became suitable for larger burrowing organisms such as mecochirid lobsters, which are commonly found in the overlying open-marine Forcall Fm (Ferratges *et al.*, 2021).

STOP 3. EARLY APTIAN: THE FORCALL FORMATION

Location

The stop takes place by the road between the villages of Josa and Cortes de Aragón, at the classical locality of La Tejería.

- » Coordinates: 40° 57' 32"N, 0° 47' 03" W, Elevation: 891m.
- » Geological map of Spain: 1:50000, sheet 493 Oliete (Quintero-Amador *et al.*, 1977).
- » Geological setting: Oliete subbasin, Western Maestrazgo Basin.
- » Lithostratigraphy: gray and whitish silt and marls, ocherish bioclastic sandstone.
- » Age: early Aptian.

Aims

- » Reconstructing the shallow marine environments of the Oliete subbasin during the lower Aptian.
- » Describing the decapod faunal associations recovered from the Forcall Fm.

Description

In the Oliete subbasin, the siliciclastic-dominated Forcall Formation represents a highly asymmetric transgressive-regressive cycle, with a short transgressive hemicycle culminating in a condensation level with diverse ammonite faunas of the *Deshayesites forbesi* biozone. The regressive hemicycle represents the transition from distal and mid-ramp environments, characterized by silts and marls (Fig. 4A) and cm-thick sandstone levels with hummocky cross-stratification, to inner ramp environments characterized by sandy floatstones with orbitolinids, echinoids, and disarticulated endobenthic bivalves (Pholadomyidae, Trigonidae), and cross-stratified coarse bioclastic sandstones. A prominent discontinuity surface on top of the Forcall Formation marks a sharp change in the depositional system towards the carbonate-dominated bioclastic packstones and marls of the lowermost Oliete Formation.

This locality coincides with the classic area where Vilanova (1870) first recorded the lobster *Oncoporeia granulosa* Vilanova, 1870 [currently recognised as *Atherfieldastacus magnus* (M'Coy, 1849) by Via-Boada (1975)] from the Lower Cretaceous in the Oliete Sub-basin. In fact this is the most abundant decapod in this locality. More recently, Ferratges *et al.* (2021) reported the highest diversified fauna of decapod crustaceans from the Spanish Aptian, an assemblage containing *Atherfieldastacus magnus*, *Aptaxiopsis longimanus*, *Crosniera forcallensis*, *Meticonaxius gracilis*, *Aptanacalliax enigma*, *Meyeria ornata*, *Cretacocalcinus josaensis* and *Mithracites vectensis*. The specimens appear in three modes reflecting different preservational states. Specimens of *Atherfieldastacus magnus* appear mostly within calcareous concretions intercalated in silt levels (Fig. 4B). Concretions are taxonomically exclusive, and only contain specimens of *A. magnus* (exceptuating scarce fish remains). Their genesis is probably related to elevated pH levels around decaying carcasses and moults, possibly inside galleries. Other taxa appear as compressed, disarticulated to articulated moults and corpses preserved in muddy levels and bedding surfaces, probably generated during rapid obrution events (Fig. 4C).

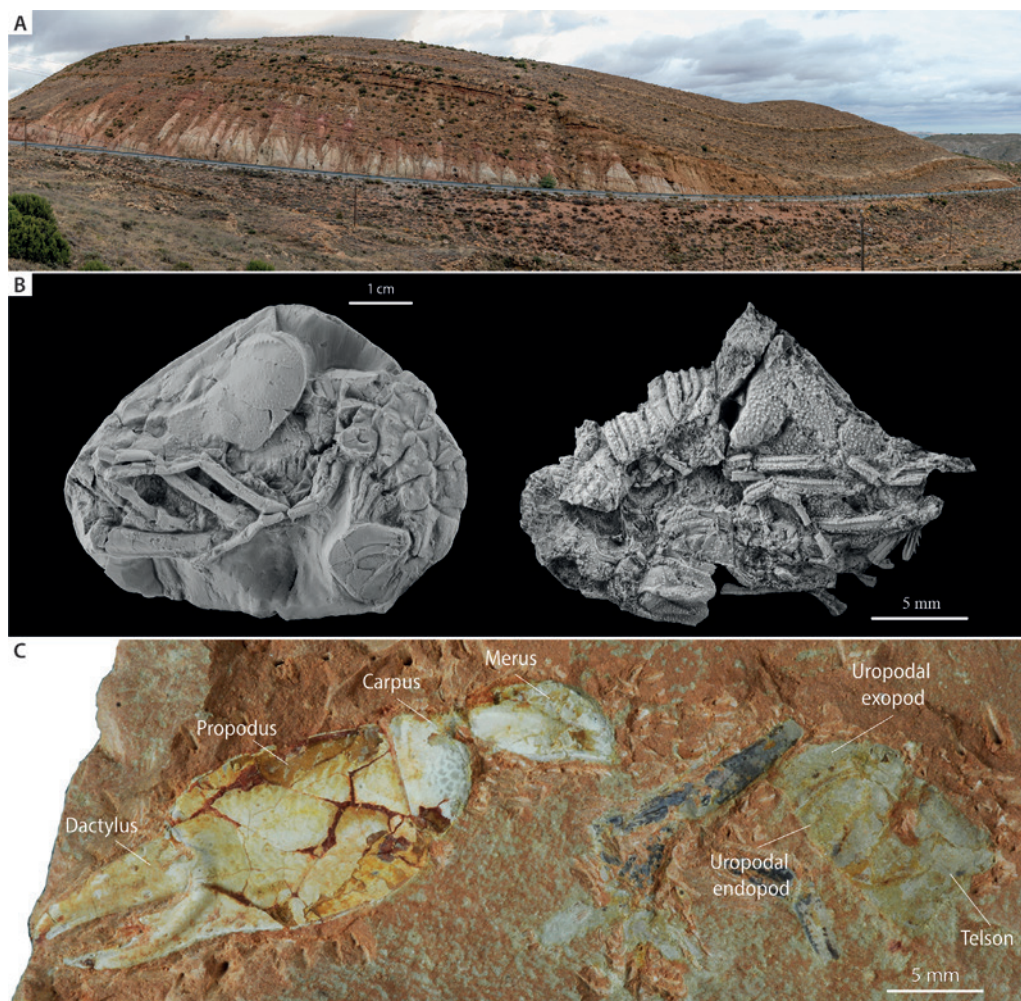


Figure 4. A. Panoramic view of the Forcall Fm at La Tejería de Josa (Stop 3). B. Two preservation modes of glypheid lobsters recovered from the Forcall Fm: Left: specimen of *Atherfieldastacus magnus* preserved inside a carbonate nodule. Right: Specimen of *Meyeria ornata* preserved inside marls. Adapted from Ferratges et al. (2021) C. *Crosniera forcallensis* preserved in an obrution level. Adapted from Ferratges et al. (2021).

STOP 4. LATE APTIAN: THE OLIETE FORMATION

Location

The stop takes place near the village of Ariño, where the road cuts the basal levels of the Oliete Formation exposing well-preserved burrow networks on the bedding surfaces.

- » Coordinates: 41° 01' 21"N, 0° 35' 30" W, Elevation: 494m.
- » Geological map of Spain: 1:50000, sheet 467 Muniesa (Ríos-Aragüés et al., 1981).
- » Geological setting: Oliete subbasin, Western Maestrazgo Basin.
- » Lithostratigraphy: ochre sandstone, whitish sandy limestone, gray marls.
- » Age: late Aptian.

Aims

- » Describing the late Aptian mixed carbonate-siliciclastic shallow marine succession of the Oliete subbasin.
- » Describing the habitat of decapod crustaceans in these shallow environments.

Description

A prominent discontinuity surface on top of the Forcall Formation marks a sharp change in the depositional system towards the carbonate-dominated bioclastic packstones and marls of the lowermost Oliete Formation (Cabezo Negro member), which contain colonial corals, rare corpus of *A. magnus* and abundant *Thalassinoides*. These levels represent the transgressive hemicycle of a long-term transgressive-regressive cycle, which culminates in a marl-dominated interval (La Dehesa member) preserving an abundance of articulated gastropods and endobenthic bivalves, as well as scarce ammonites of the *Parahoplites melchioris* and *Acanthoplites nolani* late Aptian biozones. The regressive hemicycle is represented by bioclastic-cortoidal packstones



Figure 5. A. Lower levels of the Oliete Fm by the road leading to Ariño (Stop 4). B. Three-dimensionally preserved burrow systems on a stratification plane. C. Well-preserved callianassid chelae associated to a bioturbated horizon. D. Specimen of *Atherfieldastacus* sp. recovered from the basal levels of the Oliete Fm at Ariño.

and grainstones (Los Estancos member), which are topped by a karstified discontinuity surface recognizable basinwide, separating the Oliete subbasin from the overlying transitional-to-continental Escucha Formation.

The lower levels of the Oliete subbasin outcrop in the embankments of the road leading to the village of Ariño, where they are cut almost parallel to stratification (Fig. 5A). Here, extensive burrow networks associated to callianassid remains are well-exposed on the bedding surfaces (Fig. 5B, C). Well-preserved glypheid lobsters (Fig. 5D) have also been recovered from this stratigraphic interval. Murat (1983) interprets that these levels were deposited in a shallow, low-energy ramp environment surrounded by marshy areas. Episodic fresh-water influence is evidenced by the local occurrence of oyster rudstones and generally high quartz content even in carbonate-dominated intervals.

REFERENCES

- Amiot, R., Wang, Xu, Zhou, Z., Wang, Xiaolin, Buffetaut, E., Lécuyer, C., Ding, Z., Fluteau, F., Hibino, T., Kusuhashi, N., Mo, J., Suteethorn, V., Wang, Y., Xu, X. and Zhang, F. 2011. Oxygen isotopes of East Asian dinosaurs reveal exceptionally cold Early Cretaceous climates. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 5179–5183. <https://doi.org/10.1073/pnas.1011369108>
- Aurell, M., Soria, A.R., Bádenas, B., Liesa, C.L., Canudo, J.I., Gasca, J.M., Moreno-Azanza, M., Medrano-Aguado, E. and Meléndez, A. 2018. Barremian synrift sedimentation in the Oliete sub-basin (Iberian Basin, Spain): palaeogeographical evolution and distribution of vertebrate remains. *Journal of Iberian Geology*, 44, 285–308. <https://doi.org/10.1007/s41513-018-0057-3>
- Bodin, S., Fiet, N., Godet, A., Matera, V., Westermann, S., Clément, A., Janssen, N.M.M., Stille, P. and Föllmi, K.B. 2009. Early Cretaceous (late Berriasian to early Aptian) palaeoceanographic change along the northwestern Tethyan margin (Vocontian Trough, southeastern France): $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ and Sr-isotope belemnite and whole-rock records. *Cretaceous Research*, 30, 1247–1262. <https://doi.org/10.1016/j.cretres.2009.06.006>
- Bottini, C. and Erba, E. 2018. Mid-Cretaceous paleoenvironmental changes in the Western Tethys. *Climate of the Past*, 14, 1147–1163.
- Dworschak, P.C. 2005. Global diversity in the Thalassinidea (Decapoda): an update (1998-2004). *Nauplius*, 13, 57–63.
- Ferratges, F.A., Hyžný, M. and Zamora, S. 2021. Taphonomy and systematics of decapod crustaceans from the Aptian (Lower Cretaceous) in the Oliete Sub-basin (Teruel, Spain). *Cretaceous Research*, 122. <https://doi.org/10.1016/j.cretres.2021.104767>
- Föllmi, K.B. 2012. Early Cretaceous life, climate and anoxia. *Cretaceous Research*, 35, 230–257. <https://doi.org/10.1016/j.cretres.2011.12.005>
- García, R., Moreno-Bedmar, J.A., Bover-Arnal, T., Company, M., Salas, R., Latil, J.L., Martín-Martín, J.D., Gómez-Rivas, E., Bulot, L.G., Delanoy, G., Martínez, R. and Grauges, A., 2014. Lower Cretaceous (Hauterivian-Albian) ammonite biostratigraphy in the Maestrat Basin (E Spain). *J. Iber. Geol.* 40, 99–112. https://doi.org/10.5209/rev_JIGE.2014.v40.n1.44090
- García-Penas, A., Aurell, M. and Zamora, S. 2022. Progressive opening of a shallow-marine bay (Oliete subbasin, Spain) and the record of possible eustatic fall events near the Barremian-Aptian boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 594, 110938.
- Gingras, M.K., Pemberton, S.G. and Smith, M. 2015. Bioturbation: Reworking Sediments for Better or Worse. *Oilfield Review*, 26, 46–58.



- González-León, O., Ossó, À., Bover-Arnal, T., Moreno-Bedmar, J.A., Frijia, G. and Vega, F.J. 2017 *Atherfieldastacus rapax* (Harbort, 1905) (Glyphoridae, Mecochiridae) from the Lower Cretaceous of the Maestrat Basin (NE Spain). *Cretaceous Research*, 77, 56–58.
- Hay, W.W. and Floegel, S. 2012. New thoughts about the Cretaceous climate and oceans. *Earth-Science Reviews*, 115, 262–272. <https://doi.org/10.1016/j.earscirev.2012.09.008>
- Huck, S. and Heimhofer, U. 2021. Early Cretaceous sea surface temperature evolution in subtropical shallow seas. *Scientific Reports*, 11, 1–9. <https://doi.org/10.1038/s41598-021-99094-2>
- Hyžný, M., Šimo, V. and Starek, D. 2015. Ghost shrimps (Decapoda: Axiidea: Callianassidae) as producers of an Upper Miocene trace fossil association from sublittoral deposits of Lake Pannon (Vienna Basin, Slovakia). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 425, 50–66. <https://doi.org/10.1016/j.palaeo.2015.02.012>
- Laita, E., Bauluz, B., Aurell, M., Bádenas, B., Canudo, J.I. and Yuste, A. 2020. A change from warm/humid to cold/dry climate conditions recorded in lower Barremian clay-dominated continental successions from the SE Iberian Chain (NE Spain). *Sedimentary Geology*, 403, 105673. <https://doi.org/10.1016/j.sedgeo.2020.105673>
- Liesa, C.L., Soria, A.R., Casas, A., Aurell, M., Meléndez, N., Bádenas, B., Fregenal-Martínez, M., Navarrete, R., Peropadre Medina, C. and Rodríguez-López, J.P. 2019. The Late Jurassic-Early Cretaceous rifting stage at the central and eastern Iberian Basin: The central and eastern Iberian Basin, in: Quesada, C., Oliveira, J.T. (Eds.), *The Geology of Iberia: A Geodynamic Approach. Volume 3: The Alpine Cycle*. Springer, Berlin, p. 566.
- Malkoč, M. and Mutterlose, J. 2010. The early barremian warm pulse and the late barremian cooling: A high-resolution geochemical record of the boreal realm. *Palaos*, 25, 14–23. <https://doi.org/10.2110/palo.2010.p09-029r>
- Meldahl, K.H. 1987. Sedimentologic and Taphonomic Implications of Biogenic Stratification. *Research Reports*, 2, 350–358.
- Murat, B. 1983. Contribution à l'étude stratigraphique, sédimentologique et tectonique du Bassin Éocrétacé d'Oliete (Province de Teruel, Espagne). Paul Sabatier University. Toulouse. *Travaux du Laboratoire Géologie Sédimentologie et Paléontologie*. Ph.D. Thesis, 247pp.
- Mutterlose, J., Pauly, S. and Steuber, T. 2009. Temperature controlled deposition of early Cretaceous (Barremian-early Aptian) black shales in an epicontinental sea. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 273, 330–345. <https://doi.org/10.1016/j.palaeo.2008.04.026>
- Peropadre, C. 2011. El Aptiense del margen occidental de la Cuenca del Maestrazgo: controles tectónico, eustático y climático en la sedimentación. Universidad Complutense de Madrid and Instituto de Geociencias, Madrid, Spain (2011) Ph. D. Thesis, 663 pp. (unpublished)
- Price, G.D. 1999. The evidence and implications of polar ice during the Mesozoic. *Earth Science Reviews*, 48, 183–210. [https://doi.org/10.1016/S0012-8252\(99\)00048-3](https://doi.org/10.1016/S0012-8252(99)00048-3)
- Pucéat, E., Lécuyer, C., Sheppard, S.M.F., Dromart, G., Reboulet, S. and Grandjean, P. 2003. Thermal evolution of Cretaceous Tethyan marine waters inferred from oxygen isotope composition of fish tooth enamels. *Palaeoceanography*, 18, 1–12. <https://doi.org/10.1029/2002pa000823>
- Quintero-Amador, I., Almela, A., Gómez, E. and Mansilla, H. 1975. Mapa Geológico de España 1:50000 (MAGNA), Hoja 493 (Oliete). Instituto Geológico de España, Madrid.
- Ríos-Aragüés, L.M., Beltrán, F.J. and Lanaja, J.M. 1981. Mapa Geológico de España 1:50000 (MAGNA), Hoja 467 (Muniesa). Instituto Geológico de España, Madrid.
- Salas, R., Guimerá, J., Mas, R., Martín-Closas, C., Meléndez, A. and Alonso, Á. 2001. Evolution of the Mesozoic Central Iberian Rift System and its Cainozoic inversion (Iberian chain), in:



- Ziegler, P.A., Cavazza, W., Robertson, A.H.F., Crasquin-Soleau, S. (Eds.), Peri-Tethys Memoir 6: Peri-Tethyan Rift/Wrench Basins and Passive Margins. Paris, pp. 145–185.
- Sharafi, M., Ashuri, M., Mahboubi, A. and Moussavi-Harami, R. 2012. Stratigraphic application of Thalassinoides ichnofabric in delineating sequence stratigraphic surfaces (Mid-Cretaceous), Kopet-Dagh Basin, northeastern Iran. *Palaeoworld*, 21, 202–216. <https://doi.org/10.1016/j.palwor.2012.06.001>
- Skelton, P.W., Castro, J.M. and Ruiz-Ortiz, P.A. 2019. Aptian carbonate platform development in the Southern Iberian Palaeomargin (Prebetic of Alicante, SE Spain). *BSGF - Earth Sciences Bulletin*, 190, 3.
- Soria, A.R., Martín-Closas, C., Melendez, A., Melendez, M.N. and Aurell, M. 1995. Estratigrafía del Cretácico inferior continental de la Cordillera Ibérica Central. *Estudios Geológicos*, 51, 141–152.
- Steuber, T., Rauch, M., Masse, J.P., Graaf, J. and Malkoč, M. 2005. Low-latitude seasonality of Cretaceous temperatures in warm and cold episodes. *Nature*, 437, 1341–1344. <https://doi.org/10.1038/nature04096>
- Tedesco, L.P. and Wanless, H.R. 1991. Generation of Sedimentary Facies and Facies by Repetitive Excavation and Storm Infilling of Burrow Networks, Holocene of South Florida and. *Palaios*, 6, 326–343.
- van Buchem, F.S., Al-Husseini, M.I., Maurer, F., Droste, H.J. and Yose, L.A. 2010. Sequence-stratigraphic synthesis of the Barremian – Aptian of the eastern Arabian Plate and implications for the petroleum habitat. *GeoArabia Special Publication*, 4 9–48.
- van de Velde, S. and Meysman, F.J.R. 2016. The Influence of Bioturbation on Iron and Sulphur Cycling in Marine Sediments: A Model Analysis. *Aquatic Geochemistry*, 22, 469–504. <https://doi.org/10.1007/s10498-016-9301-7>
- Vera, J.A. (coord), Arias, C., Castro, J.M., et al. 2004. Zonas Externas Béticas. In: Vera JA (ed), *Geología de España*, SGE-IGME, Madrid, 354–389.
- Vía-Boada, L., 1975. Contribución al estudio de “Mecochirus magnus” (McCoy), crustáceo decápodo del “Lower Greenand” de Inglaterra, abundante en el Cretáceo nororiental Ibérico. 1er Symposium sobre el Cretácico de la Cordillera Ibérica, Cuenca, España, 25–49.
- Vilanova, J., 1870. Ensayo de descripción geognóstica de la Provincia de Teruel en sus relaciones con la agricultura de la misma. Junta de Estadística, Años 1863, 1868, 1–312.



**DAY 2: JUNE 23rd, 2022****DISTRIBUTION OF DECAPOD COMMUNITIES FROM THE
EARLY EOCENE OF THE SOUTH-PYRENEAN CENTRAL
UNIT (TREMPE-GRAUS BASIN, SPANISH PYRENEES)****Fernando A. Ferratges¹, Álvaro García-Penas¹, Marcos Aurell¹ and Samuel Zamora^{1,2}**¹ Departamento de Ciencias de la Tierra-IUCA, Universidad de Zaragoza, 50009 Zaragoza, Spain.² Instituto Geológico y Minero de España (IGME-CSIC), C/Manuel Lasala, 44, 9B, Zaragoza E-50006, Spain.**Keywords:** Crustacea, decapoda, paleoenvironments, paleoecology, Ypresian**INTRODUCTION**

The early Eocene of the south-central Pyrenees (northeast of Spain) has provided a great diversity of fossil decapods including some representatives that help elucidating the origin of some modern families. The observed decapod diversity is in part related to the large variety of shallow marine facies, which are well exposed in continuous outcrops. The analysis of these outcrops have provided a unique opportunity to understand the spatio-temporal distribution in different sedimentary environments of different groups of decapod crustaceans (Vía, 1969, 1973; Artal *et al.*, 2005, 2013a, b; Fraaije and Pennings, 2006; Schweitzer *et al.*, 2007; van Bakel *et al.*, 2012; Ferratges *et al.*, 2019, 2021a, b, c, 2022).

The Eocene sedimentation in the south-central Pyrenean basins (i.e. Tremp-Graus, Ainsa and Jaca basins) includes a complete Eocene succession with a great diversity of sedimentary environments developed in a mixed carbonate-siliciclastic marine sedimentary system: from proximal deltaic systems and shallow environments in the eastern Tremp-Graus basin, to deep slopes in most of the Ainsa and Jaca-Pamplona basins, progressively shallower to the top (i.e., Puigdefàbregas, 1975; Millán *et al.*, 1994; Morsilli *et al.*, 2012; Pomar *et al.*, 2017; Canudo *et al.*, 2021). Offshore, the abyssal plains of the Basque-Cantabrian oceanic basin are found in the most distal part of the basin (i.e., Garcés *et al.*, 2020).

The Tremp-Graus Basin, on which the present fieldtrip focuses, corresponds to a piggy-back basin carried on the Montsec thrust sheet. It is bounded to the north and to the south by the Boixols and Montsec thrusts respectively, and is located within the South-Pyrenean Central Unit (SPCU) (Fig. 1A). Transitional siliciclastic environments with fluvial and deltaic systems formed facies belts with a SE-NW trending, which were fed by alluvial systems in a NE-SW direction (Barnolas *et al.*, 1991, 1992; Barnolas and Gil-Peña, 2001). These fluvio-deltaic systems prograded westwards due to tectonic activity and sourced the turbidite system of the Ainsa and Jaca-Pamplona basins during the Ypresian and Lutetian (lower to middle Eocene) (Garcés *et al.*, 2020 and references therein).

Four stops are envisaged during this field trip:

- 1. The lower Eocene (upper Ypresian/early Lutetian) from Morillo Formation in the road cut of the A-1605.** The limestones and marl succession of this site corresponds to the most younger levels with Eocene records of crabs in the Isabena Valley. Decapod diversity is low here but contains interesting groups of both decapod crustaceans and other benthonic organisms.
- 2. Lower Eocene (late Ypresian) from Roda Marls Formation.** This site stands out for the quantity and good conservation of fossil crabs, especially *Zanthopsis dufourii* which has in this level its highest abundance. The decapod assemblage collected in this area corresponds to taxa associated with unconsolidated soft bottoms (muddy and fine sand environments).

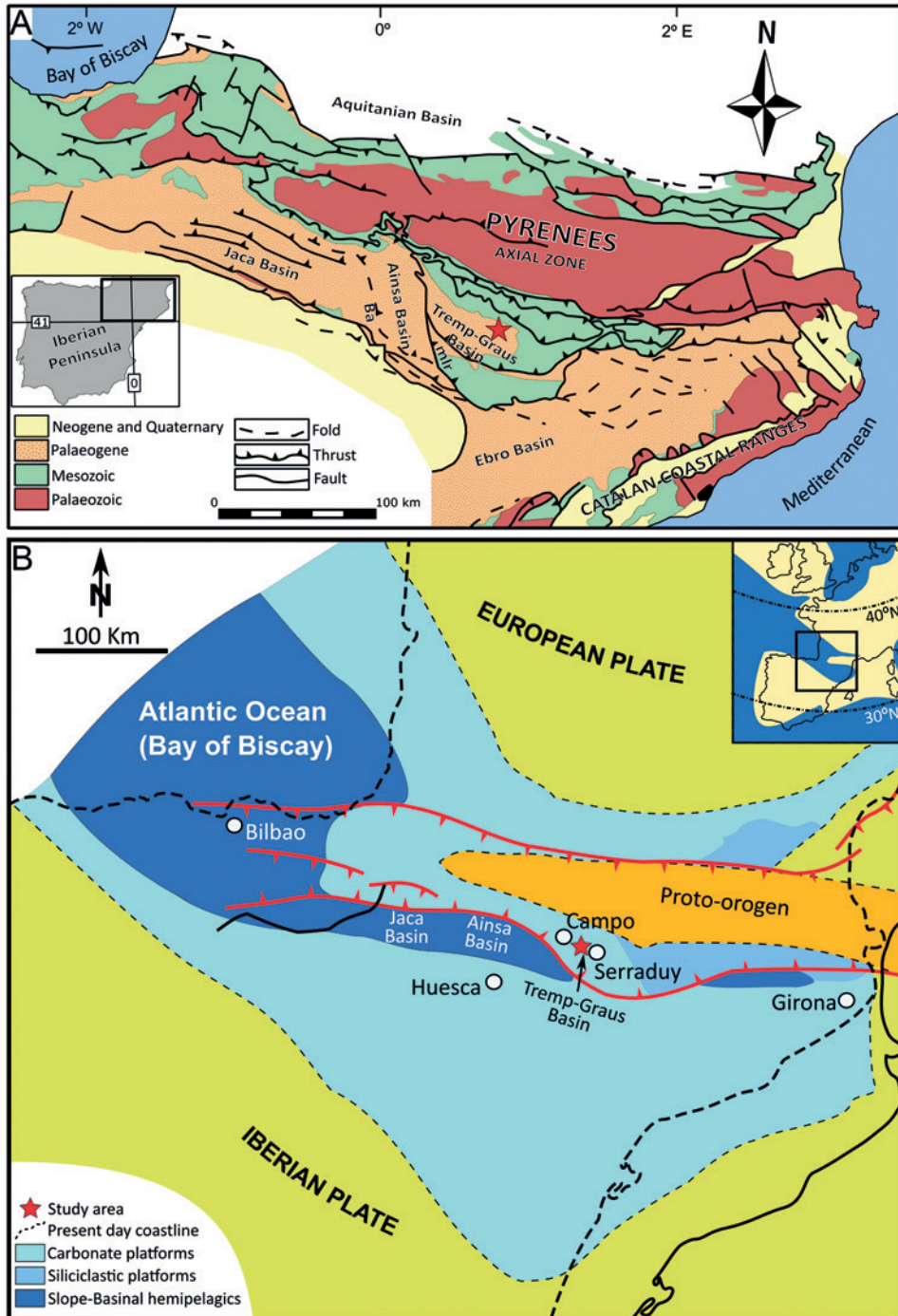


Figure 1. Location and paleogeography of the Pyrenean area. A. Geological map of the South Pyrenean Basins showing the location of the visited area (red star) in the northern part of the Tremp-Graus Basin in the south-central Spanish Pyrenees (modified after Capote et al., 2002). B. Approximate paleogeographic reconstruction of the Pyrenees and the adjacent foreland basins during the early Eocene (modified after Berástegui et al., 2010).

3. **Viewpoint of Roda de Isábena.** The high relief generated by the sandstones of the Esdolomada member of the Roda Formation offers an optimal point of view to observe and understand the arrangement of the different Eocene formations in this sector. In addition, this stop is located in the medieval town founded in the 10th century, with an interesting historical heritage.
4. **Early Eocene (Ypresian) from Serraduy Formation in La Puebla de Roda: Decapod diversity in the Ramals reefal build-up.** This outcrop has provided an exceptional early Eocene decapod fauna associated with a reef environment. The exceptional exposure of the outcrop allows direct observation of the facies arrangement and taxa distribution. The detailed study and exhaustive sampling in different facies has allowed a detailed characterization of the different species present in different sectors of the outcrop and provided information about the fossil groups that developed coeval to the different environments.

THE SOUTH PYRENEAN BASINS: BASIN EVOLUTION

During much of the Mesozoic, the evolution of the Pyrenean basins was related to an extensional tectonic regime linked to the separation of the Iberian microplate from the rest of Pangea (Rosenbaum *et al.*, 2002). The initial stages of rift development occurred around the Permian-Triassic transition. This extensive regime prevailed during the Middle Triassic to Jurassic, with sedimentation in wide shallow epicontinental seas (Meléndez and Aurell, 2004). A second rift phase during the Lower Cretaceous was related to the opening of the Bay of Biscay.

The extensional tectonic regime changed since the latest Cretaceous, onwards from the late Santonian. At that time, the inversion of the Pyrenean Mesozoic basins began due to the Alpine compression after the convergence of the African and European plates. This change in the tectonic regime resulted in the beginning of the development of a foreland basin, coeval to the development of the Pyrenean orogen (Puigdefàbregas *et al.*, 1986, 1992; Puigdefàbregas and Souquet, 1986). The uplift of the axial zone in the Pyrenees during the Paleocene in the eastern Pyrenean domain resulted in the individualization of two foreland basins: the Northern and Southern Pyrenean basins (Barnolas *et al.*, 2004).

During the lower Eocene (Ypresian) there is an increase of the tectonic activity, reaching the Tectonic Climax of the Middle Eocene. As a result of this new stage of tectonic activity, the South-Pyrenean Central Unit (SPCU) was emplaced with coeval development of highly subsident carbonate platforms in marginal areas. The development of carbonate during the Paleocene-earliest Eocene was favoured by the relative tectonic quiescence combined to the reduction of the siliciclastic supply (see Silva-Casal, 2017). All this resulted in the advance of the sedimentary systems towards the foreland and the compartmentalization of the South Pyrenean basin, giving rise to the Oriental South Pyrenean basin, the Tremp-Graus basin, the Ainsa basin and the Jaca-Pamplona basin (see Silva-Casal, 2017).

STRATIGRAPHY, ENVIRONMENTS AND PALAEOGEOGRAPHY

During the Eocene, the South Pyrenean basins spread over an elongated gulf spanning from east to west (Fig. 1B). This gulf was connected with the Cantabrian Sea in the Bay of Biscay and was limited to the north by the axial zone of the Pyrenees (Plaziat, 1981; Garcés *et al.*, 2020). The gulf was developed in tropical latitudes (i.e., Hay *et al.*, 1999; Silva-Casal *et al.*, 2019), and was flanked by shallow-water carbonate platforms, siliciclastic systems, and accumulations of hemipelagic sediments at the bottom of the basin (see Silva-Casal, 2017; Silva-Casal *et al.*, 2017). This diversity of marine environments was also conditioned by the progradation of deltaic facies towards the west, due to progressive tectonic uplift of the eastern marginal areas (Garcés *et al.*, 2020 and references therein).

The Eocene climate was much warmer than today due to the high concentration of greenhouse gases (see Pearson and Palmer, 2000; Zachos *et al.*, 2008; Pomar *et al.*, 2017). However, throughout the Eocene there was a climatic transition, gradually passing from the warm climate

that was present since the Late Cretaceous, to a cold climate, with the presence of polar ice sheets at the end of the Eocene (Pekar *et al.*, 2005; Tripathi *et al.*, 2005, 2008; Edgar *et al.*, 2007; Zachos *et al.*, 2008; Jadwiszczak, 2010). This general cooling trend was interrupted by a series of episodes or hyperthermal events that punctually affected the climate during the Paleocene and Eocene (see Payros *et al.*, 2012 and references). These tropical conditions favoured the formation of optimal environments to house a great diversity of crustaceans during the Eocene.

An almost complete Eocene succession of the SPCU crops out in the vicinity of the Roda de Isabena village (Fig. 2). This succession provides a nearly 5000-m-thick continuous record of environmental conditions during the 12 My represented by the early to middle Eocene times (54 to 42 Ma, according Honegger *et al.*, 2021). The thickness of the different Eocene formations defined within this succession has significant lateral changes, and they mostly consists of marls and sandstones, with the exception of isolated reef domes up to 5 m in some areas.

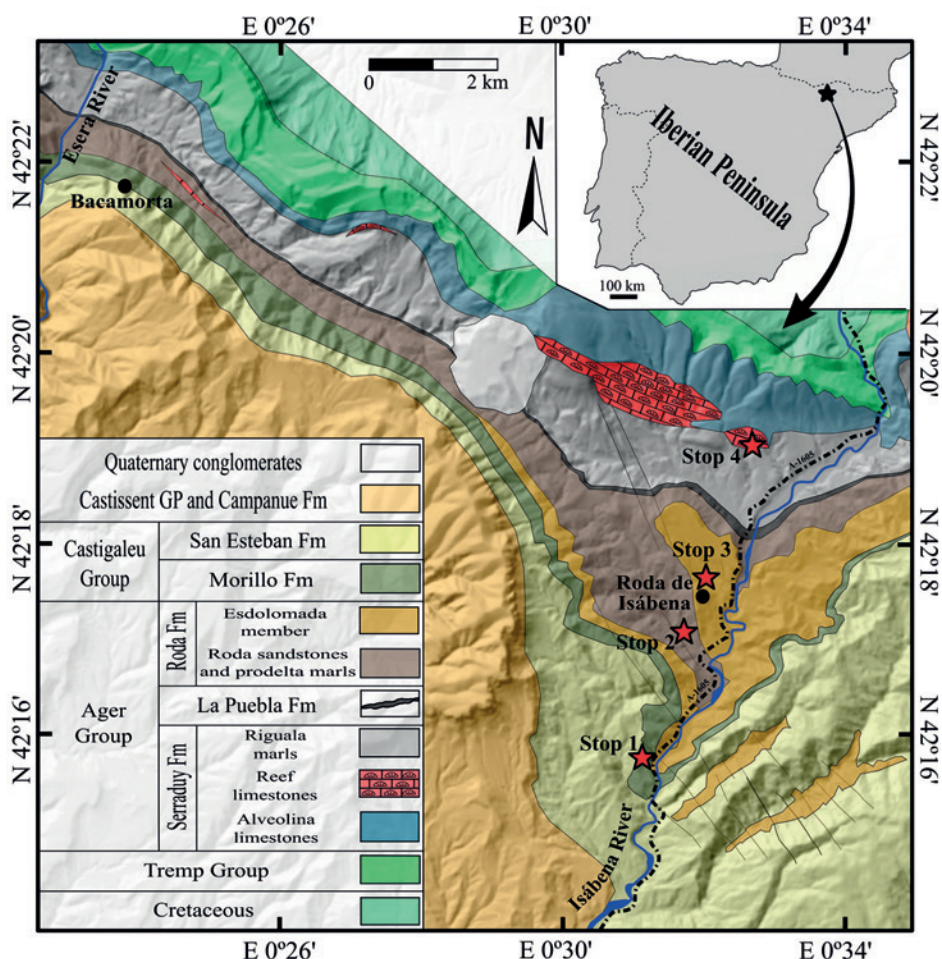


Figure 2. A. Schematic geological setting (south-central Pyrenean zone). Red stars mark the different stops detailed below. B. Synthetic stratigraphic cross section and sedimentary model of the northern margin of the Tremp area during the lower Eocene, with main facies types and the location of the main 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 Einchensee (2003) and Pomar *et al.* (2017). The lunch stop will be at stop 3.

The lower-middle Eocene succession has been divided into four marine formations (Fig. 3). The lower two units (i.e. the Serraduy and La Puebla formations) consist mostly of marls with interbedded carbonate-rich intervals, the Roda formation is mostly terrigenous (clays, silts), while carbonate productivity returns during the deposition of the Morillo formation. The Serraduy formation includes bioclastic-rich intervals represented by the Alveolina Limestones and the reef limestone member (see inset in Fig. 2).

THE EARLY EOCENE DECAPOD RECORD IN THE SOUTH-PYRENEAN CENTRAL UNIT

As explained above, south-central Pyrenean basins record one of the most complete records of Eocene marine sedimentary successions from Europe. This succession has provided several fossil decapod crustaceans (Fig. 3), described in different outcrops (i.e., Vía, 1969, 1973; Artal *et al.*, 2013, 2021; 2022; Ossó *et al.*, 2014; Domínguez and Ossó, 2016a, b; López-Horgue and Bodego, 2017; Artal and Van Bakel, 2018a, b; Ferratges *et al.*, 2019, 2020a, b).

The visited outcrops are classically known for their content of decapod crustaceans and their excellent state of preservation. The first decapod studies in the area were carried out by Vía in his major revision of Eocene decapods from Spain (see Vía, 1959, 1969). In this study, Vía stand out the great abundance and good state of preservation of fossil crabs in this region, especially the species *Zanthopsis dufourii*, as well as some interpretations about their distribution and their relationship with carcinic assemblages from other European basins.

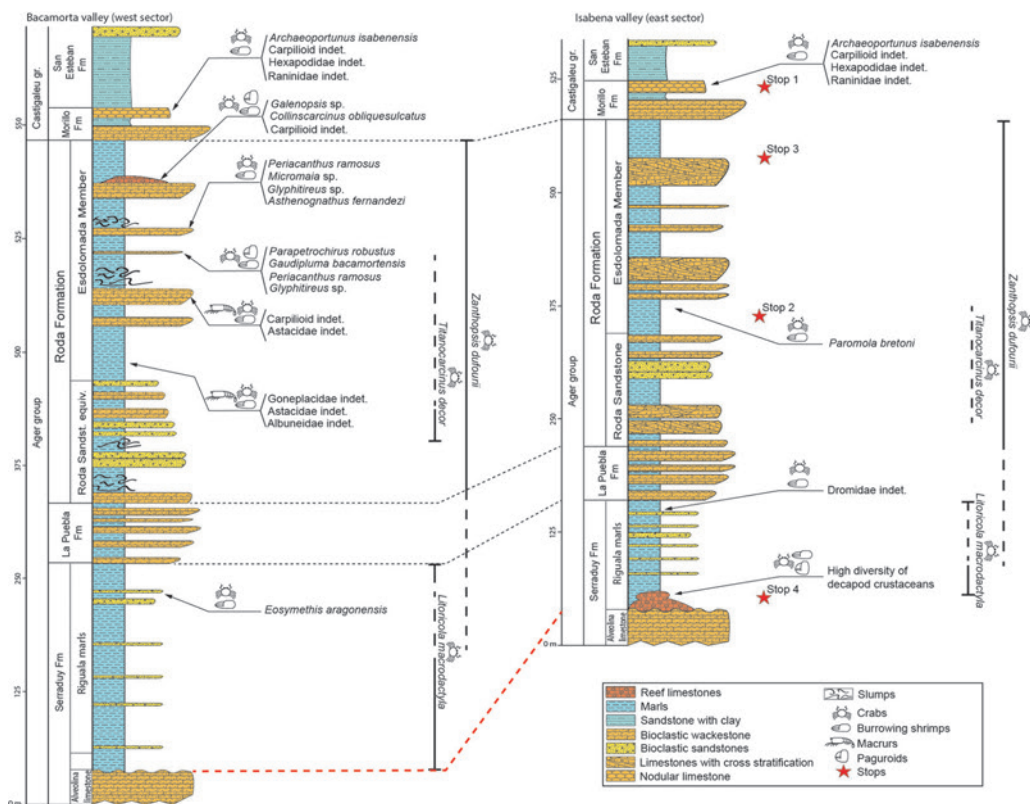


Figure 3. Synthetic stratigraphic logs of the area indicating the main lithological features of the middle Ypresian to lower Lutetian (lower Eocene) formations and the successive levels with recorded decapod associations. To see the high diversity of decapod crustaceans to the bottom of the east sector (reefal interval of the Serraduy Formation), see table 1.

Over the last decades, the knowledge of fossil decapod crustaceans of the SPCU has also substantially increased, and some authors (Vía, 1973; Fraaye, 1995; Artal *et al.*, 2005, 2013a, b; Fraaije and Pennings, 2006; Schweitzer *et al.*, 2007; van Bakel *et al.*, 2012; Ferratges *et al.*, 2019, 2021a, b, c, 2022), have highlighted the interest and relevance of these outcrops, with several new species and occurrences reported. This development is in part related to the excellent outcrop conditions exposing a large variety of shallow marine facies.

An important particular case corresponds to the outcrop known as Ramals (or Font del Oro) known since the end of the 19th century (i.e., Cotteau, 1889). However, only the high diversity and abundance of other benthic organisms such as molluscs and echinoderms was noticed. Later on, Vía (1973) reported the first specimens of brachyura associated with the distal equivalents of these materials. Artal and Vía (1988) In 1981, with described for the first time the great diversity of crustaceans in the reefal interval included in these outcrops. Since then, several systematic studies have described several species of decapod crustaceans from these materials (Artal and Castillo, 2005; Artal and Van Bakel, 2018a, 2018b; Ferratges *et al.*, 2019; Artal *et al.*, 2022; Ferratges *et al.*, in press), with some representatives that help to elucidate the origin of some modern families.

In the last years, important systematic and exhaustive sampling efforts led to a better understanding of the distribution and relative abundance of these faunas, related to the different environments, making it clear that it is a hot spot of diversity for the early Eocene, with 42 species of decapods in the same outcrop (Ferratges *et al.*, 2021). These authors attributed the decapod faunal turnovers to palaeoecological changes. The works developed since then, show an enormous diversity, with primitive forms of several groups and an unexpected diversity (Artal *et al.*, 2022; Ferratges *et al.* in press, and in preparation).

STOP 1 - LOWER EOCENE (UPPER YPRESIAN/LOWER LUTETIAN) MORILLO FORMATION.

Location

The section crops out in a road cut of the A-1605 road in its passage through the Roda de Isábena (Fig. 1).

- » Coordinates: 42°15'45"N, 0°31'03"E and 42°16'08"N, 0°31'27"E, Elevation: 693 m.
- » Geological map of Spain, 1:50,000, sheet of Arén (251).
- » Geological setting: Tremp-Graus basin, northeastern Spain.
- » Lithostratigraphical units: Morillo Formation (Fig. 4).
- » Age: Late Ypresian/early Lutetian (lower Eocene).

Aims

- » To show the general aspects of the upper early Eocene succession in the SPCU. Discuss the environment based on fossil preservation and sedimentary structures.
- » To put the decapod-bearing levels into a stratigraphical context.

Description

In this section there is a continuous exposure of the upper Ypresian -lower Lutetian Morillo Formation. The locality is about 3 km south of the small village of Roda de Isábena. The section starts with a few meters after crossing the Isabela River on the A-1605 road Graus-Serraduy.

The Morillo Formation consists of two carbonate levels (limestone or carbonate silt) rich in macroforaminifera, separated by a marly interval. The thickness of this unit increases in an E-W direction, reaching to 30 m in the Isábena river area (Serraduy section) and 57 m in the Esera river area (Campo section). It has been interpreted as a transgressive interval whose most

proximal facies (Isábena river zone) are represented by inner platform carbonates with abundant miliolids, orbitolithids and alveolinids, and the distal facies (Esera river zone) by middle platform carbonated silts with nummulitids and discocyclinids (Serra-Kiel *et al.*, 1994).

The visited outcrop consists of nodular bioclastic limestones with a great diversity of benthic fauna in the Isábena river area. Echinoderms stand out for their abundance, diversity and preservation. Among the decapod crustaceans *Archaeoportunus isabensis* Artal, Ossó and Domínguez, 2013 (previously assigned to the Roda Formation), is the best represented but other decapod crustaceans have been also recognized (Ferratges *et al.*, 2022). Tosquella (1988) interpreted a depositional setting within the photic zone of a shallow platform.

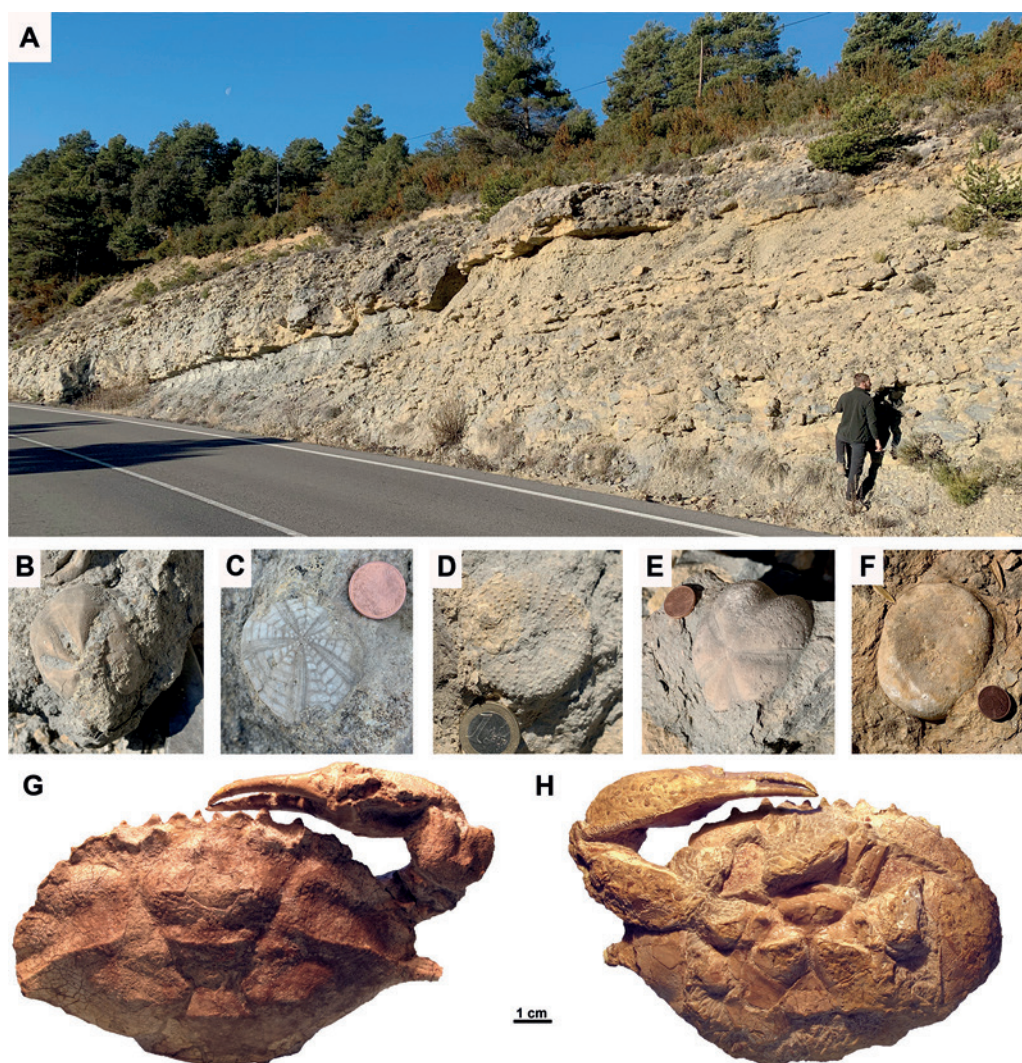


Figure 4. A. General view of the Stop 1, the upper level of Morillo Formation; B-F. Some in situ echinoderms from Morillo Fm; G-H. Holotype of *Archaeoportunus isabensis* (MGSB68576), in dorsal (G) and ventral view (H); the most iconic crab of this formation described by Artal *et al.*, 2013 and republished in Artal *et al.*, 2021. Photograph of *A. isabensis* courtesy by Á. Ossó.

STOP 2 - LOWER EOCENE (UPPER YPRESIAN) RODA FORMATION.

Location

The section crops out in a road cut of the A-1605 road in its passage through the Roda de Isábena (Fig. 5).

- » Coordinates: 42°17'09"N, 0°31'33"E, Elevation: 725 m.
- » Geological map of Spain, 1:50,000, sheet of Arén (251).
- » Geological setting: Tremp-Graus basin, northeastern Spain.
- » Lithostratigraphical units: Roda Formation (Fig. 3).
- » Age: late Ypresian (lower Eocene).

Aims

- » The aim of this stop is to observe the prodelta marls of the Roda Formation with particular emphasis in the stratigraphic levels that have provided great abundance of crabs, especially *Zanthopsis dufourii*, and occasionally other crabs (*Paromola bretoni*, *Titanocarcinus decor*, *Carpilidae* indet.).
- » Discuss environmental conditions in marly dominated bottoms.

Description

The upper Ypresian (lower Eocene) Roda Formation (Samsó *et al.*, 1990; Tosquella *et al.*, 1990) includes successive levels rich decapod faunas relevant for the understanding Ypresian decapod assemblages, preserved in a progradational deltaic systems. The Roda Formation is a coarsening and shallowing upwards succession (Molenaar and Martinus, 1990) and shows a progradational pattern to the south and southwest (i.e., Leren *et al.*, 2010 and references herein). This formation is divided in two members: (1) the lower member consists of thick prodelta marly bodies with detrital intervals (sandstones). and overlies the alternating sandstones and siltstones of the La Puebla Formation and Riguala marls member of the Serraduy Formation; (2) the upper member corresponds to the tidally influenced deltaic facies of Roda Sandstone. Elementary sequences consists of detrital sedimentary bodies separated by marly intervals rich in fauna, arranged in a set of offlap-onlap cycles of deltaic and inner platform progradational facies, respectively. This member is especially remarkable in proximal areas. West to the Isábena River, the Roda Formation rapidly transitions to prodelta and open platform marls.

In the area of the Isábena River the Roda Formation has a total thickness of 250 m. A lower 115 m-thick marly-dominated interval includes up to 1 m-thick detrital and carbonate intercalations. Westwards, in the Campo section, the unit consists of a 500 m-thick succession of marls and sandstones including highly fossiliferous shallow-marine intervals (Martinus and Molenaar, 1991). This member contains a great diversity and abundance of decapod crustaceans and have provided several important assemblages of decapods in different associations (see Fig. 2). The presence of *Zanthopsis dufourii* (H. Milne Edwards, 1850) stands out, which appears associated with other benthic fauna; *Asthenognathus fernandezi* Ferratges, Zamora and Aurell (2022), *Paromola bretoni* Ferratges, Domínguez and Ossó, 2021, *Periacanthus ramosus* Artal and Castillo, 2005, *Eosymethis aragonensis* van Bakel, Guinot, Artal, Fraaije and Jagt, 2012, *Collinscarcinus obliquesulcatus* Artal and van Bakel, 2020, *Titanocarcinus decor* Schweitzer, Artal, van Bakel, Jagt, and Karasawa, 2007; *Gaudipluma bacamortensis* Artal, van Bakel, Fraaije and Jagt, 2013 (Artal *et al.*, 2013), *Parapetrochirus robustus* Ferratges, Artal and Zamora, 2021 (Ferratges *et al.*, 2021a), have been previously documented from the Roda formation in different localities.

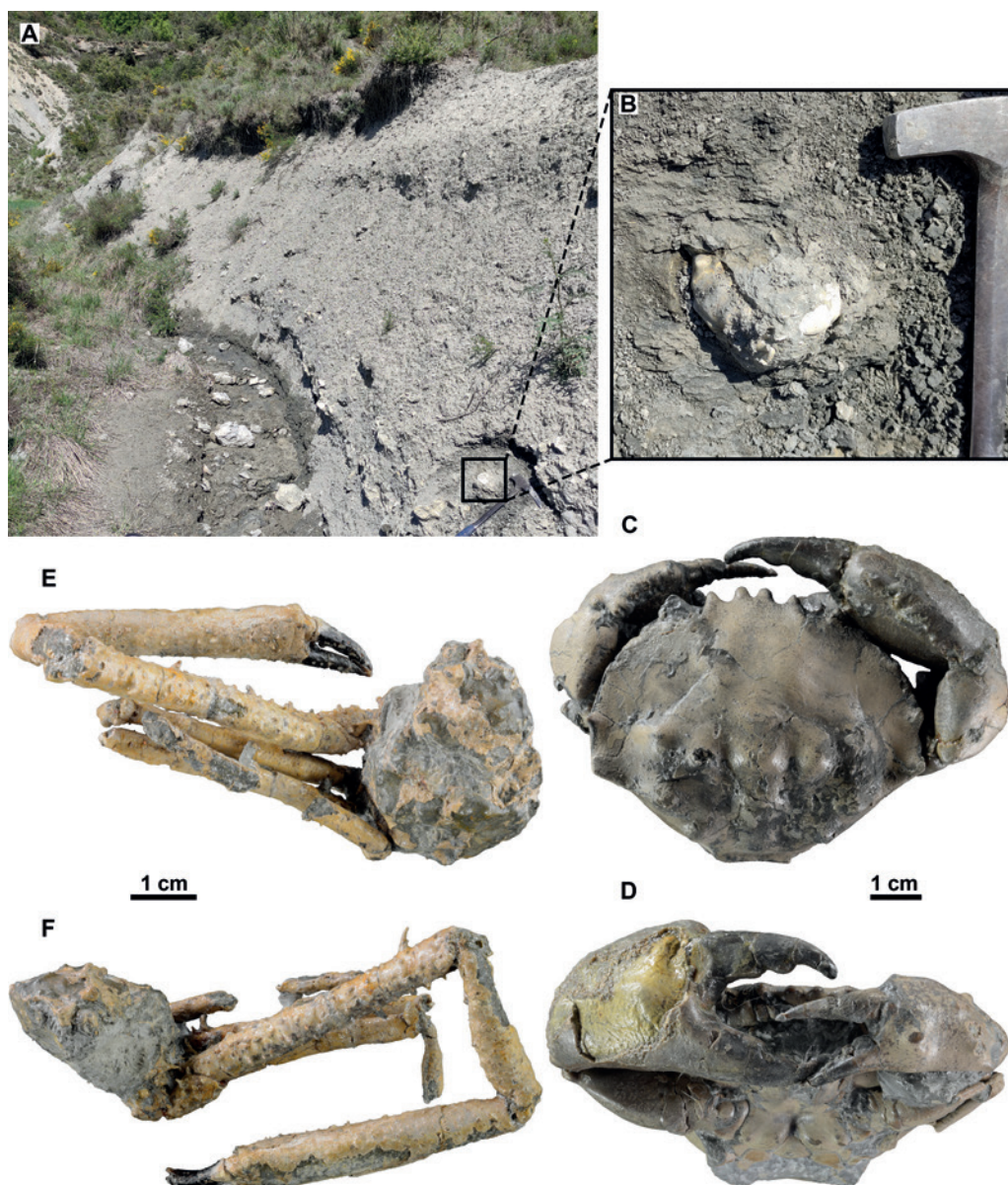


Figure 5. A. View of the visited outcrop in the Stop 3; B. detail of *in situ* articulated fossil of *Zanthopsis dufouri*; C-D. *Zanthopsis dufouri* from the same site in dorsal (C) and oblique frontal view (D); E-F. Holotype of *Paromola bretoni* (MPZ 2020/615) from the same outcrop, in dorsal (E) and frontal view (F).

STOP 3 - VIEWPOINT OF RODA DE ISÁBENA

Location

Viewpoint in the north of Roda de Isábena village (Fig. 6).

- » Coordinates: 42°17'32"N, 0°31'40"E, Elevation: 880 m.
- » Geological map of Spain, 1:50,000, sheet of Arén (251).
- » Geological setting: Tremp-Graus basin, northeastern Spain.
- » Lithostratigraphical units: Serraduy, Roda, Morillo, San Esteban and Campanue formations (Figs. 2, 3 and 6).
- » Age: Ypresian, and early Lutetian (early Eocene).

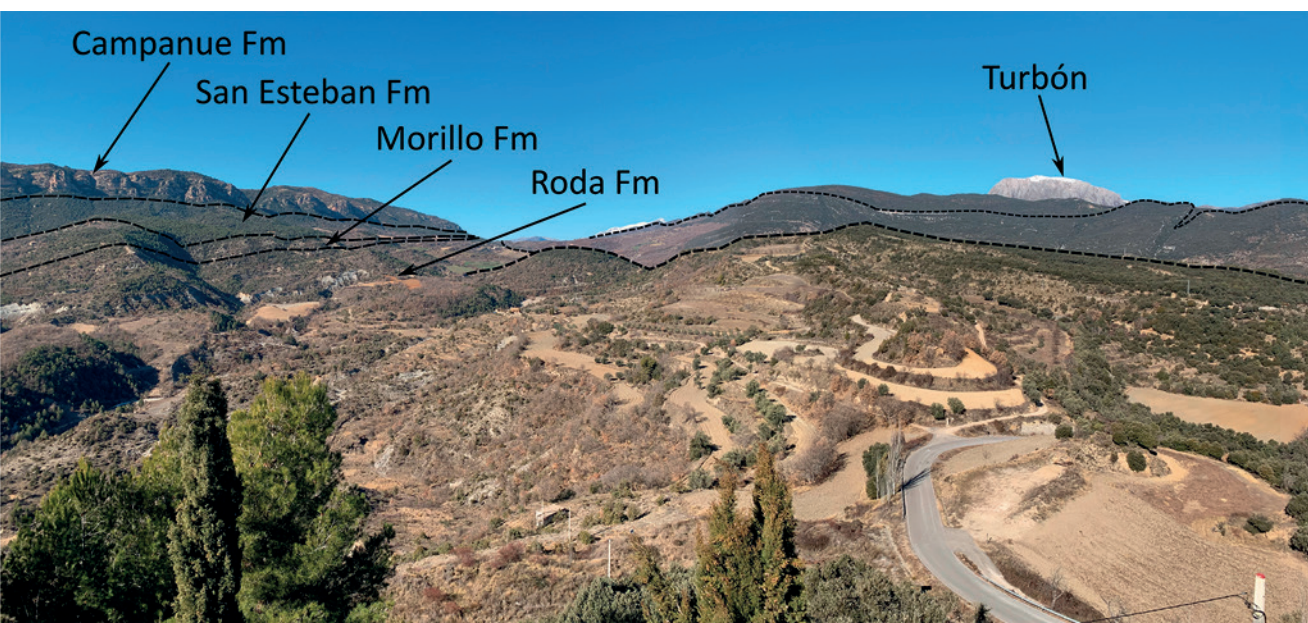
Aims

- » The objective of this stop is to observe a panoramic view of the whole lower Eocene succession in the area to explain its lithostratigraphy and sedimentary evolution.
- » To discuss the effect of the environmental change to the decapod crustacean communities.

Description

The village of Roda de Isábena is built on the proximal Roda Sandstone Member (explained above), a classical example of a well-exposed multiscale Gilbert-type delta. The elevated relief that these sandstones create with respect to the adjacent marly materials, gives rise to an excellent viewpoint of the sequence that crops out in this sector.

The oldest materials are located to the north, where the Mesozoic materials create important reliefs (Turbón peak especially stands out). Above these, and closer, is the Serraduy Formation, with its three different members (explained below). In the most depressed area of the valley, the upper member of the Serraduy Formation (Riguala marls) and the Roda Formation (Roda marls) crop, with some intercalations of sandstones corresponding to lateral equivalents of the Roda sandstones and the Morillo Formation. Finally, to the south, the great reliefs generated by the fluvial materials (conglomerates) of the Castissent Group and the Campanue Formation stand out (Fig. 6).





STOP 4 – Early Eocene (Ypresian) from Serraduy Formation in La Puebla de Roda: DECAPOD DIVERSITY IN THE RAMALS REEFAL BUILD-UP.

Location

The visited outcrop known as Ramals is a well exposed reef environment located 1.3 km to the north of Poblade Roda, in northeastern Huesca province (Aragón, Spain) (Fig. 2).

- » Coordinates: 42°18'56"N, 0°32'30"E, Elevation: 800 m.
- » Geological map of Spain, 1:50,000, sheet of Arén (251).
- » Geological setting: Tremp-Graus basin, northeastern Spain.
- » Lithostratigraphical units: Serraduy Formation, with three members: *Alveolina* limestones, Reef limestones member, and *Riguala* marls (Fig. 7).
- » Age: early to middle Ypresian (early Eocene).

Aims

- » To visit the outcrop with the highest abundance and diversity of decapod crustaceans from Spain.
- » Discuss the benthic crustacean decapod community replacement related with changes in substrate conditions.
- » To highlight and understand the distribution and high decapod diversity of this site.
- » To put the decapod-bearing levels into a stratigraphical and sedimentological context.
- » To interpret the decapod habitats based on fossil communities and facies distribution.

Description

Around the Ramals area, the Serraduy Formation forms an almost continuous ESE-WNW trending outcrop (Fig. 7A). 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* Limestone. This unit was deposited after the widespread transgression that occurred at the onset

Figure 6. Panoramic view of the Isabena valley with the relevant reliefs and outcrops indicated. In the farthest part, the Mesozoic materials of the Turbón massif can be seen. At the eastern end (right) the conglomerates give rise to the Sierra de Sis.



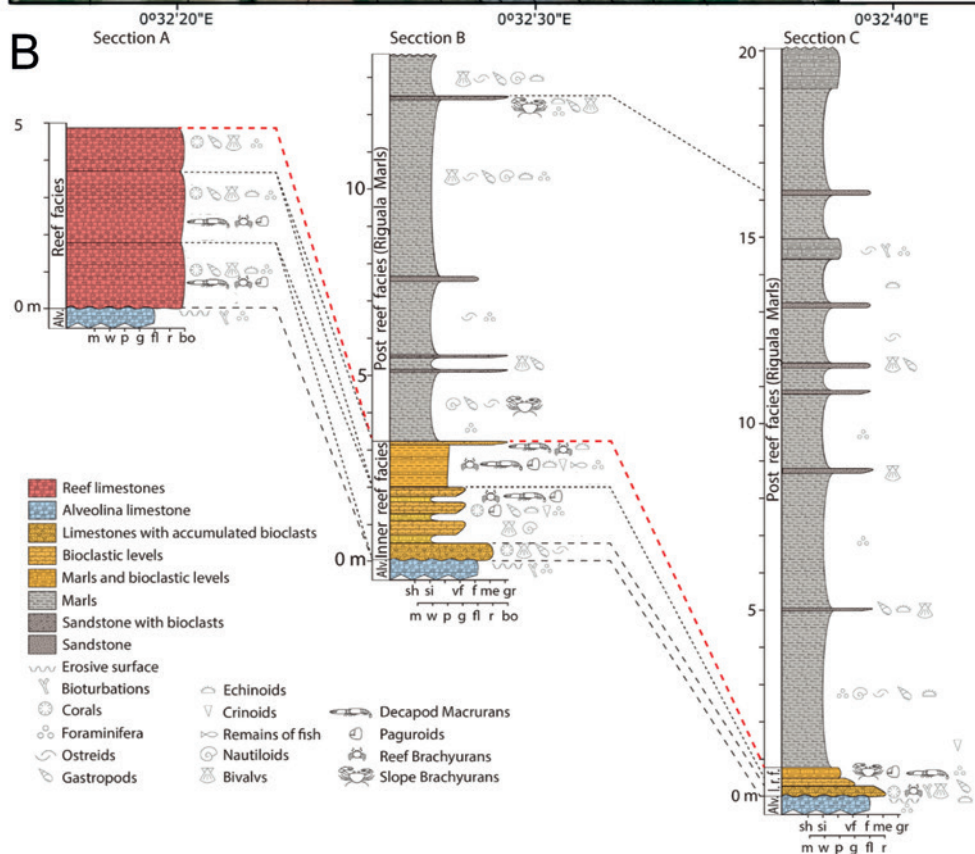
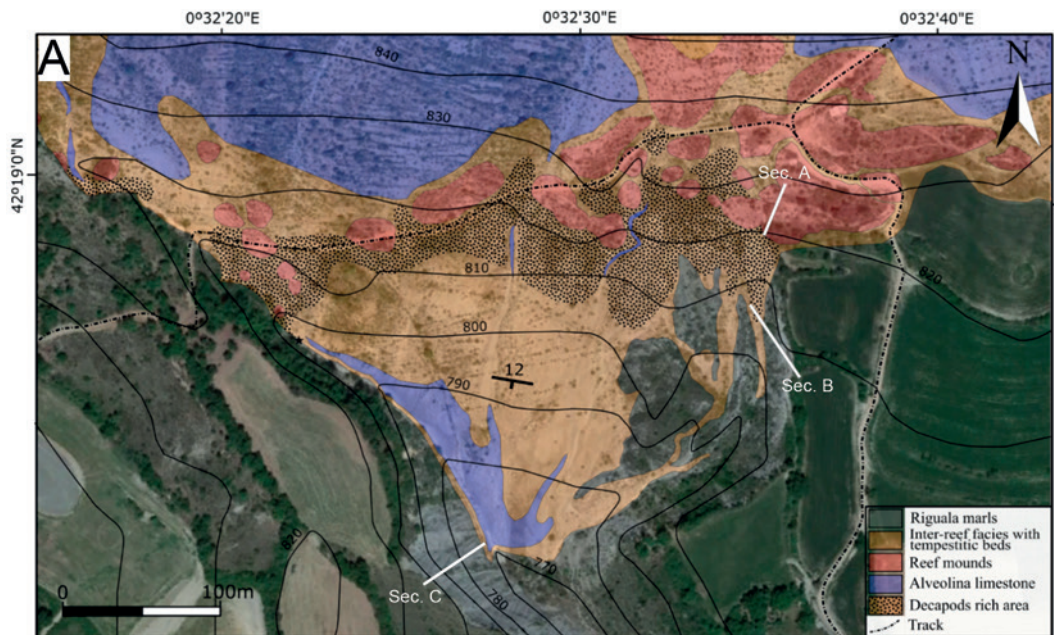
of the Eocene. The topography, together with the warm temperatures, favoured the setting of a low-relief carbonate ramp across the marginal areas of the Tremp-Graus basin at the earliest Eocene, in which the Alveolina Limestones was deposited (Ferrer, 1971; Robador *et al.*, 1991; Luterbacher *et al.*, 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 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 associated facies characterize the middle member of the Serraduy Formation (i.e., the Reef limestone member; Serra-Kiel *et al.*, 1994).

Exposed on the north-western margin of the Tremp-Graus basin is the early Eocene reef unit of the middle part of the Serraduy Formation. The classic outcrop known as Ramals exposes a reefal facies belt including closely spaced mounds up to five meters high, and associated inter- and forereef facies (Fig. 8) (Ferratges *et al.*, 2021). The reef framework consists of coral framestones with bioclastic wackestone to packstone matrix, with colonial and solitary corals, crustose red algae, encrusting foraminifers and bryozoans. Analysis of the reef framestone and associated facies, combined with characterization of the associated invertebrate assemblage, indicates that these reefs were developed at euphotic to mesophotic depths, a few tens of meters deep, around or below storm wave base (Gaemers, 1978; Eichenseer, 1988; Pomar *et al.*, 2017), with some nutrient content to maintain the diversity of associated benthic organisms. The reconstruction of the lateral and vertical relationship of the different sedimentary domains provided the overall sedimentological and stratigraphic framework, in which abundant fauna has been found and the different decapod crustacean assemblages are located from proximal to distal areas, and from deeper to shallower facies.

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 exposure on the sea floor. The studied reef mounds and associated facies allowed the establishment of a rich association of decapods consisting of 42 species (see Ferratges *et al.*, 2021).

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. 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 a top of the Alveolina limestone (Fig. 7B). 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 (Ferratges *et al.*,

Figure 7. 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.



2021). Finally, from the upper Lutetian, the fluvial-deltaic systems gradually prograded and filled the Tremp-Graus basin, reaching the Jaca-Pamplona basin (de Federico, 1981; Benthams, 1992; Nijman, 1998; Barnolas and Gil-Peña, 2001; Montes-Santiago, 2002; Chanvry *et al.*, 2018).

Statistical studies of diversity carried out in this area suggest that the distribution of the different families is not random and were distributed across different facies, as supported by the sedimentological analysis (Ferratges *et al.*, 2021). Thus, in the reef and inter-reef areas, the most representative groups are: Carpilioids, pilumnoids, xanthoids, Aethroids 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 macrodactyla* (Figs. 9-10). In addition, the only decapod that remained in the post-reef marls deposited after the collapse of the reef mounds is *Litoricola macrodactyla* (see Ferratges *et al.*, 2021). 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.

Decapod fauna

For the early Eocene, the Ramals outcrop (together with some Italian outcrops), is one of the most diverse Eocene decapod localities in the world associated with a reef environment, and its excellent exposure allows inferring the environmental preferences of certain taxa (Ferratges *et al.*, 2021). This outcrop has yielded 42 decapod species (and several isolated chelas not assignable to any taxon) from the reef mounds and associated facies, which consist of 32 brachyuran crabs, eight paguroids, and two callianassoids (Table 1), and other diverse invertebrate fauna (see Zamora *et al.*, 2018).

The state of preservation, mostly preserved as isolated carapaces or claw fragments, with little abrasion or breakage 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). The fossils material collected in this outcrop (both crustaceans, echinoderms and vertebrate remains), suggest a relatively complex taphonomic history, with resedimentation events and long periods of exposure in the water-sediment interface that lengthened the biostratinomic phase.

Figure 8. Panoramic view of the Ramals outcrop, showing the relationship between reef (red) and inter-reef (orange) facies. The Riguala marls (transparent) are the post-reef deposits. The levels marked with a red star are those that provided the largest number and diversity of decapod crustaceans.



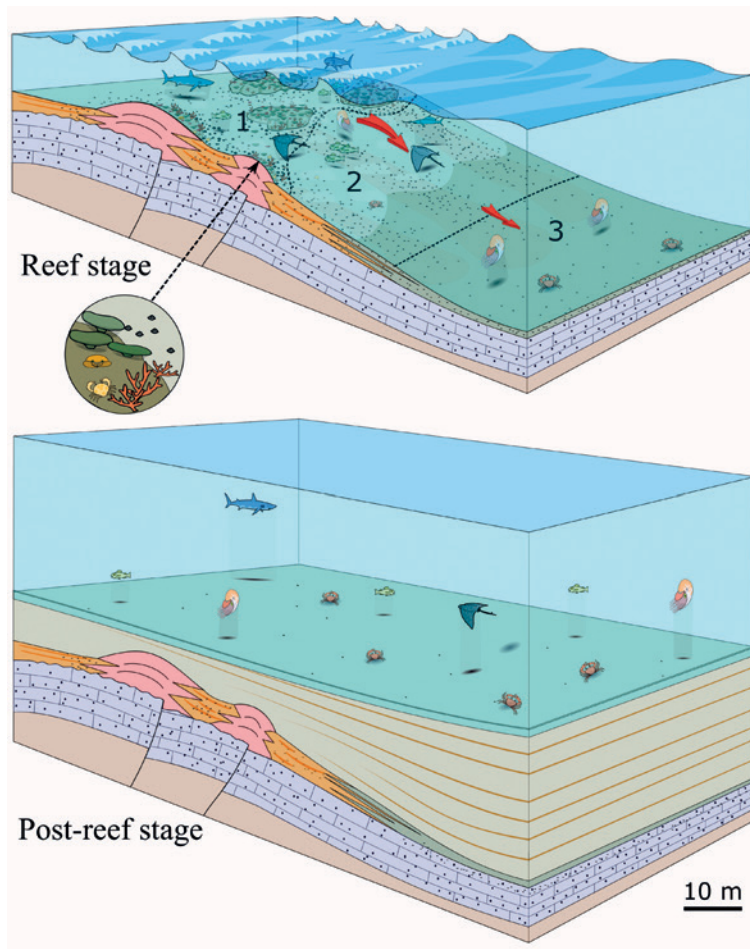


Figure 9. Simplified diagram showing the facies belt distribution. In the reef stage (top left), the reefal and inter-reef facies (1), inner fore-reef facies (2), and outer fore-reef facies (3) are differentiated. The red arrows show the dominant offshore transport of skeletal remains by episodic storm-induced currents. In the second stage (bottom left), the reefs were covered by the post-reef Riguala marls and there was a significant decrease in the diversity of the benthic fauna.



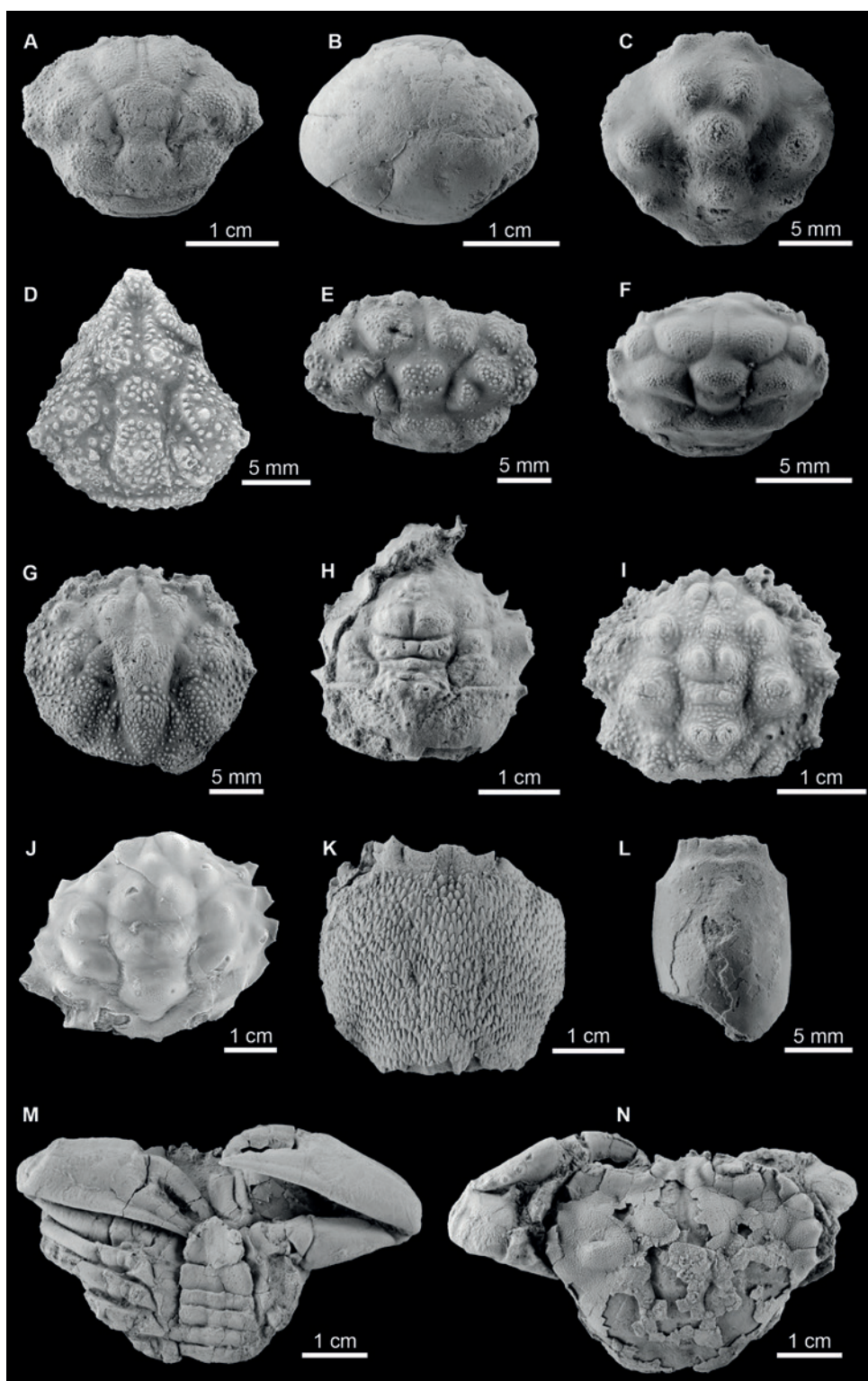
**Table 1.** Diversity of decapod crustaceans at the Ramals outcrop and their distribution according to the areas described in Ferratges et al., 2021.

Superfamily	Family	Subfamily	Taxon	Area
Callianassoidea Dana, 1852	Callianassidae Dana, 1852		Callianassidae indet.	Inner fore-reef
	Ctenochelidae Manning & Felder, 1991	Ctenochelinae Manning & Felder, 1991	<i>Ctenocheles</i> cf. <i>cultellus</i> (Rathbun, 1935)	Inner fore-reef/outer fore-reef
Paguroidea Latreille, 1802	Diogenidae Ortmann, 1892		<i>Clibanarius isabenaensis</i> Ferratges Artal, van Bakel & Zamora (in press)	Inner fore-reef
			<i>Parapetrochirus serratus</i> Ferratges Artal, van Bakel & Zamora (in press)	Inner fore-reef
			? <i>Petrochirus</i> sp.	Inner fore-reef
	Annuntidiogenidae Fraaije, Van Bakel and Jagt, 2017		<i>Paguristes perlatus</i> Ferratges Artal, van Bakel & Zamora (in press)	Inner fore-reef
	Calcinidae Fraaije, van Bakel and Jagt, 2017		<i>Dardanus balaitus</i> Ferratges Artal, van Bakel & Zamora (in press)	Reefal facies belt/Inner fore-reef
			<i>Eocalcinus veteris</i> Ferratges Artal, van Bakel & Zamora (in press)	Reefal facies belt to outer fore-reef
	Paguridae Latreille, 1802		? <i>Pagurus</i> sp.	Inner fore-reef
			<i>Anisopagurus primigenius</i> Ferratges Artal, van Bakel & Zamora (in press)	Inner fore-reef
Dromioidea De Haan, 1833	Dromiidae De Haan, 1833	Basinotopinae Karasawa, Schweitzer, and Feldmann, 2011	<i>Mclaynotopus longispinosus</i> Artal, Ferratges, van Bakel & Zamora, 2022	Inner fore-reef
		Dromiinae De Haan, 1833	<i>Torodromia elongata</i> Artal, Ferratges, van Bakel & Zamora, 2022	Inner fore-reef/outer fore-reef
		Sphaerodromiinae Guinot and Tavares, 2003	<i>Basidromilites glaessneri</i> Artal, Ferratges, van Bakel & Zamora, 2022	Inner fore-reef
			<i>Basidromilites</i> sp.	Inner fore-reef
	incertae sedis		? <i>Basinotopus</i> sp.	Inner fore-reef
	Dynomenidae Ortmann, 1892	Paradynomeninae Guinot, 2008	<i>Kromtitis isabensis</i> Artal, Ferratges, van Bakel & Zamora, 2022	Reefal facies belt/inner fore-reef
			<i>Sierradromia gladiator</i> Artal, Ferratges, van Bakel & Zamora, 2022	Reefal facies belt/inner fore-reef
Homoloidea De Haan, 1839	Homolidae De Haan, 1839		<i>Paromola</i> cf. <i>bretoni</i> Ferratges, Domínguez & Ossó, 2021	Outer fore-reef/post reef
Raninoidea De Haan, 1839	Raninidae De Haan, 1839	Cyrtorhininae Guinot, 1993	<i>Antonioranina ripacurtae</i> (Artal & Castillo, 2005)	Inner fore-reef
		Raninoidinae Lörenthey in Lörenthey & Beurlen, 1929	<i>Ranina</i> sp.	Inner fore-reef
			<i>Quasilaeviranina</i> sp.	Inner fore-reef
		Rogueinae Karasawa, Schweitzer, Feldmann & Luque, 2014	<i>Doraranina</i> sp.	Inner fore-reef
	?Orithopsidae Schweitzer et al., 2003		? <i>Necrocarcinus</i> sp.	Inner fore-reef



Superfamily	Family	Subfamily	Taxon	Area
Aethroidea Dana, 1851	Aethridae Dana, 1851		<i>Ilerdapatiscus guardiae</i> , 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		Cancridae indet.	Inner fore-reef
		<i>Cancrinae</i> Latreille, 1802	<i>Ceronnectes</i> sp.	Inner fore-reef
Carpilioidea Ortmann, 1893	Carpiliidae Ortmann, 1893		<i>Carpilius</i> sp.	Reefal facies belt/inner fore-reef
			<i>Eocarpilius ortegai</i> Artal & Van Bakel, 2018	Reefal facies belt/inner fore-reef
			<i>Oscacarpilius rotundus</i> Artal & Van Bakel, 2018	Reefal facies belt/inner fore-reef
	Tumidocarcinidae Schweitzer, 2005		<i>Xanthilites</i> sp.	Reefal facies belt/inner fore-reef
Goneplacoidea MacLay, 1838	Euryplocidae Stimpson, 1871		? <i>Alponella</i> sp.	Inner fore-reef
Hexapodoidea Miers, 1886	Hexapodidae Miers, 1886		<i>Eohexapus</i> sp.	Inner fore-reef
Parthenopoidea MacLeay, 1838	Parthenopidae MacLeay, 1838	Daldorfiinae Ng & Rodríguez, 1986	<i>Aragolambrus collinsi</i> Ferratges, Zamora & Aurell, 2019	Inner fore-reef/outer fore-reef
		Parthenopinae MacLeay, 1838	Parthenopidae indet.	Inner fore-reef
Pilumnoidea Samouelle, 1819	Pilumnidae Samouelle, 1819		<i>Galenopsis</i> sp.	Reefal facies belt
Portunoidea Rafinesque, 1815	Portunidae Rafinesque, 1815		<i>Litoricola macrodactyla</i> (Artal & Via 1988)	Outer fore-reef
	Carcineretidae Beurlen, 1930	Polybiinae Paulson, 1875	<i>Lovaroides</i> sp.	Inner fore-reef
			<i>Liocarcinus</i> sp.	Inner fore-reef
			<i>Boschettia</i> sp.	Inner fore-reef
Xanthoidea MacLay, 1838	Panopeidae Ortmann, 1893	Eucratopsinae Stimpson, 1871	<i>Glyphithyreus almerai</i> Artal & Van Bakel, 2018	Inner fore-reef
	Xanthidae MacLeay, 1838		<i>Parhalimede</i> sp.	Inner fore-reef

The most abundant genus is by far *Ctenocheles* sp. representing more than 55% of the total assemblage, but represented only by isolated chelipeds. This great abundance of this single taxon is followed by the great diverse crab assemblage; both brachyuran crabs and paguroids (see Ferratges *et al.*, 2021 for details).



Acknowledgements

This work has been supported by the projects CGL2017-85038-P subsidized by the Spanish Ministry of Science and Innovation, the European Regional Development Fund, and Project E18-20R Aragosauros: Recursos Geológicos y Paleoambientes of the government of Aragón-FEDER. The research of Fernando A. Ferratges is funded by a FPU Grant (Spanish Ministry of Science and Innovation). The research of Álvaro García-Penas is funded by a FPI Grant (Spanish Ministry of Science and Innovation). Isabel Pérez provided photographic and assistance. We are also grateful to Àlex Ossó, who has provided photos of the holotype of *Archaeoportunus isabenensis*.

REFERENCES

- Artal, P. and Castillo, J. 2005. *Periacanthus ramosus* (Crustacea, Decapoda), nueva especie del Eoceno inferior de Huesca (Aragón, España). *Batalleria*, 12, 39–44.
- Artal, P., van Bakel, B.W.M. 2018a. Aethrids and panopeids (Crustacea, Decapoda) from the Ypresian of both slopes of the Pyrenees (France, Spain). *Scripta Musei Geologici Seminarii Barcinonensis*. 22, 3–19.
- Artal, P., van Bakel, B.W.M. 2018b. Carpiliids (Crustacea, Decapoda) from the Ypresian (Eocene) of the Northeast of Spain. *Scripta Musei Geologici Seminarii Barcinonensis*, 22, pp. 20–36.
- Artal, P., Vía, L. 1988. *Xanthilites macrodactylus pyrenaicus* (Crustacea, Decapoda) nueva subespecie del Ilerdiense medio del Pirineo de Huesca. *Batalleria*, 2, 57–61.
- Artal, P. and van Bakel, B.W.M. 2020. A new xanthid crab (Decapoda, Brachyura) from the Lower Eocene (Ypresian) of Huesca (Aragón, Spain). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 296, 19–27.
- Artal, P., van Bakel, B.W.M. and Castillo, J. 2005. *Retropluma* Gill. 1894 (Crustacea, Decapoda) from the Eocene of the eastern Pyrenees (Spain, France). *Cainozoic Research*, 5, 63–69.
- Artal, P., Ossó, À. and Domínguez, J.L. 2013a. *Archaeoportunus isabenensis*, a new genus and species of portunoid crab (Crustacea, Decapoda) from the lower Eocene of Huesca (Spain). *Boletín de la Sociedad Geológica Mexicana*, 65, 307–317.
- Artal, P., van Bakel, B.W.M., Fraaije, R.H.B. and Jagt, J.W.M. 2013b. New retroplumid crabs (Crustacea, Brachyura, Retroplumidae Gill, 1894) from the Eocene of Huesca (Aragon, Spain). *Zootaxa*, 3652, 343–352.
- Artal, P., Ossó, À., and Domínguez, J. L. 2021. New genus and new species of portunoid crab: *Archaeoportunus isabenensis* from the Lower Eocene of Huesca (Aragon) and Lleida (Catalonia). *Nemus*, 11, 176–186.
- Artal, P., Ferratges, F.A., van Bakel, B.W.M. and 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. doi: 10.1017/jpa.2021.114.
- Barnolas, A. and Gil-Peña, I. 2001. Ejemplos de relleno sedimentario multiepisódico en una cuenca de antepaís fragmentada: La Cuenca Surpirenaica. *Boletín Geológico y Minero*, 112(3), 17–38.

Figure 10. Some representatives of brachyuran crabs found in the Ramals outcrop; A. *Xanthilites* sp., MPZ 2021/44; B. *Oscacarpilius rotundus* Artal & Van Bakel, 2018, MPZ 2021/49; C. *Ilerdapatiscus guardiae* Artal & Van Bakel, 2018, MPZ 2021/39; D. *Aragolambrus collinsi* Ferratges, Zamora & Aurell, 2019; E. *Xanthidae* indet., MPZ 2021/41; F. *Glyphithyreus almerai* Artal & Van Bakel, 2018, MPZ 2021/43; G. *Calappidae* indet., MPZ 2021/34; H. *Mclaynotopus longispinosus*, Artal et al., 2021, MPZ 2021/46; I. *Kromtitis isabenensis* Artal et al., 2021, MGSB77633; J. *Sierradromia gladiator* Artal et al., 2021, MGSB75454; K. *Ranina* sp., MPZ 2021/47; L. *Quasilaeviranina* sp., MPZ 2021/48; M-N. *Litoricola macrodactylus pyrenaicus* (Artal & Vía 1988), MPZ 2021/45, the only one taxon that remained in the post-reef marls deposited after the collapse of the reef mounds.

- Barnolas, A., Samsó, J.M., Teixell, A., Tosquella, J., Zamorano, M. 1991. Evolución sedimentaria entre la cuenca Graus-Tremp y la cuenca de Jaca-Pamplona. In: Colombo, F. (Ed.), I Congreso Del Grupo Español Del Terciario (Vic). Libro-Guía Excursión No 1. Universitat de Barcelona, Barcelona, pp. 1–123.
- Barnolas, A., Teixell, A., Samsó, J.M., Zamorano, M. 1992. Estructura y evolución sedimentaria del sector central de la cuenca Surpirenaica. In: III Congreso Geológico de España Y VIII Congreso Latinoamericano de Geología. Guía de Las Excursiones Geológicas. III Congreso Geológico de España, Salamanca, pp. 74–114.
- Barnolas, A., Payros, A., Samsó, J.M., Serra-Kiel, J. and Tosquella, J. 2004. La Cuenca Surpirenaica desde el llerdiense medio al Priabonense. In: Vera, J.A. (Ed.), Geología de España. SGE-IGME, Madrid, pp. 313–320.
- Bentham, P. 1992. The tectono-stratigraphic development of the western oblique ramp of the South-Central Pyrenean thrust system, Northern Spain, PhD Thesis, University of Southern California. 253 pp.
- Berástegui, X., Casas, J.M., Liesa, M., Losantos, M., Martínez, A., Muñoz, J.A. and Roca, E. 2010. Història geològica de Catalunya. In: Muñoz et al. (eds.). Atlas Geològic de Catalunya, Primera Part. *Institut Geològic de Catalunya, Institut Cartogràfic de Catalunya*, 68–77.
- Canudo, J.I., Badiola, A., Belmonte, A., Cardiel, J., Cuenca-Bescos, G., Diaz Berenguer, E., Ferratges, F.A., Moreno, M., Pérez, A., Pérez, M., Silva-Casal, R. and Zamora, S. 2021. A Window onto the Eocene (Cenozoic): The Palaeontological record of the Sobrarbe-Pirineos UNESCO Global Geopark (Huesca, Aragon, Spain). *Geoconservation Research*. [<https://doi.org/10.30486/GCR.2021.1912263.1043>].
- Capote, R., Muñoz, J.A., Simón, J.L., Liesa, C.L. and Arlegui, L.E. 2002. Alpine tectonics I: the Alpine system north of the Betic Cordillera. In: Gibbons W, Moreno T (eds) *The geology of Spain*. Geological Society, London
- Chanvry, E., Deschamps, R., Joseph, P., Puigdefàbregas, C., Poyatos-Moré, M., Serra-Kiel, J., Garcia, D. and Teinturier, S. 2018. The influence of intrabasinal tectonics in the stratigraphic evolution of piggyback basin fills: Towards a model from the TrempGraus-Ainsa Basin (South-Pyrenean Zone, Spain). *Sedimentary Geology*, 377, 34–62. [<https://doi.org/10.1016/J.SEDGEO.2018.09.007>].
- Cotteau, G.H., 1889. Échinides recueillis dans la province d'Aragon (Espagne). *Annales des sciences naturelles. Zoologie et biologie animale*, 8, 1–60.
- de Federico, A. 1981. *La sedimentación de talud en el sector occidental de la cuenca paleógena de Ainsa*. Ph.D. thesis, *Publicaciones de Geología, Universitat de Barcelona*, 12. 271 p.
- Domínguez, J.L. and Ossó, À. 2016a. New decapod fauna at midway of the Tethys Sea and Atlantic Ocean; central Pyrenees of Huesca (Aragon, Spain). In: Charbonnier, S. (Editor), 6th Symposium on Mesozoic and Cenozoic decapod crustaceans, 23–24. Villers-sur-Mer, Normandy, France.
- Domínguez, J. L. and Ossó, À. 2016b. Magyarcarcinidae new family (Crustacea: Decapoda: Goneplacoidea), and description of *Magyarcarcinus yebraensis* new species, from the Bartonian (Middle Eocene) of the Jaca basin, south-central Pyrenees (Aragón, N Spain). *Treballs del Museu de Geologia de Barcelona*, 7–18.
- Edgar, K.M., Wilson, P. a, Sexton, P.F. and Suganuma, Y. 2007. No extreme bipolar glaciation during the main Eocene calcite compensation shift. *Nature*, 448, 908–911.
- Eichenseer, H. 1988. Facies Geology of Late Maastrichtian to Early Eocene Coastal and Shallow Marine Sediments, Tremp-Graus Basin, Northeastern Spain. Ph.D. Thesis. Univ. of Tübingen (273 pp.).

- Eichenseer, H., and Luterbacher, H., 1992. The marine Paleogene of the Tremp Region (NE Spain)-depositional sequences, facies history, biostratigraphy and controlling factors. *Facies*, 27 (1), 119–151.
- Ferrer, J., 1971. El Paleoceno y Eoceno del borde sur-oriental de la Depresión del Ebro (Cataluña). *Mémoires Suisses de Paléontologie*, 90, 1–70.
- Ferratges, F.A., Artal, P. and Zamora, S. 2021a. New hermit crabs (Paguroidea, Anomura) from the Eocene of Huesca, Spain. *Boletín de la Sociedad Geológica Mexicana*, 73(3), A070121.
- Ferratges, F.A., Domínguez J.L. and Ossó, À. 2021b. First record of a homolid crab (Crustacea: Decapoda: Homoloidea) from the early Eocene of the Iberian Peninsula. *Boletín de la Sociedad Geológica Mexicana*, 73, A311220 [<https://doi.org/10.18268/BSGM2021v73n3a070121>].
- Ferratges, F.A., Zamora, S. and 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, 303–311.
- Ferratges, F.A., Zamora, S. and Aurell, M. 2021c. 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/10.1127/njgpa/2020/0893>].
- Ferratges, F.A., Zamora, S. and Aurell, M. 2022. Systematics and paleoecology 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.
- Ferratges, F.A., Zamora, S. and Aurell, M. 2020a. Systematics and distribution of decapod crustaceans associated with late Eocene coral buildups from the southern Pyrenees (Spain). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 296, 79–100.
- Ferratges, F.A., Zamora, S. and Aurell, M. 2020b. A new hermit crab out of its shell from the Eocene Arguis Formation, Huesca, Spain. *Acta Palaeontologica Polonica*, 65(4), 787-792.
- Ferratges F.A., Artal, P., van Bakel B.W.M. and Zamora, S. (in press). 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*.
- Fonnesu, F., 1984. *Estratigrafía Física y Análisis de Facies de la Secuencia de Figols, Entre el Río Noguera Pallaresa e Iscles (Prov. de Lérida y Huesca)*. Ph.D. Thesis. Universitat Autònoma de Barcelona (317 pp.).
- Fraaye, R.H.B. 1995. A new raninid crab, *Pseudorogues rangiferus* (Decapoda, Crustacea), from the Eocene of Spain. *Estudios Geológicos*, 51(1-2), 65–67.
- Fraaije, R.H.B. and Pennings, H.W. 2006. Crab carapaces preserved in nautiloid shells from the Upper Paleocene of Huesca: Pyrenees, Spain. *Revista Mexicana de Ciencias Geológicas*, 23, 361–363.
- Gaemers, P.A.M., 1978. Biostratigraphy, paleoecology and paleogeography of the mainly marine Ager Formation (Upper Paleocene Lower Eocene) in the Tremp basin, Central South Pyrenees, Spain. *Leidse. Geol. Meded.*, 51, 151–231.
- Garcés, M., López-Blanco, M., Valero, L., Beamud, E., Muñoz, J.A., Oliva-Urcia, B., Vinyoles, A., Arbués, P., Caballero, P. and Cabrera, L. 2020. Paleogeographic and sedimentary evolution of the south-pyrenean foreland basin. *Marine and Petroleum Geology*, 113, 104105. [<https://doi.org/10.1016/j.marpetgeo.2019.104105>].
- Hay, W.W., De Conto, R., Wold, C.N., Wilson, K.M., Voigt, S., Schulz, M., Wold-Rossby, A., Dullo, W.C., Ronov, A.B., Balukhovskiy, A.N. and Soeding, E. 1999: Alternative global Cretaceous paleogeography. In: Barrera, E. and Johnson, C. (eds.): The evolution of Cretaceous ocean/climate

- systems. – *Geological Society of America, Special Papers*, 332, 1–47. [doi: 10.1130/0-8137-2332-9.1].
- Honegger, L., Adatte, T., Spangenberg, J. E., Poyatos-Moré, M., Ortiz, A., Curry, M.E., Huyghe, D., Puigdefàbregas, C., Garcés, M., Vinyoles, A., Valero, L., Läubli, C., Nowak, A., Fildani, A., Clark, J.D. and Castelltort, S. 2021. Tectonics, Climate and Topography: Oxygen stable isotopes and the early Eocene growth of the Pyrenees. *Solid Earth Discussions*, 1–35.
- Jadwiszczak, P. 2010. Penguin response to the Eocene climate and ecosystem change in the northern Antarctic Peninsula region. *Polar Science*, 4, 229–235.
- Jakobsen, S.L. and Feldmann, R.M., 2004. Epibionts on *Dromiopsis rugosa* (Decapoda: Brachyura) from the late Middle Danian limestones at Fakse Quarry, Denmark: novel preparation techniques yield amazing results. *Journal of Paleontology*, 78 (5), 953–960.
- Klomp maker, A.A., Portell, R.W. and Frick, M.G. 2017. Comparative experimental taphonomy of eight marine arthropods indicates distinct differences in preservation potential. *Palaeontology*, 60 (6), 773–794.
- Krause Jr., R.A., Parsons-Hubbard, K., Walker, S.E., 2011. Experimental taphonomy of a decapod crustacean: long-term data and their implications. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 312 (3–4), 350–362.
- Leren, B.L., Howell, J., Enge, H. and Martinus, A.W. 2010. Controls on stratigraphic architecture in contemporaneous delta systems from the Eocene Roda Sandstone, Tremp-Graus Basin, northern Spain. *Sedimentary Geology*, 229, 9–40.
- López-Horgue, M.A. and Bodego, A. 2017. Mesozoic and Cenozoic decapod crustaceans from the Basque-Cantabrian basin (Western Pyrenees): new occurrences and faunal turnovers in the context of basin evolution. *Bulletin de la Société géologique de France*, 188(14), 1–28.
- Luterbacher, H.P., Eichenseer, H., Betzler, C. and Van Den Hurk, A.M. 1991. Carbonate; Depositional Systems in the Paleogene of the South Pyrenean Foreland Basin: A Sequence-Stratigraphic Approach. *Sedimentation, Tectonics and Eustasy: Sea-Level Changes at Active Margins*, pp. 391–407.
- Martinus, A.W. 2011. Contrasting styles of siliciclastic tidal deposition in developing thrust-sheet-top basins – The Lower Eocene of the Central Pyrenees (Spain). In: Davis Jr., R.A., Dalrymple, R.W. (Eds.), *Principles of Tidal Sedimentology*. Springer, Dordrecht, pp. 473–506.
- Martinus, A. W. and Molenaar, N. 1991. A coral-mollusc (*Goniaraea-Crassatella*) dominated hard-ground community in a siliciclastic-carbonate sandstone (the Lower Eocene Roda Formation, southern Pyrenees, Spain). *Palaos*, 142–155.
- Meléndez, G. and Aurell, M. 2004. El Jurásico de la vertiente sur de los Pirineos. In: Vera, J.A. (Ed.), *Geología de España*. SGE-IGME, Madrid, pp. 277–279.
- Millán, H., Aurell, M. and Meléndez, A. 1994. Synchronous detachment folds and coeval sedimentation in the Prepyrenean External Sierras (Spain): a case study for a tectonic origin of sequences and systems tracts. *Sedimentology*, 41 (5), 1001–1024.
- Miller, K.G., Kominz, M.A., Browning, J.V., Wright, J.D., Mountain, G.S., Katz, M.E., Sugarman, P.J., Cramer, B.S., Christie-Blick, N. and Pekar, S.F., 2005. The Phanerozoic record of global sea-level change. *Science*, 310, 1293–1298.
- Molenaar, N. and Martinus, A.W. 1990. Origin of nodules in mixed siliciclastic-carbonate sandstones, the Lower Eocene Roda Sandstone Member, southern Pyrenees, Spain. *Sedimentary Geology*, 66, 277–293.
- Montes-Santiago, M. J. 2002. Estratigrafía del Eoceno-Oligoceno de la Cuenca de Jaca (Sinclino rio del Guarga). Unpublished PhD Thesis, Universitat de Barcelona. 365 pp.



- Morsilli, M., Bosellini, F.R., Pomar, L., Hallock, P., Aurell, M. and Papazzoni, C.A. 2012. Mesophotic coral buildups in a prodelta setting (Late Eocene, southern Pyrenees, Spain): a mixed carbonatesiliciclastic system. *Sedimentology*, 59, 766–794.
- Mutel, M.H., Waugh, D.A., Feldmann, R.M. and Parsons-Hubbard, K.M. 2008. Experimental taphonomy of *Callinectes sapidus* and cuticular controls on preservation. *Palaios*, 23 (9), 615–623.
- Nijman, W. 1998. Cyclicity and basin axis shift in a piggyback basin: towards modelling of the Eocene TrepAger Basin, southern Pyrenees, Spain. In: Cenozoic Foreland Basins of Western Europe (Eds A. Mascle, C. Puigdefàbregas, H.P. Luterbacher and M. Fernandez) *Geological Society, London, Special Publications*, 134, 135–162.
- Ossó, À., Domínguez, J.L. and Artal, P. 2014. *Pyreneplax basaensis* new genus, new species (Decapoda, Brachyura, Vultocinidae) from the Priabonian (Late Eocene) of the Pyrenees of Huesca (Aragón, Spain), and remarks on the genus *Lobonotus* A. Milne-Edwards, 1863. *Treballs del Museu de Geologia de Barcelona*, 20, 33–43.
- Payros, A., Astibia, H., Cearreta, A., Pereda-Suberbiola, X., Murelaga, X., and Badiola, A. 2000. The Upper Eocene South Pyrenean Coastal deposits (Liedena sandstone, navarre): Sedimentary facies, benthic foraminifera and avian ichnology. *Facies*, 42, 107–131.
- Payros, A., Ortiz, S. and Alegret, L., 2012. An early Lutetian carbon-cycle perturbation: Insights from the Gorronatxe section (western Pyrenees, Bay of Biscay). *Paleoceanography*, 27, PA2213.
- Pearson, P.N. and Palmer, M.R. 2000. Atmospheric carbon dioxide concentrations over the past 60 million years. *Nature*, 406, 695–699.
- Pekar, S.F., Hucks, A., Fuller, M. and Li, S. 2005. Glacioeustatic changes in the early and middle Eocene (51–42 Ma): Shallow-water stratigraphy from ODP Leg 189 Site 1171 (South Tasman Rise) and deep-sea 180 records. *Bulletin of the Geological Society of America*, 117, 1081–1093.
- Plaziat, J. 1981. Late Cretaceous to late Eocene paleogeographic evolution of Southwest Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 36, 263–320. [[https://doi.org/10.1016/0031-0182\(81\)90110-3](https://doi.org/10.1016/0031-0182(81)90110-3)].
- Pomar, L., Baceta, J.I., Hallock, P., Mateu-Vicens, G. and Basso, D. 2017. Reef building and carbonate production modes in the west-central Tethys during the Cenozoic. *Marine and Petroleum Geology*, 83, 261–304. [<https://doi.org/10.1016/j.marpetgeo.2017.03.015>].
- Puigdefàbregas, C. 1975. La sedimentación molásica en la Cuenca de Jaca. *Pirineos*, 104, 1–188.
- Puigdefàbregas, C. and Souquet, P. 1986. Tecto-sedimentary cycles & depositional sequences of the mesozoic & tertiary from the Pyrenees. *Tectonophysics*, 129, 173–203.
- Puigdefàbregas, C., Muñoz, J.A. and Marzo, M. 1986. Thrust belt development in the eastern Pyrenees and related depositional sequences in the southern foreland basin. In: Allen, P.A., Homewood, P. (Eds.), *Foreland Basins. IAS Spec. Publ.*, 8. pp. 229–246.
- Puigdefàbregas, C., Muñoz, J.A. and Vergés, J. 1992. Thrusting and foreland basin evolution in the southern Pyrenees. McClay, K. *Thrust Tectonics*. Chapman Hall, London, 247–254.
- Pujalte, V., Baceta, J.I., Schmitz, B., Orue-Etxebarria, X., Payros, a., Bernaola, G., Apellaniz, E., Caballero, F., Robador, a., Serra-Kiel, J. and Tosquella, J. 2009. Redefinition of the Ilerdian Stage (early Eocene). *Geologica Acta*, 7, 177–194.
- Robador, A., Samsó, J.M., Serra-Kiel, J., and Tosquella, J. 1991. Field guide. Introd. to Early Paleogene South Pyrenean Basin. Field-trip Guid. 1st Meet IGCP Proj. 286, 131–159.
- Rosenbaum, G., Lister, G.S. and Duboz, C. 2002. Relative motions of Africa, Iberia and Europe during Alpine orogeny. *Tectonophysics*, 359, 117–129.



- Samsó, J.M., Tosquella, J. and Serra-Kiel, J. 1990. Los géneros *Alveolina* y *Nummulites* (Macroforaminíferos) del llerdiense Medio-Cuisiense Medio de la Cuenca de Graus, Huesca. I. Sistemática de *Alveolina*. *Boletín Geológico y Minero*, 101: 219-252.
- Schweitzer, C.E., Artal, P., van Bakel, B.W.M., Jagt, J.W.M. and Karasawa, H. 2007. Revision of the genus *Titanocarcinus* (Decapoda: Brachyura: Xanthoidea) with two new genera and one new species. *Journal of Crustacean Biology*, 27, 278–295.
- Serra-Kiel, J., Canudo, J.I., Dinares, J., Molina, E., Ortiz, N., Pascual, J.O., Samsó, J.M., and Tosquella, J. 1994. Cronoestratigrafía de los sedimentos marinos del Terciario inferior de la Cuenca de Graus-Tremp (Zona Central Surpirenaica). *Revista de la Sociedad Geológica de España*, 7, 273–297.
- Silva-Casal, R. 2017. *Las plataformas carbonatadas del Eoceno medio de la cuenca de Jaca-Pamplona (Formación Guara, Sierras Exteriores): análisis estratigráfico integral y evolución sedimentaria*. Tesis doctoral. Universidad de Zaragoza (Inédita). 345 pp
- Silva-Casal, R., Payros, A., Martínez-Bracerías, N. and Aurell, M. 2017. The Eocene marine sedimentation in the southern Pyrenean Basin: a basin-slope-platform transect. – International Meeting of Sedimentology 2017 (33rd IAS and 16th ASF Joint Meeting), Field Trip 1, Guidebook: 56 pp. Toulouse.
- Silva-Casal, R., Aurell, M., Payros, A., Pueyo, E.L. and Serra-Kiel, J. 2019. Carbonate ramp drowning caused by flexural subsidence: the South Pyrenean middle Eocene foreland basin. *Sedimentary Geology*, 393, 1–23. [<https://doi.org/10.1016/j.sedgeo.2019.105538>].
- Tosquella, J. 1988. *Estudi sedimentològic i bioestratigràfic de la Formació Gresos de Roda (Eocè, Conca de Tremp-Graus)*: Barcelona, University of Barcelona, masters thesis, 540 p.
- Tosquella, J., Samsó, J.M. and Serra-Kiel, J. 1990. Los géneros *Alveolina* y *Numulites* (macroforaminíferos) del llerdiense medio-Cuisiense medio de la Cuenca de Graus, Huesca. II. Sistemática de *Nummulites*. *Boletín Geológico y Minero*, 101, 351–403.
- Tripathi, A., Backman, J., Elderfield, H. and Ferretti, P. 2005. Eocene bipolar glaciation associated with global carbon cycle changes. *Nature*, 436, 341–6.
- Tripathi, A.K., Eagle, R.A., Morton, A., Dowdeswell, J.A., Atkinson, K.L., Bahé, Y., Dawber, C.F., Khadun, E., Shaw, R.M.H., Shorttle, O. and Thanabalasundaram, L. 2008. Evidence for glaciation in the Northern Hemisphere back to 44 Ma from ice-rafted debris in the Greenland Sea. *Earth and Planetary Science Letters*, 265, 112–122.
- van Bakel, B.W.M., Guinot, D., Artal, P., Fraaije, R.H.B. and Jagt, J.W.M. 2012. A revision of the Palaeocorystoidea and the phylogeny of raninoidian crabs (Crustacea, Decapoda, Brachyura, Podotremata). *Zootaxa*, 3215, 1–216.
- Vía, L., 1959, Decápodos fósiles del Eoceno español: *Boletín del Instituto geológico y Minero de España*, 70, 331–402.
- Vía, L. 1969. Crustáceos decápodos del Eoceno español. *Pirineos*, 91–94, 1–469.
- Vía, L. 1973. Datos para el estudio de los crustáceos decápodos del Eoceno circumpirenaico. *Pirineos*, 107, 55–70.
- Zachos, J.C., Dickens, G.R. and Zeebe, R.E. 2008. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature*, 451, 279–83.
- Zamora, S., Aurell, M., Veitch, M., Saulsbury, López-Horgue, M.A., Ferratges, F.A., Arz, J.A. and Baumiller, T.K. 2018. Environmental distribution of post-Palaeozoic crinoids from the Iberian and south-Pyrenean basins (NE Spain). *Acta Palaeontologica Polonica*, 63, 779–794.

DAY 3: JUNE 24th, 2022

DECAPOD CRUSTACEAN DIVERSITY AND HABITATS IN THE UPPER ALBIAN DEPOSITS OF NAVARRE (WESTERN PYRENEES, SPAIN): THE KOSKOBILLO QUARRY LIMESTONES AND THEIR COEVAL DEPOSITS

Mikel A. López-Horgue¹, Adiël A. Klompmaker² and René H. B. Fraaije³

¹ Geologia saila/Dept. of Geology, Faculty of Science and Technology, Euskal Herriko Unibertsitatea/University of the Basque Country UPV/EHU, Sarriena z/g, 48940, Leioa, Biscay (Basque Country), Spain.

² Department of Museum Research and Collections & Alabama Museum of Natural History, University of Alabama, Box 870340, Tuscaloosa, Alabama 35487, USA.

³ Oertijdmuseum, Bosscheweg 80, 5283 WB, Boxtel, The Netherlands.

Keywords: Crustacea, Decapoda, Diversity, Habitats, upper Albian, Western Pyrenees

INTRODUCTION

The Upper Albian successions of the Basque Cantabrian Basin (Western Pyrenees; North Spain) yield a high diversity of decapod crustaceans, which helps to understand the evolution of this group from the Early to the Late Cretaceous (Fig. 1). As for ammonoids and other groups, decapod diversity during this time is related to paleoecological changes linked to changing environmental conditions during basin evolution.

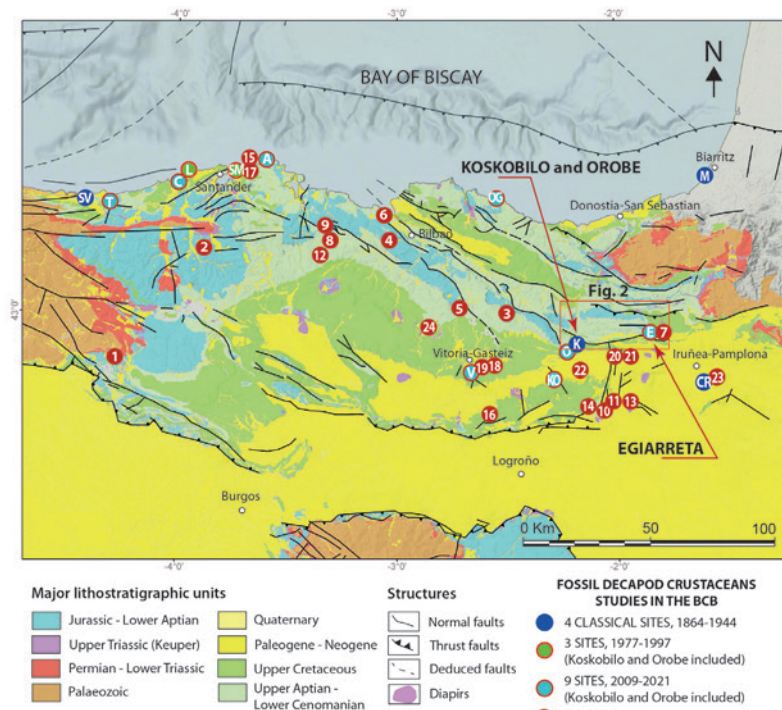


Figure 1. Geological map of the Basque-Cantabrian Basin (Western Pyrenees) with indication of the sites with decapod crustacean fossils arranged into 4 categories: historical references from the 19th and early 20th centuries; late 20th century works; last important references of the earliest 21st century; and the basin-scale compilation of new faunas from the Jurassic to the Miocene. Modified from López-Horgue and Bodego (2017: fig. 1).

The Basque-Cantabrian Basin (BCB) was a rift basin related to the continental break-up occurring in the Permian-Triassic transition (e.g., Robles, 2014). Several rift phases led to the deposition of continental to transitional and marine sediments from the Permo-Triassic to the Early Cretaceous (Aptian). During the late Aptian to the early Cenomanian, a hyperextensional phase took place (e.g., Tugend *et al.*, 2014), leading to extreme crustal thinning, mantle exhumation, and extreme subsidence rates that were accompanied by very high sedimentation rates. In this context, submarine volcanism spread in the basin center, seaways changed, and new areas of shallow to deep marine settings developed, creating a new paleoecological scenario rich in carbonate platforms with reefal margins facing deeper environments.

On this field trip, we will concentrate on the lower upper Albian outcrops of the Sakana Valley (Navarre province), where a rich decapod fauna has been reported from (e.g., López-Horgue *et al.*, 1996; Fraaije *et al.*, 2008; Klompmaker *et al.*, 2011, 2013a; Van Bakel *et al.*, 2012a; Artal *et al.*, 2012; Klompmaker, 2013; López-Horgue and Bodego, 2017). Here, this succession is mainly composed of shallow marine carbonates forming isolated carbonate build-ups of the Eguino Formation (García-Mondéjar, 1982) and ramps surrounded by deeper siliciclastic successions; the whole succession is called the Albeniz unit (López-Horgue *et al.*, 1996). This unit crops out extensively between the localities of Araia (Araba) and Irurtzun (Navarre) to the south of the Aitzgorri and Aralar mountains (Fig. 2).

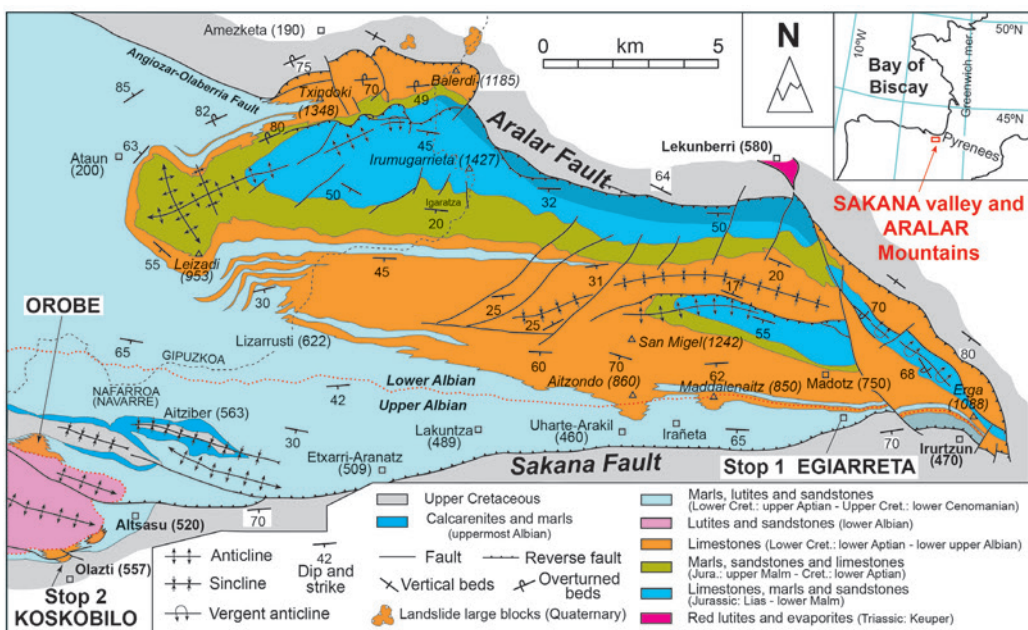


Figure 2. Simplified geological map of the the Sakana Valley and Aralar mountains. The sites with decapod crustacean faunas to be visited are indicated. The reef limestones of Koskobilo and Orobe are well-known sites of decapod biodiversity for the Cretaceous. The Egiarreta site has yielded decapods from siliciclastic muddy bottoms coeval to that of Koskobilo and Orobe. The Orobe site is here considered part of the field-trip due to its historical and scientific value but, unfortunately, it is not possible to visit it. See figure 1 for location in the western Pyrenean area.

Two stops are envisaged:

1. **Egiarreta village (near Irurtzun city).** The silty marl succession of this site forms a deeper marine succession stratigraphically equivalent to the carbonate build-ups of the Koskobilo and Orobe sites. Decapod diversity is relatively low here.

2. **Koskobilo quarry (Olazti).** Concrete factories exploited this site in the 1940s, destroying one of the best Pleistocene cave sites (e.g., Arlegi *et al.*, 2018). However, the upper Albian reef limestones contain a collection of decapods known as one of the most diverse Cretaceous decapod localities in the world (Klompmaier, 2013).

Another important site is added as an appendix:

- » **Orobe quarry (N of Alsasua city).** This site was created to provide ballast for the Madrid-Irun railway in the 19th and 20th centuries. A taxonomically similar decapod fauna to that of Koskobilo has been found here as shown in the pioneer papers of Van Straelen (1940, 1944), Ruiz de Gaona (1943, 1952), and Via (1981).

THE BASQUE CANTABRIAN BASIN: Basin evolution and environmental changes

During the latest Permian to Early Triassic, the Pangaea supercontinent underwent a first fracturing phase that led to crustal thinning and the formation of different intracontinental sedimentary basins. Continental extension gave way to plate separation and to a progressive increase in subsidence. Accordingly, the extended area between the Iberian and European plates led to the opening of the Bay of Biscay in the context of crustal thinning in the North Atlantic rifting system. This area is the so-called Basque-Cantabrian Basin (BCB), a sedimentary basin geodynamically related to other basins in the Pyrenean area sharing a similar extension and inversion evolution.

Succeeding environmental changes in the basin led to the creation of new ecological niches through time. Consequently, decapod crustaceans can show a high diversity locally in the Mesozoic and Cenozoic, having occupied continental, transitional, and marine environments (Klompmaier, 2013; López-Horgue and Bodego, 2017, 2018).

Several rifting phases separated by relative quiescent intervals are distinguished through the BCB evolution from an intracontinental rift to an extended pericratonic rift:

- » Late Permian-Triassic rifting phase (intracontinental rift). Active faulting created tectonic depressions with a high subsidence rate that were filled with siliciclastics deposited from alluvial fans and braided rivers (Permian Buntsandstein facies). Calc-alkalin volcanism affected the basin margins. Rifting subsidence decreased during the Middle and Late Triassic and the basin became filled as a result. However, a transgressive phase permitted the sedimentation of shallow marine carbonates (Muschelkalk facies). Later, the shallowing phase of the Late Triassic is characterised by the deposition of red mudstones and evaporites in a very shallow intracontinental salt-lake environment (sabkha).
- » Latest Triassic (Rhaetian)-Middle Jurassic inter-rift phase. Faulting was not so active and subsidence is mainly related to a slow thermal contraction affecting large areas in the basin (sag-type). Progressive sagging permitted the development of marine epicontinental areas characterized by shallow carbonate ramp environments with a high organismal diversity, such as ammonoids, sponges, and brachiopods. Black shales were deposited in the center of the basin. The glypheid lobster *Paraglyphea* inhabited these hypoxic bottoms. Sponge build-ups punctuated these ramps during the Middle Jurassic (e.g., Fontana *et al.*, 1994).
- » Late Jurassic-Early Cretaceous (early Aptian) rifting. This new extensional phase led to a widening of the basin, the creation of new sedimentary depocenters, and the uplift of basin margins. The subsidence rate increased but was offset by the deposition of thick successions of fluvial origin and coeval coastal to shallow marine environments. Freshwater inhabiting mecochirid lobsters are found in these continental environments. Faulting slowed and transgression took place during the early Aptian: coastal environments in the basin margins were accompanied by coastal lagoons and shallow carbonate areas in the central part. Mecochirids flourished in these new shallow-marine environments, whereas atyid shrimps inhabited coastal brackish lagoons (López-Horgue and Bodego, 2017).

- » Late Aptian-late Albian hyperextended rift phase. A severe increase in continental extension led to extreme crustal thinning and mantle exhumation in the basin center. Thick successions of submarine basalts and volcanoclastites were deposited mainly during the late Albian. Plate separation and basin widening increased substantially and resulted in the opening of the Bay of Biscay, sea deepening, the onset of oceanic conditions, and the connection with nearby marine areas. In this scenario, differential subsidence controlled the sedimentation of shallow marine carbonate environments on uplifted blocks facing deeper marine siliciclastic and mixed successions on hanging wall blocks. Reef communities flourished in these transitional areas where microbial and corallgal communities dominated in the early Albian and in the late Albian, respectively. In these reef facies, one of the highest Cretaceous decapod diversities worldwide is found (Klompaker, 2013).
- » Cenomanian-Santonian/Campanian boundary: thermal subsidence phase. The early Cenomanian marked the transition from the maximum cortical extension of the basin to a passive margin stage. Fault-related subsidence gave way to a progressive long-ranging slow subsidence. This fact and the onset of a major transgressive episode worldwide (e.g., Haq, 2014) led to the deepening of sea environments, the flooding of continental areas, and, consequently, the creation of new ecological niches. In this context, coastal environments migrated toward basin margins and carbonate ramps facing deep marine environments developed over large areas. Ammonoids and fish turnovers are examples of the faunal replacement associated with the relatively abrupt palaeoecological changes (e.g., López-Horgue *et al.*, 2014).
- » Santonian/Campanian boundary-Eocene/Oligocene: compressive phase. The European and Iberian plates started converging and, consequently, the BCB basin underwent flexure subsidence related to tectonic load. The basin changed from a foredeep to a foreland basin type. At the beginning of this stage, coastal siliciclastic environments prograded over deeper ramps causing a regressive phase in the basin. The Paleocene is a time of relative quiescence of the compressive forces leading to a transgression and the development of carbonate platforms and ramps facing deep marine environments. During the Eocene, a time of high temperatures worldwide, carbonate ramps developed in a tectonic context of migration of foreland areas that gave way to the progressive uplift and encroachment of terrestrial conditions. Eocene carbonate ramp environments were inhabited by zanthopsid crabs typical of the Pyrenean area. One of the earliest representatives of potamid crabs inhabited shallow brackish lakes created after basin inversion atop of diapiric structures (López-Horgue and Hernández, 2003).

THE DECAPOD RECORD IN THE BCB (WESTERN PYRENEES)

The first studies in the area refer to Eocene fossils from the eastern and western margins: the Muliña site near Biarritz (Jacquot, 1864) and San Vicente de la Barquera in Cantabria (Quiroga, 1887; Mengaud, 1920). In the first so-called modern study on decapods in the Iberian Peninsula, Van Straelen (1927) formally described the Eocene specimens referred to by Mengaud (1920). Also from the Eocene, Ruiz de Gaona (1943) referred to one species from the Lutetian of El Carascal (Navarre). Via (1969) studied the Eocene faunas from Cantabria and Navarre in his major revision of Eocene decapods from Iberia.

It is not until 1940 that Mesozoic decapods were first reported when Van Straelen described mid-Cretaceous decapods from the Orobe quarry. His work was based on the collection amassed by Máximo Ruiz de Gaona from 1935-1940 in this quarry located near Alsasua (Navarre), the limestones of which were used in the refurbishment of the Norte (Madrid-Irun) railway line (previously, in the 1860-1870s, Norte Railway Company also extracted limestone here). Van Straelen and Ruiz de Gaona described several species from 1940 to 1954 (e.g., Van Straelen, 1940, 1944; Ruiz de Gaona, 1943). Via (1981, 1982) revised these decapods adding a new galatheid species to the

known record. Some decades later, substantial collecting efforts mainly during 2008–2010 within the coeval Aldoirar limestones of the Koskobilo quarry led to the discovery of a diversity hotspot for the Cretaceous (e.g., Klompmaker *et al.*, 2011, 2012a, 2012b, Klompmaker, 2013; Fraaije *et al.*, 2012, 2019), with 39 decapod species. A rare isopod species has also been described in the same limestones (Fraaije *et al.*, 2019).

The knowledge of fossil decapods of the BCB besides Koskobilo has also substantially increased due to intense research activity in the last 15 years, with several new species and occurrences from the Aptian, Albian, Santonian, and Campanian (e.g., López-Horgue, 2009; Van Bakel *et al.*, 2012a, 2012b; Ossó and Díaz-Isa, 2014; González-León *et al.*, 2016).

The enhanced exploration and revision of successions from the Lower Jurassic to the Miocene in the BCB permitted the updating of the stratigraphical record of Decapoda in the area (López-Horgue and Bodego, 2017, 2018) with the description of 24 new sites, 29 new occurrences, and 3 new species. These authors attributed the decapod faunal turnovers to palaeoecological changes in the context of basin evolution (see Fig. 1).

An updated decapod species and occurrences list in the BCB is presented here (Table 1).

Table 1. The updated record of Decapoda from the Basque-Cantabrian Basin (Western Pyrenean area), with listed taxa, environments, and age.

Localities	Taxon	Environment	Age
(in López-Horgue and Bodego, 2017)			
1-Aguilar de Campó	<i>Paraglyphea</i> sp.	Hemipelagic carbonate ramp	Pliensbachian-Toarcian
2-Ontaneda	Mecochiridae indet.	Shallow fresh-water lake	Berriasian
3-Eskoriatza	<i>Delclosia almeni</i> López-Horgue and Bodego, 2017	Shallow coastal lagoon	Hauterivian-Barronian
4-Zaramillo	<i>Atherfieldastacus magnus</i> (M' Coy, 1849)	Prodelta, shallow marine	early Aptian
C-Cuchía	Callianassidae indet. 1	Id.	early Aptian
5-Gorbea	<i>Atherfieldastacus magnus</i> (M' Coy, 1849)	Distal shallow marine mixed ramp	late Aptian
6-Sestao	Callianassidae indet. 2	Distal marine siliciclastic ramp	late Aptian
A-Ajo	<i>Hoploparia</i> sp. 1	Shallow marine mixed ramp	early Albian
7-Irurtzun	<i>Joeranina</i> sp.	Siliciclastic trough in shallow marine carbonate platform	late Albian
E-Egiarreta	<i>Cenomanocarcinus sakanaensis</i> López-Horgue and Bodego, 2017	Id.	early late Albian
8-La Escrita, 9-Sopeña, 10-Zubielki, 11-Larrión	Callianassidae indet. 3 (8); Callianassidae indet. 4 (9); Callianassidae indet. 5 (10-11)	Prodelta	late Albian
12-Baljerri	<i>Cenomanocarcinus</i> aff. <i>cantabricus</i> Van Bakel <i>et al.</i> , 2012a, b	Offshore siliciclastic platform	early late Albian
13-Allotz	<i>Etyxanthosia inflata</i> López-Horgue and Bodego, 2017	Id.	latest Albian
L-Liencres	<i>Hoploparia</i> sp. 2	Shoreface-offshore carbonate ramp	early Cenomanian
14-Antzin	? Paguroidea	Offshore carbonate ramp	Coniacian
15-Langre beach	? <i>Caloxanthus</i> sp.	Shallow marine carbonate platform	late Santonian



Localities	Taxon	Environment	Age
16-Bajauri	<i>Mesostylus</i> sp.	Shoreface carbonate ramp	early Campanian
17-Loredo-1	Callianassidae indet. 6; <i>Brachyura</i> indet.	Offshore carbonate ramp	early Campanian
V-Vitoria Pass	<i>Enoploclytia</i> aff. <i>collignoni</i> Secrétan, 1964; <i>Cretacorantina</i> aff. <i>schloenbachi</i> (Schlüter, 1879)	Prodelta	late Campanian
18-Ullibarri-Jauregi, 19-Egileta	Callianassidae indet. 7	Prodelta	late Campanian
20-Andia 1	<i>Zanthopsis leachii</i> (Desmarest, 1817)	Offshore carbonate ramp	late Ypresian
21-Andia 2	<i>Harpactoxanthopsis quadrilobatus</i> (Desmarest, 1817)	Offshore carbonate ramp	early Lutetian
22-Urbasa	<i>Harpactoxanthopsis</i> sp.	Shallow marine carbonate ramp	early Bartonian
23-Ardanaz	Decapoda indet.	Delta front to prodelta	early Bartonian
24-Izarra	Potamidae	Freshwater to brackish swamp	early Miocene
(in González-León et al., 2016)			
C-Cuchía	<i>Rathbunopon viai</i> González-León et al., 2016 <i>Mithracites vectensis</i> Gould, 1859	Prodelta	early Aptian
(in Ossó and Moreno-Bedmar, 2020)			
C-Cuchía	<i>Etyus tresgalloi</i> Ossó and Moreno-Bedmar, 2020	Prodelta	early Aptian
(in Ossó et al., 2021)			
C-Cuchía	<i>Cuchiadromites jadeae</i> Ossó et al., 2021	Prodelta	early Aptian
(in López-Horgue, 2009)			
A-Ajo	<i>Meyeria magna</i> M'Coy, 1849 (= <i>Atherfieldastacus magnus</i> (M'Coy, 1849) sensu Robin et al., 2016)	Shallow marine mixed ramp	early Albian
(in Van Bakel et al., 2012a)			
A-Ajo	<i>Cenomanocarcinus cantabricus</i> Van Bakel et al., 2012a	Shallow marine mixed ramp	early Albian
(in Agirrezabala et al., 2013)			
OG-Ogella	<i>Callianassa</i>	Offshore; deep marine siliciclastic trough	late Albian
(in Van Bakel et al., 2012a)			
E-Egiarreta	<i>Joerania gaspari</i> Van Bakel et al., 2012a	Siliciclastic trough in shallow marine carbonate platform	early late Albian
13-Allotz	<i>Eucorystes navarrensis</i> Van Bakel et al., 2012a	Offshore siliciclastic platform	latest Albian
V-Pto. Vitoria	<i>Cretacorantina schloenbachi</i> (Schlüter, 1879)	Prodelta	late Campanian
(in Van Straelen, 1940, 1944; Ruiz de Gaona, 1943; Via, 1981, 1982; Artal et al., 2012; Fraaije et al., 2008, 2009, 2012, 2013, 2019; Klompmaker, 2013; Klompmaker et al., 2011a,b,c, 2012a,b, 2013a, 2020)			
K-Koskobilo quarry-Aldoir carbonate build-up, and Orobe quarry-Orobe carbonate build-up	KOSKOBILIO Achelata <i>Paleopalpinurus serratus</i> Fraaije et al., 2019 Brachyura <i>Acareprosope bouvieri</i> (Van Straelen, 1944) <i>Albenizus minutus</i> Klompmaker, 2013 <i>Caloxanthus paraornatus</i> Klompmaker et al., 2011c <i>Cretamaja granulata</i> Klompmaker, 2013 <i>Distefania incerta</i> (Bell, 1863) <i>Distefania renefraaijei</i> Klompmaker et al., 2012b <i>Eodromites cristinarobinsae</i> Klompmaker et al., 2020 <i>Etyxanthosia fossa</i> (Wright and Collins, 1972) <i>Faksecarcinus koskobiloensis</i> (Klompmaker et al., 2011c) <i>Glyptodynomene alsasuensis</i> Van Straelen, 1944	Shallow marine carbonate platform (coral and microbialite facies)	early late Albian



Localities	Taxon	Environment	Age
	<p><i>Goniodromites laevis</i> (Van Straelen, 1940) <i>Graptocarcinus texanus</i> Roemer, 1887 <i>Koskobilius postangustus</i> Klompmaker, 2013 <i>Laeviprosopon crassum</i> Klompmaker, 2013 <i>Laeviprosopon edoi</i> Klompmaker, 2013 <i>Laeviprosopon hispanicum</i> Klompmaker, 2013 <i>Laeviprosopon planum</i> Klompmaker, 2013 <i>Navarradromites pedroartali</i> Klompmaker et al., 2012b <i>Navarrahomola hispanica</i> Artal et al., 2012 <i>Navarrara betsiei</i> Klompmaker, 2013 <i>Rathbunopon obesum</i> (Van Straelen, 1944) <i>Viaia robusta</i> Artal et al., 2012</p> <p>Galatheoidea <i>Eomunidopsis aldoirarensis</i> Klompmaker et al., 2012a <i>Eomunidopsis navarrensis</i> (Van Straelen, 1940) <i>Eomunidopsis orobensis</i> (Ruiz de Gaona, 1943) <i>?Palmunidopsis</i> sp. (see Klompmaker et al., 2012a; Fraaije, 2014) <i>Hispanigalathea pseudolaevis</i> Klompmaker et al., 2012a <i>Hispanigalathea tuberosa</i> Klompmaker et al., 2012a <i>Nykteripteryx rostrata</i> Klompmaker et al., 2012a <i>Serraphylctaena multisquamata</i> (Vía Boada, 1981) <i>Vasconilia ruizi</i> (Van Straelen, 1940a) <i>Vasconilia straeleni</i> (Ruiz de Gaona, 1943)</p> <p>Gastrodoroidea <i>Gastrodorus cretahispanicus</i> Klompmaker et al., 2011a</p> <p>Paguroidea <i>Annuntidiogenes worfi</i> Fraaije et al., 2009 (carapace) <i>Cretatrizocheles olazagutiensis</i> Fraaije et al., 2012 (carapace) (?=<i>Pylochelitergites alatus</i> Fraaije et al., 2013 (tergite)) <i>Mesoparapylocheles michaeljacksoni</i> Fraaije et al., 2012 (carapace) (?=<i>Parapylochelitergites pustulosus</i> Fraaije et al., 2013 (tergite)) <i>Paguritergites yvonnecoleae</i> Fraaije et al., 2013 (tergite) <i>Pylochelitergites rugosus</i> Fraaije et al., 2013 (tergite)</p> <p>OROE</p> <p>Brachyura <i>Acareprosopon bouvieri</i> (Van Straelen, 1944) <i>Etyxanthosia fossa</i> (Wright and Collins, 1972) <i>Eodromites grandis</i> (von Meyer, 1857) <i>Glyptodynomene alsasuensis</i> Van Straelen, 1944 <i>Goniodromites laevis</i> (Van Straelen, 1940) <i>Graptocarcinus texanus</i> Roemer, 1887 <i>Necrocarcinus labeschei</i> (Eudes-Deslongchamps, 1835) <i>Rathbunopon obesum</i> (Van Straelen, 1944) <i>Sabellidromites scarabaea</i> (Wright and Wright, 1950)</p> <p>Galatheoidea <i>Eomunidopsis navarrensis</i> (Van Straelen, 1940) <i>Eomunidopsis orobensis</i> (Ruiz de Gaona, 1943) <i>Serraphylctaena multisquamata</i> (Vía Boada, 1981) <i>Vasconilia ruizi</i> (Van Straelen, 1940a) <i>Vasconilia straeleni</i> (Ruiz de Gaona, 1943) <i>Annieporcellana dhondtae</i> Fraaije et al., 2008</p> <p>Paguroidea <i>Annuntidiogenes ruizdegaonai</i> Fraaije et al., 2008</p>		
(in Ossó, 2017)			
T-Trasvía	<i>Cenomanocarcinus</i> sp. 2	Offshore carbonate ramp	middle Turo-nian
(in Van Bakel et al., 2012b)			
KO-Kontrasta	<i>Graptocarcinus urbasaensis</i> Van Bakel et al., 2012b	Offshore carbonate ramp	Santonian
O-Olazagutia	<i>Graptocarcinus urbasaensis</i>	Id.	Santonian
SM-Santa Marina	<i>Graptocarcinus urbasaensis</i>	Id.	Santonian



Localities	Taxon	Environment	Age
(in Ossó and Díaz-Isa, 2014)			
17-Loredo-2	<i>Cantabroxanthus loredoensis</i> Ossó and Díaz-Isa, 2014	Offshore carbonate ramp	early Campanian
(in Via, 1969)			
SV-San Vicente de la Barquera (first ref.: Quiroga, 1887)	<i>Ctenocheles</i> cf. <i>cultellus</i> (Rathbun, 1935); <i>Harpactocarcinus jacquoti</i> A Milne-Edwards, 1865; <i>Xanthopsis bruckmanni</i> (von Meyer, 1862) (<i>Neozanthopsis bruckmanni</i> sensu Schweitzer, 2003); <i>Harpactoxanthopsis quadrilobatus</i> (Desmarest, 1817)	Offshore carbonate ramp	early Lutetian
CR-El Carrascal (first ref. Ruiz de Gaona, 1943)	<i>Lophoranina reussi</i> Woodward, 1866; <i>Notopella vareolata</i> Lörentz and Beurlen, 1929	Offshore carbonate ramp	middle Lutetian
M-Mulíña (Larralde; first ref. Jacquot, 1864)	<i>Harpactocarcinus jacquoti</i> A. Milne-Edwards, 1865	Offshore carbonate ramp	late Lutetian-Bartonian

THE UPPER ALBIAN SUCCESSION IN THE SAKANA VALLEY (NAVARRRE): Stratigraphy, Environments, and Palaeontology

The Albian stage in the BCB represents an interval of very high subsidence due to extreme faulting and crustal thinning. Both the increasing siliciclastic input and the favorable conditions of the sea (temperature, nutrient level, oceanic currents, and seaways connecting other adjacent basins) allowed the deposition of very thick shallow carbonate successions on paleogeographic highs and siliciclastics in coeval deeper troughs. High sedimentation rates accompanied the tectonic subsidence leading to stratigraphic thicknesses up to 6.5 km in the depocenter of the basin (S of Bilbao) and 3 km in the Sakana Valley. From these thicknesses, up to 5 km and 2 km correspond to the upper Albian substage in Bilbao and the Sakana Valley, respectively. Hence, it is clear that the late Albian represented a time of extreme subsidence and corresponding environmental changes.

The extreme input of siliciclastics during the late Albian substantially filled the accommodation space created by subsidence and led to an overall shallowing of the BCB margins. The shallow marine carbonate sedimentation was confined to the more elevated areas, and the deeper troughs were siliciclastic ramps (e.g., López-Horgue et al., 1999). The basin center and some parts of the northern margin show substantially deeper troughs with steep slopes and are filled mainly with turbidites (e.g., Agirrezabala and López-Horgue, 2017). Volcanic successions in the basin center reached up to 500 m in thickness (e.g., Castañares et al., 2001).

The change to a thermal subsidence and the onset of the transgression during the latest Albian resulted in diminished siliciclastic input in the BCB and the drowning of the shallow marine carbonate platforms in the area.

In the Sakana Valley, the upper Albian succession is divided into two main intervals:

- lower upper Albian

In the eastern part, it is composed of shallow-marine carbonate ramp deposits (Aralar platform, late stage) with siliciclastic intraplatform troughs and reef build-ups facing deeper siliciclastic facies (Aitzondo-Maddalenaitz areas). In the western part, shallow marine carbonates formed at least four reef build-ups of variable extension (Egino, Aldoirar-Koskobilo, Altsasu and Orobe), separated by marly troughs and forming an overall shallow-marine carbonate area. Between these two contrasting shallow carbonate areas, a N-S oriented deeper turbiditic trough developed (Lizarrusti) (Fig. 3).

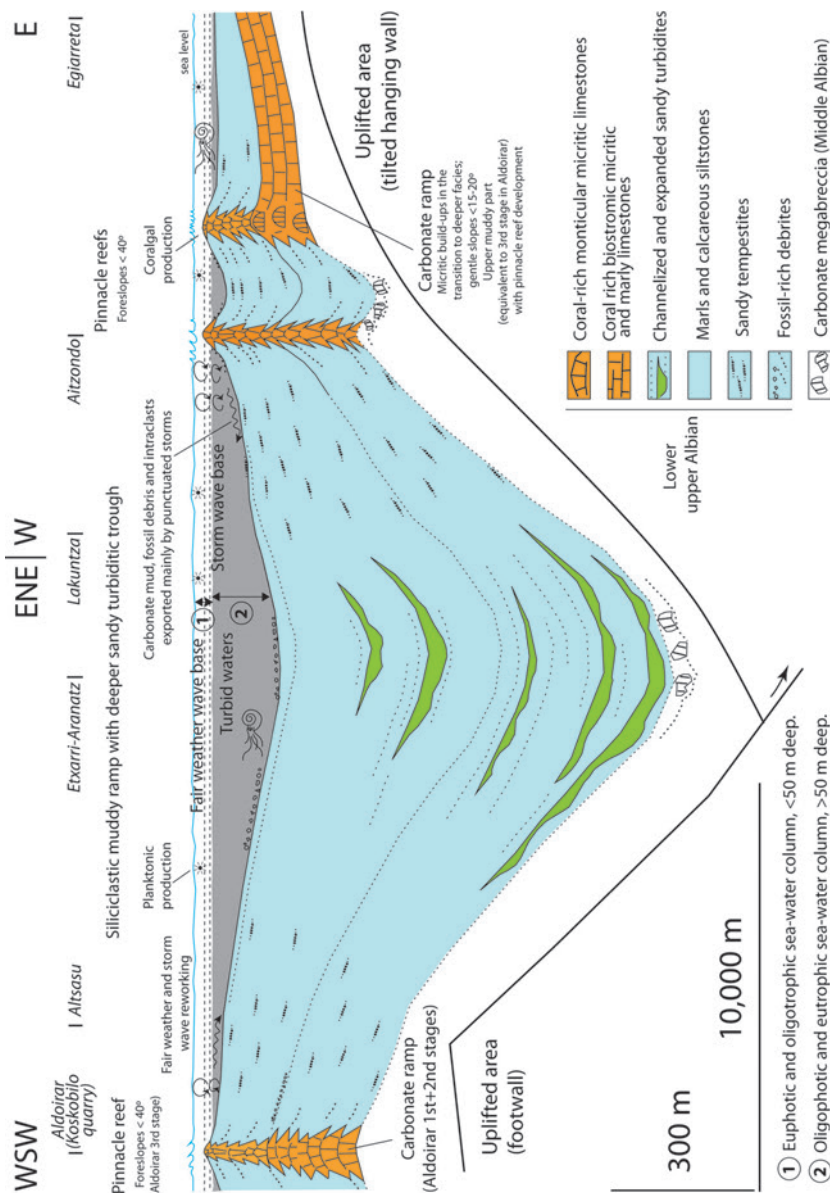


Figure 3. Sedimentary model of the lower upper Albian interval in the Sakana Valley (Navarre). Tectonic synsedimentary control created areas with differential subsidence. Uplifted areas were places of shallow marine carbonate sedimentation facing deeper areas with muddy and sandy sedimentation affected by storms and turbiditic currents. Breccia deposits may be linked to carbonate margin erosion after tectonic activity. Carbonates evolved from ramps to pinnacle structures with an overall reduction of the carbonate sedimentary area; in deeper siliciclastic areas there is a marked fining upwards trend. A shallow intraplatform muddy area developed between Aitzondo and Egiarreta. Decapod crustaceans are mainly found in limestones of the pinnacle carbonates and also in the muddy area of Egiarreta. Carbonate production on reefal areas occurred under clear waters (euphotic zone) and likely oligotrophic conditions. Deeper areas are characterized by turbid waters (oligotrophic) and eutrophic conditions.

Carbonate build-ups are composed of micritic limestones rich in corals (e.g., flabeloids of the *Plesiosmilia* group; O. A. Bonilla, pers. comm. 2019), rudists, and green algae that lived in shallow marine euphotic conditions (e.g., Klompmaker *et al.*, 2013a; Zamora and López-Horgue, 2022). Red algae, platy corals, sponges, bryozoans, and the crinoid *Proholopus holopiformis* (Remeš, 1902) are characteristic of the fore-reef in transition to an oligophotic marly deeper area, periodically affected by local storm waves.

Decapod crustacean diversity in these carbonate build-ups is the highest known worldwide for the Cretaceous thus far, with representatives of 45 decapod species reported from the Eguino Formation (Albeniz unit) (Klompmaker, 2013; Fraaije *et al.*, 2019).

In the shallowest siliciclastic areas coeval to these carbonates, representatives of only two decapod families (palaeocorystid and cenomanocarcinid crabs) have been found thus far (Van Bakel *et al.*, 2012a; López-Horgue and Bodego, 2017).

Ammonites of the genera *Desmoceras*, *Hamites*, *Kossmatella*, and the orbitolinids *Mesorbitolina subconcava* Leymerie, 1878, and *M. aperta* (Erman, 1854) have been found in the Koskobilo build-up, indicating an early late Albian age (Klompmaker, 2013; López-Horgue and Bodego, 2017) rather than Cenomanian or Albian/Cenomanian as was used previously. This is supported by the occurrence of ammonites of the same age (*Mortoniceras cf. geometricum* (Spath, 1932), *Hystero-ceras* sp., *Kossmatella muhlenbecki* (Fallot, 1885), *Hamites* (*Stomohamites*) *virgulatus* (Brongniart, 1822), *Hamites* (*Plesiohamites*) *multicostatus* (Brown, 1837), *Hypophylloceras seresitense* (Pervinquiere, 1907), and *H. algeriense* Wiedmann, 1962) in coeval and overlying deposits from the Etxarri-Aranaz locality, studied by Wiedmann (1962).

- upper upper Albian

Carbonate drowning occurred near the start of the latest Albian. The top of the carbonates near Altsasu show in places dissolution features and banded cements that suggest the stop of the shallow marine carbonate factory and a non-depositional time (hiatus). The coeval interval in the siliciclastic areas is marked by carbonate breccias. Accordingly, this mid upper Albian unconformity in the Sakana Valley is marked by a tectonic event (García-Mondéjar *et al.*, 2004), which caused the erosion of previous sediments, the end of marked deeper troughs, and the retreat of the sandy coastal systems. In other parts of the basin, this event is indicated by an angular unconformity (e.g., López-Horgue *et al.*, 2000; western margin of the BCB) and represents the end of an important volcanic phase (e.g., López-Horgue *et al.*, 2009; BCB center).

A shallow marine siliciclastic platform dominated in the whole Sakana Valley except for a small area (Aitziber) to the north of Altsasu where calcarenite deposits formed in a shallow marine, wave-dominated uplifted tectonic block. The sediments are mainly fine-grained: calcareous siltstones, marls, and scattered thin fine-sand tempestites. This type of sedimentation extended towards the south (Estella-Lizarra in López-Horgue *et al.*, 1999) and represents the retreat of sandy input in the basin.

The transition to the lower Cenomanian deposits is marked by a gradual decrease of silt input, a feature that continues during the earliest Cenomanian, being diachronous towards the southern margin of the BCB while the transgression was taking place.

Etyid and paleocorystid crabs are the only known decapods from the shallow-marine muddy environments of this age to the south of the Sakana Valley, in the Estella-Lizarra area (Van Bakel *et al.*, 2012a; López-Horgue and Bodego, 2017).

Ammonites ascribed to *Cantabrigites cf. subsimplex* (H. G. Owen, pers. comm. 2000) found in the calcareous siltstones stratigraphically overlying the Koskobilo limestones are indicative of a latest Albian age. However, the topmost marls stratigraphically overlying Koskobilo limestones are of middle Cenomanian age (López-Horgue *et al.*, 1996), indicating a hiatus encompassing the latest Albian and most of the early Cenomanian (Fraaije *et al.*, 2019).



STOP 1 - DECAPODS IN SEA MUDDY-BOTTOMS: THE EGIARRETA INNER PLATFORM SUCCESSION.

Location

The Egiarreta village is located to the west of the Iruztzun town (Navarre) but is part of the Arakil municipality. The locality was settled on the southern flank of the Aralar mountains near the northern bank of the Arakil river, in the eastern end of the Sakana (or Barranca) Valley (Fig. 2).

- » Coordinates: 42°55'33.74"N, 1°51'46.11"W, Elevation: 491 m.
- » Geological map of Navarre 1:25.000, sheet 114(II) Uharte-Arakil (López-Horgue *et al.*, 1997a).
- » Geological setting: Southern margin of the inverted BCB, Western Pyrenees.
- » Lithostratigraphy: Calcareous siltstones, marly limestones, and fine-grained sandstones of an intra-platform trough coeval to the upper part of the lower upper Albian limestones of the Sakana Valley (Fig. 3). Time-equivalent to the Aldoirar carbonate build-up (see Koskobilo quarry stop).
- » Age: early late Albian.

Aims

- » To show the siliciclastic facies succession coeval to the Koskobilo and Orobe carbonate build-ups with decapods.
- » To put the decapod-bearing levels into a stratigraphical context.
- » To show the decapod habitats based on fossil communities and facies interpretation.

Description

This siliciclastic unit is usually covered by forest in the Sakana Valley. The Egiarreta outcrops developed due to deforestation and grazing.

The decapod-bearing siliciclastic muddy succession (Fig. 4) is overlying limestones and marly limestones (rich in corals, orbitolinids, and rudists) and underlying calcareous siltstones and tempestites. Laterally to both the west and east, this muddy series changes to coralline limestones, in the Maddalenaitz and Etxeberri sites, respectively.

All units in the southern flank of the Aralar mountains are cut by low-displacement faults orthogonal to the regional 60/180 bedding.

Egiarreta succession

A gradual increase in the subsidence of the Sakana area during the late Albian led to a more than 50% areal reduction of the carbonate production environments from the early to the late Albian (García-Mondéjar *et al.*, 2004; see Fig. 2).

The upper Albian carbonate platform is divided into shallow platform areas with siliciclastic muddy input in the Egiarreta area, and a coralline micritic rim with gentle slopes facing deeper muddy facies in the Maddalenaitz area.

Platy and tabular coral limestones alternate with orbitolinid-rich muddy beds; green algae and rudists are common in certain beds. The siliciclastic content in these inner platform carbonates increases upwards in the succession leading to the silty succession of Egiarreta (Fig. 4). The lower part shows a transition from orbitolinid-coral rich limestones to silty marls with scattered limy beds with orbitolinids, as well as scarce ahermatypic corals and siderite nodules (28 m thick). The marly succession shows an upwards increase in the carbonate content leading to a top interval (8 m thick) of coral-chaetetid rich marly limestones.

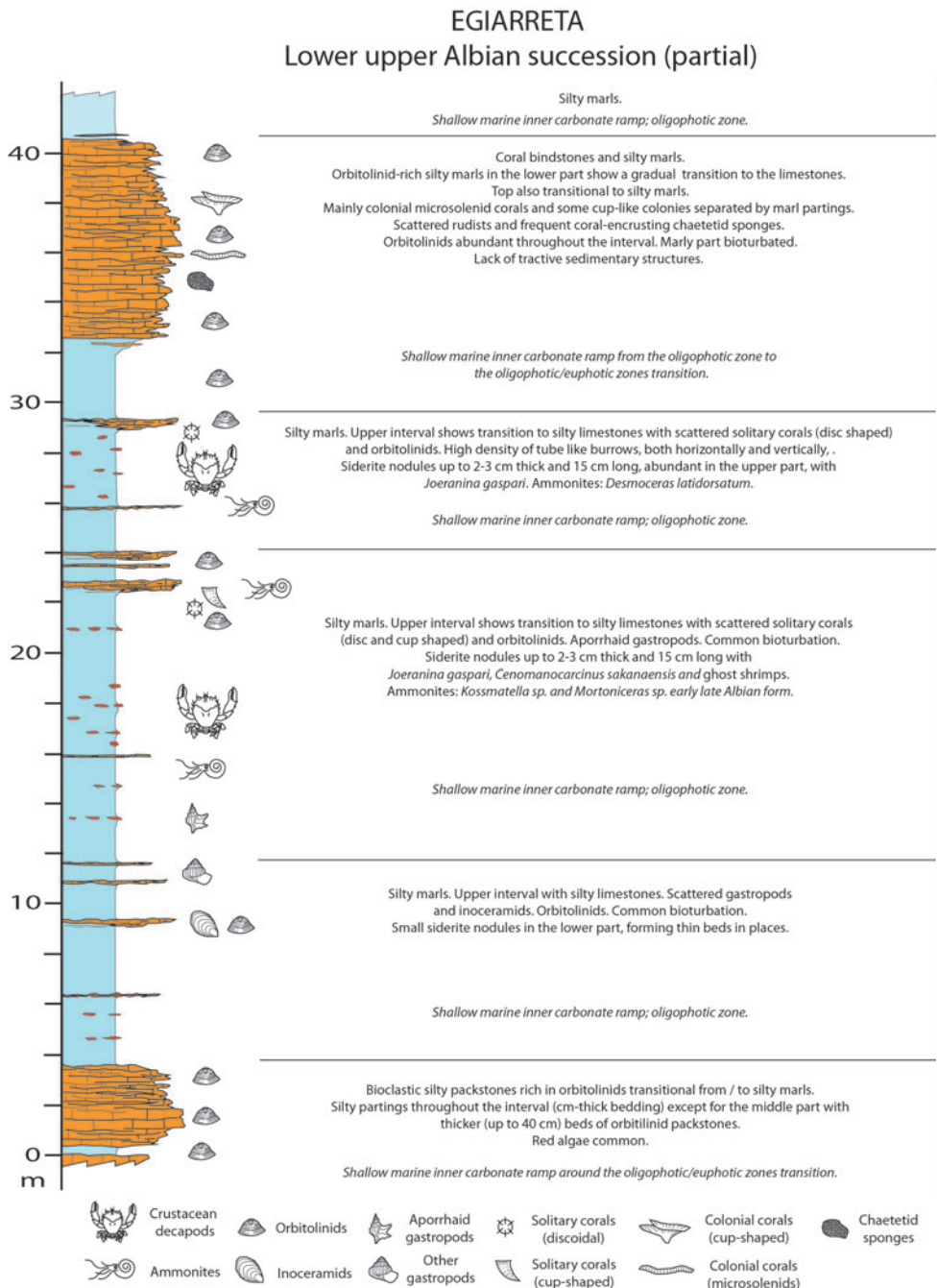


Figure 4. Intraplatform setting section of the lower upper Albian succession in Egiarreta (Navarre). A shallow marine muddy setting was developed after carbonate accumulation dominated by orbitolinid and coral macrofossils. At least 3 metric-scale cycles of siltstones to silty marls are distinguished in the muddy interval. The recovery of the carbonate producers atop of the succession is represented by platy corals and orbitolinids that tolerated some input of siliciclastic silt and mud, after which the drowning of the carbonate platform took place before the latest Albian. See figure 3 for location.

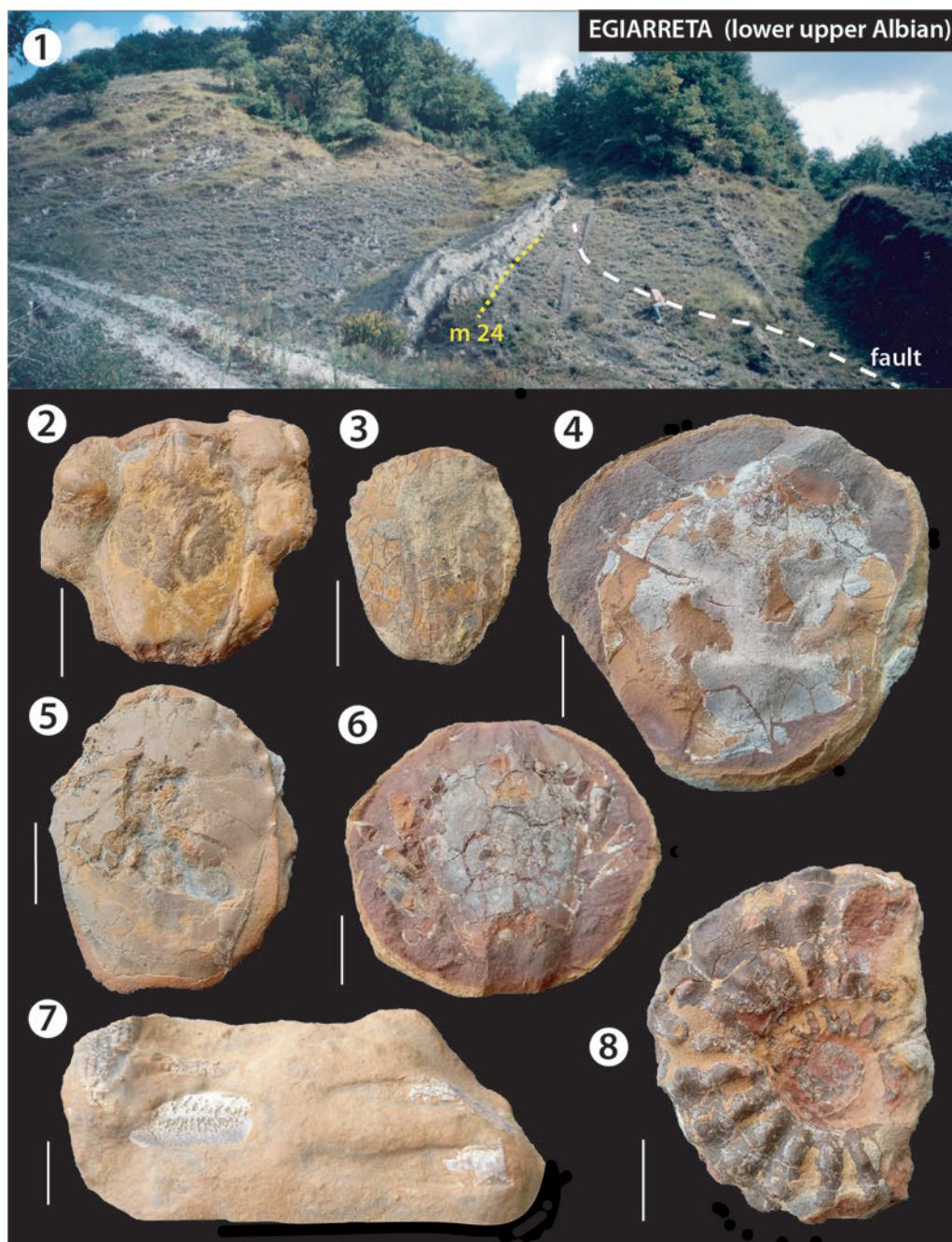


Figure 5. Egiarreta site (Navarre). 1. Outcrop of the muddy intraplatform setting represented in figure 4. Representative fossils of the upper part of the succession: 2, 3. *Joeranina gaspari* Van Bakel et al., 2012a. And from the lower part: 4. *Cenomanocarcinus sakanaensis* López-Horgue and Bodego, 2017, holotype BCB-D16; 5, 6. *J. gaspari*; 7. Callianassidae indet.; 8. *Mortoniceras* sp., early late Albian form. Scale bar: 1.0 cm. Specimens housed in the collections of the Geology department of the University of the Basque Country; waiting for repository after formal description.



Decapods are preserved in the siderite nodules from the marly interval where ammonites have also been found (Fig. 5). Ammonites indicate a substantially deeper environment. In the Maddalenaitz area, crinoids inhabited fore reef environments near 50 m depth in transition to deeper silty facies with ammonites (Zamora and López-Horgue, 2022).

Only two decapod species are known from this site thus far: *Joeranina gaspari* Van Bakel et al., 2012a, and *Cenomanocarcinus sakanaensis* López-Horgue and Bodego, 2017 (Fig. 5). Both crab species are typical of muddy substrates in siliciclastic coastal environments, areas of high nutrient levels.

STOP 2 - DECAPOD DIVERSITY IN THE ALDOIRAR CARBONATE BUILD-UP: THE KOSKO-BILO QUARRY.

Location

Koskobilo is the name of a limestone hill located to the north of Olazti locality (Navarre), near the northern bank of the Arakil river, at the western end of the Sakana (or Barranca) Valley (fig. 2).

- » Coordinates: 42°52'57.03"N, 2°11'56.48"W, Elevation: 562 m.
- » Geological map of Navarre 1:25.000, sheet 113(IV) Olazagutia (López-Horgue et al., 1997b).
- » Geological setting: Southern margin of the inverted BCB, Western Pyrenees.
- » Lithostratigraphy: Aldoirar carbonate reef build-up (Figs. 3, 6) of the former Eguino limestone Formation; today included in the Albeniz unit.
- » Age: early late Albian.

Aims

- » To show the facies architecture of a carbonate build-up surrounded by siliciclastics. To put the decapod-bearing levels into a stratigraphical context.
- » To show the decapod habitats based on fossil communities and facies interpretation.
- » To highlight and understand the high decapod diversity of this site.

Description

The Koskobilo hill and other coeval limestone bodies in the area were intensely quarried in the 19th and 20th centuries for concrete and railway track purposes (Fig. 7). Ruiz de Gaona highlighted the paleontological importance of the quarry through the discovery of a key Pleistocene fauna in karstic cavities of the limestone due to quarry exposures in 1940 (Arlegi et al., 2018).

The regional bedding is around 90/60S - 60/60SSE near the top. Two faults of only metric-scale displacement cut across the limestone, located in the southern flank of the Aitzgorri anticline.

Abandonment of active limestone mining for at least the last 30 years provided the opportunity for both geological and paleontological exploration in the 2010s, during which a peak Albian decapod diversity was found (e.g., Klompmaker, 2013).

The Aldoirar carbonate build-up is surrounded by calcareous silty facies, with a lateral extension around 1.3 km and a total thickness around 400 m (Fraaije et al., 2019). The build-up shows three main limestone intervals (Fraaije et al., 2019; Fig. 6). The Koskobilo quarry is excavated mainly in the upper interval, where the majority of decapod fauna was found (Klompmaker et al., 2013a).

Recently, the municipality of Olazti initiated a project to preserve Koskobilo as an important paleontological site for future generations.

Aldoirar limestones

The lower limestone interval of the Aldoirar build-up is made up of floatstones to packstones rich in platy corals and chaetetids with a ramp-like architecture and rapid transitions to fine-grained sandstones and siltstones. Upward in the succession, marly limestones with planar corals and sponges are at the base of the middle limestone interval with wackestones and floatstones rich in large planar corals, algae and rudists; gentle clinoforms are at the transition to siltstones. The top of this second interval is marked by a limestone breccia with ammonoids and marls; this marks the development of a local discontinuity likely related to tectonic pulses in the area. Above this, carbonate production recovered. The upper limestone interval shows the steepest clinoforms in transition to calcareous siltstones and a striking reduction of the limestone depositional area through time.

The limestones exposed at the Koskobilo quarry have been further subdivided into a wackestone/carbonate mudstone, a floatstone, and a boundstone zone (Klompmaier *et al.*, 2013a; Figs. 7-3). Paleocological analyses has shown that water depth varied between 20–80 m and energy levels may have increased toward younger strata.

Overall, the Aldoirar facies architecture shows a wedding cake form, indicative of the progressive abandonment of carbonate production and ultimate drowning of the build-up, likely linked to the inability of carbonate producers to keep up with increasing depths and to the siliciclastic trapping (e. g., López-Horgue *et al.*, 1993).

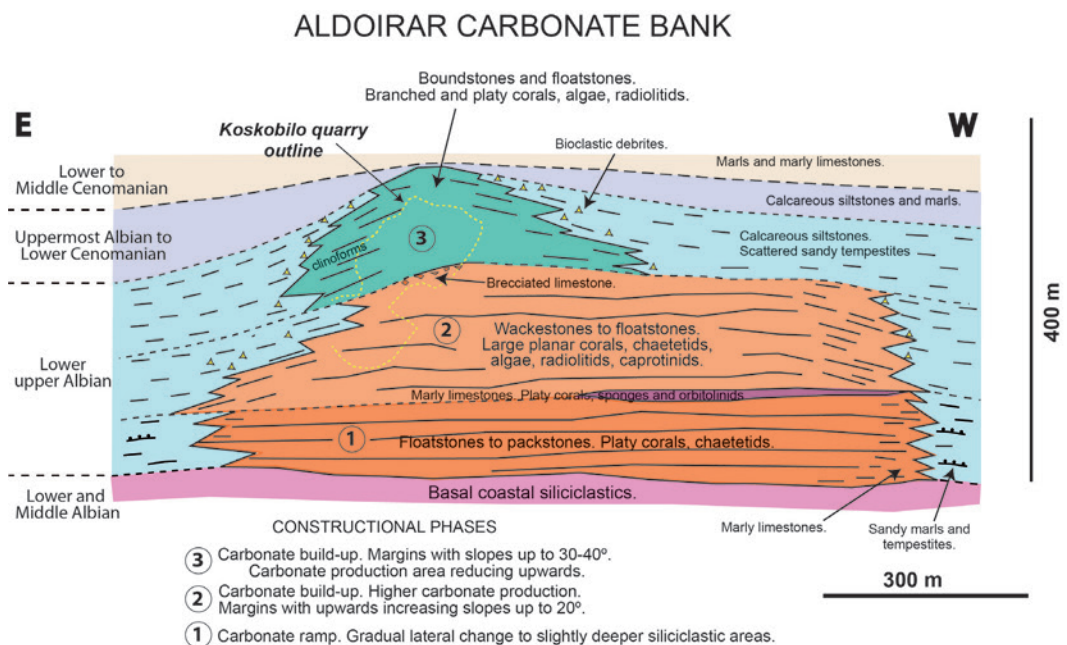


Figure 6. Aldoirar carbonate bank model with lateral changes to siliciclastic muddy deeper troughs. This carbonate system is divided into three constructional stages that show an upwards overall reduction of the carbonate sedimentation area and development of steeper clinoforms in the transition to siliciclastics. The approximate position of the Koskobilo quarry is highlighted. The main decapod fauna has been found in the third interval.

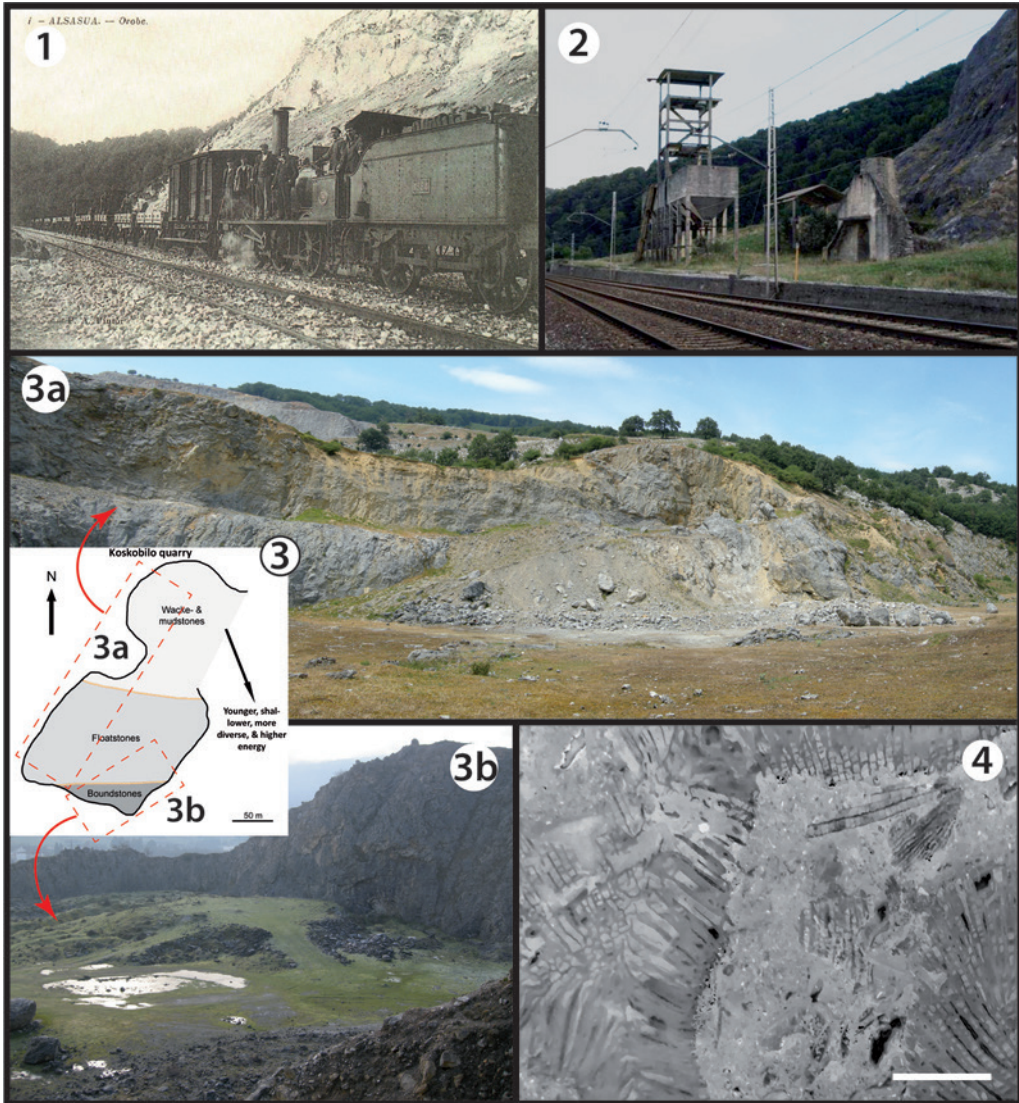


Figure 7. Koskobilo (Aldoirar carbonate bank) and Orobe (Orobe carbonate bank) quarries. 1. Historical photo of a ballast train of the Norte Railway Company in ca. 1910 during the exploitation of the Orobe quarry, likely to be full of thousands of decapods and other fossils. 2. Orobe quarry in the 1990s after the abandonment of the quarry, showing the train loading system. 3. Inset showing the location of panoramic views of the Koskobilo quarry, modified from Klompmaker *et al.* (2013: fig. 4), with permission: 3a, northwestern part of the quarry with wackestones and carbonate mudstones in the NW part and floatstones in the SW part; 3b, southern part, where most of the decapods have been found in floatstones and boundstones. 4. Boundstone of the Koskobilo quarry, showing branched corals of the *Plesiosmilina* group and a micritic matrix rich in bioclasts; decapods are common in this facies. Scale bar: 1.0 cm.

Decapod fauna

For the Cretaceous, the Koskobilo quarry is one of the most diverse decapod localities in the world (Klompmaker, 2013: fig. 16). Thus far, this quarry has yielded a decapod fauna consisting of 39 species based on well over 1,000 specimens (Fraaije *et al.*, 2009, 2012, 2013, 2019;

Klomp maker *et al.*, 2011a-c, 2012a-b, 2013a, 2020; Klomp maker, 2013). Those 39 species consist of 22 brachyuran crabs, 10 galatheid squat lobsters, five paguroids (hermit crabs), one gastrodoroid, and one achelatan lobster (Table 1). Swimming shrimps ascribed to Dendrobranchiata and Caridea have not been found so far, almost certainly due to their relatively low preservation potential as shown experimentally (Klomp maker *et al.*, 2017). The eight most abundant species include (in descending order) *Eomunidopsis navarrensis*, *Goniodromites laevis*, *Vasconilia ruizi*, *Distefania incerta*, *Graptocarcinus texanus*, *Acareprosopon bouvieri*, *Caloxanthus paraornatus*, and *Eomunidopsis orobensis* (Klomp maker, 2013: table 5; Fig. 8). Jointly, they make up ~83% of specimens of the decapod fauna.

Besides a high species diversity, a relatively high number of specimens can be found. A quantitative assessment collecting nine hours each at four sites in the southern part of the quarry yielded 235 decapods, or 6.5 specimens per hour on average (Klomp maker *et al.* 2013a). In terms of ecology, nearly all species were living exclusively on or in the bottom, but *Faksecarcinus koskobilensis* was almost certainly a swimmer given its flattened, wider than long carapace with a short height.

The highest diversity of decapods is found in the southeastern part of the quarry (Fig. 7-3) based on several diversity analyses (Klomp maker *et al.*, 2013a). Here, boundstones consisting of branching corals (Fig. 7-4) are common in between which decapods are frequently encountered. Paguroid carapaces are most commonly found in this part of the quarry too. Decapod sizes, using maximum carapace width, are statistically smaller in this part of the quarry because of (a) the relative scarcity of species with a large maximum size (b) the relatively frequent occurrence of species with a small maximum size, and (c) the common presence of small individuals of *Goniodromites laevis* (Klomp maker *et al.*, 2013a).

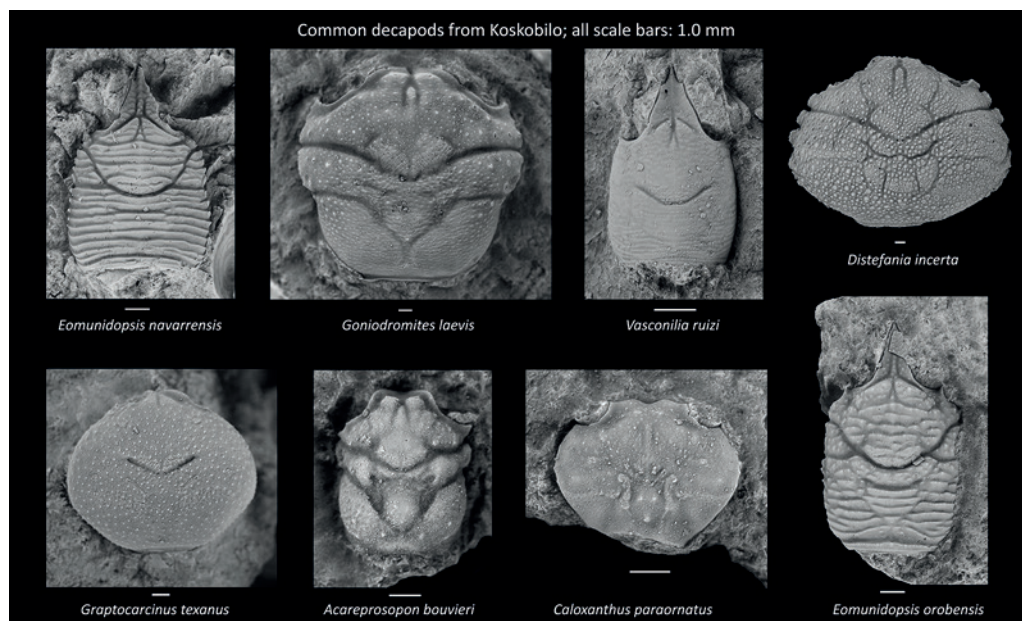


Figure 8. Eight (of the 39) most commonly encountered decapod species from the diverse southern part of the Koskobil quarry, arranged from most common to less common. These eight species comprise ~83% of all decapod specimens found from 2008–2010 (Klomp maker, 2013: table 5). Specimen images reproduced with permission from Klomp maker *et al.* (2011a, 2012a-b) and Klomp maker (2013). Image of *Acareprosopon bouvieri* specimen is new. Specimen museum numbers from upper left to bottom right: MAB k2535, MAB k2608, MAB k2972, MAB k2938, MAB k2669, MAB k2482, MAB k2649, and MAB k2932 (all Oertijdmuseum, Boxtel, The Netherlands).

Despite the very high diversity, the preservation of decapods in Koskobilo is not exquisite. None of the specimens have been found with the appendages, sternum, and/or abdomen attached to the carapace. This result suggests that favorable preservational circumstances cannot explain the high diversity. Instead, the reef environment with various subhabitats at Koskobilo providing ample places for shelter and food can explain this high diversity, as is known from modern reef habitats. Highly diverse decapod faunas have been found as well in other Meso- and Cenozoic reefs (e.g., Müller, 1984; Fraaije, 2003; Schweitzer and Feldmann, 2009; Beschin *et al.*, 2016; Robins and Klompmaker, 2019; Ferratges *et al.*, 2021; Hyžný and Dulai, 2021) and decapod diversity and reef abundance are positively correlated in the Mesozoic (Klompmaker *et al.*, 2013b).

While most species from Koskobilo have been described, discover additional species may be possible because the rarefaction curve has not fully flattened out yet (Klompmaker, 2013: fig. 15). For example, a single specimen (Klompmaker *et al.*, 2012b: fig. 12; Fraaije, 2014) ascribed to the galatheid *?Palmunidopsis* sp. is insufficiently complete to ascribe it to a species, but would almost certainly constitute a new species had it been complete. Additional paguroid carapace-based taxa are also expected because only three carapace-based species are known compared to the four tergite-based taxa (Fraaije *et al.*, 2009, 2012, 2013). Only two of the tergites can be provisionally linked to their carapaces (Fraaije *et al.*, 2013).

Koskobilo was also home to other crustaceans such as a cyclid (Van Bakel *et al.*, 2011), a cirrolanid isopod (Fraaije *et al.*, 2019), myodocopid ostracods, and almost certainly multiple species of epicaridean isopods (Klompmaker *et al.*, 2014). Body fossils of epicarideans have not been found due to their low preservation potential (Klompmaker *et al.*, 2017, 2022), but they have caused swellings in the gill chamber of ten decapods species in 4.2% of the specimens in the assemblage suitable for this analysis (Klompmaker *et al.*, 2014). This swelling received the trace fossil name *Kanthyoloma crusta* Klompmaker *et al.*, 2014.

The still active, larger Olazagutia quarry in the same Koskobilo hill has also yielded some decapods such as unidentified propodi of ghost shrimps not reported from the Koskobilo quarry thus far and the squat lobster *Vasconilia ruizi* (Klompmaker *et al.*, 2012b-c). This quarry has not been explored extensively for decapods.

Appendix - ANOTHER REEFAL HOT SPOT OF DIVERSITY: THE OROBE QUARRY.

Here, we include the Orobe decapod site since it is coeval to that the Koskobilo quarry. Unfortunately, only 4X4 vehicles can reach the Orobe quarry easily so it is not possible to visit this classic site. Because of the importance of this site and its relevance for this day, information is given to present a more comprehensive overview of the reef limestones and their crustacean fauna during an environmentally changing late Albian episode of the Basque-Cantabrian Basin.

Location

Orobe is the name of a place where a limestone quarry started producing aggregates for the Norte Railway at the end of the 19th century (Figs. 2, 7).

- » Coordinates: 42°55'03.19"N, 2°12'31.79"W, Elevation: 595 m.
- » Geological map of Navarre 1:25.000, sheet 113(IV) Olazagutia (López-Horgue *et al.*, 1997b) and 113(II) Zegama (López-Horgue *et al.*, 1997c).
- » Geological setting: Southern margin of the inverted BCB, Western Pyrenees.
- » Lithostratigraphy: Orobe carbonate reef build-up of the former Eguino limestone Formation; today included in the Albeniz unit.
- » Age: early late Albian.

Description

The quarry exploitation has been intimately linked to the needs for ballast used in the construction of the railway Madrid-Irun in the nearby area at several times (end of 19th and 20th centuries). Thanks to the excellent outcrops, Ruiz de Gaona found the first decapod remains around 1935 just before the Spanish civil war (1936-1939). Limestone mining intensified after the war, reaching a volume of 60 railway wagons per day (Ruiz de Gaona, 1954). The limestone was directly put onto the train in the quarry. Up to 1150 war prisoners were working on the refurbishment of the railway track between 1938 and 1944 (https://altsasumemoria.wordpress.com/category/batallontrab_altsasu/).

The Orobe build-up is located on the northern flank of the Aitzgorri anticline. This is the classic site from which Van Straelen (1940, 1944), Ruiz de Gaona (1943), and Via (1981, 1982) studied decapods. The limestone is about 200 m thick, and divided into three main limestone intervals (Gómez-Alday and Fernández-Mendiola, 1994).

Orobe limestones

Compared to the Aldoirar limestones, the Orobe build-up is thinner, indicating a less subsiding area for the early late Albian. The lower unit at Orobe is composed of calcarenites and marly limestones rich in sponges, orbitolinids, bryozoans, and red algae, with scarce radiolitic clusters, overlying lutites with tempestite beds. This unit can be divided into two intervals separated by silty marls and limestones. A gradual increase in carbonate production gave way to the upper interval composed of alternating floatstones with planar corals and orbitolinid-rich packstone-grainstones changing laterally to silty marls by means of clinoforms (Gómez-Alday and Fernández-Mendiola, 1994). The top of the Orobe limestones is an irregular surface overlain by Santonian marls and marly limestones, indicating a hiatus of ~15 Ma (e.g., Quintanar-Soto, 2003). Decapods are most abundant in the Orobe upper unit in association with corals. This upper part is time-equivalent to the upper part of Aldoirar build-up as suggested by orbitolinids and time-equivalent marls with ammonoids (López-Horgue *et al.*, 1997; Quintanar-Soto, 2003).

Decapod fauna

The general palaeontology and sedimentology of the Monte Orobe locality was described in detail by Ruiz de Gaona (1943, 1952, 1954) and López-Horgue *et al.* (1996). In addition to Ruiz de Gaona's 1943 paper, decapod crustaceans from this locality have also been recorded by Van Straelen (1940, 1944), Via (1981, 1982), Gómez-Alba (1989) and López-Horgue *et al.* (1996). Fraaije *et al.* (2008), Artal *et al.* (2012), Klompmaker *et al.* (2012b), Robins *et al.* (2013, 2016) also studied one or several specimens from this site.

Via (1981) listed the then known decapod crustacean species from this locality, nineteen in total (see Fraaije *et al.*, 2008: table 1). Klompmaker (2013: appendix A) provided an updated list of 24 decapod species found at Monte Orobe, nearly all of which have also been found at Koskobilu. Exceptions include the galatheid *Annieporcellana dhondtae* Fraaije *et al.*, 2008 (see Robins *et al.*, 2016), the paguroid *Annuntidiogenes ruizdegaonai* Fraaije *et al.*, 2008, the brachyuran *Necrocarcinus labeschei* (Eudes-Deslongchamps, 1835), and the brachyuran *Sabellidromites scarabaea* (Wright and Wright, 1950).

Collecting on two (parts of) days in 2008 and 2009 have yielded species commonly found in Koskobilu: *Eomunidopsis navarrensensis*, *Goniodromites laevis*, *Vasconilia ruizi*, *Distefania incerta*, and *Graptocarcinus texanus* (Florida Museum of Natural History collection). One of use (RHBF) recalls that some decapods at Orobe may be larger on average than conspecifics from Koskobilu.



Acknowledgements

This work is dedicated to the memory of Hugh Gwyn Owen, palaeontologist of the Natural History Museum of London and a lovely kind person who taught L-H very much on palaeontology.

Benjamin Botanz Apestegia (Irañeta, Navarre) helped very much in the field, providing a key ammonite from Egíarreta. Olazti and Arakil municipalities (Navarre) are also acknowledged.

The work (MAL-H) has been supported by the Gobierno Vasco/Eusko Jaurlaritza funds for the Research Group IT-1044-16 and IT-1418-19 and the project PID2019-105670 GB-I00/AEI/10.13039/501100011033 (Spanish research State Agency). Decapod research in Koskobilo by AAK was in part supported by a Molengraaff Fonds, an Amoco Alumni Scholarship, a Kent State University Graduate Student Senate research grant, and a Sigma Gamma Epsilon (Gamma Zeta Chapter) research grant to AAK and by NSF grant EF0531670 to Feldmann and Schweitzer. Cementos Portland Valderrivas is thanked for access to the Koskobilo quarry, and Pedro Artal, Barry van Bakel, Yvonne Coole, Rodney Feldmann, and Carrie Schweitzer for much appreciated help during field campaigns in the 2010s.

REFERENCES

- Agirrezabala, L.M., Kiel, S., Blumenberg, M., Schäfer, N. and Reitner, J. 2013. Outcrop analogues of pockmarks and associated methane-seep carbonates: a case study from the Lower Cretaceous (Albian) of the Basque-Cantabrian Basin, western Pyrenees. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 390, 94-115.
- Agirrezabala, L-M. and López-Horgue, M.A. 2017. Environmental and ammonoid faunal changes related to Albian Bay of Biscay opening: Insights from the northern margin of the Basque-Cantabrian Basin. *Journal of Sea Research*, 130, 36-48.
- Arlegi, M., Rios-Garaizar, J., Rodríguez-Hidalgo, A., López-Horgue, M.A. and Gómez-Olivencia, A. 2018. Koskobilo (Olazti, Nafarroa): nuevos hallazgos y revisión de las colecciones. *Munibe*, 69. <https://doi.org/10.21630/maa.2018.69.07>
- Artal, P., Van Bakel, B.W.M., Fraaije, R.H.B., Jagt, J.W.M. and Klompmaker, A.A. 2012. New Albian-Cenomanian crabs (Crustacea, Decapoda, Podotremata) from Monte Orobe, Navarra, northern Spain. *Revista Mexicana de Ciencias Geológicas*, 29, 398-410.
- Bell, T. 1863. A Monograph of the Fossil Malacostracous Crustacea of Great Britain, Pt. II, Crustacea of the Gault and Greensand. *Palaeontographical Society Monograph*, London, 40 pp., 11 pls.
- Beschin, C., Busulini, A., Tessier, G. and Zorzin, R. 2016. I crostacei associati a coralli nell'Eocene inferiore dell'area di Bolca (Verona e Vicenza, Italia nordorientale). *Memorie del Museo Civico di Storia Naturale di Verona - 2. serie. Sezione Scienze della Terra*, 9, 1-189.
- Brongniart, B.G. 1822. Sur quelques terrains de Craie hors du Bassin de Paris. Cuvier, *Recherches sur les Ossements fossiles*, 2, 316-337.
- Brown, T. 1837-1849. Illustrations of the Fossil Conchology of Great Britain and Ireland. Smith, Elder, London, vii+273 pp.
- Castañares, L.M., Robles, S., Gimeno, D. and Vicente-Bravo, J.C. 2001. The submarine volcanic system of the Errigoiti formation (Albian-Santonian of the Basque-Cantabrian Basin, northern Spain): stratigraphic framework, facies and sequences. *Journal of Sedimentary Research*, 71, 318-333.
- Desmarest A.G. 1817. Crustacés fossiles, in Société de Naturalistes et d'Agriculteurs (eds), Nouveau Dictionnaire d'Histoire naturelle, appliquée aux Arts, à l'Agriculture, à l'Économie rurale et domestique, à la Médecine, etc. Tome 7 [COR-CUN]. Deterville, Paris, 495-519.

- Erman, A. 1854. Elinige Beobachtungen über die Kreide-formation an der Nordküste von Spanien. *Zeitschrift der Deutschen Geologischen Gesellschaft*, 6, 596-611, 2 pl.
- Eudes-Deslongchamps, J.A. 1835. Mémoire pour servir à l'histoire naturelle des Crustacés fossils. *Mémoire de la Société Linnéenne de Normandie*, 5, 37-46, pl. 1.
- Fallot, E. 1885. Etude géologique sur les étages moyens et supérieurs du terrain Crétacé dans le Sud-Est de la France. *Annales des Sciences géologiques*, 18 (1885), 1-262.
- Ferratges, F.A., Zamora, S. and Aurell, M. 2021. Unravelling the distribution of decapod crustaceans in the Lower Eocene coral reef mounds of NE Spain (Trempe-Graus Basin, southern Pyrenees). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 575, 110439, doi: 10.1016/j.palaeo.2021.110439.
- Fontana, B., Gallego, M.R., Meléndez, G., Aurell, M. and Badenas, B. 1994. Las calizas con esponjas del Bajociense de la Cordillera Vasco-Cantábrica oriental (Navarra). *Geogaceta*, 15, 30-33.
- Fraaije, R.H.B. 2003. Evolution of reef-associated decapod crustaceans through time, with particular reference to the Maastrichtian type area. *Contributions to Zoology*, 72, 119-130, doi: 10.1163/18759866-0720203010.
- Fraaije, R.H.B. 2014. A new shallow-marine munidopsid (Anomura, Galatheaidea) from the upper Miocene in the Maroni-Psematismenos Basin of Cyprus. *Scripta Geologica*, 147, 233-239.
- Fraaije, R.H.B., Artal, P., Van Bakel, B.W.M., Jagt, J.W.M. and Klompmaker, A.A. 2013. An array of sixth abdominal tergite types of paguroid anomurans (Crustacea) from the mid-Cretaceous of Navarra, northern Spain. *Netherlands Journal of Geosciences*, 92, 109-117.
- Fraaije, R.H.B., Klompmaker, A.A. and Artal, P. 2012. New species, genera and a family of hermit crabs (Crustacea, Anomura, Paguroidea) from a mid-Cretaceous reef of Navarra, northern Spain. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen*, 263, 85-92.
- Fraaije, R.H.B., López-Horgue, M.A., Bruce, N.L., Van Bakel, B.W.M., Artal, P., Jagt, J.W.M. and Klompmaker, A.A. 2019. New isopod and achelatan crustaceans from mid-Cretaceous reefal limestones in the Basque-Cantabrian Basin, northern Spain. *Cretaceous Research*, 101, 61-69, doi: 10.1016/j.cretres.2019.04.012.
- Fraaije, R.H.B., Van Bakel, B.W.M., Jagt, J.W.M. and Artal, P. 2008. New decapods crustaceans (Anomura, Brachyura) from mid-Cretaceous reefal deposits at Monte Orobe (Navarra, northern Spain), and comments on related type-Maastrichtian material. *Bulletin de l'institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre*, 78, 193-208.
- Fraaije, R.H.B., Van Bakel, B.W.M., Jagt, J.W.M., Klompmaker, A.A. and Artal, P. 2009. A new hermit crab (Crustacea, Anomura, Paguroidea) from the mid-Cretaceous of Navarra, northern Spain. *Boletín de la Sociedad Geológica Mexicana*, 61, 211-214.
- García-Mondéjar, J. 1982. Aptiense-Albiense, Región Vasco-Cantábrica y Pirineo navarro. In: García A. (Ed.), *El Cretácico de España*, Universidad Complutense, Madrid, 63-84.
- García-Mondéjar, J., Fernández-Mendiola, P.A., Agirrezabala, L.M., Aranburu, A., López-Horgue, M. A., Iriarte, E. and Martínez de Rituerto, S. 2004. El Aptiense-Albiense de la Cuenca Vasco-Cantábrica. In: Vera, J. A. (Ed.), *Geología de España*. Sociedad Geológica de España-Instituto Geológico y Minero de España, Madrid, 291-296.
- González-León, O., Ossó, A., Moreno-Bedmar, J. A. and Vega, F. 2016. Brachyura from the Lower Cretaceous (Aptian) of Spain: a new species of *Rathbunopon* (Homolodromioidea, Prosopidae) and the second record of *Mithracites vectensis* (Homoloidea). *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen*, 282, 115-124.

- Gómez-Alba, J. 1989. Decápodos fósiles de España (Decapoda, Cretácico-Pleistoceno) conservados en el Museu de Geologia de Barcelona. *Museu de Geologia de Barcelona, Catàleg de Col·leccions*, 1, 1–48.
- Gómez-Alday, J.J. and Fernández-Mendiola, P. A. 1994. Las calizas de Motho (Albiense superior, Alsasua, Navarra): análisis de facies. *Kobie (serie ciencias naturales)*, XXII, 5-12.
- Haq, B.U. 2014. Cretaceous eustasy revisited. *Global and Planetary Change*, 113, 44-58.
- Hyzný, M. and Dulai, A. 2021. *Badenian Decapods of Hungary*. Geolitera Publishing House, Institute of Geosciences, University of Szeged, Hungary, Szeged, 290 pp.
- Jacquot, E. 1864. Description géologique des Falaises de Biarritz, Guétary et Saint Jean de Luz. *Actes de la Société linnéenne de Bordeaux, 3ème série*, 5, 1-58.
- Klomp maker, A.A. 2013. Extreme diversity of decapod crustaceans from the mid-Cretaceous (Late Albian) of Spain: Implications for Cretaceous decapod paleoecology. *Cretaceous Research*, 41, 150-185, doi: 10.1016/j.cretres.2012.12.003.
- Klomp maker, A.A., Artal, P., Van Bakel, B.W. M., Fraaije, R.H.B. and Jagt, J.W.M. 2011a. Etyid crabs (Crustacea, Decapoda) from mid-Cretaceous reefal strata of Navarra, northern Spain. *Palaeontology*, 54, 1199-1212, doi: 10.1111/j.1475-4983.2011.01072.x.
- Klomp maker, A.A., Artal, P., Fraaije, R.H.B. and Jagt, J.W.M. 2011b. Revision of the family Gastrodoridae (Crustacea, Decapoda), by description of the first species from the Cretaceous. *Journal of Paleontology*, 85, 226-233.
- Klomp maker, A.A., Artal, P. and Gulisano, G. 2011c. The Cretaceous crab *Rathbunopon*: revision, a new species and new localities. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen*, 260, 191-202, doi: 10.1127/0077-7749/2011/0170.
- Klomp maker, A.A., Feldmann, R.M. and Schweitzer, C.E. 2012a. A hotspot for Cretaceous goniodromitids (Decapoda: Brachyura) from reef associated strata in Spain. *Journal of Crustacean Biology*, 32, 780-801, doi: 10.1163/193724012X635340.
- Klomp maker, A.A., Feldmann, R.M., Robins, C.M. and Schweitzer, C.E. 2012b. Peak diversity of Cretaceous galatheoids (Crustacea, Decapoda) from northern Spain. *Cretaceous Research*, 36, 125-145, doi: 10.1016/j.cretres.2012.03.003.
- Klomp maker, A.A., Feldmann, R.M. and Schweitzer, C.E. 2012c. New European localities for coral-associated Cretaceous decapods crustaceans. *Bulletin of the Mizunami Fossil Museum*, 38, 69-74.
- Klomp maker, A.A., Ortiz, J.D. and Wells, N.A. 2013a. How to explain a decapod crustacean diversity hotspot in a mid-Cretaceous coral reef. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 374, 256-273, doi: 10.1016/j.palaeo.2013.01.024.
- Klomp maker, A.A., Schweitzer, C.E., Feldmann, R.M. and Kowalewski, M. 2013b. The influence of reefs on the rise of Mesozoic marine crustaceans. *Geology*, 41, 1179-1182, doi: 10.1130/G34768.1.
- Klomp maker, A.A., Artal, P., Van Bakel, B.W.M., Fraaije, R.H.B. and Jagt, J.W.M. 2014. Parasites in the fossil record: a Cretaceous fauna with isopod-infested decapod crustaceans, infestation patterns through time, and a new ichnotaxon. *PLoS One*, 9, e92551, doi: 10.1371/journal.pone.0092551.
- Klomp maker, A.A., Portell, R.W. and Frick, M.G. 2017. Comparative experimental taphonomy of eight marine arthropods indicates distinct differences in preservation potential. *Palaeontology*, 60, 773-794, doi: 10.1111/pala.12314.



- Klomp maker, A.A., Starzyk, N., Fraaije, R.H.B. and Schweigert, G. 2020. Systematics and convergent evolution of multiple reef-associated Jurassic and Cretaceous crabs (Decapoda, Brachyura). *Palaeontologia Electronica*, 23, a32, doi: 10.26879/1045.
- Klomp maker, A.A., Robins, C.M., Portell, R.W. and De Angeli, A. 2022. Crustaceans as hosts of parasites throughout the Phanerozoic. In De Baets, K. and Huntley, J. W. (eds), *The Evolution and Fossil Record of Parasitism*. Springer International Publishing, Cham, Topics in Geobiology 50, 121-172, doi: 10.1007/978-3-030-52233-9_5.
- Leymerie, A. 1878-1881. Description géologique et paléontologique des Pyrénées de la Haute Garonne. E. Privat. Édité., Toulouse, 2t., 1010 p (1878 text), pl. A-Z (1881 atlas).
- López-Horgue, M.A. 2009. New occurrences of *Meyeria magna* McCoy, 1849 (Decapoda, Mecochiridae) in the early Aptian and early Albian of the Basque-Cantabrian Basin (North Spain). *Geogaceta*, 47, 25-28.
- López-Horgue, M.A., Aranburu, A., Fernández-Mendiola, P.A. and García-Mondéjar, J. 1993. Existencia de una plataforma carbonatada entre materiales terrígenos de mar somero (Karrantza-Trucíos, Bizkaia). *Geogaceta*, 13, 65-68.
- López-Horgue, M.A., Lertxundi, D. and Baceta, J.I. 1996. Evolución sedimentaria del episodio mixto carbonatado-terrágeno del Albiense superior-Cenomaniense inferior entre Altsasu (Nafarroa) y Asparrena (Araba): la unidad Albeniz. *Príncipe de Viana, Suplemento de Ciencias*, 14, 81-96.
- López-Horgue, M.A., Hernández, A., Baceta, J.I., Faci, E. and Larrañaga, M.J. 1997a. Mapa geológico de Navarra a escala 1:25.000, hoja 114-II (Uhart-Arakil). Gobierno de Navarra, Servicio de Obras Públicas, Pamplona.
- López-Horgue, M.A., Baceta, J.I., Faci, E. and Larrañaga, M.J. 1997b. Mapa geológico de Navarra a escala 1:25.000, hoja 113-IV (Olazagutia). Gobierno de Navarra, Servicio de Obras Públicas, Pamplona.
- López-Horgue, M.A., Baceta, J.I., Faci, E. and Larrañaga, M.J. 1997c. Mapa geológico de Navarra a escala 1:25.000, hoja 113-II (Zegama). Gobierno de Navarra, Servicio de Obras Públicas, Pamplona.
- López-Horgue, M.A., Owen, H.G., Rodríguez-Lázaro, J., Orue-Etxebarria, X., Fernández-Mendiola, P. A. and García-Mondéjar, J. 1999. Late Albian-Early Cenomanian stratigraphic succession near Estella-Lizarrá (Navarra, central northern Spain) and its regional and interregional correlation. *Cretaceous Research*, 20, 369-402.
- López-Horgue, M.A., Aranburu, A., Fernández-Mendiola, P.A. and García-Mondéjar, J. 2000. Existencia de una discordancia angular con laguna del Albiense medio en el complejo Urgoniano de Ranero (Ramales-Karrantza, Región Vasco-Cantábrica). *Geogaceta*, 28, 89-92.
- López-Horgue, M.A. and Hernández, J.M. 2003. La cuenca terciaria continental del diapiro de Murgoa: la Formación Izarra (Oligoceno superior-Mioceno inferior, Cuenca Vasco-Cantábrica). *Geogaceta*, 33, 123-126.
- López-Horgue, M.A., Owen, H.G., Aranburu, A., Fernández-Mendiola, P.A. and García-Mondéjar, J. 2009. Early late Albian (Cretaceous) of the central region of the Basque-Cantabrian Basin, northern Spain: biostratigraphy based on ammonites and orbitolinids. *Cretaceous Research*, 30, 385-400.
- López-Horgue, M.A., Poyato-Ariza, F.J., Cavin, L. and Bermúdez-Rochas, D.D. 2014. Cenomanian transgression in the Basque-Cantabrian Basin (northern Spain) and associated faunal replacement. *Journal of Iberian Geology*, 40, 489-506.

- López-Horgue, M.A. and Bodego, A. 2017. Mesozoic and Cenozoic decapod crustaceans from the Basque-Cantabrian Basin (Western Pyrenees): new occurrences and faunal turnovers in the context of basin evolution. *Bulletin de la Société Géologique de France*, 188, 14, doi: 10.1051/bsgf/2017180.
- López-Horgue, M.A. and Bodego, A. 2018. Grandes desconocidos del registro fósil: los crustáceos decápodos del Mesozoico y Cenozoico de los Pirineos occidentales. In Badiola, A., Gómez-Olivencia, A. and Pereda-Suberbiola, X. (eds.), *Registro fósil de los Pirineos occidentales. Bienes de interés paleontológico y geológico. Proyección Social*. Servicio Central de Publicaciones del Gobierno Vasco, Vitoria-Gasteiz, 109-116.
- Lőrenthey, E. and Beurlen, K. 1929. Die fossilen Dekapoden der Länder der Ungarischen Krone. *Geologica Hungarica, Series Palaeontologica*, 3, 1–420, 16 pls.
- M'Coy, E. 1849. On the classification of some British fossil Crustacea, with notices on the new forms in the University collection at Cambridge. *Annals and Magazine of Natural History*, 2nd series, 4(21), 161-179.
- Mengaud, L. 1920. Recherches géologiques dans la Région Cantabrique. Thèse présentée à la Faculté des Sciences Université Paris, 374 pp., 87 figs., láminas 1-14, A-D, Toulouse.
- Meyer, H. von 1857. Briefliche Mitteilungen. *Neues Jahrbuch für Mineralogie, Geologie, Geognosie und Petrefaktenkunde* 1857, 556.
- Meyer, H. von 1862. Tertiäre Decapoden aus den Alpen, von Öningen und dem Taunus. *Paleontographica* 10, 147-178.
- Milne Edwards, A. 1865. Monographie des Crustacés de la famille des Cancériens (suite). *Annales des Sciences Naturelles, Zoologie*, 5, 3, 297-351.
- Müller, P. 1984. Decapod Crustacea of the Badenian. *Geologica Hungarica, (Palaeontologica)*, 42, 1-317, pls. 1-97.
- Ossó, A. 2017. New records of Palaeocorystoidea from the Iberian peninsula and remarks on the taxonomic significance of the posterior margin of *Cenomanocarcinus* Van Straelen, 1936 and *Hasaracancer* Jux, 1971 (Decapoda; Brachyura; Cenomanocarcinidae). *Zootaxa*, 4303(2), 273-283.
- Ossó, A. and Díaz-Isa, M. 2014. *Cantabroxanthus loredoensis* new genus, new species (Decapoda, Brachyura, Etyoidea) from the Middle Campanian of Loredo, Ribamontán al Mar (Cantabria, northern Spain). *Boletín de la Sociedad Geológica Mexicana*, 66, 483-489.
- Ossó, A. and Moreno-Bedmar, J.A. 2020. A new species of *Etyus* Leach in Mantell, 1822 (Decapoda, Brachyura, Etyidae) from the lower Aptian (Lower Cretaceous) of Cantabria, Spain. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen*, 296/1-2, 175-183.
- Ossó, A., van Bakel, B.W.M. and Ferratges, F.A. 2021. *Cuchiadromites jadeae*, a new genus and species of primitive crab (Crustacea: Decapoda: Podotremata) from the Aptian of Cantabria (Spain), with comments on its peculiar surface ornament. *Cretaceous Research*, 117. <https://doi.org/10.1016/j.cretres.2020.104636>
- Pervinquière, L. 1907. Etudes de Paléontologie Tunisienne I, Céphalopodes des terrains secondaires. Carte géologique Tunisie, Direction Générale des Travaux Publics, 438 S., 27 pl., Paris.
- Rathbun, M.J. 1935. Fossil Crustacea of the Atlantic and Gulf Coastal Plain. *Geological Society of America, special paper*, 2, viii+160.
- Quintanar-Soto, A.B. 2003. El Cretácico medio del extremo suroccidental del Anticlinorio de Bilbao: Estratigrafía y Sedimentología. Unpublished Ph. D. Thesis, UPV/EHU, 217 pp.



- Quiroga, F. 1887. Nummulítico de Castillo de la Barquera y Cabo Oyambre. *Anales de la Sociedad Española de Historia Natural*, 16, 220-222.
- Remeš, M., 1902. Nachträge zur Fauna von Stramberg, VI. Crinoiden-. Asteriden- und Echinoiden-resten aus dem Weissen Kalkstein von Stramberg. *Beiträge zur Paläontologie und Geologie Österreich-Ungarns*, 14, 195-217.
- Robin, N., Charbonnier, S., Merle, D., Simpson, M.I., Petit, G. and Fernandez, S. 2016. Bivalves on mecochirid lobsters from the Aptian of the Isle of Wight: Snapshot on an Early Cretaceous palaeosymbiosis. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 453, 10-19.
- Robins, C.M. and Klompmaker, A.A. 2019. Extreme diversity and parasitism of Late Jurassic squat lobsters (Decapoda: Galatheaidea) and the oldest records of porcellanids and galatheids. *Zoological Journal of the Linnean Society*, 187, 1131-1154, doi: 10.1093/zoolinnean/zlz067.
- Robins, C.M., Feldmann, R.M. and Schweitzer, C.E. 2013. Nine new genera and 24 new species of the Munidopsidae (Decapoda: Anomura: Galatheaidea) from the Jurassic Ernstbrunn Limestone of Austria, and notes on fossil munidopsid classification. *Annalen des Naturhistorischen Museums in Wien, Serie A*, 115, 167-251.
- Robins, C.M., Feldmann, R.M., Schweitzer, C.E. and Bonde, A. 2016. New families Paragalatheididae and Catilloagalatheididae (Decapoda: Anomura: Galatheaidea) from the Mesozoic, restriction of the genus *Paragalathea*, and establishment of 6 new genera and 20 new species. *Annalen des Naturhistorischen Museums in Wien, Serie A*, 118, 65-131.
- Robles, S. 2014. Evolución geológica de la Cuenca Vasco-Cantábrica. In Bodego, A., et al., (eds.), *Geología de la Cuenca Vasco-Cantábrica*. Servicio editorial de la Universidad del País Vasco, Bilbao, 9-104.
- Roemer, F. A. 1887. *Graptocarcinus texanus*, ein Brachyure aus der Kreide von Texas. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie*, 1887, 173-176.
- Ruiz de Gaona, M. 1943. Nota sobre crustáceos decápodos de la cantera del Monte Orobe (Alsasua). *Boletín de la Real Sociedad Española de Historia Natural*, 40, 425-433, pl. 28.
- Ruiz de Gaona, M. 1952. Algunos datos geológico-paleontológicos sobre el Valle de la Barranca (Navarra). *Primer congreso internacional del Pirineo del Instituto de Estudios Pirenaicos, Zaragoza, CSIC*, 3-14.
- Ruiz de Gaona, M. 1954. La fauna paleontológica de Orobe (Navarra). *Boletín de la Real Sociedad Española de Historia Natural. Tomo Extraordinario*, 573-577.
- Schlüter, C. 1879. Neue und weniger gekannte Kreide- und Tertiär-Krebse des nördlichen Deutschlands. *Zeitschrift der deutschen geologischen Gesellschaft*, 31, 586-615, pls. 13-18.
- Schweitzer, C.E. 2003. Utility of proxy characters for classification of fossils: an example from the fossil xanthoidea (Crustacea: Decapoda: Brachyura). *Journal of Paleontology*, 77, 1107-1128.
- Schweitzer, C.E. and Feldmann, R.M. 2009. Revision of the Prosopinae sensu Glaessner, 1969 (Crustacea: Decapoda: Brachyura) including four new families, four new genera, and five new species. *Annalen des Naturhistorischen Museums in Wien, Serie A*, 110, 55-121.
- Secrétan, S. 1964. Les Crustacés décapodes du Jurassique supérieur et du Crétacé de Madagascar. *Mémoires du Muséum national d'Histoire naturelle, Paris, new series*, C14, i-viii+1-226, pls. 1-20.
- Spath, L. F. 1932. A monograph of the Ammonoidea of the Gault, part IX. XXXVII-XLII pl., 379-410. The Palaeontographical Society, London.



- Tugend, J., Manatschal, G., Kuszniir, N.J., Masini, E., Mohn, G. and Thionon, I. 2014. Formation and deformation of hyperextended rift systems: Insights from rift domain mapping in the Bay of Biscay-Pyrenees. *Tectonics*, 33, 1239-1276, doi: 10.1002/2014TC003529
- Van Bakel, B.W.M., Jagt, J.W.M., Fraaije, R.H.B. and Artal, P. 2011. A new family, genus and species of cyclid (Crustacea, Branchiura, Cyclida) from mid-Cretaceous reefal deposits in northern Spain. *Bulletin of the Mizunami Fossil Museum*, 37, 47-49.
- Van Bakel, B.W.M., Guinot, D., Artal, P., Fraaije, R.H.B. and Jagt, J.W.M. 2012a. A revision of the Palaeocorystoidea and the phylogeny of raninoidian crabs (Crustacea, Decapoda, Brachyura, Podotremata). *Zootaxa*, 3215, 1-216.
- Van Bakel, B.W.M., Guinot, D., Corral, C. and Artal, P. 2012b. Graptocarcininae n. subfam., an extinct subfamily of Dynomenidae Ortmann, 1892 (Crustacea, Brachyura, Podotremata). *Zootaxa*, 3534, 40-52.
- Van Straelen, V. 1927. Contribution à l'étude des Crustacés décapodes fossiles de la Péninsule Ibérique. *Eos: Revista Española de Entomología*, 3(1), 79-94.
- Van Straelen, V. 1940. Crustacés décapodes nouveaux du Crétacique de la Navarre. *Bulletin du musée d'histoire naturelle de Belgique*, 16, 1-5, pl. 1.
- Van Straelen, V. 1944. Anomoure et brachyures du Cénomanien de la Navarre. *Bulletin du musée d'histoire naturelle de Belgique* 20, 1-12, pl. 1.
- Via, L. 1969. Crustáceos decápodos del Eoceno español. *Pirineos*, 91-94, 1-479, 39 pls.
- Via, L. 1981. Les crustacés décapodes du Cénomanien de Navarre (Espagne): premiers résultats de l'étude des Galatheidae. *Geobios*, 14, 247-251.
- Via, L. 1982. Les Galatheidae du Cénomanien de Navarre (Espagne). *Annales de Paléontologie*, 68, 107-131.
- Wiedmann, J. 1962. Ammoniten aus der Vascogotischen Kreide (Nordspanien), I. Phylloceratina, Lytoceratina. *Palaeontographica Abteilung A*, 118,, 119-237.
- Woodward, H. 1866. Note on a new species of *Ranina* (*Ranina porifera*) from the Tertiary strata of Trinidad. *Quarterly Journal of the Geological Society of London*, 22, 591-592.
- Wright, C.W. and Wright, E.V. 1950. Some dromiacean crabs from the English Cretaceous. *Geological Magazine*, 82, 126-129, pl. 5.
- Wright, C. W. and Collins, J. S. H. 1972. British Cretaceous crabs. *Palaeontographical Society Monographs*, 126, 1-113.
- Zamora, S. and López-Horgue, M.A. 2022. A shallow-water cyrtocrinid crinoid (Articulata) from the upper Albian of the Western Pyrenees, North Spain. *Cretaceous Research*, 134, 105161. doi: 10.1016/j.cretres.2022.105161

**AUTHOR INDEX****A**

Abelló 82
Aguirre-Urreta 29
Ando 27, 66
Andrada 29
Arasa 75
Artal 79
Audo 32, 34
Aurell 47, 53, 99, 113

B

Bádenas 86
Bakel 49, 51, 61, 79, 91, 93
Belaústegui 36
Beschinn 42, 90
Bracken-Grissom 21
Braig 40
Brezina 66
Briggs 21
Busulini 42, 90

C

Canudo 86
Charbonnier 34, 45, 68, 70
Ćosović 56

D

Devillez 32
Domínguez 47

F

Ferratges 47, 53, 86, 99, 113
Forel 68, 70
Fraaije 49, 51, 61, 91, 93, 137

G

Gaete 72
Galán 86
Garassino 45
García-Penas 53, 99, 113
Gašparič 56, 70
Glamuzina 56

H

Hachiya 27
Haug 40
Hayashi 27
Heteš 59
Hitij 70
Hof 61
Huang 32, 34
Hyžný 11, 59, 63

J

Jagt 49, 51, 61, 63, 91, 93
Jakobsen 89
Jauvion 34
Jenkins 21
Jovanović 56

K

Kawai 32, 34
Kloess 66
Klompemaker 66, 89, 137
Krobicki 51

L

Landman 66
Laville 68, 70
Lazo 29
Lindgren 21
López-Horgue 137
Luci 29
Luque 21, 47

M

Makiguchi 27
Medina 82
Méndez 72
Mizuno 27
Moreno-Bedmar 79
Muñiz 36

N

Núñez-Lahuerta 86
Nyborg 66

O

O'Flynn 32
Oji 27
Ortega-Hernandez 21
Ossó 47, 72, 75, 79, 82, 91

P

Palmer 21
Pastó 75
Pérez-Pueyo 86
Porter 21
Puértolas-Pascual 86

R

Robins 89

S

Sellés 72
Sheldon 89
Simpson 91

T

Tessier 42, 90
Tshudy 63

V

Veselská 63
Vila 72
Vrabac 56

W

Wallaard 49, 51, 93
Wolfe 21

Y

Yamaoka 27

Z

Žalohar 70
Zamora 47, 53, 99, 113
Zorzin 90



**Universidad
Zaragoza**



**GOBIERNO
DE ARAGON**



Instituto Universitario de Investigación
en Ciencias Ambientales
de Aragón
Universidad Zaragoza



MUSEO DE
CIENCIAS
NATURALES
UNIVERSIDAD
ZARAGOZA



Ayto. de Olazti
Olaztiko Udala

