

9th Symposium on Fossil Decapod Crustaceans

9–13 June 2025
Faxe, Denmark

Abstract and program book

Edited by

Adiël A. Klompmaker & Jesper Milàn



GEOMUSEUM
FAXE
ØSTSJÆLLANDS MUSEUM



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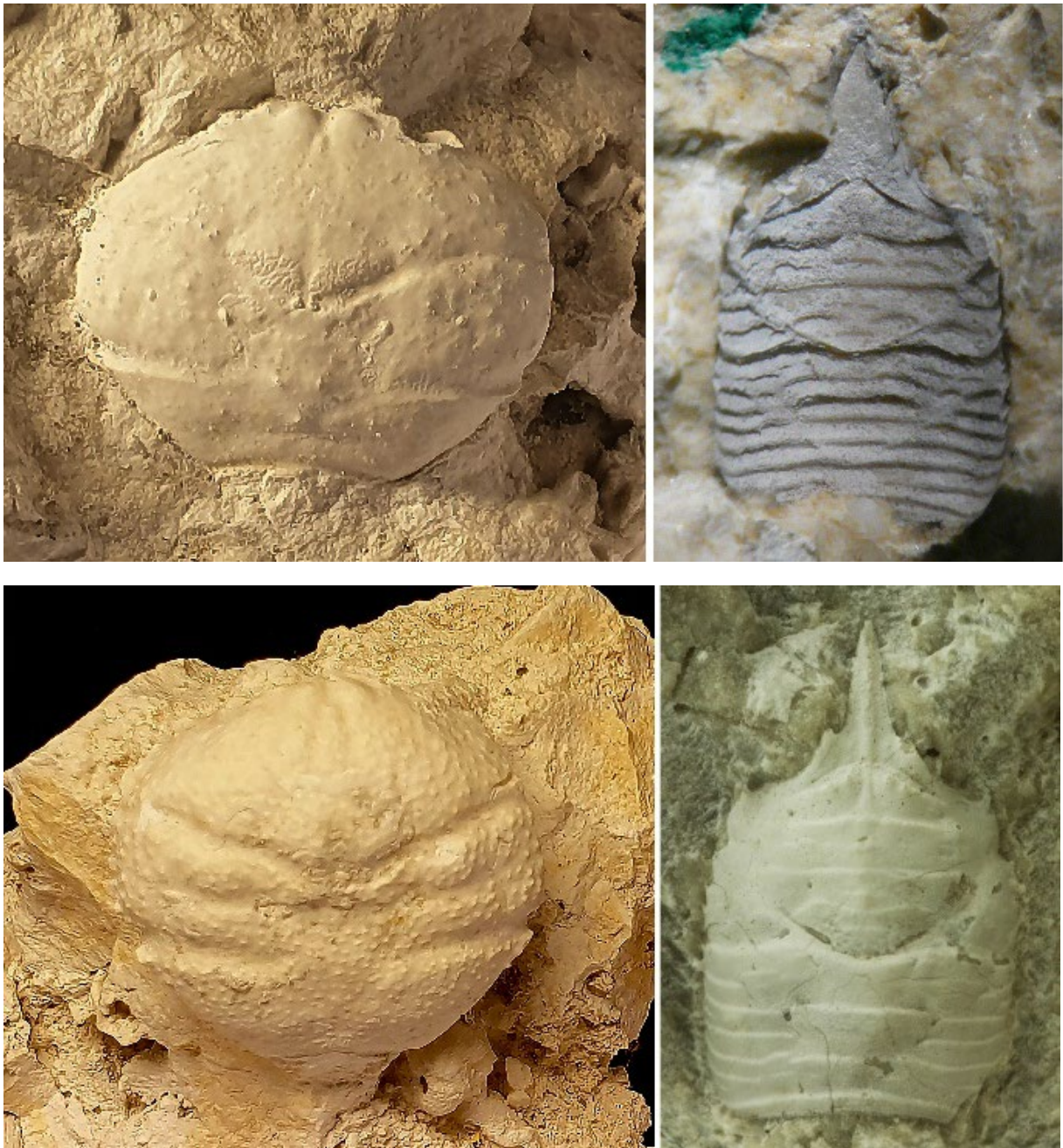
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Front cover: Photo of *Dromiopsis rugosa* (von Schlotheim, 1820) in frontal view embedded in coral limestone from the Faxe Quarry. Photo: Steen Knarberg



Examples of Danian decapods from Denmark: *Dromiopsis elegans* Reuss, 1858, *Galathea strigifera* von Fischer-Benzon, 1866, *Dromiopsis rugosa* (von Schlotheim, 1820), and *Protomunida bennickei* Klompmaker et al., 2022. Photos: Sten Jakobsen (brachyurans) and Adiël Klompmaker (galatheoids, from Klompmaker et al., 2016, 2022).

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Preface

We welcome all of you to the Geomuseum Faxe to participate in the 9th Symposium on Fossil Decapod Crustaceans. This conference is co-organized by the Geomuseum Faxe and the University of Alabama (Department of Museum Research and Collections & Alabama Museum of Natural History). Although the conference is focused on fossil decapod crustaceans, research on other crustaceans is also well-represented by various abstracts.

The conference venue is next to the Faxe Limestone quarry, which is the type locality for the Danian age, and has preserved the remains of a 63 million-year-old cold-water coral reef. The quarry is famous for its high number of well-preserved fossils, including very abundant decapod fossils that have been formally reported from Faxe since 1820 [*Dromiopsis rugosus* (von Schlotheim, 1820)] There is free public access to the quarry, so there are ample opportunities to collect in the quarry during the conference, and also as part of the 1st day of the conference field trips.

For the scientific program of the conference, we have 21 talks and 14 posters. During the field trip days, we will visit latest Cretaceous (Maastrichtian) and early Paleocene (Danian) outcrops, including two Cretaceous-Paleogene boundary sections. We wish you a wonderful conference with many exciting presentations, posters, field trips, and discussions, as well as reconnecting with friends and colleagues.

Organizing committee

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Impression of a part of the Faxe quarry. Photo: Jesper Milàn

Map with key locations for conference



Conference program

Icebreaker and registration, 9 June

19:00 Icebreaker and registration reception in Geomuseum Faxe, sponsored by Royal Unibrew

Scientific program day 1, 10 June

9:00 – 9:15 Registration

9:15 – 9:20 Opening remarks Geomuseum and conference committee

Oral session 1 (Mesozoic Decapoda), chair: Javier Luque

9:20 – 10:00 **Keynote.** Fernando A. Ferratges – An overview of the Mesozoic Decapod Revolution in Iberia

10:00 – 10:20 Barry W.M. van Bakel – Ecological guilds in Mesozoic Brachyura: a functional and macroevolutionary framework

10:20 – 10:40 A. Mariel Andrada & Beatriz Aguirre-Urreta – Preliminary notes on decapods preserved in ammonite shells from the Middle Jurassic of Argentina

10:40 – 11:00 Break

Oral session 2 (Jurassic Decapoda), chair: Cristina Robins

11:00 – 11:20 Michał Krobicki – Distribution of the Late Jurassic crabs (Brachyura) between Europe and Asia – palaeobiogeographical migration route riddle

11:20 – 11:40 Adam Heteš & Matúš Hyžný – Diversity and dominance of Late Jurassic decapod assemblages: a case study from southern Poland

10:40 – 12:00 Günter Schweigert, Matthias Wulf & Marina Wulf – Wattendorf, the stratigraphically oldest Solnhofen-type Plattenkalk site in Germany and its decapod fauna

12:00 – 13:20 Lunch

Oral session 3 (Cretaceous and other Decapoda), chair: Mariel Andrada

13:20 – 13:40 Javier Luque – The Cretaceous Crab Revolution: exceptional preservation, novel forms, and phylogenetic implications

13:40 – 14:00 Florian Braig, Carolin Haug, Ireen J. Schröder, Florian P. Ille & Joachim T. Haug – Plesiomorphic shapes in the megalopa phase and the evolution of crab morphologies

14:00 – 14:20 Adiël A. Klompmaker, Sten L. Jakobsen, Emma Sheldon, Jesper Milàn & Annette A. Jørgensen – Assessing the effect of the Cretaceous-Paleogene mass extinction on malacostracan crustaceans in Denmark and progress on some Danian decapod assemblages

14:20 – 14:40 Break

Oral session 4 (Late Cenozoic Decapoda), chair: Sten Jakobsen

- 14:40 – 15:00 Matúš Hyžný, Ján Schlögl & Adam Tomašových – Preservation of burrowing shrimps (Malacostraca: Decapoda: Axiidea) in hypoxic environments from the Miocene of the Central Paratethys
- 15:00 – 15:20 Àlex Ossó, Joaquín Sánchez, Miquel Fernández, Josep Florit & Francesc Xavier Roig-Munar – Preliminary report of Neogene decapod fauna from Menorca (Balearic Islands, Western Mediterranean)
- 15:20 – 15:40 Jonathan J.W. Wallaard, Barry W.M. van Bakel, René H.B. Fraaije, Crispin T.S. Little & John W.M. Jagt – A new decapod crustacean fauna from the Pliocene of Cyprus

Scientific program day 2, 11 June

9:15 – 9:20 Opening remarks conference committee

Oral session 5 (Crustaceans and Imaging Techniques), chair: Guenter Schweigert

- 9:20 – 10:00 **Keynote.** Sylvain Charbonnier – Fossil crustaceans in the UV and X-ray spotlight
- 10:00 – 10:20 Flavien Lagrange, Denis Audo, Giliane P. Odin & Sylvain Charbonnier – A new acanthephirid shrimp with 3D-preserved organs from the Middle Jurassic La Voulte-sur-Rhône Lagerstätte
- 10:20 – 10:40 Thomas Laville, Joachim T. Haug & Carolin Haug – A new look at *Pygocephalus cooperi* Huxley, 1857, from the Coseley Lagerstätte (Pennsylvanian, Carboniferous), UK, using X-ray micro-tomography: implications for the phylogenetic affinities of Pygocephalomorpha

10:40 – 11:00 Break

Oral session 6 (Peracarida and Stomatopoda), chair: Denis Audo

- 11:00 – 11:20 Javier Luque & Sarah Gerken – The fossil record of comma shrimp (Malacostraca: Peracarida: Cumacea): new findings and evolutionary perspectives
- 11:20 – 11:40 Rok Gašparič, Javier Luque, Tomaž Hitij, Primož Miklavc, Martina Kočová Veselská, Tomáš Kočí & Jure Žalohar – Exceptionally preserved peracarid crustaceans from the Middle Triassic of Kamnik – Savinja Alps (Slovenia)
- 10:40 – 12:00 Sarah Plischek, H. Alicia Byrom-Stengel, Florian Braig, Carolin Haug & Joachim T. Haug – Using quantitative morphology to compare adults and larvae of extant and fossil mantis shrimps

12:00 – 13:20 Lunch

Oral session 7 (Crustaceans from Europe), chair: Matúš Hyžný

- 13:20 – 13:40 Davide Di Franco – GeoSphere Austria's fossil crustacean collection: a key resource for palaeocarcinological research
- 13:40 – 14:00 René H.B. Fraaije, Barry W.M. Van Bakel, John W.M. Jagt, Eduard V. Mychko & Jonathan J.W. Wallaard – A new enigmatic alsasuacaridid (Pancrustacea, Cyclida) from the Maastrichtian type area in the Netherlands (Upper Cretaceous)
- 14:00 – 14:20 John W.M. Jagt – Late Cretaceous–early Paleogene cirripedes (Crustacea, Thoracica) from Liège-Limburg: an update

14:20 – 14:40 Break

Poster session, chair: Barry van Bakel

14:40 – 15:50 Presentation of posters (up to 5 minutes per poster)

15:50 – 16:20 Instructions conference dinner and field work
Discussion conference proceedings volume
Discussion next fossil decapod conference

16:20 – 18:30 Optional trip to fossil collections of Kulturmuseum Øst in collections building
(Rådhusvej 2, 4640 Faxe) ~900 m south of Geomuseum Faxe

19:00 Conference dinner in Danhostel Faxe

Field trip day 1, 12 June

9:00 Meet at Geomuseum Faxe (bring own lunch)

9:15 – 12:00 Guided tour by Jesper Milàn and Sten Lennart Jakobsen and fossil collecting in the
Faxe quarry

12:00 – 12.30 Lunch break

12:30 – 13:00 Bus to Rødvig at Stevn Klint (UNESCO site)

13:00 – 14:30 Walk to see the K/Pg boundary section near Rødvig (no *in situ* collecting allowed).
Note: stairs and walking a few hundred meters along the rocky coastline with flint.

14:30 – 15:00 Bus close to the Holtug limestone quarry at Stevns Klint. Walk ~500 m to quarry.

15:00 – 17:00 Limited fossil collecting in the Holtug limestone quarry with K-Pg boundary

17:00 – 17:30 Bus return to Geomuseum Faxe

Field trip day 2, 13 June

9:00 Meet at Geomuseum Faxe (bring own lunch)

9:15 – 10:15 Bus to Natural History Museum of Denmark (Priorparken, W Copenhagen)

10:15 – 12:00 Visit to the collections of Natural History Museum of Denmark

12:00 – 13:00 Bus to Limhamn quarry near Malmö (Sweden)

13:00 – 16:00 Guided tour by Anders Lindskog and fossil collecting in Limhamn quarry

16:00 – 17:30 Bus return to Faxe

Abstracts

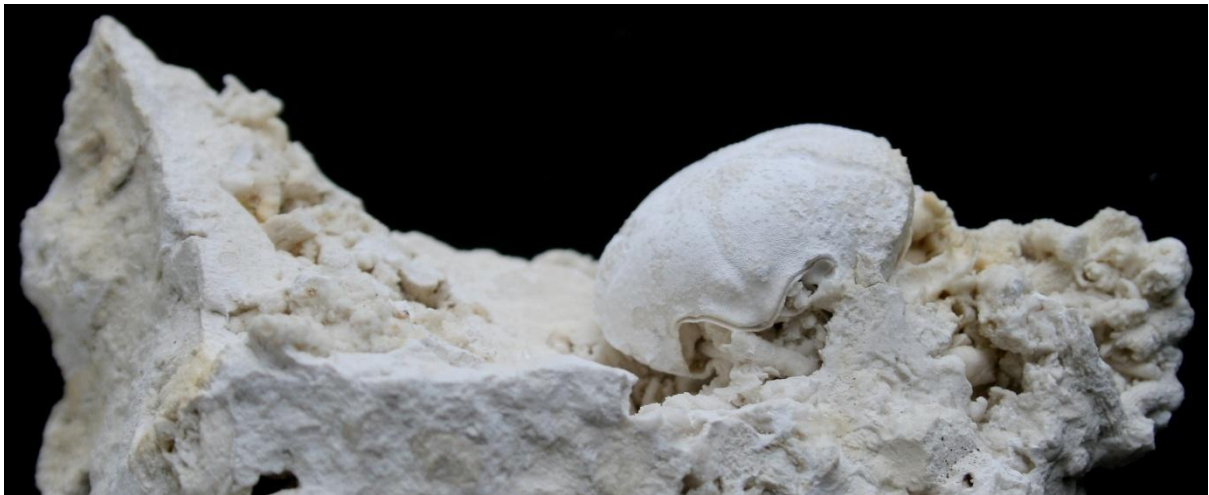


Photo of *Dromiopsis rugosa* in frontal view embedded in coral limestone from the Faxø Quarry. Photo: Jesper Milàn

Preliminary notes on decapods preserved in ammonite shells from the Middle Jurassic of Argentina

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Although rare, the association of fossil decapods with mollusks has been reported since the Triassic by several authors, including interpretations of inquilinism, sheltering and gregarious behaviour (e.g., Fraaye & Jäger, 1995; Klompmaker & Fraaije, 2012; Landman et al., 2014; Fraaije et al., 2020). The aim of this contribution is to document the presence of two erymoids in ammonite shells from the upper Bathonian of Los Patillos Formation, Paso del Espinacito locality, San Juan province, Argentina (Alvarez, 1997; Riccardi, 2008). This unit, dominated by calcareous sandstones and limestones, has been interpreted as an open shelf marine setting (Álvarez et al., 1994; Álvarez, 1997).

The first specimen consists of half a carapace of *Eryma* sp. (Figure 1A-B) preserved in the body chamber of *Bullatimorphites* (*K.*) cf. *bullatus* (d'Orbigny, 1846). The anterior part of the carapace is oriented towards the aperture. Ongoing research using CT scanning may provide further information about the possible presence of additional exoskeletal elements within the sediment infill, as the lobster is small relative to the ammonoid body chamber.

The second specimen consists of a pair of chelipeds of an erymoid, including dactylus, propodus, carpus and a mold of the merus, preserved in a fragment of a body chamber of an ammonoid (Figure 1C). The tip of the fingers are directed towards the phragmocone. The preservation of both chelipeds, along with the massive sediment infill of the body chamber devoid of other fossil remains, suggests that the lobster remains were not introduced into the ammonite shell by an external agent. Instead, the lobster may have entered the vacant shell on its own (either to molt, retreating backward and leaving the shelter, or dying inside it), leaving both chelae together as they were not subjected to transport.

As these are the only two records of decapods in Los Patillos Formation, a taphonomic factor is likely preventing their preservation. The use of ammonite shells as shelters may have played an important role in the fossilization of decapods in this unit.

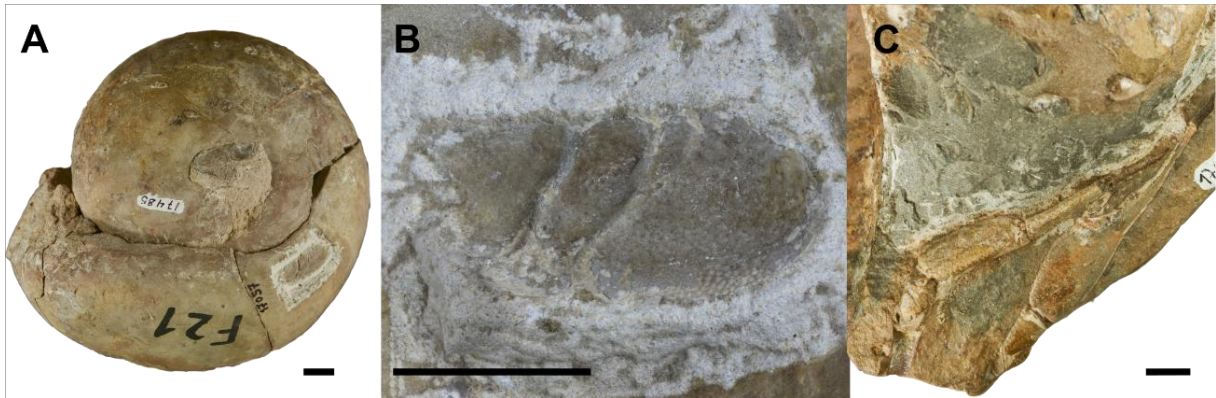


Figure 1. A, *Bullatimorphites* (K.) cf. *bullatus* containing a carapace of *Eryma* sp. B, Close up of the carapace of *Eryma* sp. C, Fragment of body chamber of an ammonoid with a pair of chelipeds of an erymoid. Scale bar: 10.0 mm.

Acknowledgements

We thank L. Marin for helping with information about the ammonites and P. Caccia for providing information of Los Patillos Formation. This is contribution C- of the Instituto de Estudios Andinos “Don Pablo Groeber” (UBA-CONICET).

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New specimens of *Cycleryon propinquus* (von Schlotheim, 1822) from the Upper Jurassic Canjuers Konservat-Lagerstätte

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Polychelidan lobsters are typically found in Konservat-Lagerstätten, where peculiar taphonomic conditions such as the absence of scavengers and bioturbators, and high sedimentation rates allow their preservation. Konservat-Lagerstätten are rather rare, so polychelidan lobster occurrences can be separated by long time spans and large geographical distances even though some polychelidans may have been cosmopolitan.

Polychelidans are relatively diverse in the Upper Jurassic (Kimmeridgian-Tithonian: Schweigert, 2007) lithographic limestones of Solnhofen-type Konservat-Lagerstätten (Garassino & Schweigert, 2006; Audo et al., 2021). These outcrops, mainly known from Germany but also occurring in France and Poland (Kin et al., 2013), correspond to micritic sediments deposited in lagoons and lagunas, in a reefal context (dead sponge-microbial bioherms with living corals – Schmid et al., 2005).

In Solnhofen-type outcrops, the specific diversity of polychelidans reaches its highest value in the fossil record (14 species). At this time, the diversity of polychelidans is dominated by the Eryonidae (11 species), and within the Eryonidae, by the genus *Cycleryon* Glaessner, 1965 (5 species) (Audo et al., 2021).

Here we describe two new subcomplete specimens of *Cycleryon* from the Canjuers Konservat-Lagerstätte in France. They were discovered during scientific excavations in the summer of 2024 in the military firing range of Canjuers. The specimens have been imaged under cropped light and UV-light and compared with other *Cycleryon* specimens, including another subcomplete specimen from Canjuers.

Both specimens have the typical rounded cephalothoracic shield of *Cycleryon*, with deep, U-shaped ocular incisions, deep cervical and hepatic incisions, and a short anterolateral cervical spine at the anterior angle of the cervical groove. The uropodal exopodite is not articulated (no visible diaeresis) and with a straight outer margin. Within *Cycleryon*, the anterolateral cervical spine only occurs in *Cycleryon propinquus* (von Schlotheim, 1822) and *C. bourseaui* Audo et al., 2014. *Cycleryon bourseaui* and *C. propinquus* differ little from each other: *Cycleryon bourseaui* has a slightly larger anterolateral cervical spine and a wider hepatic incision with a more curved anterior margin. Our new specimens resemble *C. propinquus* more because of their relatively shorter anterolateral cervical spine and straighter hepatic incision.

In Audo et al. (2014), another specimen of *Cycleryon* from Canjuers, more altered than our new specimens was described as a *C. bourseaui*. However, a careful re-examination of this material and the original illustrations suggests that it is also more similar to *C. propinquus*, for the same reasons: a comparatively smaller anterolateral cervical spine and a straighter hepatic incision.

Thus, the biogeographic distribution of *Cycleryon propinquus* appears wider than previously accepted, with species occurring in the Kimmeridgian and Tithonian of Germany and in the early Tithonian of Canjuers. Although the number of occurrences is too small for reliable comparisons, we note that *Cycleryon propinquus*, which is the most frequent *Cycleryon* species in Germany, also has a relatively wide biogeographic distribution. This is also the case for the older *Proeryon hartmanni* (von Meyer, 1836), the most frequent species of Toarcian polychelidans in Germany, and also known for its broad biogeographic range, from western France to Siberia (Audo et al., 2020).

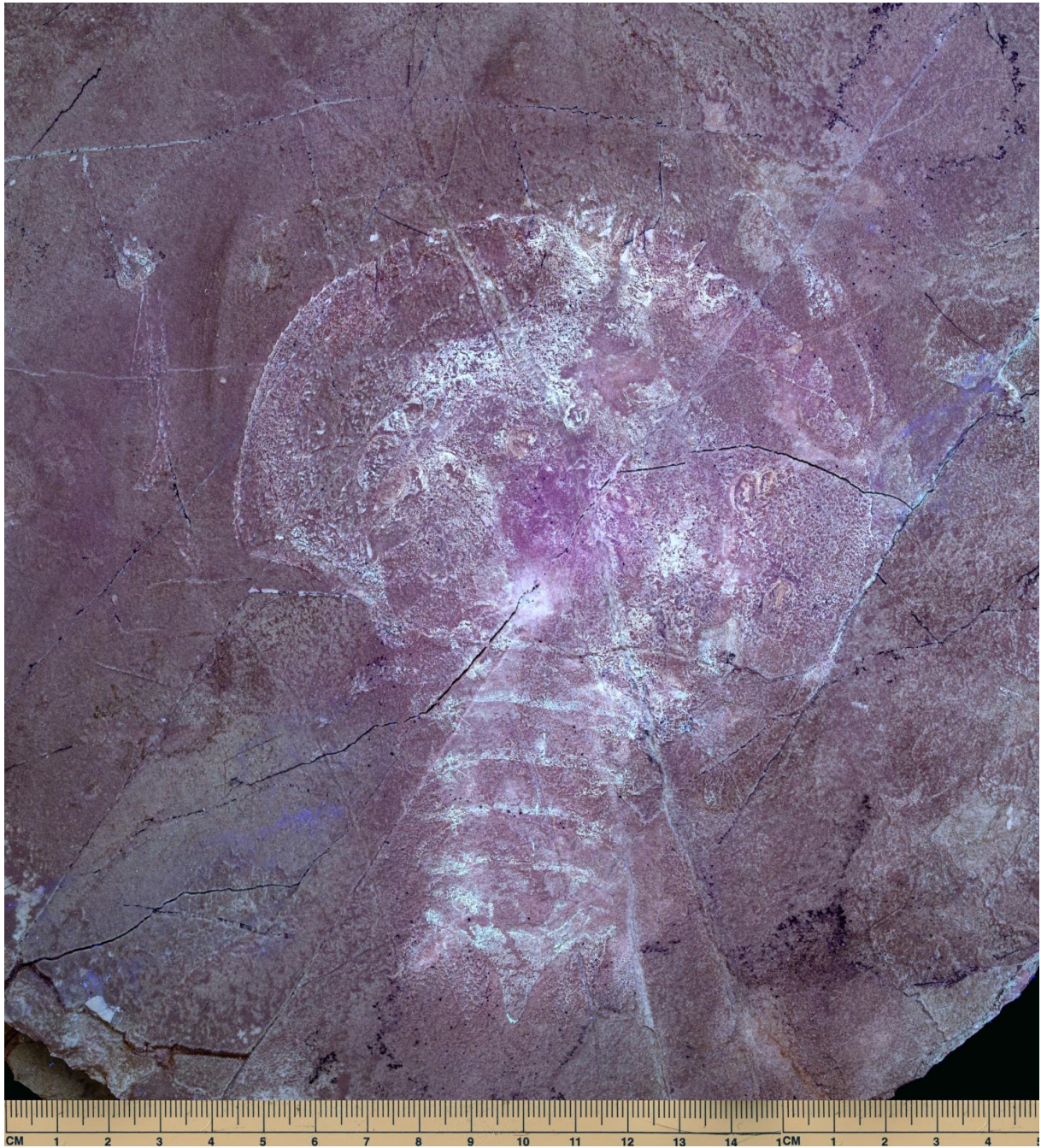


Figure 1. One of the two new specimens of *Cycleryon propinquus* from Canjuers under UV-light.

Acknowledgements

We thank Lilian Cazes and Christian Lemzaouda for the photographic work and the fossil preparator team for their careful work on the specimens.

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A decapod-serpulid association from middle Eocene volcanoclastics at Main quarry (Arzignano - Vicenza - NE Italy)

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The middle Eocene decapod fauna from Main quarry (Arzignano, Chiampo Valley - Vicenza - NE Italy) has been known since the 1980s (Busulini et al., 1982). The abundant crustacean remains there found are part of a fossil association including also molluscs (gastropods and bivalves), corals, larger foraminifera, echinoderms and coralline algae preserved in a thick volcano-arenitic level interlayered between two nummulitic calcarenite banks. The limestones belong to the informal Unit "Calcari Nummulitici" (Nummulitic Limestone) referred to the "San Giovanni Ilarione Horizon" (Middle Eocene) while the basaltic volcanoclastic deposits originate from reworking of Eocene submarine volcanic rocks of the so-called Venetian Tertiary Volcanism (Barbieri et al., 1991; Zampieri, 1995, 2022). The palaeoenvironment where these crustaceans lived would have been the bottom of a shallow-shelf exposed to ashes and toxic substances produced by volcanic eruptions.

The crustacean fauna from Main quarry is very rich. Up to now 68 species have been recognized and hundreds of specimens considered (Busulini et al., 1982; Beschin et al., 2002, 2004; De Angeli et al., 2019). Most of them consist only of carapaces which may be parts of exuviae, but individuals of some species show exceptional condition of fossilization preserving not only the whole carapace but also thoracic sternum, abdomen and pereopods. The most iconic species is probably the xanthid crab *Lathahyposia aculeata* (Busulini et al., 1984) very flashy for its large size and its showy ornamentation made of many large spines on anterior margins of carapace and on appendages. A recent analysis carried out on the specimens of *L. aculeata*, most males, housed in three Museums in Veneto (NE Italy) (namely Natural History Museum of Venice "Giancarlo Ligabue"; Museum of Nature and Humankind of the University of Padua [MGP-PD]; Museum of Archaeology and Natural Sciences "Giuseppe Zannato" at Montecchio Maggiore, Vicenza) has revealed the presence of encrusting serpulids on the pereopods and the ventral parts of many of these crabs (Beschin et al., in press) (Figure 1A-C).

Serpulids are marine, sessile, suspension-feeding polychaetes with a protective carbonate tube. They show symbiotic relationships with different groups of organisms such as corals, crustaceans and cephalopods (Andrew et al., 2011; Vinn et al., 2021).

The presence of skeletobionts (*sensu* Taylor & Wilson, 2002) on fossil crustaceans has been frequently reported, but while encrustations by molluscs, barnacles and bryozoans are relatively common, records of worms encrusting decapods are quite scarce. The new discovery is particularly noteworthy because, although the crustaceans collected in the Eocene rocks of western Veneto consist of hundreds of species and thousands of specimens (De Angeli & Garassino, 2006; De Angeli et al., 2019), it represents up to now the unique evidence of fossil serpulids encrusting crabs from this geographic area and it concerns only *L. aculeata*.

The exoskeletons of nine out of 15 specimens of *L. aculeata* are fouled by worms. Their tubes are entirely attached to the crab surface and reach a length up to 3 cm, only slightly increasing in diameter; they have a triangular cross section with a dorsal longitudinal smooth keel; these characters allow them to be attributed to the genus *Propomatoceros* Ware, 1975. Their shape is sinuous and they can form one or two U-shaped folds or be irregularly wrapped on themselves (figg. 1D-G). This is so far the first record of *Propomatoceros* from the Cenozoic; the genus was known until now for ranging from the Late Triassic to the Late Cretaceous (Ippolitov et al., 2014). Minute characters of the tube reveal that these specimens represent the types of a new species within *Propomatoceros* (Beschin et al., in press) representing the first fossil serpulid epibiont on a fossil crab determined at species level.

Lathahyposia aculeata was an epibenthic species inhabiting soft bottoms (Beschin et al., 2002; Zampieri, 2022) so its exoskeleton must have constituted small hard substrates on which larvae of serpulids could settle and grow, but these substrates had a relatively short life-span due to moulting. Anyway all the examined crab specimens show an adult size and therefore, if they were not even in their terminal moult stage, they should have had a relatively long inter-moult phase.

Taphonomic observations let one suppose that the analyzed specimens of *L. aculeata* were still alive at the time of their burial; in fact the ones with chelipeds and other pereopods raised upward, such as MGP-PD 437 (Figure 1A-B), show an escape position (*sensu* Bishop, 1986) while others found with chelipeds and legs arranged at the sides of the carapace might have died smothered and were rapidly buried by sediments. Also, the encrusting worms show an adult size and a discrete degree of preservation.

Records of serpulids encrusting fossil crabs from literature show epibionts on the dorsal carapaces, most frequently as *post-mortem* colonizations: among them we can report the example of *Dromiopsis rugosa* (von Schlotheim, 1820) from the lower Paleocene of Faxø Quarry (DK) (Jakobsen & Feldmann, 2004). In *L. aculeata* instead encrustations occur only on the ventral sides of the crabs and on appendages. Tens of serpulid specimens were counted, most of them localised on chelipeds and on thoracic sternites. Others colonized 3rd maxillipeds, pleon and other pereopods. According to McGaw (2006), this particular pattern could depend on ecological needs of serpulid species whose photo-negative larvae prefer sciaphilic microhabitats like the bottom-facing ventral parts of crabs. The abundance of serpulids also on the claws, and particularly on the internal side of the propodus, could be explained with the advantage derived from eating residual food particles present in the area near the mouth. The association between this serpulid and its host can be interpreted as commensalism and appears to be species-specific since the occurrence of this serpulid has not been detected on any other crab or type of substratum in the considered area.

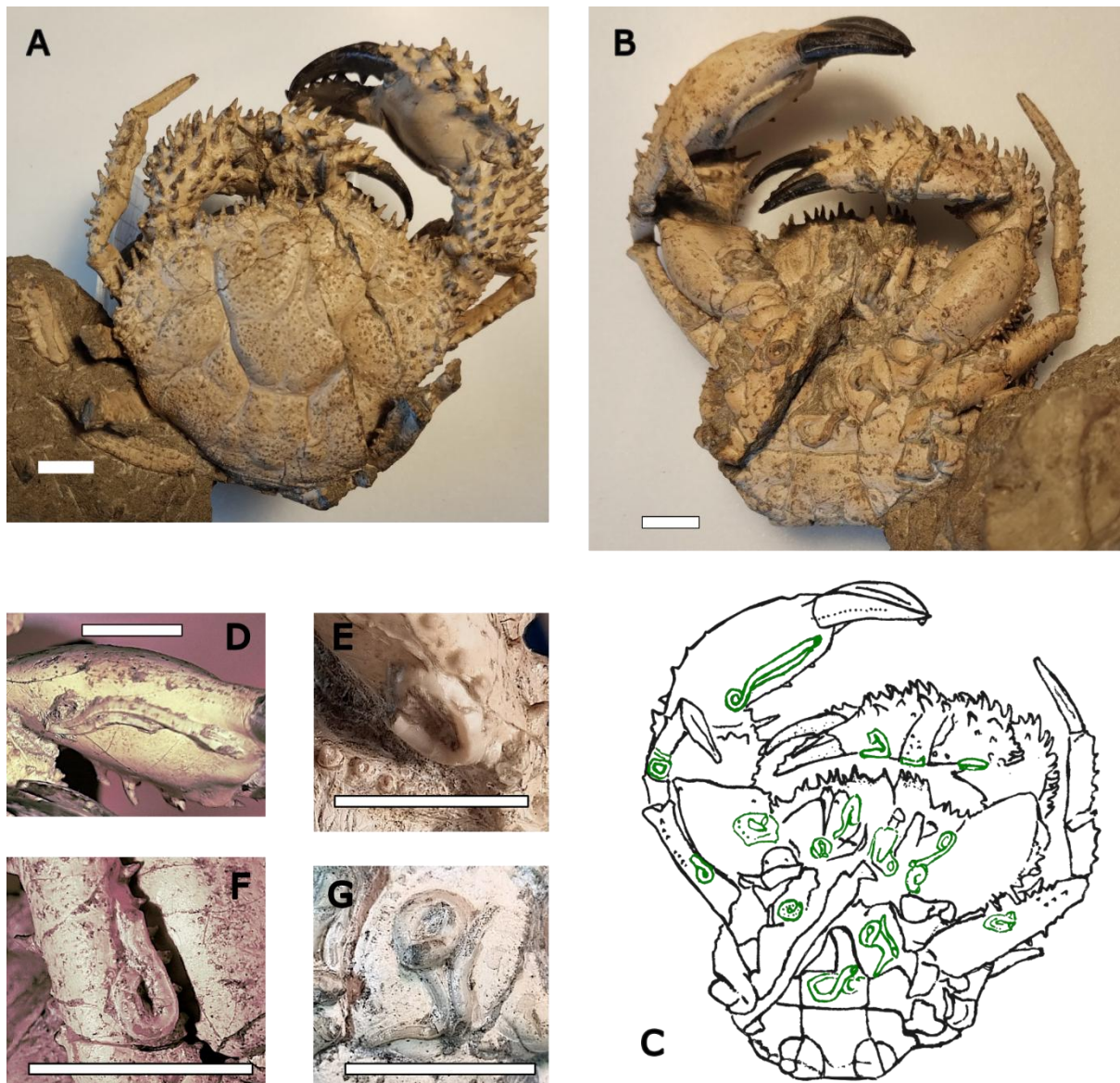


Figure 1. *Lathahyposia aculeata* (Busulini et al., 1984) specimen MGP-PD 437. A, dorsal view. B, ventral view. C, line drawing of the ventral view displaying encrusting *Propomatoceros* sp. highlighted in green. D, serpulids on the right-cheliped propodus. E, serpulid on the left-cheliped propodus. F, serpulid on the right merus of the second pereiopod. G, serpulid on the thoracic sternum. Scale bars = 1.0 cm.

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Plesiomorphic shapes in the megalopa phase and the evolution of crab morphologies

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Brachyura and Anomala (or Anomura) form Meiura, a group commonly referred to as crabs. They are prominent crustaceans with a global distribution. They show a large biological and morphological diversity, counting almost 10,000 species, and they have conquered marine, limnic, and terrestrial habitats around the world (Taylor & Schram, 1999). The earliest representatives of the group are known from the Triassic (Chablais et al., 2011). From this point on, by a process called carcinization, different lineages of Meiura have seemingly convergently evolved the same body shape with a broad shield and the tail flipped under the body ventrally. Especially in Brachyura, the group of true crabs, this process is abundant. The evolutionary success of both groups is sometimes attributed to this process (Scholtz, 2014; Keiler et al., 2017), but might also be connected to the megalopa phase, a specific transitional larval phase. We investigated the evolution of morphological diversity within the group, using elliptic Fourier outline analysis of the shield shapes (carapaces) of more than 1500 meiuran crabs (Braig et al., 2024). We compared the morphological diversity of representatives of the zoea, megalopa, juvenile and adult phase of major ingroups of true and false crabs. We found that the megalopa phase of meiuran crabs appears to show plesiomorphic morphology in its shield form, as it overlaps between true and false crabs and shows little diversity. Causes may be common evolutionary constraints on a developmental phase specialized for transitioning. This implies, that the adult morphology of crabs is an evolutionary new addition to the developmental pathway. We furthermore find increasing morphological disparity of adults of true and false crabs with increasing phylogenetic distance, indicating diverging evolution of the shield morphology of adult representatives of Meiura.

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Anomalous features in crabs from the Eocene of western Veneto (NE Italy)

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Analyses of the great number of the Brachyura and the Anomura constituting the fossil crustacean faunas from the Eocene of the Lessini Mountains (NE Italy) have revealed over the years the presence of specimens with different kinds of peculiarities. Even if their percentage is low, swellings on carapaces (the ichnotaxon *Kanthyloma crusta* Klompmaker et al., 2014) caused by epicaridean isopods hosted in branchial chambers have been often reported above all in the Galatheoidea (Anomura), the Dromioidea, the Raninoidea and the Trapezioidea (Brachyura) from Italy (Cecccon & De Angeli, 2013; Beschin et al., 2022).

More recently, the presence of epibionts encrusting the exoskeleton of some fossil crabs has been recognised, too. It may seem strange, but this concerns specimens studied many years ago, such as a few types of *Lathahyposia aculeata* (Busulini et al., 1984) fouled by serpulids on their ventral parts (Beschín et al., in press) and a paratype of *Daira salebrosa* Beschín et al., 2002, showing an oyster on its dorsal carapace (Figure 1A) (both species were found in middle Eocene volcanoclastics in Main quarry (Arzignano - Vicenza) (Beschín et al., 2002)).

Anomalies in the structure of the carapace are extremely uncommon in fossil crabs but some of them have been observed in few specimens from western Veneto of *Harpactoxanthopsis quadrilobata* (Desmarest, 1822), an Eocene Zanthopsidae widespread in Eocene levels above all in France, Spain, Italy and Hungary. On its anterolateral margins, *H. quadrilobata* shows three teeth (four in young specimens after Vía, 1969), the outer two larger and spiny. The exceptionally preserved specimen 23.582 housed in the Palaeontological Museum of Roncà (Verona) has three well developed triangular and pointed teeth that are asymmetrically distributed on the two sides (Figure 1B) (Beschín et al., 2025). Anomalous distribution of marginal teeth on *H. quadrilobata* had been already reported by De Angeli & Bellin (2015), who described a specimen with three frontal teeth instead of the usual four. This species therefore had a variability in number, characteristics and distribution of marginal teeth that has been never observed in other fossil brachyurans before.

Lophoranina marestiana (König, 1825) is another fossil species from western Veneto sometimes found in an exceptional condition of preservation showing complete carapace, ventral parts, chelipeds and other pereopods. Among the specimens from "Lophoranina Tuff" (Lower Lutetian) cropping out in Zanconato quarry (Chiampo Valley - NE Italy) MCZ 8210, housed in the Museum of Archeology and Natural Sciences "G. Zannato" of Montecchio Maggiore (Vicenza), presents an asymmetrical growth of chelipeds while in the Raninidae the two chelipeds have the same size and structure. A similar situation is well known in *Ranina*

ranina (Linnaeus, 1758) living in warm Indo-Pacific seas (Matondo & Demayo, 2015) in crabs that are regenerating a chela lost may be for autotomy or for a damage due to a predator. The process can be completed during a few successive moults and the original functionality of the appendage can be restored. The specimen found in the Chiampo Valley has a small size and preserves only its ventral parts (thoracic sternum, pleon, chelipeds): its right chela is much smaller than the left one (Figure 1C). This is so far the first report of claw regeneration in fossil crabs.

Another peculiarity in *L. marestiana* from Vicenza territory has been recently observed (Beschlin et al., 2025): the exoskeleton of some specimens found in Lovara quarry and housed in the Palaeontological Museum of Roncà shows an unusual red colour (Figure 1D): at the moment it has not been determined yet if this character is a trace of the original pigmentation of the carapace or if it has a secondary origin. The result of our analysis will be the object of a future study.

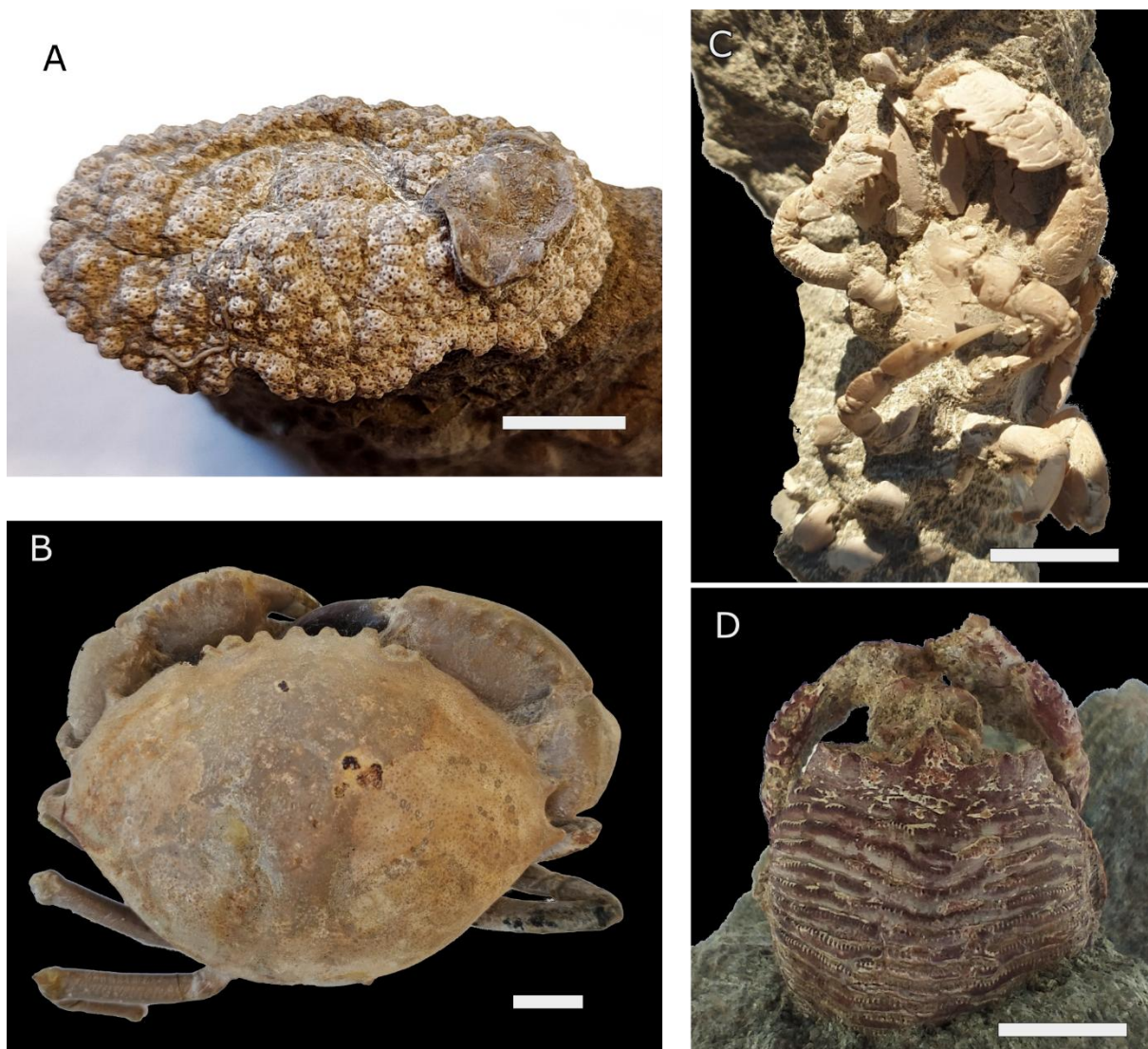


Figure 1. A, *Daira salebrosa* (Beschlin et al., 2002) specimen MCZ 2272, frontal view. B, *Harpactoxanthopsis quadrilobata* (Desmarest, 1822) specimen 23.582, dorsal view. C, *Lophoranina marestiana* (König, 1825) specimen MCZ 8210, ventral view. D, *Lophoranina marestiana* (König, 1825) specimen 23.587, dorsal view. Scale bars = 1.0 cm.

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The genus *Dromiopsis* from Eocene patch reefs in NE Italy

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When it was erected, the genus *Dromiopsis* Reuss, 1859, included only few species found in the Danian cold-water coral reef of Faxe (DK) [species reported in Schweitzer et al. (2010) are *D. rugosa* (von Schlotheim, 1820), the type species, *D. elegans* Reuss, 1859 and *D. laevior* Reuss, 1859]. Afterwards the genus was reported not only from Northern Europe but also from the United States and Madagascar with a range from Lower Cretaceous to Paleocene (Schweitzer et al., 2012).

In recent years, more species referred to *Dromiopsis* were found in lower Eocene coral-algal buildups widespread in western Veneto (NE Italy) and namely *D. ceratoi* Beschin et al., 2016a (Figure 1C), *D. longitudovata* Beschin et al., 2016a (Figure 1D), *D. parvula* Beschin et al., 2016a (Figure 1B), *D. paucigranosa* Beschin et al., 2007 (Figure 1A). Their tiny carapaces (average width about 5 mm) share an almost circular shape, a triangular rimmed front, large ovate orbits, cervical, branchial and branchiocardiac grooves, but they differ from each other in their width/length ratio, number and feature of small spines arming lateral margins, depth of grooves, abundance of granulation on their surface.

During the Middle Eocene, the shallow lagoon with patch reefs in which these small crabs dwelt, was replaced by a shallow shelf where the carbonate deposition, that originated banks of calcarenites (Nummulitic Limestones), was interrupted by volcanic eruptions. Within the volcanoclastics produced from reworking of submarine basaltic rocks, rich fossil associations were yielded. Among the crustaceans from the lower Lutetian "Lophoranina tuff" (Beschin et al., 2016b) only one carapace of *Dromiopsis* was found. It is the holotype of *D. vicetinus* Beschin et al., 2016b (Figure 1F). This carapace is larger than the Ypresian ones: it is about 15 mm wide.

Another lagoon with widespread patch reefs settled in western Veneto for part of the Late Eocene (Beschin et al., 2018, 2019). In this new environment the taxa of the Dromioidea were much rarer than during the Ypresian. Up to now, only one tiny species of *Dromiopsis* was found, namely *D. marginospinosa* Beschin et al., 2019 (Figure 1E): on its smooth enlarged carapace grooves are only slightly sunk and there are small tubercles on the lateral margins. Another species was doubtfully referred to the genus, i.e., ?*D. rocchetti* Beschin et al., 2019.

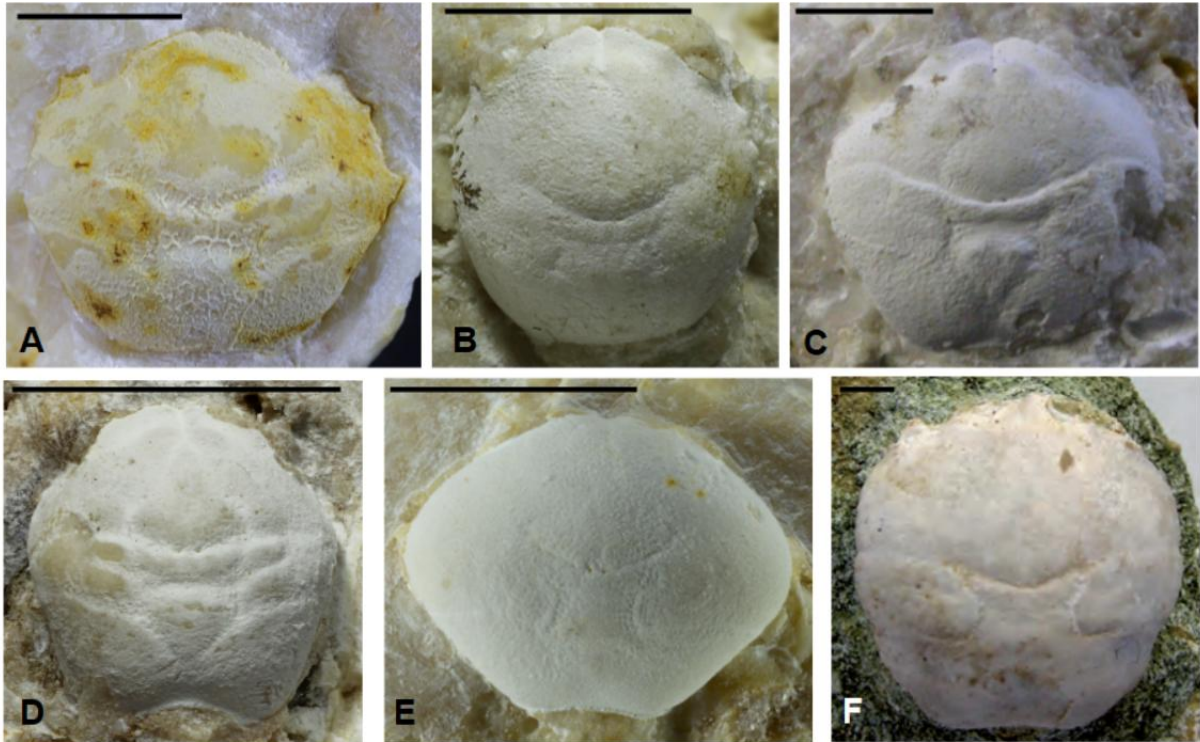


Figure 1. Species referred to the genus *Dromiopsis* found in western Veneto (NE Italy); the specimens are housed in the Civic Museum of Natural History in Verona (VR) and in the Museum of Archaeology and Natural Sciences "Giuseppe Zannato" at Montecchio Maggiore, Vicenza (MCZ). A, *Dromiopsis paucigranosa*, carapace MCZ 5961, dorsal view. B, *Dromiopsis parvula*, carapace VR 93966, dorsal view. C, *Dromiopsis ceratoi*, carapace VR 93954, dorsal view. D, *Dromiopsis longitudovata*, carapace VR 93962, dorsal view. E, *Dromiopsis marginospinosa*, carapace VR 19.1742, dorsal view. F, *Dromiopsis vicetinus*, carapace MCZ 3905, dorsal view. Scale bars = 3.0 mm.

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Fossil crustaceans in the UV and X-ray spotlight

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Over the last 10 years, the study of exceptionally well-preserved crustaceans from Jurassic and Cretaceous Konservat-Lagerstätten has provided many discoveries in terms of systematics (increase of paleobiodiversity), palaeobiology (reproduction, sexual dimorphism), palaeoecology (morphological adaptations, modes of life), palaeoenvironment (bathymetry, pathway of colonization) and evolutionary history (phylogeny). Progress has been made in particular through the use of X-ray microtomography as a non-invasive tool for studying the internal and external anatomy of specimens preserved in concretions or nodules in three dimensions, but also through the systematisation of observations under UV light on specimens preserved more or less flattened on the surface of lithographic limestones.

Presented here are results on crustaceans from the Middle Jurassic (Callovia) La Voulte-sur-Rhône Lagerstätte, France [general anatomy, reproductive, digestive, respiratory and cardiovascular systems (Vannier et al., 2016; Audo et al., 2019; Jauvion et al., 2020a; Charbonnier et al., 2024)], from the Late Jurassic lithographic limestones of Europe [e.g., Solnhofen and neighbouring outcrops, Canjuers, Cerin (Laville et al., 2021)], and from the Late Cretaceous of Lebanon [Cenomanian of Hakel, Hadjoula & Santonian of Sahel Alma (Charbonnier et al., 2017; Audo et al., 2021)] with new taxa and focus on fossil eyes and adaptation of vision to depth.

At the same time, studies to understand the fossilisation of crustaceans have also made considerable progress (e.g., Gueriau et al., 2020; Jauvion et al., 2020b). Even if the processes leading to the exceptional morphological preservation of fossils in these deposits remain incompletely understood, the mineralogical characterization of crustacean fossils is a prerequisite for improving the robustness of palaeontological reconstructions.

Finally, deposits of an “intermediate” nature also exist and provide fossil crustaceans relatively well preserved in volume within siliceous or carbonate concretions of flattened on shales, without reaching a Lagerstätten-type preservation. These intermediate deposits still provide high quality anatomical details as well as new palaeobiological information on sexual dimorphism, paleosymbiosis and phenomena of moulting and autotomy. This is the case for the crustaceans found in some assemblages in the Jurassic of France [Callovia of Normandy (Chény et al., 2023a)] and in the Cretaceous of France [Cenomanian of Pays de La Loire (Charbonnier et al., 2023b)].

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New ghost shrimps (*Axiidea*, *Callianassidae*) from the Paleogene of north-eastern Italy

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Recent findings of axiideans claws have contributed to the study of new callianassids for the Paleogene of north-eastern Italy. *Callianassa ferox* Bittner, 1893, was described based on some claws from the Rupelian of Törökvágás (Klausenburg, Romania) and subsequently illustrated in Lőrenthey & Beurlen (1929) and reported by Hyžný (2016a) and Hyžný et al. (2022). The Italian specimens come from the Bartonian volcanicdetritic marls of Roncà (Verona) and correspond to the characteristics of the types illustrated by Bittner (1893, figs. 6-12). In particular because of the long and little developed in height fixed finger and the deep notches on the internal surface of the propodus (Plate 1, figs. 6-8). *Callianassa ferox* probably developed in the shallow marine environments of north-eastern Italy during the Lutetian-Bartonian and subsequently spread into the lower Oligocene of Romania (De Angeli, 2024).

Other specimens of propodi of chelipeds were found in the lower Oligocene (Rupelian) of the Berici Mountains (Vicenza). *Callianassa canavarii* described by Ristori (1889) from the Rupelian of the Ligure-Piemontese Basin, was found in the volcanic-detrital levels of Soghe (Plate 1, fig. 1a, b). Other specimens of this species come from the Rupelian of Sant’Urbano (Vicenza) (Ceccon & De Angeli, 2019).

Three other propodus from the Soghe deposit have been attributed to *Balsscallichirus* Sakai, 2011, a genus that includes five living species (Sakai, 2011). *Balsscallichirus soghensis* Coole & De Angeli, 2023, has a long and smooth left propodus, a manus slightly longer than it is tall and with parallel margins; a serrated lower margin; a long fixed finger, with a smooth occlusal margin, external and internal surfaces of the manus and the fixed finger with a tuberculate crest (Plate 1, figs. 2a, b, 3a, b, 4a, b).

Balsscallichirus bericensis Coole & De Angeli, 2023, instead comes from the Rupelian of Monte Berico and has a propodus of the cheliped with a manus that is higher than it is long, with parallel margins; a serrated lower margin, with some orifices; a manus with an internal surface with three orifices on the upper part and a granulated crest that continues onto the fixed finger. Long, curved fixed finger, with three teeth in the occlusal margin (Plate 1, fig. 5a-c).

Hyžný (2016b), based on known fossil axiideans, provides a possible stratigraphic distribution of the genus *Balsscallichirus*, probably starting with ?*B. wellsii* (Schweitzer et al., 2004) from the Bartonian-Priabonian of Pakistan and then spreading to the European Tethys and Paratethys with the three Miocene-Pliocene species *B. florianus* (Glaessner, 1928), *B. laepaensis* (Hyžný & Muñiz, 2012) and *B. sismondai* (A. Milne Edwards, 1860). The discovery of *Balsscallichirus soghensis* and *B. bericensis* extends the stratigraphic distribution of this genus in the fossil record to the lower Oligocene (Coole & De Angeli, 2023).

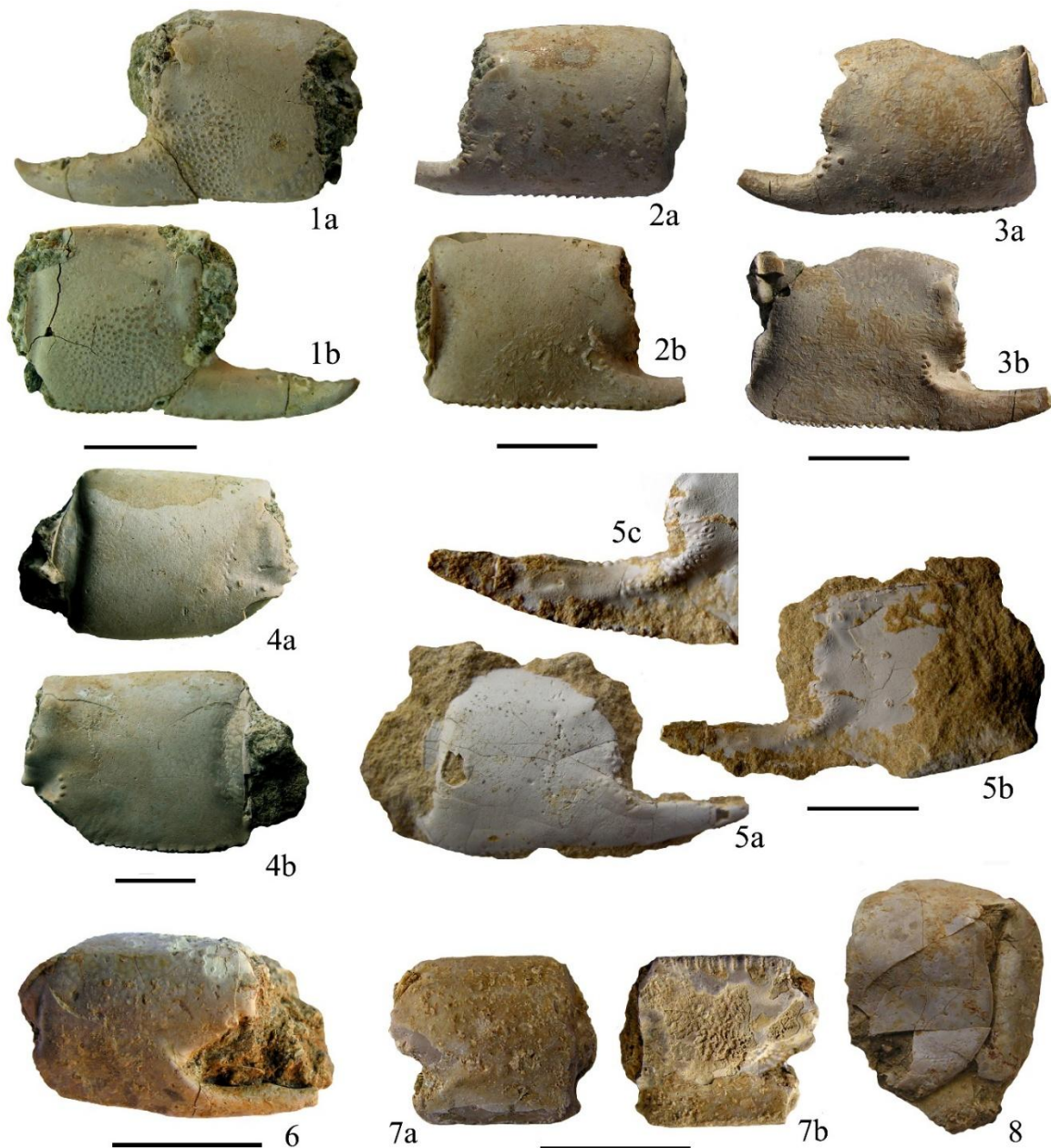


Plate 1. Fig. 1, *Callianassa canavarii* Ristori, 1889 (MCZ.7953), left chela in outer (a) and in inner (b) views. Fig. 2, *Balsscallichirus soghensis* Coole & De Angeli, 2023 (MCZ.7954), left chela in outer (a) and in inner (b) views. Fig. 3, *Balsscallichirus soghensis* Coole & De Angeli, 2023 (MCZ.7955), left chela in outer (a) and in inner (b) views. Fig. 4, *Balsscallichirus soghensis* Coole & De Angeli, 2023 (MCZ.7957), right chela in outer (a) and in inner (b) views. Fig. 5, *Balsscallichirus bericensis* Coole & De Angeli, 2023 (MCZ.7956), right chela in outer (a) and in inner (b) views, and detail of the tubercles on the fixed finger (c). Fig. 6, *Callianassa ferox* Bittner, 1893 (MCZ.7958), right chela in outer view. Fig. 7, *Callianassa ferox* Bittner, 1893 (MCZ.7959), left chela in outer (a) and in inner (b) views. Fig. 8, *Callianassa ferox* Bittner, 1893 (MCZ.7961), carpus of the left cheliped. Scale bars = 10.0 mm (adapted from Coole & De Angeli, 2023, and De Angeli, 2024).

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Oligocene and Miocene crustaceans of the Vicenza territory (NE Italy)

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A recent study on the crustaceans of the Oligocene of Vicenza examined 662 specimens in the paleontological collection of the Civic Museum "D. Dal Lago" at Valdagno (Vicenza) from various locations in the province of Vicenza (NE Italy). Two new species were identified among the examined material (Figure 1): *Noetlingocarcinus minutus* De Angeli et al., 2024 (Basinotopidae) and *Pilumnus pianetatensis* De Angeli et al., 2024 (Pilumnidae) both found associated with corals.

A list of the isopod, stomatopod and decapod crustaceans known for the Oligocene and Miocene of the Vicenza territory is also provided. The carcino-fauna includes 85 species of which 13 of uncertain attribution. The species are attributed to the isopods, stomatopods and decapods (79 from the Oligocene and 2 from the Miocene) that lived in lagoonal or coralline environments in clear, warm and relatively deep marine waters.

The carcino-fauna list includes (full references in De Angeli et al., 2024):

ISOPODA

Cirolana fabianii De Angeli & Rossi, 2006; *Eosphaeroma obtusum* (von Meyer, 1858).

STOMATOPODA

Pseudosquilla berica De Angeli & Messina, 1996; *Lysiosquilla messinai* De Angeli, 1997.

DECAPODA

Penaeus sorbinii Beschin & Garassino, 1999; *Penaeus vanzoi* Beschin & Garassino, 1999; *Palaemon fabricii* Michelotti, 1861; Palinuridae gen. et sp. Indet.; *Callianassa canavarii* Ristori, 1889; "Callianassa" sp. 1; "Callianassa" sp. 2; "Callianassa" sp. 3; *Balsscallichirus soghensis* Coole & De Angeli, 2023; *Balsscallichirus bericensis* Coole & De Angeli, 2023; *Thalassina* sp.; *Upogebia perarolensis* De Angeli & Messina, 1992; *Galathea valmaranensis* De Angeli & Garassino, 2002; *Galathea* cf. *G. weinfurteri* Bachmayer, 1950; *Palaeomunida defecta* Lőrenthey, 1901; *Petrolisthes vicetinus* Beschin et al., 2001; *Dardanus caporiondoi* Ceccon & De Angeli, 2019; *Paronapaguropsis* cf. *P. latidactylus* (Müller & Collins, 1991); Paguridae gen. et sp. indet.; *Dromia corvini* Bittner, 1893; *Noetlingocarcinus minutus* De Angeli et al., 2024; *Dynomene lessinea* Beschin et al., 2001; *Kromtitis* sp.; *Ranina bouilleana* A. Milne Edwards, 1872; *Ranina pellatieroi* De Angeli & Beschin, 2011; *Ranina speciosa* (von Münster, 1840); *Antonioranina* cf. *A. globosa* (Beschin et al., 1988); *Caporiondulus bericus* De Angeli, 2016; *Ethusa berica* De Angeli & Beschin, 2008; *Calappilia vicetina* Fabiani, 1910; *Stenodromia mainii* (Allasinaz, 1987); *Mursia lienharti* (Bachmayer, 1961); *Osachila berica* De Angeli & Beschin,

1999; *Ebalia pumicosa* Ceccon & De Angeli, 2019; *Merocryptus altavillensis* De Angeli et al., 2010; *Achaeus parvulus* De Angeli & Caporiondo, 2010; *Hyastenus corallinus* De Angeli & Beschin, 2008; *Maja prealpina* Ceccon & De Angeli, 2019; *Micippa antiqua* Beschin et al., 2001; *Phrynoslambrus italicus* De Angeli & Beschin, 2008; *Daldorfia fabianii* Beschin et al., 2001; *Corystites vicetinus* De Angeli et al., 2010; *Daira depressa* (A. Milne Edwards, 1865); *Coeloma vigil* A. Milne Edwards, 1865; *Euronectes grumiensis* (Beschin et al., 2001); *Portunus arcuatus* (A. Milne Edwards, 1860); *Portunus incertus* (A. Milne Edwards, 1860); *Portunus obtusus* (A. Milne Edwards, 1860); *Portunus kochi* (Bittner, 1893); *Portunus suessi* (Bittner, 1875); *Portunus* cf. *P. ristorii* Karasawa et al., 2008; *Portunus* cf. *P. radobojanus* (Bittner, 1884); *Portunus* cf. *P. stenaspis* (Bittner, 1884); *Eocarpilius vicetinus* Ceccon & De Angeli, 2019; *Palaeocarpilius aquitanicus* A. Milne Edwards, 1862; *Tethyscarpilius bericus* De Angeli & Alberti, 2016; *Galenopsis similis* Bittner, 1875; *Pilumnus pedemontanus* Ceccon & De Angeli, 2019; *Pilumnus pianetensis* De Angeli et al., 2024; *Pilumnopeus priscus* Ceccon & De Angeli, 2019; *Glabropilumnus soghensis* De Angeli & Beschin, 2008; *Glabropilumnus tuberculatus* Ceccon & De Angeli, 2019; *Glabropilumnus granulatus* De Angeli et al., 2010; *Panopeus santurbanensis* Ceccon & De Angeli, 2019; *Haydnella oligocenica* De Angeli & Beschin, 2008; *Actaeites lobatus* Müller & Collins, 1991; *Bernuffius ornatus* De Angeli et al., 2010; *Cherisius oligocenicus* (Beschin et al., 2001); *Eurotetralia loerentheyi* (Müller, 1975); *Tetralia vicetina* De Angeli & Ceccon, 2013; *Eomaldivia trispinosa* Müller & Collins, 1991; *Priabonocarcinus gallicus* Müller & Collins, 1991; *Prochlorodius ellipticus* Müller & Collins, 1991; *Branchioplax rossii* De Angeli & Beschin, 2008; *Branchioplax albertii* De Angeli & Beschin, 2002; *Eopalicus semicarinatus* De Angeli & Beschin, 2000; *Daragrapsus trispinosus* Müller & Collins, 1991; *Percnon santurbanensis* Ceccon & De Angeli, 2019; *Asthenognathus laverdensis* De Angeli & Garassino, 2006; *Brachynotus oligocenicus* De Angeli, 2010.

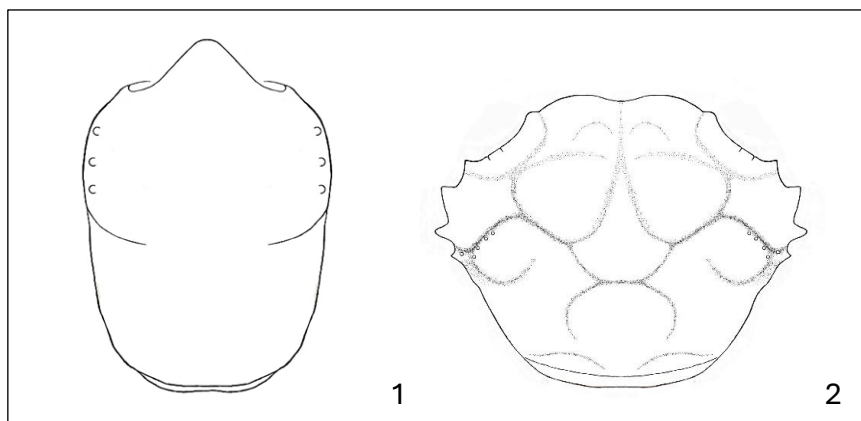


Figure 1. 1, *Noetlingocarcinus minutus*, carapace width: 2.2 mm (carapace reconstruction). 2, *Pilumnus pianetensis*, carapace width: 3.0 mm (carapace reconstruction).

Reference

De Angeli, A., Ceccon, L. & Caporiondo, F. 2024. Crostacei oligocenici del territorio vicentino (Italia nordorientale). *Bollettino del Museo Civico di Storia Naturale di Verona, Geologia Paleontologia Preistoria* 48, 43-65. <https://doi.org/10.61006/bgpp202405>

A new assemblage of the decapod crustaceans from the Eocene of Alonte (Vicenza, NE Italy)

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The study reports a rich crustacean fauna from the middle-upper Eocene (Bartonian-Priabonian) of the Manfrinato quarry at Alonte (Berici Mountains, Vicenza, NE Italy), preserved in the Civic Museum “D. Dal Lago” of Valdagno (NE Italy). The stratigraphic section of the Manfrinato quarry is reported by Beccaro (2003). Above the Bartonian volcanoclastic sandstones, which can be observed along the road leading up to the quarry, there are calcarenites with loose bioclasts and limestone contaminated by material of volcanic origin, with bioclasts of characteristic facies in which *Microcodium* sedimentary structures have been identified, indicating an emersion condition, which has led to the lower part of the section being attributed to the Bartonian. This is followed by a series of yellowish, slightly earthy, limonitic calcarenites, with numerous internal models of molluscs, coral remains, plant traces, rare echinoids, sirenian bone remains (*Prothotherium veronense* De Zigno, 1875), axiidean claws and decapod carapaces (Bartonian).

The middle and upper part of the stratigraphic section of the quarry is represented by marly limestones and nummulite calcarenites, orthofragmines, rhodolites and echinoid remains. Limestones contain oysters and other bivalves, numerous whole echinoids, *Tubulostium spirulaeum* and crustacean remains. Calcarenites come with algal remains, rare internal models of molluscs, some corals and crustaceans. Marly limestones contain scattered single corals. Micritic limestones bear corals and crustaceans while limestones yield nummulites and algal remains (Priabonian).

The specimens of the Manfrinato quarry are assigned to 50 species of decapods. Nine of these species have been studied previously: *Spathagalathea minuta* De Angeli & Garassino, 2002; *Italiabunea lutetiana* (Beschin & De Angeli, 1984); *Ranina* sp. indet.; *Portunites eocenica* Lőrenthey in Lőrenthey & Beurlen, 1929; *Tethyscarpilus bericus* De Angeli & Alberti, 2016; *Bericocarcinus alontensis* De Angeli, 2018; *Alontecarcinus buratoi* De Angeli & Caporiondo, 2019; *Eopalicus imbricatus* De Angeli & Beschin, 2000; and *Spinipalicus italicus* Beschin & De Angeli, 2003 (Beschin & De Angeli, 1984, 2003; De Angeli, 1998, 2018; De Angeli & Beschin, 1999, 2000; De Angeli & Garassino, 2002; De Angeli & Alberti, 2016; De Angeli & Caporiondo, 2019).

The other 41 species in this recent study are: *Karumballichirus borensis* (Beschin et al., 2006); *Calliuxina altavillensis* Beschin & De Angeli, 2012; *Palaeomunida defecta* Lőrenthey, 1902; *Palaeomunida multicristata* De Angeli & Garassino, 2002; *Paronapaguropsis latidactylus* (Müller & Collins, 1991); *Dromia subglobosa* (Müller & Collins, 1991); *Pseudodromilites hilarionis* (Bittner, 1883); *Gemmellarocarcinus loerentheyi* Checchia-Rispoli, 1905; *Cyamocarcinus angustifrons* Bittner, 1883; *Lophoranina reussi* (Woodward, 1866); *Lophorani-*

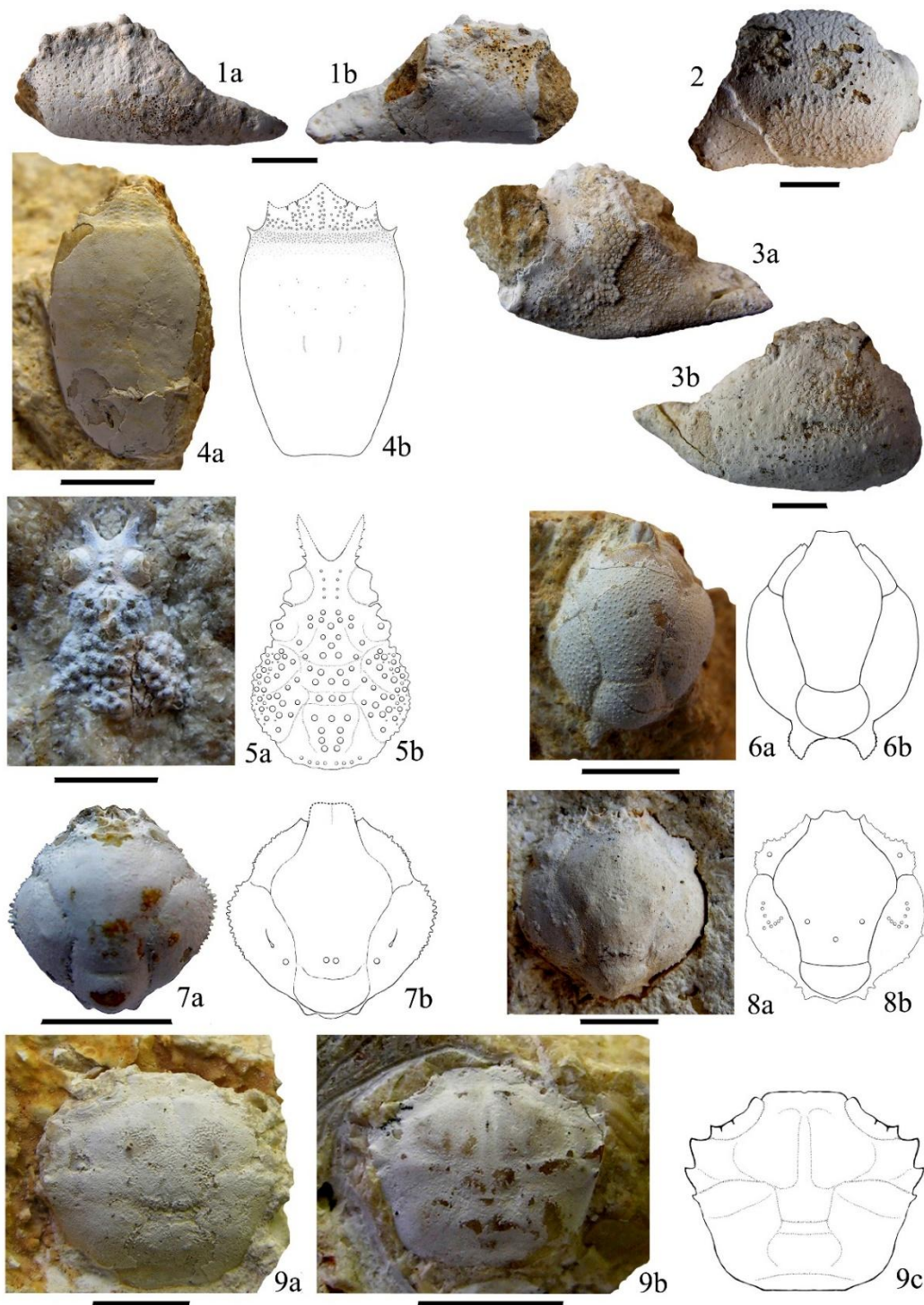


Plate 1. Fig. 1, *Paguristes dallagoi* (MCV.24/060-24.106), right chela in outer (a) and in inner (b) views. Fig. 2, *Eocalcinus manfrinatoensis* (MCV.24/048-24.94), left chela in outer view. Fig. 3, *Batypaguropsis alontensis* (MCV.24/049-24.95), left chela in inner (a) and in outer (b) views. Fig. 4, *Quasilaeviranina yvonnecooleae* (MCV.24/061-24.107), carapace dorsal view (a), carapace reconstruction (b). Fig. 5, *Hyastenus bericus* (MCV.24/034-24.80), carapace dorsal view (a), carapace reconstruction (b). Fig. 6, *Palaeomyra eocaenica* (MCV.24/041-24.87), carapace dorsal view (a), carapace reconstruction (b). Fig. 7, *Philyra antiqua* (MCV.24/043-24.89), carapace dorsal view (a), carapace reconstruction (b). Fig. 8, *Alonteucosia hepatituberculata* (MCV.24/045-24.91), carapace dorsal view (a), carapace reconstruction (b). Fig. 9, *Santeella italica*, MCV.24/050-24.96, carapace dorsal view (a), MCV.24/052-24.98, carapace dorsal view (b), carapace reconstruction (c). Scale bars = 5.0 mm. (from De Angeli & Marangon, 2025).

na laevifrons (Bittner, 1875); *Calappilia dacica* Bittner, 1893; *Calappilia* sp.; *Priabonella violatii* Beschin et al., 2006; *Periacanthus horridus* sp. *bericus* De Angeli & Caporiondo, 2009; *Phrynotambrus italicus* De Angeli & Beschin, 2008; *Montezumella elegans* (Lőrenthey in Lőrenthey & Beurlen, 1929); Corystidae gen. et sp. indet.; *Daira eocaenica* (Lőrenthey, 1898); *Carpilius petreus* Beschin et al., 2007; *Palaeocarpilius macrochelus* (Desmarest, 1822); *Galenopsis crassifrons* A. Milne Edwards, 1865; *Panopeus granulineatus* Müller & Collins, 1991; *Phlyctenodes krenneri* Lőrenthey, 1897; *Phlyctenodes steinmanni* Lőrenthey, 1902; *Pseudophlyctenodes hantkenii* (Lőrenthey, 1897); *Actaeites lobatus* Müller & Collins, 1991; *Pyreneoplax sommarugai* (Beschin et al., 2009); *Eurotetralia loerentheyi* (Müller, 1975); *Prochlorodius ellipticus* Müller & Collins, 1991; and nine species are new: *Eocalcinus manfrinatoensis* De Angeli & Marangon, 2025; *Paguristes dallagoi* De Angeli & Marangon, 2025 (Diogenidae Ortmann, 1892); *Batypaguropsis alontensis* De Angeli & Marangon, 2025 (Paguridae Latreille, 1802); *Quasilaeviranina yvonnecooleae* De Angeli & Marangon, 2025 (Raninidae de Haan, 1839); *Hyastenus bericus* De Angeli & Marangon, 2025 (Epiplatidae MacLeay, 1838); *Palaeomyra eocaenica* De Angeli & Marangon, 2025; *Alonteucosia hepatituberculata* De Angeli & Marangon, 2025; *Philyra antiqua* De Angeli & Marangon, 2025 (Leucosiidae Samouelle, 1819); and *Santeella italica* De Angeli & Marangon, 2025 (Pilumnidae Samouelle, 1819) (Plate 1, figs. 1-9).

The new species come from Bartonian yellowish-white calcarenites, richly fossiliferous with mollusc molds. The scarcity of benthic foraminifera indicates a warm and shallow sea, while the presence of marine, brackish and freshwater molluscs, plants (wood and leaves) and freshwater potamonid crabs highlights a terrestrial contribution. The middle and upper part of the quarry is represented by limestones with nummulites, rhodoliths, bivalves and echinoderms and limestones with corals and coralline algae that indicate the Priabonian marine transgression. A rich and diversified decapod fauna is present, consisting of 50 different species, some endemic to this part of the Berici Mountains and others also present in other contemporary Venetian and European deposits.

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GeoSphere Austria's fossil crustacean collection: a key resource for palaeocarcinological research

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GeoSphere Austria in Vienna (formerly the Geological Survey of Austria) houses one of the country's most significant paleontological collections, with around 160,000 datasets and over a million fossils. Spanning from the Cambrian to the Quaternary, the collection includes a diverse range of taxa, from protists to vertebrates and invertebrates. Notably, about 26,000 specimens constitute type material, highlighting its scientific importance. The paleozoological collection features specimens collected and described by renowned Austrian geologists and paleontologists such as Franz von Hauer, Rudolph Hörnes, Melchior Neumayr, and Edmund Mojsisovics, who were instrumental in shaping Austrian paleontology and geology.

Among the specimens, the institution houses an extensive crustacean collection, comprising specimens from 22 countries and spanning a geological timeframe from the Ordovician (~485 Ma) to the Miocene (~5.3 Ma). The collection includes representatives of four major crustacean clades: Malacostraca, Branchiopoda, Ostracoda, and Merostomata, encompassing at least eight orders, over 30 families, and more than 320 species.

Of particular importance are several historical palaeocarcinological collections dating back to the late 19th century, including the pioneering work of Alexander Bittner (1875, 1877, 1883, 1884, 1893, 1895) and Reuss (1858a). The type material of several monotypic Triassic genera described by Glaessner (1931) from the Reingraben Beds ("Reingrabener Schiefer", Carnian, ~237–227 Ma) is also preserved within the collection. Moreover, the repository continues to yield unexpected discoveries, including material previously considered lost or unknown (De Angeli & Garassino, 2006; Hyžný and Zorn, 2016), such as numerous type specimens of Bittner.

In total, the decapod collection of GeoSphere Austria includes more than 400 fossils, among which 55 are type specimens, consisting of eight holotypes, three paratypes, 14 lectotypes, and 30 paralectotypes, representing 23 valid taxa. The decapod specimens originate from twelve countries: Austria (>150 specimens), Bosnia (1 specimen), Croatia (11 specimens), the Czech Republic (12 specimens), Germany (41 specimens), Hungary (4 specimens), Italy (147 specimens), Romania (1 specimen), Slovakia (3 specimens), Slovenia (20 specimens), Ukraine (3 specimens), and the United Kingdom (1 specimen) (Hyžný & Zorn, 2020). A large portion of the collection (47% of the total) derive from the Miocene of Austria and the Eocene of Italy (Hyžný & Zorn, 2020).

Fossil decapods housed at the institute have been studied in numerous taxonomic and systematic revisions, including works by Reuss (1858a), Glaessner (1924, 1930), Lőrenthey & Beurlen (1929), Müller (1998), Schweitzer & Feldmann (2008, 2009), Hyžný (2014), Hyžný & GašParič (2014), and Hyžný et al. (2015, 2016, 2020). The catalogue compiled by Hyžný & Zorn (2016) laid the foundation for the reevaluation of numerous type specimens, culminating in a

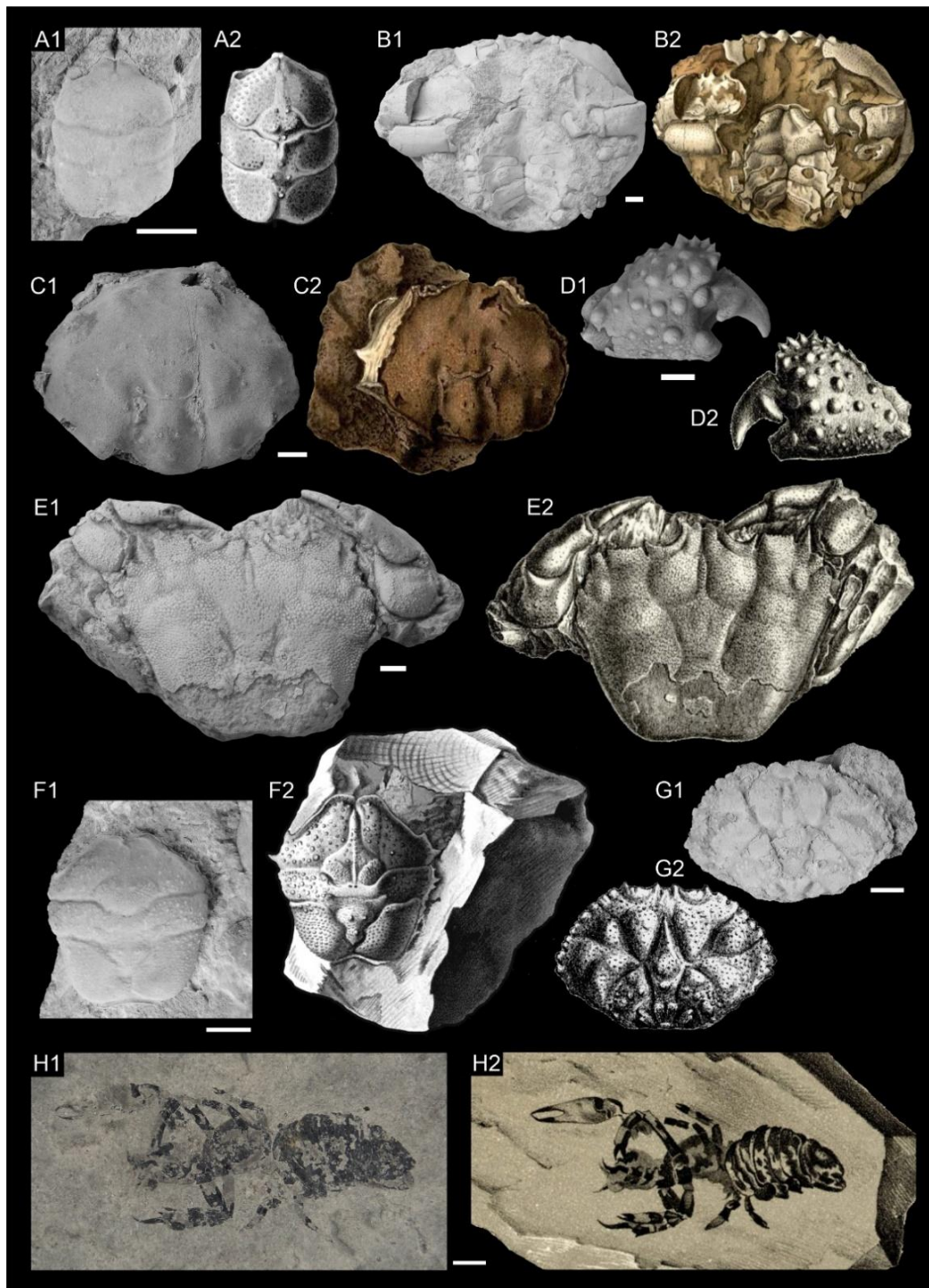


Figure 1. Selected fossil decapod crustaceans from the collection of GeoSphere Austria, previously described and figured by Hyžný & Zorn (2016). A1-2, *Eodromites rostratus* (von Meyer, 1840), dorsal view (A1) and original drawing (Reuss, 1858a: Pl. 24, Fig. 2) (A2); B1-2, *Harpactocarcinus punctulatus* (Desmarest, 1822), ventral view (B1) and original drawing (Reuss, 1858a: Pl. 13, Fig. 5) (B2); C1-2, *Zanthopsis bispinosa* M'Coy, 1849 dorsal view (C1) and original drawing (Reuss, 1858a: Pl. 14, Fig. 5) (C2); D1-2, *Bittnerilia* sp., lateral view (D1) and original drawing (Bittner, 1875: Pl. 1, Fig. 7a) (D2); E1-2, *Coeloma vigil* A. Milne-Edwards, 1865, dorsal view (E1) and original drawing (Bittner, 1875: Pl. 5, Fig. 4a) (E2); F1-2, Lectotype of *Goniodromites polyodon* Reuss, 1858a, dorsal view (F1) and original drawing (Reuss, 1858a: Pl. 24, Fig. 4) (F2); G1-2, *Tasadia carniolica* (Bittner, 1884), dorsal view (G1) and original drawing (Bittner, 1884: Pl. 1, Fig. 8a) (G2); H1-2, *Tetrachela raiblana* (Bronn, 1858), dorso-lateral view (H1) and original drawing (Reuss, 1858b: Pl. 1, Fig. 2).

comprehensive taxonomic framework for all fossil decapod crustaceans housed at GeoSphere Austria in 2020 (Hyžný & Zorn, 2020). As part of this effort, several historically significant specimens were reassessed, clarifying taxonomic uncertainties and designating lectotypes where necessary. The plate presented herein illustrates selected specimens from this collection, including *Eodromites rostratus* (von Meyer, 1840), *Harpactocarcinus punctulatus* (Desmarest, 1822), *Zanthopsis bispinosa* M'Coy, 1849, *Bittnerilia* sp., *Coeloma vigil* A. Milne-Edwards, 1865, *Goniodromites polyodon* Reuss, 1858c, *Tasadia carniolica* (Bittner, 1884), and *Tetrachela raiblana* (Bronn, 1858), all of which were previously investigated and figured by Hyžný & Zorn (2016) (Figure 1). These specimens originate from various Mesozoic and Cenozoic deposits, spanning the Triassic to the Miocene, and represent a diverse range of paleoenvironmental settings. Their broad temporal distribution and exceptional preservation provide valuable insights into decapod evolution and diversity, reinforcing their significance for future comparative studies.

The scientific significance of this collection is underscored by the high number of type specimens, rare taxa, and historically important material, making GeoSphere Austria a key international reference point for researchers studying decapod crustaceans across different geological periods. Additionally, the vast diversity of crustaceans, alongside the wealth of fossils representing other taxonomic groups, solidifies GeoSphere Austria as an invaluable resource for paleontological research on a global scale.

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An overview of the Mesozoic Decapod Revolution in Iberia

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The study of the diversity and distribution of decapod crustaceans during the Mesozoic is critical to understand their origin and evolution. The fossil record indicates that this era was crucial, marking the appearance of major clades and the diversification of crabs, lobsters, and anomurans (i.e., Klompmaker et al., 2013a; Schweitzer & Feldmann, 2015; Luque et al., 2019), with significant diversity peaks. In particular, the Mesozoic Decapod Revolution (Klompmaker et al., 2013a, 2015) represents an evolutionary turning point, with the emergence of 80% of the major clades (Luque et al., 2019; Wolfe et al., 2024). This revolution coincides with the expansion and contraction of reefs, such as those of the Upper Jurassic in Central Europe (i.e., Müller et al., 2000; Schweitzer and Feldmann, 2009; Franțescu, 2010; Klompmaker et al., 2020; Van Bakel et al., 2021), those of the Early Cretaceous, like those of Olazagutía, Navarra, Spain (see Klompmaker et al., 2013b), and with the early stages of the Late Cretaceous (i.e., Luque et al., 2019, 2021).

New findings from deposits ranging from the Middle Jurassic (Bathonian) to the early Late Cretaceous (Cenomanian) in Aragón, Spain, provide new insights into the morphology and paleoecology of decapods at key moments in their evolution. These fossils reveal significant anatomical traits (Figure 1), while the outcrops from which they originate offer valuable information on the environments where these groups diversified.

These discoveries refine the paleobiogeographic distribution of Mesozoic decapods and provide crucial evidence for understanding their origin, morphological variability, and environmental affinities. By addressing knowledge gaps regarding their early diversification, this study contributes to reconstructing the evolutionary trajectory of modern decapods and discerning the spatiotemporal patterns underlying their evolution.

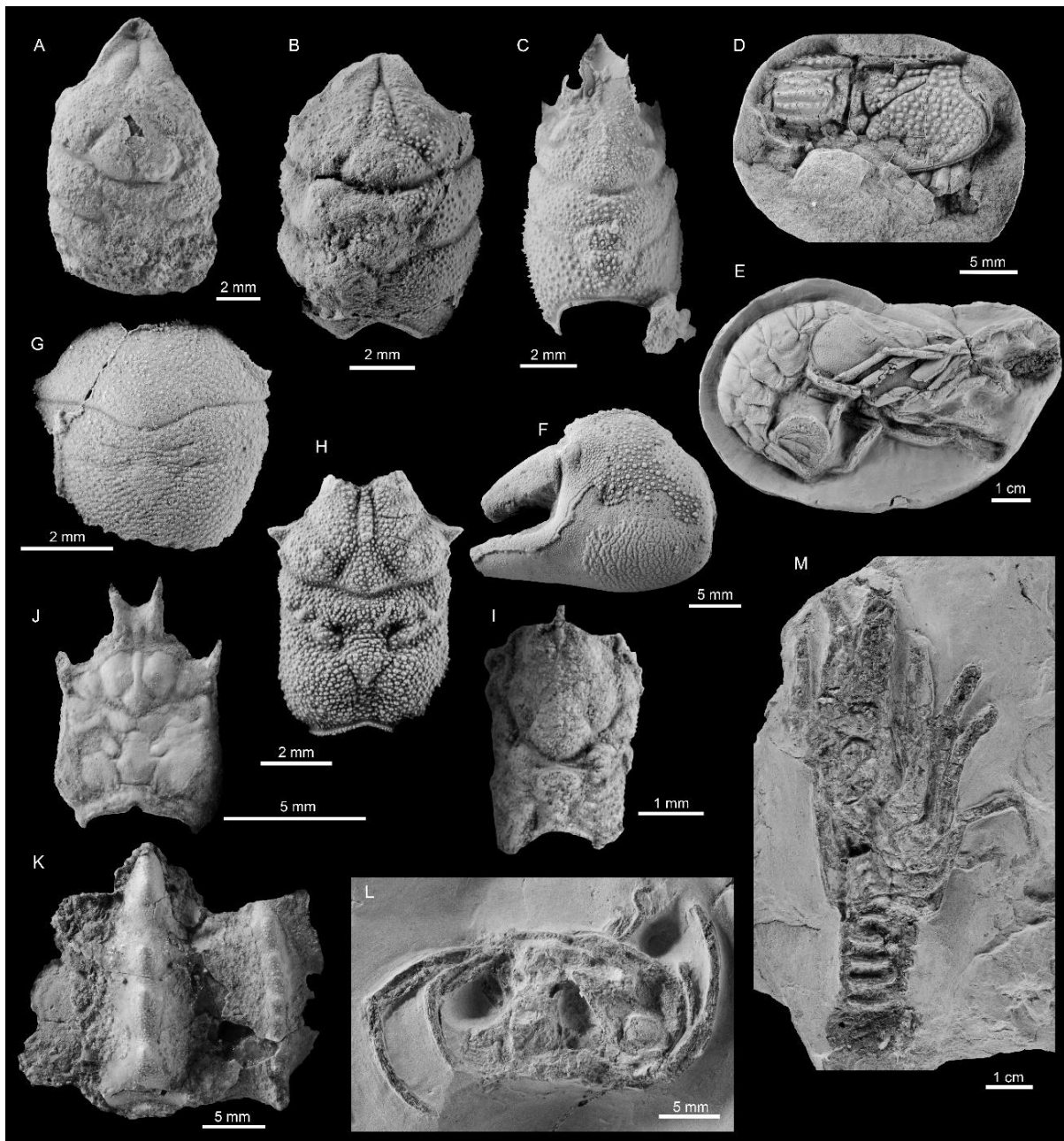


Figure 1. Some of the studied decapod crustaceans from the Mesozoic outcrops of Aragon; A-C, Bathonian (Middle Jurassic) sponge meadows of Zaragoza; A, *Tanidromites* sp. (MPZ 2025/49); B, ?*Nodoprosopon* sp. (MPZ 2025/50); C, Decapoda indet. (MPZ 2025/51); D-F, Oxfordian (Upper Jurassic) marly deposits of Teruel; D, *Glypheus* sp. (MPZ 2025/55); E, *Atherfieldasthacus* sp. (MPZ 2025/56); F, Paguridae indet. (MPZ 2025/57); G-I, Oxfordian (Upper Jurassic) sponge meadows of Zaragoza; G, *Goniodromites* sp. (MPZ 2025/52); H, *Planoprosopon* sp. (MPZ 2025/53); I, *Gastrodorus* sp. (MPZ 2025/54); J-M, Cenomanian (lower Upper Cretaceous) siliciclastic deposits of Teruel; J, Brachyura indet. (MPZ 2025/61); K, *Cenomanocarcinus* sp. (MPZ 2025/58); L, Paguridae indet. (MPZ 2025/59); M, *Linuparus* sp. (MPZ 2025/60).

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A new enigmatic alsasuacaridid (Pancrustacea, Cyclida) from the Maastrichtian type area in the Netherlands (Upper Cretaceous)

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A new, diminutive arthropod belonging to the cyclidan family Alsasuacarididae is described from upper Maastrichtian strata in the type area of that stage. It is the second member of the genus known to date, extending the stratigraphical and palaeobiogeographical ranges of this genus considerably, the type species, *A. nostradamus* Van Bakel, Jagt, Fraaije & Artal, 2011, having been recorded from the Albian of northern Spain. The new species constitutes only the third representative of the family Alsasuacarididae, and the first in three-dimensional preservation and with ventral morphology exposed (Fraaije *et al.*, in prep.). Morphologically and stratigraphically speaking, alsasuacaridids are quite distinct from other Cyclida recorded to date, but no alternative taxonomic classification is possible at the moment. The presence of more than one cyclidan in the diverse faunal assemblages from the Meerssen Member (Maastricht Formation, upper Maastrichtian) in the south-east Netherlands, may suggest that it is feasible that more of such taxa will be discovered in strata of Mesozoic age, and possibly even of Paleogene date, when also millimetre-sized faunal elements are screened in detail. Although cyclidans do have a crab-like appearance, it is highly likely that alsasuacaridids occupied other ecological niches than brachyurans. The new species will be described in full, and compared with its congener, *Alsasuacaris nostradamus*, in a forthcoming paper (Fraaije *et al.*, in prep.).

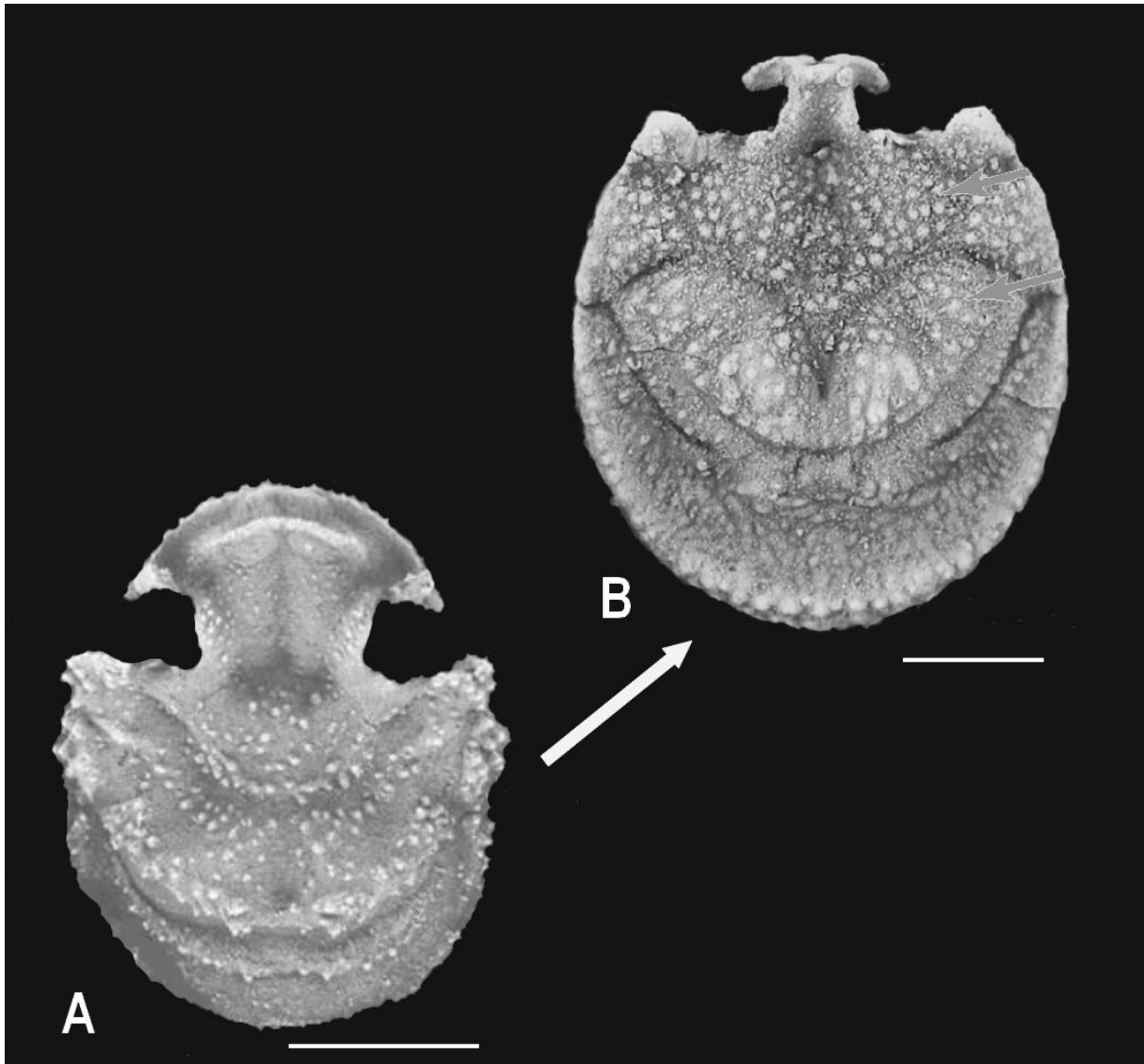


Figure 1. Alsasuacarididae. A) *Alsasuacaris nostradamus*, Albian, north-east Spain (from Van Bakel et al., 2011, fig. 1.1) B) *Maastrichtiocaris rostrata* Fraaije, Schram & Vonk, 2003, upper Maastrichtian, the Netherlands (from Schweitzer et al., 2020, fig. 9.1). Scale bar 1 mm. Photos by Barry van Bakel.

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Deepwater crustacean assemblage from Early Miocene ophiuroid beds of Meljski hrib (Slovenia)

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The Meljski hrib locality is known among collectors for its early Miocene invertebrate fossils and petrified wood. Located on the northeastern outskirts of Maribor, its fossiliferous beds form nearly vertical cliffs approximately 100 meters high. Although the preservation of fossils is remarkable, the taxa are unevenly distributed, occurring in distinct assemblages across different stratigraphic layers (Mikuž and Gašparič, 2014).

Nannoplankton analyses confirm an early Miocene age (Bartol et al., 2013; Gašparič et al., 2021). The assemblage is attributed to the lower NN4 (Ottangian/Karpatian) Paratethyan biozone based on the co-occurrence of *Sphenolithus heteromorphus* Deflandre, 1953, and *Helicosphaera ampliaperta* Bramlette and Wilcoxon, 1967, with the absence of *Helicosphaera waltrans* Theodoridis, 1984. Most of the section consists of dark grey siltstones with rare macrofauna dominated by the bivalves *Solemya doederleini* Mayer, 1861, and *Limaria labani* (Meznerics, 1936). Gašparič and Halasova (2015) reported occurrences of decapod crustaceans, including the crab *Styrioplax exiguous* (Glaessner, 1928) and axiidean ghost shrimps that can be attributed to *Callianopsis jahringensis* (Glaessner, 1928).

Higher up in the section, in a less accessible part, there is a lithologically distinct layer of yellowish marls. This layer is characterized by a mass mortality accumulation of brittle stars, and because of the well-preserved fauna, these ophiuroid beds are classified as a Konservat-Lagerstätte (Gašparič et al., 2025). Though ophiuroids are abundant, fossil remains are generally rare, with most taxa represented by single specimens. However, these specimens exhibit extraordinary detail, including well-preserved soft tissues with minimal postmortem disturbance from water currents or scavengers.

Notably, a deep-water nephropid lobster, *Metanephrops serendipitus* Gašparič et al., 2021, was described from the ophiuroid beds (Figure 1). Much like its modern counterparts, this fossil lobster lived in a fine-grained deep-sea environment that was frequently associated with brittle stars. As the first fossil representative of the genus found in the northern hemisphere, *M. serendipitus* expands its known palaeobiogeographical range. Although a comprehensive account of the associated fauna remains forthcoming, we have identified

several accompanying bivalves, including *Solemya doederleini* Mayer, 1861; *Limaria labani* (Meznerics, 1936); *Lentipecten denudatus* (Reuss, 1867); and *Macoma elliptica* (Brocchi, 1814), as well as the scaphopod *Gadilina taurogracilis* Sacco, 1897 (Gašparič et al., 2021) and the ghost shrimp *Callianopsis jahringensis* (Figure 2a). Additional remarkable finds include a marine vertebrate coprolite containing basking shark gill rakers, an exceptionally preserved complete deep-water holothurian, and at least two more crustacean taxa.



Figure 1. A nephropid lobster *Metanephrops serendipitus*, holotype specimen RGA/SMNH 2295 (carapace) and RGA/SMNH 1591 (chelipeds). Scale bar equals 50 mm.

We herein report the discovery of a new brachyuran fossil. A single dorsal carapace specimen, attributable to the genus *Bathynectes* Stimpson, 1871, was recently recovered from the ophiuroid beds by one of the authors (Figure 2b). To date, the only fossil representative of this genus, *Bathynectes muelleri* Ossó & Stalennuy, 2011, was found in Middle Miocene shallow-water reef limestones in Ukraine. In contrast, the specimen from the Early Miocene of Slovenia aligns with the ecological preferences of extant *Bathynectes* species, which inhabit soft, deep substrates in the Mediterranean Basin and Atlantic Ocean (Ossó & Stalennuy, 2011).

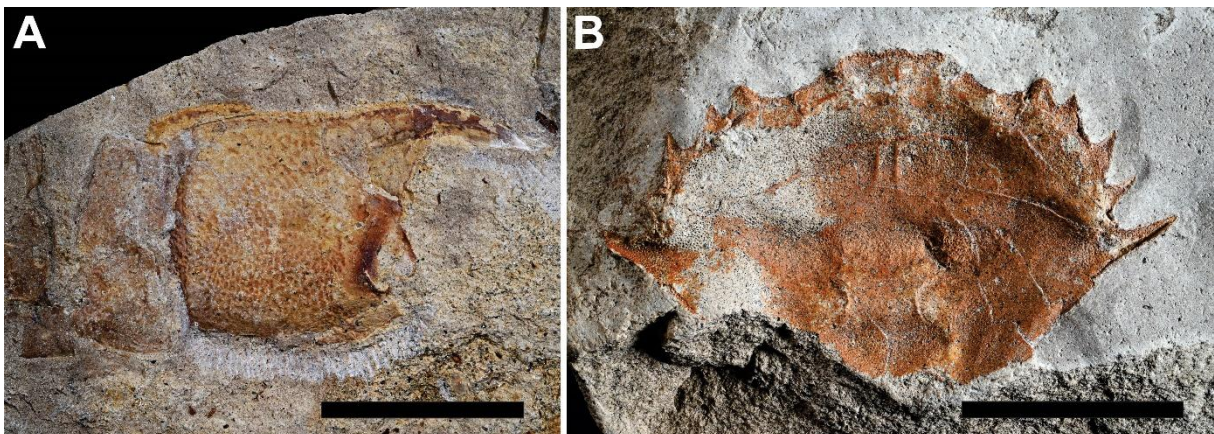


Figure 2. A – Ghost shrimp *Callianopsis jahringensis*, major cheliped, specimen RGA/SMNH 7126. B – *Bathynectes* sp. in dorsal view, specimen RGA/SMNH 6949. Scale bars equal 10.0 mm.

Another noteworthy crustacean discovery from the ophiuroid beds is a mantis shrimp, likely a member of the Squillidae Latreille, 1802. The articulated stomatopod specimen includes pereopods, although its carapace is less well preserved than its abdomen, with the raptorial thoracopods and mouthparts folded beneath the carapace. This mode of preservation suggests that the specimen was either buried alive or remained undisturbed after death, since unfolding typically occurs as muscles decay (Hof & Briggs, 1997). The abdomen is exceptionally preserved, revealing individual muscle bundles within the abdominal somites (Figure 3). There is evidence for soft tissue preservation via replication in calcium phosphate, a process observed in various crustacean groups with phosphate-rich cuticles under anaerobic conditions (Klompaker et al., 2019).

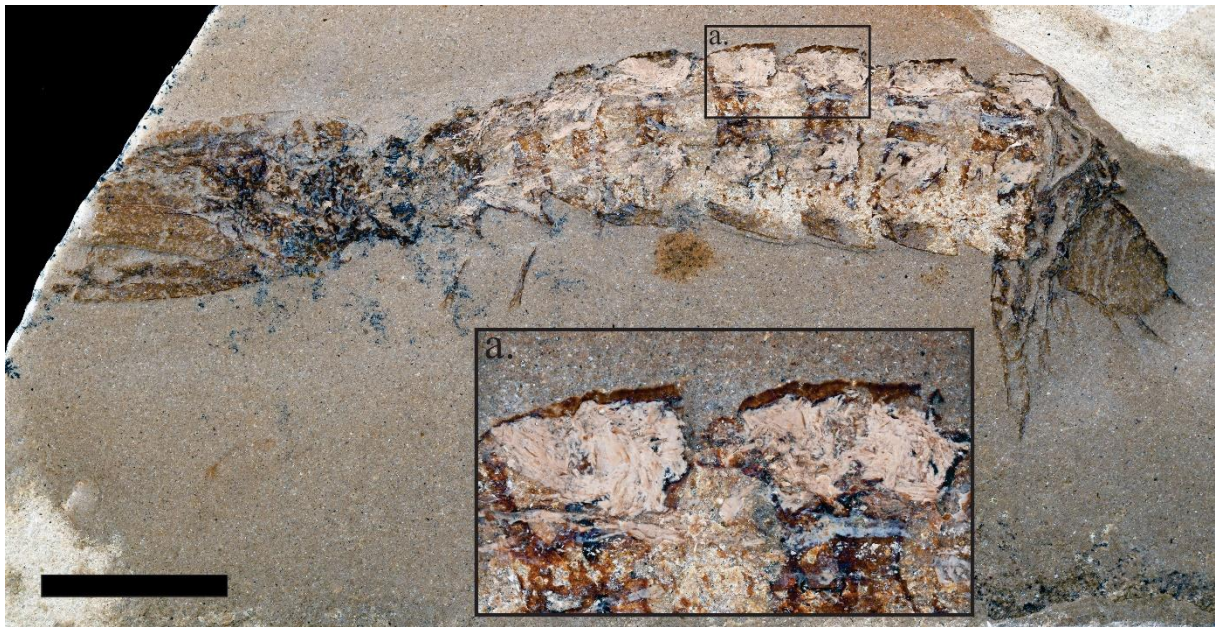


Figure 3. Stomatopod, specimen RGA/SMNH 5241 with exceptionally preserved abdominal muscle tissue (in closeup 3a). Scale bar equals 10.0 mm.

Deepwater decapod crustacean assemblages are relatively rare in the fossil record (Harzhauser et al., 2011). The associated fauna from the ophiuroid beds suggests a depositional environment ranging from an outer shelf to a slope setting, with water depths of at least 150 meters and likely exceeding 250 meters (Gašparič et al., 2021). Ophiuroid beds from Meljski hrib locality preserve a unique taphonomic window into the early Miocene fauna of Central Paratethys, and a reminder of the hidden biodiversity that resided in the poorly sampled fossil record of the deep-marine ecosystems.

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Exceptionally preserved peracarid crustaceans from the Middle Triassic of Kamnik – Savinja Alps (Slovenia)

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The crustacean order Spelaeogriphacea Gordon, 1957, consists of four extant species that are eyeless, lack pigmentation, and inhabit only subterranean waters. These species are found in freshwater environments on southern continents, specifically within ancient cratons that have remained free from marine transgressions since at least the Early Cretaceous, when Gondwana began to break apart.

The first known living species *Spelaeogriphus lepidops* was described by Isabella Gordon (1957) from a remote freshwater stream flowing through Bats Cave on Table Mountain near Cape Town in South Africa, and later located in other similar environments within the region (Poore & Humphrys, 1998). Another species, *Poticoara brasiliensis* Pires, 1987, was identified from caves within Brazil's Mato Grosso region. Further discoveries have expanded the order's known range. Two more species were identified in an aquifer in Western Australia: *Mangkurtu mityula* Poore & Humphries, 1998, and *Mangkurtu kutjarra* Poore & Humphries, 2003. These findings suggest that additional spelaeogriphaceans may exist in other regions with Gondwanan and Tethyan connections, following distribution patterns similar to those of another Peracarida order, Thermosbaenacea.

The external morphology of extant representatives is well documented, however identifying spelaeogriphacean fossils can be challenging, especially when the limbs are not well preserved. Given their highly specialized, cave-dwelling nature, a fossil record for this group might seem unlikely. Yet, four fossil taxa have been identified so far, ranging from Palaeozoic marine "proto-spelaeogriphacean," *Acadiocaris novascotica* (Copeland, 1957), to youngest freshwater form from Early Cretaceous of Spain (Jaume et al., 2013).

Here, we present a mass occurrence of exceptionally preserved spelaeogriphacean fossils from the Middle Triassic (Anisian) of Slovenia. The Strelovec Formation extends across

the Kamnik–Savinja Alps and the Julian Alps (Celarc et al., 2013). The deposition of the Strelovec Formation occurred on a drowned section of the carbonate platform, likely within a restricted outer ramp environment associated with an intraplateau basin, where laminated hemipelagic limestones were deposited in a restricted, anoxic environment (Figure 1). Periodic input of clay and sediments from gravity mass flows interrupted hemipelagic sedimentation (Miklavc & Celarc, 2022). The dark laminated bituminous limestones of Strelovec Formation contain well preserved fauna including algae, plants, molluscs (gastropods, bivalves, ammonoids), echinoderms (crinoids, echinoids, ophiuroids), lingulate and articulate brachiopods, fully articulated actinopterygian fishes, sauropterygians, and rare ichthyosaurs. Additionally, various euarthropods have been found, including decapods, xiphosurids, and thylacocephalans (Hitij et al., 2010; Bicknell et al., 2021; Laville et al., 2024).



Figure 1. Laminated limestones of Strelovec Formation, with dark layer (hammer) of green claystones with spelaeogriphacean fossils.

Interbedded between the dark bituminous limestones are thinly laminated green claystones with exceptionally preserved fossils. A rich crustacean fauna was discovered within these finely laminated strata, dominated by an abundance of spelaeogriphaceans (Figure 2). Thousands of tiny specimens, ranging from 1 to 7 mm in length and representing various stages of development, were recovered (Figure 3). Specimens are found in abundance of up to 20 specimens per 1 dm². They are consistently complete, with fully articulated body segments and limbs, in some cases even traces of internal anatomy are visible. Due to their unique preservation, the fossils had to be processed in large numbers and photographed under wet conditions before they could be properly observed.



Figure 2. Two exceptionally preserved spelaegriphacean specimens RGA/SMNH 6680/3 in dorsal and ventral aspect. Photographed wet. Scale bar equals 5.0 mm.

The oldest representative, *Acadiocaris novascotica* (Copeland, 1957) from the Lower Carboniferous of Canada was originally described as a syncarid, however Schram (1974) subsequently reassigned it as a spelaegriphacean. From sediments of nearshore marine environment, *A. novascotica* was until now considered the only marine representative of Spelaegriphacea. *Liaoningogriphus quadripartitus* Shen et al., 1998, from the Early Cretaceous of China exhibits a more typical spelaegriphacean traits. As reconstructed by Shen et al. (1999), this modest-sized spelaegriphacean (1–2 cm in length) inhabited freshwater lacustrine ecosystems. In 1993, Tchindonova and Tchesunov described what they believed to be an Early Cretaceous isopod from the Transbaikal region of Siberian, naming it *Squilloides longiabdominalis*. Hegna et al. (2016) noted that the Siberian species closely resembled *L. quadripartitus*, and reassigned the species to the genus *Liaoningogriphus* as *L. longiabdominalis*. A fourth fossil species, *Spinogriphus ibericus*, occurs in the Early Cretaceous deposits of central Spain (Jaume et al., 2013). This species appears to have been a freshwater form, deposited under geological conditions that may indicate cave or crevicular environments. If confirmed, Jaume et al. (2013) suggested that *S. ibericus* would represent the oldest known stygobiont among crustaceans (Schram & Koenemann, 2021).

The new record of fossil spelaegriphaceans from the Middle Triassic of Slovenia corroborates the palaeobiogeographical distribution of the order, where all four extant taxa have a southern hemisphere distribution, while the fossil representatives are described from the northern hemisphere. The new occurrence also fits with the currently accepted scenario that spelaegriphaceans evolved in marine environments and became isolated in freshwater habitats and entered the groundwater systems following a drop in sea level, somewhere between Middle Triassic and Early Cretaceous.



Figure 3. Juvenile specimens RGA/SMNH 6570/4 in dorsal and lateral aspect. Photographed wet. Scale bar equals 1.0 mm.

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Diversity and dominance of Late Jurassic decapod assemblages: a case study from southern Poland

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The sponge megafacies represents a deep-neritic sediment accumulated along the northern margin of the Tethys ocean during the Late Jurassic (Müller et al., 2000). Its occurrences range from Portugal through France, Germany and Poland to the North Caucasus.

The studied material consists of 356 specimens and was collected directly from the exposed strata of sponge megafacies at seven localities in the Kraków-Wieluń Upland (southern Poland): Bobrowniki and Lisowice (Bimammatum and Planula ammonite zones, early Kimmeridgian), Zawodzie (Bifurcatus ammonite zone, late Oxfordian), Młynka and Wysoka (Plicatilis ammonite zone, middle Oxfordian), Niegowonice and Ogrodzieniec (Transversarium ammonite zone, middle Oxfordian). Almost half of the collection (172 specimens) consists of the carapaces which were identified on the genus and/or species level (Figure 1, Table 1). The assemblages at respective localities are dominated by different combinations of genera (Figure 2). Representatives of *Goniodromites* Reuss, 1858, dominate at every locality; the differences in assemblages are in the abundance ratio of *Gastrodorus* von Meyer, 1864, and *Tanidromites* Schweitzer & Feldmann, 2008, representatives to *Goniodromites* Reuss, 1858, representatives. The localities of Młynka, Wysoka, and Zawodzie yielded 1, 5, and 2 specimens respectively, thus, assessing the dominant taxa is not possible. All the identified species at these three localities also occur at the other localities.

To investigate differences in decapod assemblages during the Late Jurassic, a non-metric multidimensional scaling (NMDS) analysis was conducted using presence/absence data of 202 decapod crustacean species from 22 European (Austria, the Czech Republic, Germany, Poland, and Romania) localities of Oxfordian to Tithonian age, exposing either sponge-microbial or coral-dominated reef-facies. Jaccard similarity index was applied. The results show that (1) the localities are grouped together based on the age, with Oxfordian, Kimmeridgian and Tithonian localities being separated from each other; (2) Oxfordian and Kimmeridgian localities are closer to each other than to Tithonian ones; (3) localities with both Oxfordian and Kimmeridgian strata slightly overlap with localities with only Kimmeridgian strata; and (4) the studied Polish localities are close to selected German localities and to Stránska skála locality (the Czech Republic). Nevertheless, the presented results should be taken as preliminary because no unified approach in collecting has been applied, with the majority of data coming from the published literature only. Further research should include a uniform collecting method accompanied with the rarefaction analysis.

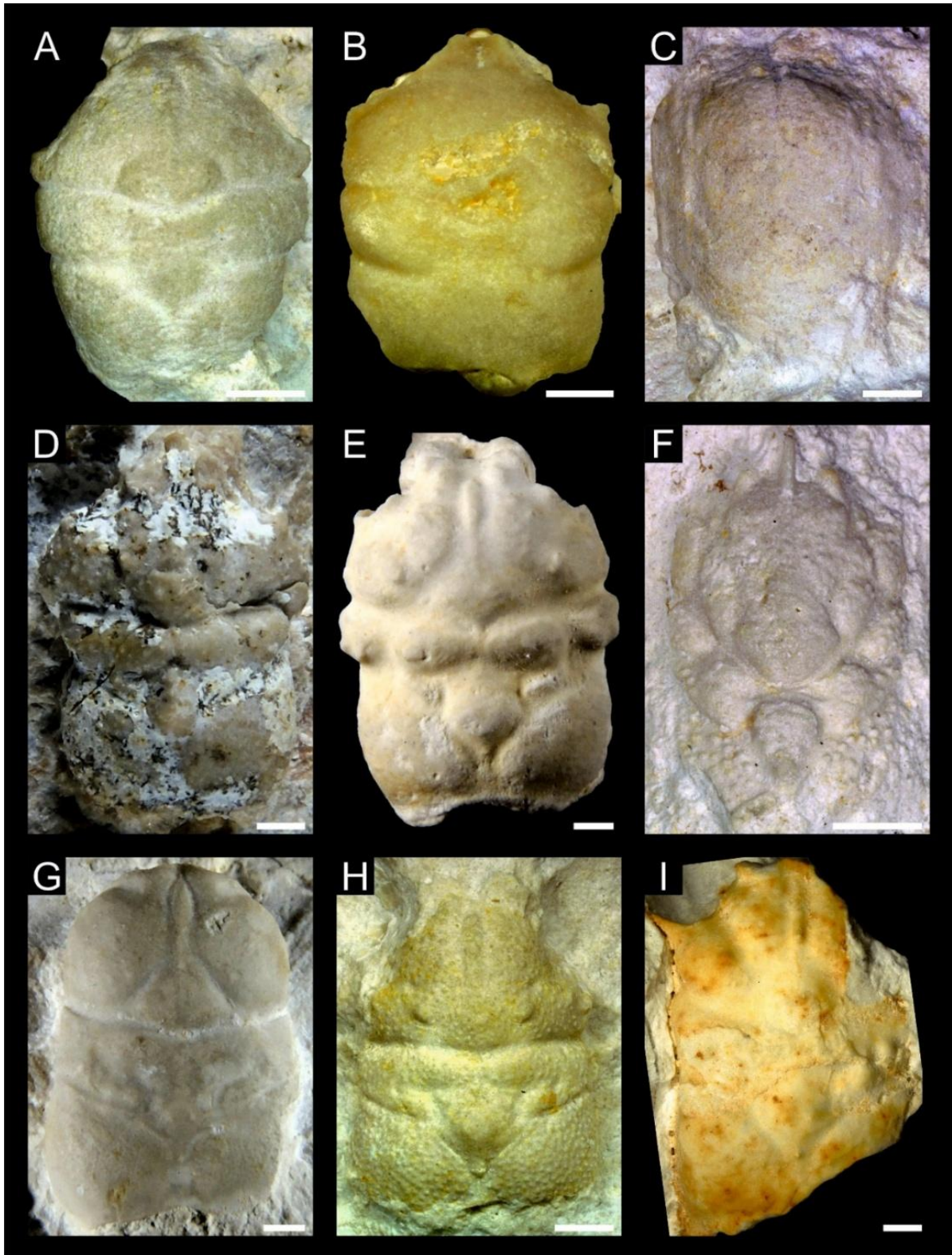


Figure 1. Some of the examined late Jurassic decapod species from Kraków-Wieluń Upland. A, *Goniidromites kubai*. B, *Tanidromites alexandrae*. C, *Ammopylocheles* sp. D, *Bucculentum bucculentum*. E, *Abyssopthalmus spinosus*. F, *Gastrodorus bzowiensis*. G, *Gabriella biburgensis* H. *Planoprosopon rhathamungus*. I, *P. heydeni*. A-C and E-G from Lisowice, D from Niegowonice. Scale bars: 1.0 mm.

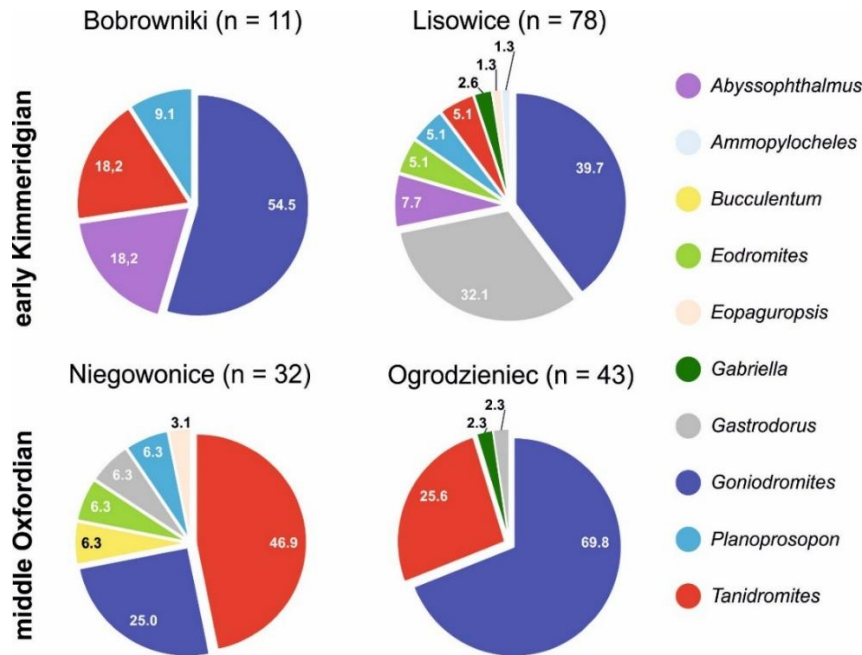


Figure 2. Composition of decapod assemblages from four investigated localities of Kraków-Wieluń Upland.

Table 1. The abundance of identified decapod species at studied localities of Kraków-Wieluń Upland. Specimens identified only on the genus level (n = 30) are not included. BO: Bobrowniki, LI: Lisowice, NI: Niegowonice, OG: Ogródzieniec.

Taxon	BO	LI	NI	OG	n
<i>Abyssopthalmus mirus</i> (Moericke, 1897)		1			1
<i>Abyssopthalmus spinosus</i> (von Meyer, 1842)	2	4			6
<i>Ammopylocheles</i> sp.		1			1
<i>Bucculentum bucculentum</i> (Wehner, 1988)			2		2
<i>Eodromites bernchrisdomiorum</i> Klompmaker et al., 2020		4			4
<i>Eopaguropsis blausteinensis</i> Fraaije et al., 2017		1	1		2
<i>Gabriella biburgensis</i> (Wehner, 1988)		2		1	3
<i>Gastrodorus bzowiensis</i> Krzemińska et al., 2015		25	2	1	28
<i>Goniodromites kubai</i> Starzyk et al. 2012	1	6	2	10	19
<i>Goniodromites narinosus</i> Frantescu, 2010	1	4	1	4	10
<i>Goniodromites serratus</i> Beurlen, 1929	3	15	2	13	33
<i>Planoprosopon heydeni</i> (von Meyer, 1857)	1	2			3
<i>Planoprosopon rhathamungus</i> Schweitzer & Feldmann, 2009		2	2		4
<i>Tanidromites alexandrae</i> Starzyk, 2015	1	1	2	4	8
<i>Tanidromites insignis</i> (von Meyer, 1857)			1	2	3
<i>Tanidromites longinosa</i> Starzyk, 2016		1			1
<i>Tanidromites nightwishorum</i> Klompmaker et al., 2020			2		2
<i>Tanidromites sculpta</i> (Quenstedt, 1858)				1	1
<i>Tanidromites scheffnerae</i> Schweigert & Koppka, 2011			2		2
<i>Tanidromites schweitzerae</i> Starzyk, 2016			1		1
	9	69	20	36	134

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Preservation of burrowing shrimps (Malacostraca: Decapoda: Axiidea) in hypoxic environments from the Miocene of the Central Paratethys

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Burrowing shrimps of the infraorder Axiidea are soft-bodied, usually heterochelous decapods representing major bioturbators of muddy and sandy marine substrates and having great impact on physicochemical properties of the sediment (Dworschak et al., 2012, and references therein). Their fossil record is robust, and their remains are present in most assemblages of Cenozoic decapod crustaceans (Glaessner, 1969; Hyžný & Klompmaker, 2015). Much of the burrowing shrimp's integument is reduced because the burrow walls replace many of the cuticle's functions. Due to the delicate nature of most of the cuticle, only the hardened parts are usually preserved, with heavily calcified chelipeds preserved most frequently, although other parts are sometimes preserved as well. Three main types of preservation in terms of completeness of the material can be observed (Bishop & Williams, 2005; Hyžný & Klompmaker, 2015): (1) (Near) completely-articulated body fossils, in which the majority of all three main parts of the shrimp are preserved (i.e., carapace, legs, and pleon; Figure 1A); (2) Disassociated body fossils represented by some but not all exoskeleton elements that are still articulated and preserved together (i.e., cheliped disassociation unit, pleonal disassociation unit, etc.); (3) Isolated elements of the exoskeleton not associated with any other parts from the same specimen. In Miocene siliciclastic sediments of the Central Paratethys, all these three types of preservation can be documented at various localities (e.g., Müller, 1984; Hyžný & Hudáčková, 2012; Hyžný et al., 2015; Hyžný, 2016). However, in the Schlier-type deposits formed by diatom-rich sandy mudstones (siltstones and claystones), yet another type of preservation was identified: the disassociation unit is preserved as a set of isolated elements that are partly or fully disarticulated and preserved apart from each other but simultaneously close enough to be identified as originating from the same individual (Figure 1B-C). This intermediate type of preservation (in respect to the categorization outlined above) required only minor transport and virtually no physical disintegration following the final deposition near the sediment-water interface. Recently, a seasonal or permanent hypoxia was identified as a key factor that limited scavengers or bulldozers and thus reduced exoskeleton disintegration and displacement. These conditions allowed the preservation of intact or dislocated, weakly time-averaged remains of macrobenthic fauna (Tomašových et al., 2024). Hypoxic conditions can create a unique taphonomic window for preservation of benthic macrofauna which still actively colonize the sea-floor but disintegration and mixing rates are slow or spatially limited (Briggs et al., 2015; Tomašových et al., 2018, 2024). An example of the association preserved in such a way is that from the succession of the lower Miocene (Bur-

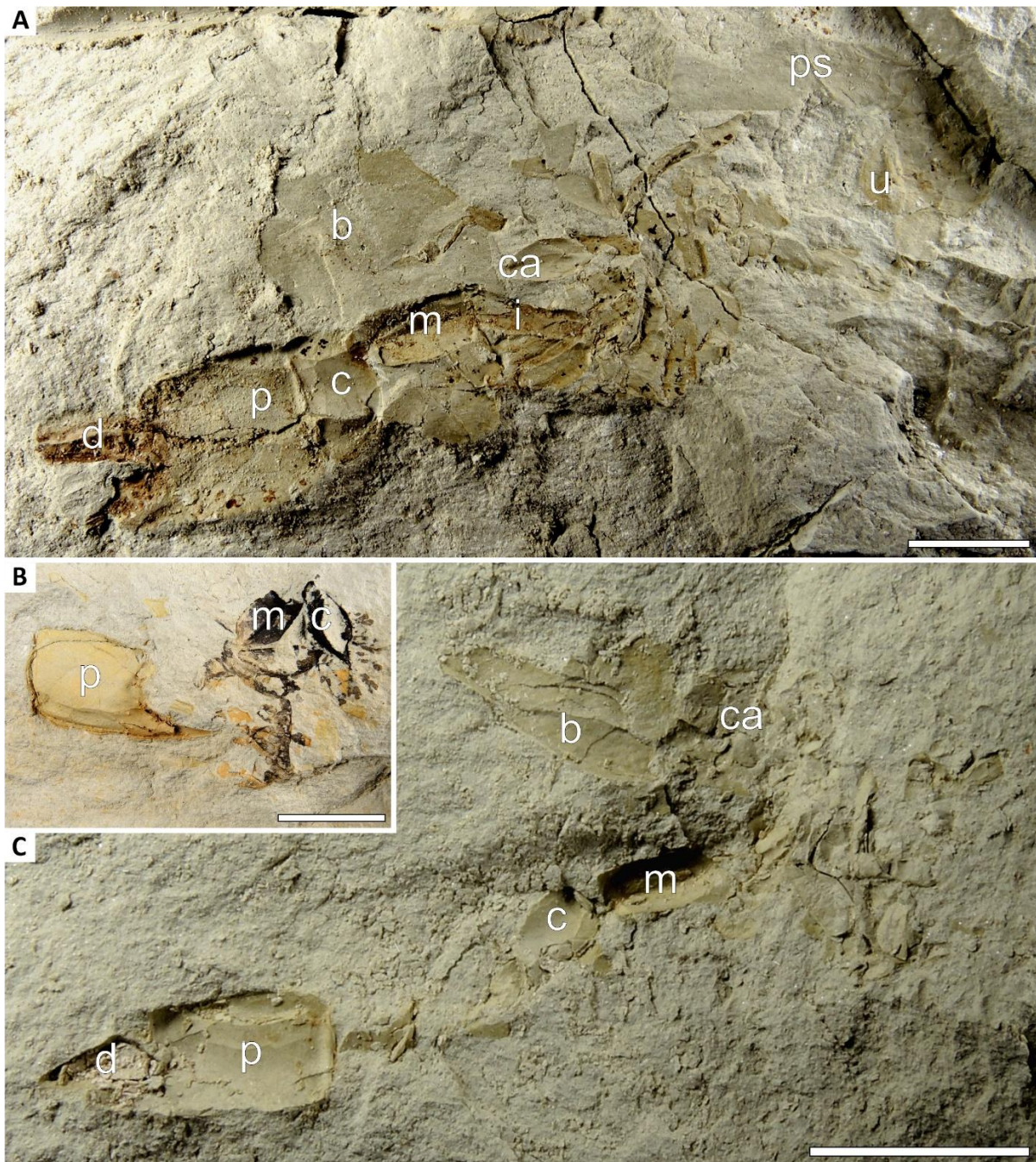


Figure 1. *Callianopsis marianae* Hyžný & Schlögl, 2011, from the Burdigalian Schlier-type deposits of Cerová, Slovakia. A, Intactly preserved near-complete individual. B, Dislocated cheliped disassociation unit. C, Near-complete individual preserved as dislocated assemblage of elements. Abbreviations: b=branchiostegite; c=carpus; ca=carapace; d=dactylus; i=ischium; m=merus; p=propodus; ps=pleonal somites; u=uropod. Scale bars equal 10.0 mm.

digalian) Schlier-type mudstone (of the Lakšárska Nová Ves Formation) exposed at the Cerová section in the northern Vienna Basin, Slovakia (Schlögl et al., 2011). Benthic foraminiferal assemblages suggest the deposition in outer shelf-upper bathyal conditions, with the estimated depth of ca. 150–500 m (Schlögl et al., 2011). Deep-water faunal elements have been identified also in molluscs (Harzhauser et al., 2011; Schlögl et al., 2011), chondrichthyans (Underwood & Schlögl, 2013), and sponges (Łukowiak et al., 2014). The macrofaunal association is dominated by the shallow-burrowing irregular echinoid *Lovenia mortenseni*

Čtyroký, 1965, small-shelled bivalves, and burrowing ghost shrimp *Callianopsis marianae* Hyžný & Schlögl, 2011. Preserved exoskeletons of *C. marianae* exhibit the preservation suggesting hypoxic conditions as discussed above. Although many decapod crustaceans are mobile animals showing little tolerance to anoxia or hypoxia, with larval stages of brachyuran crabs being among the most sensitive marine organisms to oxygen supply (Vaquer-Sunyer & Duarte, 2008), burrowing shrimps do not show any pronounced decreases in metabolic activity under hypoxic/anoxic conditions of up to 48 hours, with some species being able to survive up to five days under anoxia (Thompson & Pritchard, 1969; Felder, 1979; Anderson et al., 1994; Powilleit & Graf, 1996). Their tolerance to low oxygen levels is directly linked with their fossorial lifestyle as burrows often reach pore waters that are strongly hypoxic or anoxic. Presumed metabolic adaptations of *C. marianae* allowed its thriving in habitat affected by seasonal hypoxic events which in turn promoted the exceptional preservation of shrimps as fossils.

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Late Cretaceous–early Paleogene cirripedes (Crustacea, Thoracica) from Liège-Limburg: an update

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The first detailed descriptions of thoracican cirripedes from the wider environs of Maastricht are those by Bosquet (1854, 1857), who also corresponded and exchanged material and publications with Charles Darwin (Jagt, 2011). His collections were subsequently revised by Withers (1935), who added a number of new species from the area. During the last three decades, a lot of material has been recovered, mostly from bulk samples, and this has resulted in the recognition of both novel records and taxa, as follows:

Vaals Formation (lower lower to lower upper Campanian): *Cretiscalpellum obtusum* Jagt & Collins, 1989, *Arcuatocalpellum dortangsi* (Collins & Jagt, 1999) new comb., *Fallaxlepas fallax* (Darwin, 1851) and *Zeugmatolepas cretae* (Steenstrup, 1837).

Gulpen Formation, Zeven Wegen Member (lower upper Campanian): an indeterminate stramentid, *Cretiscalpellum glabrum* (Roemer, 1841), *Jagtscalpellum striatum* (Darwin, 1851), *Regioscalpellum maximum* (J. de C. Sowerby, 1929), *Diotascalpellum fossula* (Darwin, 1851), *Virgiscalpellum beisseli* (Bosquet & Müller, in Bosquet, 1857), *Brachylepas naissantii* (Hébert, 1855), *Fallaxlepas fallax*, *Proverruca* n. sp. and *Priscoverruca prisca* (Bosquet, 1854). Semi-articulated capitula are available of *D. fossula*.

Gulpen Formation, Vijlen and Lixhe members (upper lower to upper Maastrichtian): *Bosquetlepas darwiniana* (Bosquet, 1854), *Cretiscalpellum paucistriatum* (Woodward, 1906), *Cretiscalpellum glabrum*, *Regioscalpellum maximum*, *Diotascalpellum fossula*, *Virgiscalpellum hagenowianum* (Bosquet, 1854), *Pycnolepas industriosa* Jagt, 2007, and *Priscoverruca prisca*.

Gulpen Formation, Lanaye Member (upper Maastrichtian): *Bosquetlepas darwiniana*, *Cretiscalpellum glabrum*, *Jagtscalpellum striatum*, *Diotascalpellum gracile* (Bosquet, 1854) new comb., *Regioscalpellum* n. sp. (?), *Arcuatocalpellum* n. sp., *Virgiscalpellum radiatum* (Bosquet, 1857), *Virgiscalpellum darwinianum* (Bosquet, 1854) and *Priscoverruca prisca*.

Maastricht Formation, lower part (Valkenburg, Gronsveld, Schiepersberg and Emael members) (upper Maastrichtian): *Bosquetlepas darwiniana*, *Cretiscalpellum glabrum*, *Virgiscalpellum darwinianum*, *Virgiscalpellum radiatum*, *Diotascalpellum gracile*, *Arcuatocalpellum* n. sp. and '*Arcoscalpellum*' *pulchellum* (Bosquet, 1854). Of special note is the find of a piece of driftwood, with dispersed valves (> 1,130) of at least six species of pedunculate cirripede and a minimum number of 126 individuals (Jagt & Collins, 1999), which allowed a better characterisation of *Virgiscalpellum radiatum* and the erection of a new species ('*Arcoscalpellum*' *mosense*).

Maastricht Formation, upper part (Nekum and Meerssen members) (uppermost Maastrichtian): *Bosquetlepas darwiniana*, *Bosquetlepas gracilis* (Roemer, 1841), *Bosquetlepas* (?) *bosqueti* (Withers, 1935), *Diotascalpellum gracile*, *Virgiscalpellum ryckholti*

Withers, 1935, *Virgiscalpellum exsertum* Withers, 1935, *Brachylepas guascoi* (Bosquet, 1857), *Proverruca* (?) *smeetsi* (Bosquet, 1857) and *Verruca jagti* Gale, 2014.

Houthem Formation, Geulhem Member (lower to middle Danian): Indeterminate scalpellids, *Faxelepas bruennichi* (Withers, 1914) and *Priscoverruca* gr. *prisca*. The second species is of particular importance in providing a link with the (middle) Danian of Denmark (Jagt & Collins, 1988).

Particularly during deposition of the Vaals Formation (predominantly during the early Campanian), the upper Gulpen Formation (Lanaye Member) and lowermost Maastricht Formation (Valkenburg and Gronsveld members), there are clear links with the Atlantic seaboard and Gulf Coast of the United States, with a number of sibling species (Table 1).

Recent and ongoing work on other Late Cretaceous cirripede assemblages elsewhere in Europe, and southern Sweden in particular, has provided numerous insights into the taxonomy and palaeobiology of calanticomorph, scalpellomorph, verrucomorph and balanomorph taxa (Gale, 2014, 2015a, b; Gale & Sørensen, 2014, 2015; Gale & Vidovic, 2023). Alongside all of Charles Darwin's originals and other material in the vast collections of the Natural History Museum, London (NHMUK) are being revised. In a series of three parts, part 1 has already come out in print (Gale, 2024).

North America	North-west Europe
<i>Arcoscalpellum bakeri</i> Collins, 1973	' <i>Arcoscalpellum</i> ' <i>mosense</i> Jagt & Collins, 1999
<i>Arcoscalpellum campus</i> Collins, 1973	<i>Diotascalpellum fossula</i> (Darwin, 1851)
<i>Arcoscalpellum hubrichti</i> Collins, 1973	<i>Regioscalpellum</i> gr. <i>maximum</i> (Sowerby, 1836)
<i>Arcoscalpellum withersi</i> Collins, 1973	<i>Diotascalpellum gracile</i> (Bosquet, 1854)
<i>Brachylepas americana</i> Zullo et al., 1987	<i>Brachylepas guascoi</i> (Bosquet, 1857)
<i>Cretiscalpellum harnedi</i> Collins, 1973	<i>Cretiscalpellum paucistriatum</i> (Woodward, 1906)
<i>Cretiscalpellum macrum</i> Collins, 1973	<i>Cretiscalpellum glabrum</i> (Roemer, 1841)
<i>Cretiscalpellum vallum</i> Collins, 1973	<i>Cretiscalpellum obtusum</i> Jagt & Collins, 1989
<i>Cretiscalpellum venustum</i> Collins, 1973	<i>Jagtscalpellum striatum</i> (Darwin, 1851)
<i>Virgiscalpellum gabbi gabbi</i> (Pilsbry, 1933)	<i>Virgiscalpellum radiatum</i> (Bosquet, 1854)

Table 1. Sibling cirripede species from Campanian-Maastrichtian strata on both sides of the Atlantic Ocean (see Jagt, 2011). Note that the generic attribution of most North American species has not yet been revised, in contrast to European ones, with the exception of '*Arcoscalpellum*' *mosense*.

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Turonian stalked barnacles from the Opole area, south-west Poland

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In general, records of Late Cretaceous cirripedes from Poland (calanticomorphs, scalpellomorphs, verrucosomorphs and balanomorphs) are few and far between (compare Collins & Radwański, 1982; Jagt et al., 2008), but from personal experience we know this to be mostly a matter of insufficient sampling. Through bulk processing, quite rich assemblages are now available from Campanian and Maastrichtian strata in southern and eastern Poland, awaiting assessment and description.

Amongst cirripede taxa recorded to date from Poland, long-ranging and widely distributed species such as *Jagtscalpellum striatum* (Darwin, 1851) and *Cretiscalpellum glabrum* (Roemer, 1841) predominate. Both occur quite commonly in the middle and upper Turonian in the wider vicinity of Opole (Odra Nowa and Folwark quarries; see Kędziński, 2008; Jagt-Yazykova et al., 2022). In recent years, special attention in the field was paid to these crustaceans, enabling us to record here the first representatives of the archaeolepadomorph family Stramentidae, both as dissociated capitular plates and attached to medium-sized phragmocones of the desmoceratoid (pachydiscid) ammonite *Lewesiceras peramplum* (Mantell, 1822) (Figure 1). Although preparation and assessment are still under way, this find looks to correspond to previous records of *Stramentum pulchellum* (G.B. Sowerby, 1843) from the United Kingdom, Germany and the Czech Republic (Withers, 1935; Oekentorp, 1989; Hauschke, 1994; Wittler, 1996; Kočová Veselská et al., 2013; Gale, 2015, 2024).

In a historical perspective, rare, isolated cirripede plates from the study area were first recorded by C.F. Roemer (1870), Leonhard (1898) and Wegner (1913). Following a preliminary revision (Jagt & Mazurek, 2011), we know that C.F. Roemer's record of *Pollicipes conicus* Reuss, 1845, actually refers to *Cretiscalpellum glabrum* (F.A. Roemer, 1841). Three decades later, Leonhard (1898) recorded *Pollicipes glaber* (= *C. glabrum*), on the basis of several valves from various localities in the Opole area and said to have come from the *Inoceramus brongniarti* inoceramid Zone of early Coniacian age. Subsequently, Wegner (1913) recorded *Scalpellum angustatum* [now *Diotascalpellum angustatum* (Geinitz, 1843)] from 'displaced' Cretaceous rocks at Königlich Neudorf (= Nowa Wieś Królewska), as well as *Pollicipes glaber* (now *C. glabrum*).

More recent records (Collins & Radwański, 1982; Jagt et al., 2008) include mostly fairly wide-ranging species such as *Zeugmatolepas cretae* (Steenstrup, 1839), *Diotascalpellum fossula* (Darwin, 1851), *Regioscalpellum maximum* (J. de C. Sowerby, 1829), *Brachylepas naissantii* (Hébert, 1855), *Priscoverruca prisca* (Bosquet, 1854) and *Eoverruca hewitti* Withers, 1935.



Figure 1. Two individuals of *Stramentum pulchellum* attached to the venter of a phragmocone of the pachydiscid ammonite, *Lewesiceras peramplum*, from the middle Turonian of Odra Nowa quarry, Opole (Uniwersytet Opolski collections, Opole). Photographs: Piotr Janecki.

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Testing for sexual dimorphism in Danian decapod crustaceans from the Faxø Limestone Quarry

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Brachyuran crabs have a highly specialized morphology with a wide, short, and flattened carapace (Rasmussen, 1977; Scholtz, 2014). The carapace is decorated with different patterns in the form of sculptures, grooves, and elevated areas (Moore, 1969). The pleons of brachyurans are strongly reduced and folded onto the ventral side (Rasmussen, 1977; Scholtz, 2014) and is used in recent crabs to determine the sex (Moore, 1969).

Sexual dimorphism is morphological differences in animal groups with separate sexes. The body size might affect both survival and reproduction by affecting fitness. Many adult animals show dimorphic body sizes between the sexes, or sexual size dimorphism (SSD). Different biological features drive sexual dimorphism, like female fecundity selection, sexual selection, or natural selection, favoring one larger sex compared to the other (Ceballos et al., 2013). Sexual selection might influence a population to develop larger males because sexual selection drives male combat. But if it is an advantage that the males are more mobile and therefore faster, sexual selection will enhance smaller males. Fecundity selection influences the females to be the larger sex (Ceballos et al., 2013), leading to a higher reproductive output and increased fitness (Baeza et al., 2012). The last type is natural selection, which via ecological conditions, enhances one larger sex compared to the other, where the type of habitat enhances different SSD. For terrestrial, semi-aquatic species and bottom walkers, larger males are favored compared to females, due to male combat and forced insemination. In these situations, it is an advantage to be larger as a male. Among the aquatic species, the females usually get larger compared to males, when the females select their partner. The larger sex (commonly males) in groups following Rensch's rule drives the differences in body size, where the smaller sex passively adapts to match the size of the dominating sex. If the dominating sex gets very large, the smaller sex will also get larger than average (Ceballos et al., 2013). Before maturity, some body parts disproportionally grow to optimize fitness when reaching maturity (Baeza et al., 2012). It is common within brachyuran crabs that females invest many resources in reproductive output (Baeza et al., 2012), expressed by a broader pleon, while males invest resources in mating success, expressed by larger chelae (Schenk and Wainwright, 2001; Baeza et al., 2012; Frigotto et al., 2013). These dimorphic secondary characters are used

to estimate maturity in brachyuran crabs (Saher and Qureshi, 2011; Silva et al., 2014), and to investigate sexual dimorphism. Growth patterns within crustaceans can illustrate sexual dimorphism and are used in studies about maturity (Saher and Qureshi, 2011; Frigotto et al., 2013; Silva et al., 2014)

It is known that crustaceans' growth rates differ between juveniles and adults, as well as between immature and mature specimens (Frigotto et al., 2013; Silva et al., 2014). Many crustaceans exhibit discontinuous growth with distinctive growth stages (Saher and Qureshi, 2011). Some body parts might grow disproportionately compared to the carapace width (allometric growth). The puberty molt from immature to mature crustaceans is a transitional molt. Significant morphological changes appear, where sexual dimorphism might be observed (Schejter and Spivak, 2005; Silva et al., 2014).

In this research, the focus is on three fossil brachyuran crab species from the Faxø limestone quarry (Paleocene, middle Danian). The hypothesis was that the carapace of females might have a broader posterior margin compared to males, due to a broader pleon for the reproductive outcome. The ontogeny and allometric growth for the three species, *Dromiopsis rugosa* (von Schlotheim, 1820), *Dromiopsis elegans* Reuss, 1858, and *Caloxanthus ornata* (Fischer-Benzon, 1866) was also investigated by using a logarithmic growth model, where the carapace width was the independent variable and all the other variables were dependent variables as in other studies (Saher and Qureshi, 2011; Baeza et al., 2012; Frigotto et al., 2013; Simpson et al., 2016). To investigate sexual dimorphism within the three brachyuran species, principal component analyses and other statistical methods were used. Furthermore, a taxonomic characterization was made. Though the posterior margin of some specimens appeared proportionally larger, it was not possible to find any sexual dimorphism from the measurements made. When looking at the allometric growth of the three species, *D. rugosa* seems to primarily have isometric growth, while *D. elegans* and *C. ornata* have more allometric growth. *Dromiopsis elegans* undergoes major differences between the small and larger specimens, which corresponds to the allometric growth.

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Assessing the effect of the Cretaceous-Paleogene mass extinction on malacostracan crustaceans in Denmark and progress on some Danian decapod assemblages

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The Cretaceous-Paleogene (K-Pg) extinction is one of the most severe mass extinctions in Earth's history, linked to a meteorite impact near Chicxulub in Mexico and Deccan Trap volcanism in India. Many major groups became extinct (ammonites, belemnites, non-avian dinosaurs, etc.) or experienced major losses in their biodiversity (bivalves, insects, echinoids, etc.). Conversely, decapod crustaceans, major contributors to marine ecosystems since the Mesozoic Decapod Revolution, appear to have experienced limited to some losses based on global analyses depending on the type of analyses (Schweitzer & Feldmann, 2005, 2023; Brösing, 2008; Klompmaker et al., 2016). Scenarios for this apparent pattern include: (1) decapod diversity was not affected significantly by the K-Pg event; (2) there was a substantial loss in diversity, but taxon richness rebounded rapidly and was not detectable in coarse global analyses; or (3) uneven sampling has distorted the true signal. Distinguishing between these scenarios has never been carried out thus far by controlled, quantitative sampling on both sides of the K-Pg boundary at sites where both latest Cretaceous (late Maastrichtian) and earliest Paleogene (early Danian) crustacean-bearing sediments are exposed. Previous research has attempted to assess a possible crustacean K-Pg extinction at a more regional scale, but sampling strategies were not provided and/or only very few decapod species were encountered on either side of the boundary (Feldmann & Tshudy, 1989; Collins & Jakobsen, 1994; Feldmann et al., 1995; Fraaije, 2003), insufficient for detailed comparative analyses.

Extensive sampling was carried out at two decapod-bearing sites, one far away (~8000 km) from the disaster area at the UNESCO site at Stevns Klint (Denmark) and one in central Alabama (USA) relatively close (~1200 km) to the impact site. For this talk, results regarding the K-Pg boundary will focus on the Danish limestone deposits near Rødvig at Stevns Klint in eastern Zealand. We performed standardized sampling per weight unit from relatively comparable sediments on both sides of the boundary. Specimens from museum collections from those sites augmented the specimens collected during our fieldwork in 2022 and 2023. After unravelling the taxonomy and biostratigraphy, we assessed the diversity, abundance, composition, and body size of the crustaceans. Preliminary results indicate a relatively low species richness in the late Maastrichtian at Stevns Klint, but species richness is higher in the

early Danian, also when augmenting our data with that of museum material and the literature. Abundance and species richness per kilogram sediment is also higher in the early Danian. Brachyuran species dominate in both the Maastrichtian and Danian strata. The most common decapod in the Danian is *Caloxanthus ornatus* von Fischer-Benzon, 1866 (>75% of specimens), while also other brachyurans and galatheoids are present in the Danian. One species of *Dromiopsis* Reuss, 1859, crosses the K-Pg boundary in the Stevns Klint area. The limited number of specimens from the Maastrichtian thus far precludes many body size analyses. To summarize, we find limited evidence for a long-term effect of the extinction event on decapods at Stevns Klint.

In addition to Stevns Klint, there are multiple other Danian sites in Denmark that may shed light on decapods after the K-Pg boundary. One site is the Sangstrup/Fornæs Klint area in eastern Jutland for which one informal report on Decapoda exists (Jensen, 2013). A new nannofossil biostratigraphic analysis has constrained the age to the early Danian. Renewed *in situ* sampling of the limestone at the site has yielded close to 1000 specimens, and we have identified more than ten species, part of which are also known from the middle Danian of Faxe quarry in eastern Zealand and the early Danian of Stevns Klint. Another site is Hesnæs Strand in southern Zealand, where various *ex situ* limestone boulders have yielded over 200 specimens. One galatheoid species, *Protomunida bennickei* Klompmaker et al., 2022, was described recently, but most of the assemblage remained unstudied. Our new studies indicate that there are about 15 decapod species present in the assemblage. Nannofossil biostratigraphic analyses suggest that the assemblage consists of a mixture of early and middle Danian decapods, however. Both assemblages are dominated by brachyurans and some galatheoids. For comparison, the very well-studied middle Danian assemblage of Faxe has yielded over 20 decapod species (e.g., Jakobsen & Collins, 1997; Klompmaker et al., 2016; Jakobsen et al., 2020; Jakobsen in Milàn et al., 2022), some of which are also reported from the middle Danian of Limhamn in Sweden (Segerberg, 1900). To summarize, though Danian decapods from the area have been studied for two centuries, ongoing research on these assemblages can shed more light on regional decapod development throughout the Danian.

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Cirripedes from Slovenia – overview, past, present and future

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Despite nearly two centuries of palaeontological research on Miocene deposits in the Central Paratethys of Slovenia, knowledge of cirripedes remains limited. Until recently, cirripedes were mentioned only sporadically, either left in open nomenclature, as epibionts on fossil specimens of interest (Mikuž, 1998; Mikuž & Horvat, 1998) or as components of studied faunal assemblages (Križnar & Mikuž, 2014). Systematic research on fossil cirripedes from Slovenia's Cainozoic deposits has only begun in recent years.

To date, only acorn barnacles have been described from this region (Buckeridge et al., 2020; Kočí et al., 2023). However, Kočová et al. (2024) recently recorded the first occurrence of the pedunculate cirriped *Scalpellum burdigalense* in Badenian (Middle Miocene) deposits at Cirknica near Šentilj, Slovenia. Additionally, Gašparič et al. (2024) briefly mentioned five species of coral-dwelling barnacles.

This abstract aims to provide an overview of cirripedes in Slovenia in light of these recent discoveries. A list of cirripede distributions in Slovenian strata is presented in Table 1 below. The potential for new finds remains promising, as a large number of undetermined acorn barnacles have been recorded in private collections from Miocene deposits. Future research will be particularly intriguing, especially in examining cirripede larvae attached to fossil leaves.

Taxon	Stratigraphic range	Locality
<i>Scalpellum burdigalense</i> Des Moulins, 1875	Miocene	Šentilj
<i>Actinobalanus sloveniensis</i> Buckeridge et al., 2020	Oligocene, Miocene	Trbovlje (Ojstro), Kamnik (Košiše)
<i>Amphibalanus venustus</i> (Darwin, 1854)	Miocene	Dolnja Stara Vas
<i>Concavus concavus</i> (Bronn, 1831)	Miocene	Podgračen, Dolnja Stara vas
<i>Balanus</i> sp.	Miocene	Lipovica
<i>Perforatus perforatus</i> (Bruguière, 1789)	Miocene	Dolnja Stara vas
<i>Creusia miocaenica</i> Procházka, 1893	Miocene	Lipovica
<i>Ceratoconcha</i> sp. 1	Miocene	Duplek, Šentilj, Ciringa
<i>Ceratoconcha?</i> <i>krambergeri</i>	Miocene	Duplek, Šentilj, Ciringa
<i>Ceratoconcha?</i> <i>darwiniana</i>	Miocene	Duplek, Šentilj, Ciringa
<i>Ceratoconcha?</i> <i>sturi</i>	Miocene	Duplek, Šentilj, Ciringa
<i>Pyrgomina?</i> <i>costata</i>	Miocene	Duplek, Šentilj, Ciringa

Table 1. The cirripedes fauna of Slovenia *sensu* Procházka, 1893, Mikuž & Horvat, 1998, Križnar & Mikuž, 2014, Buckeridge et al., 2020, Kočí et al., 2023, and Gašparič et al., 2024.

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Brachyuran crab *dactyli* of the Late Cretaceous near-shore facies in the Bohemian Cretaceous Basin, the Czech Republic

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Based on last 16 years of intensive research in the Cenomanian–Turonian near-shore deposits situated along the south and southeastern margin of the Bohemian Cretaceous Basin (Chrníky, Nová Lhota, Kaňk, Radim, Turkaňk, Velim, Vítězov, Zbyslav, Kamajka), a rich brachyuran crab assemblage is described. Numerous specimens were also found in sieved residues coming from currently overgrown and inaccessible outcrops (Předboj, Zbyslav, Vítězov). Brachyurans from dynamic near-shore environment (Žítt et al., 1997a, b) were affected by frequent transport and physical disturbance, and thus only more calcified parts (mainly cheliped *dactyli*) were more likely to be preserved in the sediment. Most of the carapaces were probably destroyed under high hydrodynamic energy regimes, which explains their scarcity in the area. Our research follows the paper of Kočová Veselská et al. (2014) in which we reported on dozens of dynomenid cheliped fragments from various late Cenomanian–early Turonian near-shore localities as well as one necrocarcinoid carapace fragment and two dynomenid carapaces of *Graptocarcinus texanus* Roemer, 1887. These carapaces are Fritsch's originals (in Fritsch & Kafka, 1887) from the lower Turonian calcareous siltstones at Kamajka representing the only known carapaces from near-shore deposits in the Bohemian Cretaceous Basin to date. Although the authors conducted 120 additional fieldworks to accessible outcrops and washed and screened a total weight of cca. 8 tons of residue through a 1 mm sieve, no other carapaces have been found in this type of paleoenvironment. This effort, however, yielded hundreds of chelipeds and isolated *dactyli* of dynomenid and dozens of etyoid brachyurans indicating that these crabs dominated the late Cenomanian–early Turonian high-energy marine environment in the Bohemian Cretaceous Basin. One paguroid *dactylus* additionally found in sieved residue from Předboj near Prague represents the first record of the group in the Bohemian Cretaceous Basin. The etyids and graptocarcinid *dactyls* were picked up from new material of Zbyslav (rescue research - the picking mesofossils under binocular microscope was started March 2023 and it is continuing by today), this material was gained by Dr. Žítt in 70s of last century and the newest

unpublished material comes from cca, over than 30 kg washed material of Dr. Jan Sklenář, that he collected in in 2012. The future research will focus on non-picked material from localities: Starkoč, Kamajka, Turkaňk and reopened overgrown localities e.g. Velim and concentrate on hemipelagic localities in Bohemian Paradise and quarry in Úpohlavy in North Bohemia.

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We are indebted to Dr. Žítt from Geological Institute of Czech Academy Sciences and Dr. Jan Sklenář (Paleontological department, Natural History Museum of National Museum in Prague), that they allowed to study their material from the locality Zbyslav (JŽ 10 kg approximately washed and dried material; JS 35 kg). We thank Ing. Lenka Váchová (Paleontological department, Natural History Museum of National Museum in Prague) who have taken images of dozens specimens under SEM in Laboratory of Paleontological department, Natural History Museum of National Museum in Prague.

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A new acanthephyrid shrimp with 3D-preserved organs from the Middle Jurassic La Voulte-sur-Rhône Lagerstätte

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Shrimps of the infraorder Caridea Dana, 1852, are extremely diverse, with more than 3000 species (De Grave & Fransen, 2011). They inhabit a wide range of environments, from tidal pools to the abyss, from freshwater environments to marine environments, and have also colonized more unusual environments such as caves and hydrothermal vents (Bauer, 2004). To trace this rich evolutionary history, one must turn to the fossil record of carideans. Unfortunately, this fossil record is relatively patchy and comparisons between living and fossil carideans are complex, as caridean systematics rely heavily on minute anatomical details that are rarely preserved in the fossil record.

Here, we use synchrotron imaging to study an exceptionally preserved fossil caridean (MNHN.F.A58277, Figure 1) from the La Voulte-sur-Rhône Konservat-Lagerstätte and compare it to modern carideans preserved in the MNHN zoological collections.

The fossil is preserved within a sideritic nodule which also encompassed a small cumacean. The specimen is exquisitely preserved, retaining most of its original volume and organs: muscles, part of the nervous system, digestive gland (hepatopancreas), heart, antennal glands, oesophagus, stomach, and proctodeum. These organs are preserved in at least two types of minerals: denser than the sideritic matrix, and lighter than the sideritic matrix. More precisely, ventrally, organs are more often replaced by the denser mineral(s), whereas dorsally, they tend to be more often replaced by the lighter mineral(s). Besides, bundles of dense mineral grains are quite abundant ventrally, around the appendages.

The detailed preservation of the specimen allowed it to be assigned to the Acanthephyridae C.S. Bate, 1888, based upon the shape of the mandibular molar process and the shape of the pereopodal epipods – features not usually visible in most fossil carideans. The stomach of our specimen is entirely filled by fragments of cuticles, mostly of two types: small cylinders, often grouped end-to-end; curved plates, some with spines. Similar fragments are also visible in the proctodeum.

Extant acanthephyrids are typically either mesopelagic (between 200-4000 m) or pelagic (1000-4000 m) (Chan et al., 2010; Poore & Ahyong, 2023). Such life habits are consistent with geological and palaeontological evidence suggesting that La Voulte-sur-Rhône was deposited in a deep-water setting. The fossilized gut contents also suggest that the specimen fed in the water column. Indeed, the abundant cuticle cylinders found within it may well correspond to multiarticulated appendages such as antennae, exopods, and pleopods, all

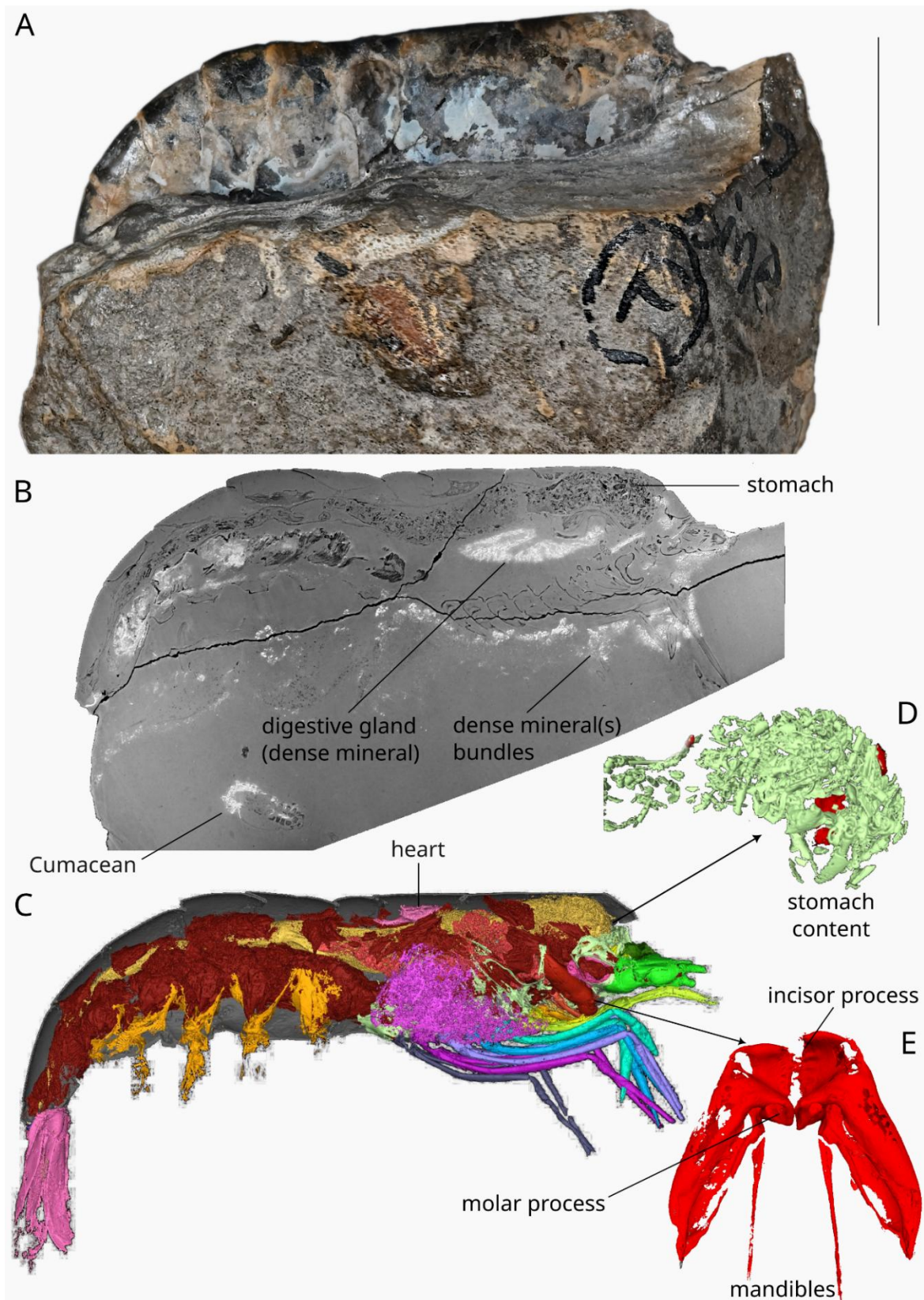


Figure 1. New species of acanthephyrid shrimp (MNHN.F.A58277) from the Callovian Konservat-Lagerstätte of La Voulte-sur-Rhône, France. A, whole specimen outside view. B, virtual slice in sagittal view. C, 3D model showing the organs. D, gut content in 3D. E, mandibles.

of which are more commonly found in planktic arthropods. As the specimen shows no visible injuries, it is possible that it was poisoned by the hydrothermal activity at La Voulte. If so, it may have come into contact with poisonous waters either while feeding in the rich environment of La Voulte or when returning to the bottom to rest after feeding in the water column.

From a taphonomic perspective, as posited by Jauvion et al. (2020), we can infer that the lighter mineral(s) correspond to fluorapatite and the denser minerals correspond to sulfides. Their prevalence in the ventral area would suggest the source of metallic ions (iron, lead) was extraneous. Indeed, the ventral side may have been an area of higher exchange rate with the outside, due to the decay of the numerous thin arthroal membranes of appendages. Moreover, the disposition of the specimen, with pereopods partially aligned on the right side of the animal, and more dense mineral grains bundles on that side, suggest it may have laid on its right side after death and during burial.

This new Acanthephiridae is the oldest known occurrence of this family. It provides a more comprehensive view of the palaeoenvironment of La Voulte and offers valuable insights into the taphonomic processes that led to the exceptional preservation of fossils in La Voulte.

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A new look at *Pygocephalus cooperi* Huxley, 1857, from the Coseley Lagerstätte (Pennsylvanian, Carboniferous), UK, using X-ray microtomography: implications for the phylogenetic affinities of Pygocephalomorpha.

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Malacostraca Latreille, 1802, is a diverse clade of crustaceans with an extensive fossil record, dating back from the Cambrian (Collette & Hagadorn, 2010). In the Late Palaeozoic (Devonian–Permian), peculiar ingroups of eumalacostracans became diversified and widespread (Schram, 1981). However, although they are well-diversified and known since the 19th century for a large proportion of them, the phylogenetic affinities of several of these Palaeozoic malacostracans are unknown due to the "problematic" nature of their anatomy. The latter is either unknown due to poor preservation or it presents a unique character states combination that prevents a direct assignment to the current malacostracan ingroups. This is particularly the case for Pygocephalomorpha Beurlen, 1930, a group of eumalacostracans with a shrimp-to lobster-like morphology known from the Late Devonian (e.g. Gueriau et al., 2014) to the Cisuralian (i.e. Early Permian; e.g. Pazinato et al., 2016). Pygocephalomorphans are particularly recognizable by their well-developed shield, their thorax bearing two pairs of maxillipeds, and by the oöstegites of the females, i.e. the specialized epipodites of the thoracic appendages, which hold the marsupium (or brood pouch). This latter character state is one of the autapomorphies of Peracarida Calman, 1904, which therefore led to the assignation of Pygocephalomorpha to Peracarida (W.T. Jones et al., 2016). However, some debates on their affinities and monophyly still exist, as Tealliocarididae, a pygocephalomorph ingroup, has been interpreted as being part of Decapoda (Clark, 2013; Gueriau et al., 2014), implying that Pygocephalomorpha might be non-monophyletic.

Nowadays, pygocephalomorphans are studied only sporadically, despite being a major component of certain faunas. For the most part, they have rarely been the subjects of "modern" work. To resolve these issues, we decided to restudy pygocephalomorphans from the Coseley Lagerstätte (Westphalian B, Pennsylvanian, Carboniferous), near Dudley, Staffordshire, United Kingdom. The Coseley Lagerstätte contains an important diversity of arthropods, remarkably preserved in 3D inside nodules (Braznell, 2006). X-ray microtomography has proven to be efficient to reconstruct their anatomy, in particular for arachnidans (e.g. Garwood et al., 2009; F.M. Jones et al., 2014). We therefore decided to apply this technique to the pygocephalomorphans, allowing us to redescribe in detail their morphology and anatomy. We were in particular able to determine their segmentation and their appendage morphology, and therefore were able to discuss their phylogenetic affinities.

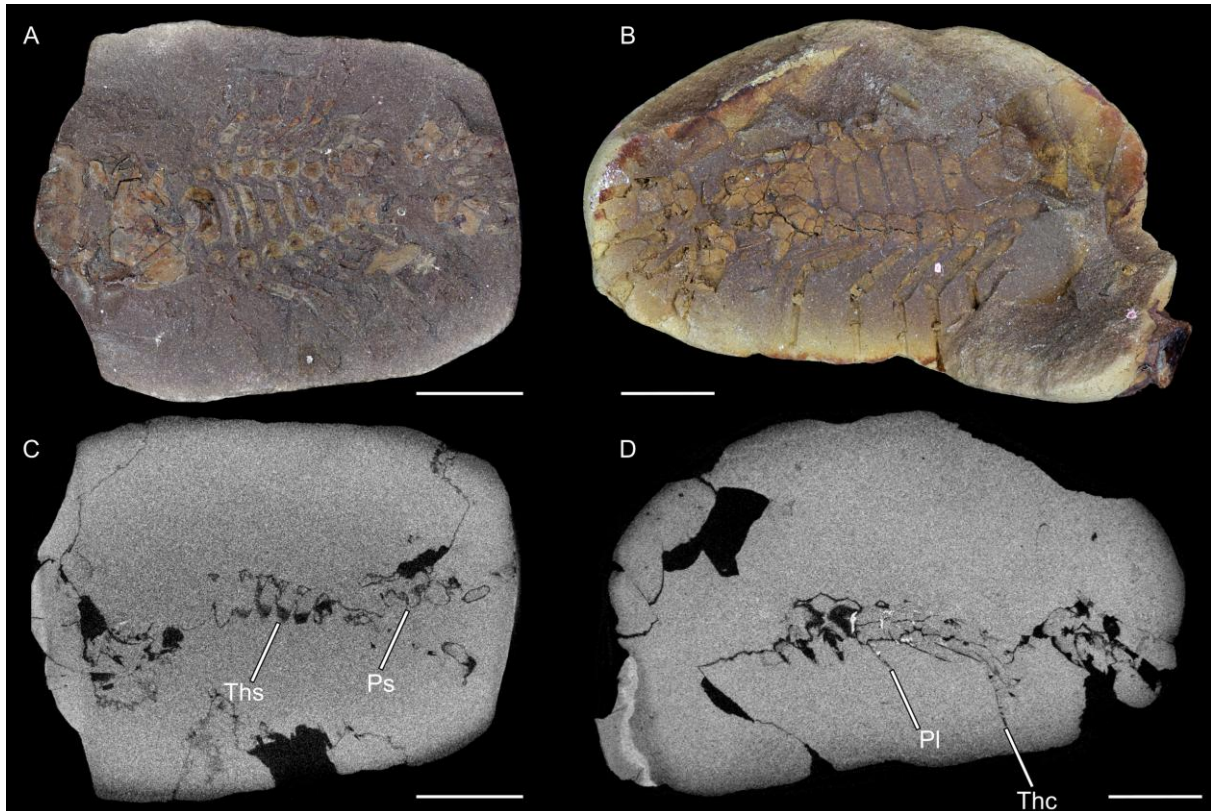


Figure 1. *Pygocephalus cooperi* Huxley, 1857, from the Coseley Lagerstätte, UK (Westphalian B, Pennsylvanian, Carboniferous). A, C, NHMUK In22847. A, ventral view. C, sagittal virtual section. B, D, NHMUK In22848. B, ventral view. D, sagittal virtual section. Abbreviation: Pl, pleopod; Ps, pleon segment; Thc, thoracopods; Ths, thoracic segment. Scales: A, C, 10.0 mm; B, D, 5.0 mm.

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The Cretaceous Crab Revolution: exceptional preservation, novel forms, and phylogenetic implications

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Brachyurans, or ‘true’ crabs, form a speciose, ecologically, behaviourally, and anatomically diverse clade of crustaceans, considered to be reciprocal sister groups with anomurans (jointly known as ‘false’ crabs and allies), and forming the clade Meiura (= Anomura + Brachyura) (Scholtz & Richter, 1995; Schram & Dixon, 2004; Hegna et al., 2020). Comprehensive molecular and morphological phylogenetic studies strongly support a monophyletic Brachyura (i.e., a group that includes their most recent common ancestor and all of its descendants), and provide solid backbones to investigate internal evolutionary relationships among and within groups, including the now widely-recognized paraphyletic (non-natural grouping) podotremes and the heterotreme eubrachyurans (Zhang et al., 2022; Poore & Ahyong, 2023; Luque et al., 2024; Wolfe et al., 2024; Pan et al., 2024, and references therein).

While molecular and morphological phylogenetics fossils provide fresh views on the brachyuran phylogenetic relationships, the fossil record offers unique and critical anatomical, spatial, and temporal information inaccessible from extant species alone (Luque et al., 2019a). Unfortunately, i) reliable fossil occurrences of early stem, crown, and structurally intermediate groups are scarce, ii) they are often fragmentary and poorly preserved, iii) convergence is pervasive among crabs, often leading to inaccurate systematic placements based on superficial similarity, and iv) they generally lack testable, quantitative assessments of such phylogenetic affinities (Luque et al., 2019a, 2024). Moreover, despite their earliest reliable fossils dating back to the Early Jurassic and the abundant and often well-preserved Cenozoic fossil occurrences (see Luque et al., 2024), most of their Cretaceous evolutionary history remains sparse and fragmentary, principally from tropical latitudes (Luque et al., 2017, 2019a), resulting in considerable biases when addressing major phylogenetic, biogeographic, and evolutionary questions (Luque et al., 2019a, 2025).

Here, I present new key and exceptionally-preserved fossil discoveries, which reveal increased anatomical and ecological experimentation during the Cretaceous, including the origins of several crown groups, unique body plans (e.g., Guinot et al., 2019; Luque et al., 2019a; Vega et al., 2022), the earliest evidence of active swimming among brachyurans (Luque et al., 2019a), fossoriality, heterochelity, and durophagy, modern-like larval forms, different visual systems (Luque et al., 2019b; Jenkins et al., 2022), multiple convergent instances of gain/loss of the crab-like body plan (i.e., carcinisation and decarcinisation) (Luque et al., 2019a; Wolfe, Luque & Bracken-Grissom, 2021), and several independent incursions into non-marine habitats (Luque et al., 2021; Wolfe et al., 2024). A growing number of key palaeontological discoveries, and the critical re-interpretations of several previous Cretaceous fossil findings using novel technologies, permits us to better assess homology and homoplasy in fossils, to re-examine earlier systematic views that were based on traditional alpha taxonomy, and to bridge the gaps between predicted molecular divergences and younger

fossil records, while challenging the paradigm of high-latitude origins of several taxa (Luque et al., 2019a, 2024).

Although several early brachyuran lineages have pre-Cretaceous origins (e.g., Klompmaker et al., 2013; Schweitzer and Feldmann, 2015; Hegna et al., 2020; Luque et al., 2024; and references therein), it is during the Cretaceous Crab Revolution that ~80% of the main brachyuran groups appear, underwent major adaptive radiations, diversification, and morphological experimentation, before settling into the modern forms seen today (Luque et al., 2019a).

Acknowledgements

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The fossil record of comma shrimp (Malacostraca: Peracarida: Cumacea): new findings and evolutionary perspectives

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Comma shrimp (Cumacea) are a group of small peracarid crustaceans with 8 families, 38 genera, and over 1900 extant species currently described (WoRMS, 2019). Surprisingly, despite their global distribution, anatomical diversity, species richness, and abundance, the fossil record of cumaceans is one of the poorest among arthropods, hindering our understanding of their evolution in deep time. This is likely due to i) their small size (1–35 mm), ii) their delicate and lightly biomineralized integument, which may reduce preservation in the fossil record, and iii) considerable taxonomic biases due to their unfamiliar anatomy, making fossil cumaceans overlooked or unrecognized both in the field and in museum samples, compared to more typical crustacean forms (Luque & Gerken, 2019; Luque & Gerken, 2024).

Here, we present a summary of the current state of knowledge of the cumacean fossil record, including a revision of stem and crown fossils, and new palaeontological findings ranging from mid-Cretaceous to Quaternary. Although a handful of Late Paleozoic fossil crustaceans have tentatively been considered as stem group cumaceans (see Luque & Gerken, 2019 for a detailed discussion), only four fossils can be reliably assigned to the crown group. These are: *Palaeocuma hessi* Bachmayer, 1960 (family unknown), from the Middle Jurassic (~165 Ma) of France; the exceptionally preserved *Eobodotria muisca* Luque & Gerken, 2019 (family Bodotriidae Scott, 1901), from the mid-Cretaceous (~95 Ma) of Colombia (Luque et al., 2019; Luque & Gerken, 2019); *Marmacuma samimei samime* Artüz & Sakiñç, 2020 (family Nannastacidae Bate, 1865), from the Late Pleistocene of Turkey (<1 Ma) (Artüz & Sakiñç, 2020); and *Makrokyllindrus itoi* Luque & Gerken, 2024 (family Diastylidae Bate, 1856), from the Plio-Pleistocene (~2.5 Mya) of Japan (Luque & Gerken, 2024). These fossils, together with a few other species from the mid-Cretaceous to the Quaternary currently under study by us, indicate that the fossil record of cumaceans is more widespread and diverse than previously known.

We suggest that the scarce and sparsely known fossil record of cumaceans likely reflects a lack of recognition due to their small size and unfamiliar anatomy, making fossil cumaceans easily misidentified, confused with crustacean larvae of unknown affinities, or interpreted as fragments of other crustaceans (taxonomic bias), rather than a lack of fossilization potential (taphonomic bias) (Luque & Gerken, 2024).

Our findings bridge a gap of more than 160 million years in the evolution of true comma shrimp, expand our understanding of the geographic and temporal distribution of higher cumacean taxa in deep time (Luque & Gerken, 2019; Luque & Gerken, 2024), and provide new and reliable data for morphological and phylogenetic studies (Gerken et al., 2022; Luque &

Gerken, 2019), understanding the appearance of key adaptations and novel forms, for tip and node dating, and molecular divergence time estimates for cumaceans in the peracarid and eumalacostracan trees of life.

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Simon Robič and his "Carniolan crab" *Tasadia carniolica* (Bittner, 1884)

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Simon Robič - a passionate naturalist

Simon Robič was born on 11. February 1824 in Kranjska Gora (Figure 1A). In his youth he was interested in fossils and plants. He attended grammar school in Ljubljana, where he also studied theology. As a priest he worked in Metlika, Loški Potok, Dob, Preddvor, Borovnica, Šenčur, Olševik and finally he stayed the longest in Šenturška Gora, where he is buried. He died on 7. March 1897. As a naturalist, Simon Robič worked in the fields of botany, zoology and paleontology. He was a passionate advocate of the use of the Slovene language, including in scientific terminology. Simon Robič began collecting fossils at an early age, when he found the first specimens in the vicinity of his native Kranjska Gora. He often shared his geological and paleontological knowledge of the surrounding area by writing popular articles. Robič began to study and collect fossils more actively and systematically after his arrival in Šenturška Gora, where he remained until his death. From there he often visited the surrounding peaks and some caves of the Kamnik-Savinja Alps and the Karavanke Mts. and explored the ridges and ravines of the Tunjice hills and the wider Kamnik area. Among the first fossils he discovered were the large Miocene gastropod *Pleurotomaria carniolica* Hilber, 1908 (Figure 1C) and the here presented "Carniolan crab" *Cancer carniolicus* (= *Tasadia carniolica*) (Bittner, 1884) (Križnar, 2013). Robič also collected and made at least a dozen paleontological collections, which he later donated or sold to schools and museums, of which only two are still preserved in Slovenia. One of such paleontological-geological collections is today kept in the Slovenian Museum of Natural History. The collection contains 269 inventoried fossil units, 116 of which are from Slovenian sites and were collected between 1880 and 1887. Among the specimens are also several fossils from classical European sites in Germany, Austria and France. Simon Robič cooperated also with some Austrian geologists and paleontologists, informing them of his knowledge of the Miocene strata in the vicinity of Šenturška Gora (Križnar & Hočevár, 2025). Robič knew at least ten caves, which he visited regularly, searching for both fossil remains of mammals and living cave fauna, especially beetles and snails (Križnar, 2024). In Mokriška jama he found the skull of a cave bear *Ursus spelaeus* Rosenmüller, 1794 (Figure 1B) and sent it to the curator of the Provincial Museum for Carniola (originally Krainisches Landesmuseum) Karl Dežman (1821-1889) (Križnar, 2024a). A species of cave beetle *Ceuthmonocharis robici* (Ganglbauer, 1899), which he discovered in the Ihanšica cave near Ihan, was also named after him. Furthermore, Robič taxidermized birds, mammals and snakes, which he bred in his garden under the church on Šenturška Gora. Initially he was also interested in flowering plants and even offered his herbarium of mountain plants for sale, but later he devoted himself entirely to non-flowering plants and fungi. He was an avid collector of mosses and lichens and was in contact with some leading experts

such as Johann Breidler (1828-1913) and Jacob Juratzka (1821-1878). Robič found four species of fungi that were described as new to science by his friend Wilhelm Voss (1849-1895) (Križnar, 2024).

In the second half of the 19th century, he was one of the most active and recognised naturalists in Carniola (today's Slovenia), and his work left its mark on the history of paleontology in Slovenia. In 2008, paleontologists discovered the remains of a Miocene dragonfly in Tunjice hills and named it *Sloveniatrum robici* Zessin, Žalohar & Hitij, 2008 in honour of Simon Robič (Zessin et al., 2008).



Figure 1. A, Portrait of Simon Robič (1824-1897) (Archive of the National Museum of Slovenia). B, Skull of a cave bear from Mokriška jama (photo: Matija Križnar). C, Original photograph of the Miocene snail *Pleurotomaria carniolica* Hilber, 1908 (after Hilber, 1908).

Discovery of the "Carniolan crab"

In the summer of 1880, Simon Robič began to actively collect fossils in the Tunjice hills, mainly in the streams southern of Šenturška Gora. It is assumed that his search for fossils was inspired by a short note by Theodor Fuchs (1842-1925) entitled Tertiary structure of the Kamnik area in Carniola (Fuchs, 1875). In the same year, during his summer holidays, he was expected to receive a visit from the Graz paleontologist Rudolf Hoernes (1850-1912), with whom he was to explore the area together, and Hoernes is said to have helped him identify some of the fossils he had collected (Kos, 1925). In 1881, Robič published a short notice in Novice on a new species of land snails, in which he also mentioned new discoveries of some fossils between Šenturška Gora and Sidraž (Robič, 1881). Robič received the identifications of these new fossil finds in the review article written by the paleontologist and geologist Vinzenz Hilber (1853-1931).

Simon Robič published an interesting three-part geological-paleontological article in a Carniolan newspaper entitled "A brief review of some hills and creeks in the foothills of Šenturska Gora from a geological and paleontological perspective" (Robič, 1882), where he wrote: "*The third fossil was a small crab, similar to the crab "Cancer brachychelus". I found six of them in the brownish sandstone by the road from Tunjice to Kamnik. Two of them still have front legs with claws*".

Through the intermediary of Vinzenz Hilber these first collected specimens of Miocene crustaceans also came into the hands of the Viennese paleontologist Alexander Bittner (1850-1902) (Bittner, 1884). Upon receipt of the decapod specimens, Bittner wrote: "*From the*

parish priest Father S. Robič from Šenturška Gora near Kamnik in Carniola, I received four specimens of rather well-preserved crabs, which this avid collector found in the deposits between Tunjice and Kamnik and which most probably belong to the Miocene" (Bittner, 1884). Based on Robič's specimens, Bittner then described a new species, *Cancer carniolicus* Bittner, 1884, today's *Tasadia carniolica* (Bittner, 1884) (Figure 2B, 2E-H). Simon Robič's collaboration with Alexander Bittner is also evidenced by several specimens now kept in the Robič paleontological-geological collection at the Slovenian Museum of Natural History. One such example is a Miocene echinoid found with a label attached to it. On the back of the label is a manuscript written by Alexander Bittner, who mentions that he found a similar species of a sea urchin between Trbovlje and Hrastnik, referring to his extensive geological-paleontological research of the Zasavje Tertiary beds (Bittner, 1884a) (Figure 2D).

Records of preserved labels and specimens confirm that Simon Robič discovered the first specimens of the "Carniolan crab" as early as 1881. This is also confirmed by one of the labels found in a small Robič's collection of fossils now kept at the Novo mesto Gymnasium (Mikuž et al., 1998) (Figure 2A). On that label, we can read that he found the fossil along the road between Tunjice and Kamnik, where the type locality of the species is and where new specimens in the Miocene sandstones can be found. This locality of the crab *Tasadia carniolica* (Bittner, 1884) should certainly be studied more thoroughly, both from a stratigraphic and paleontological point of view.

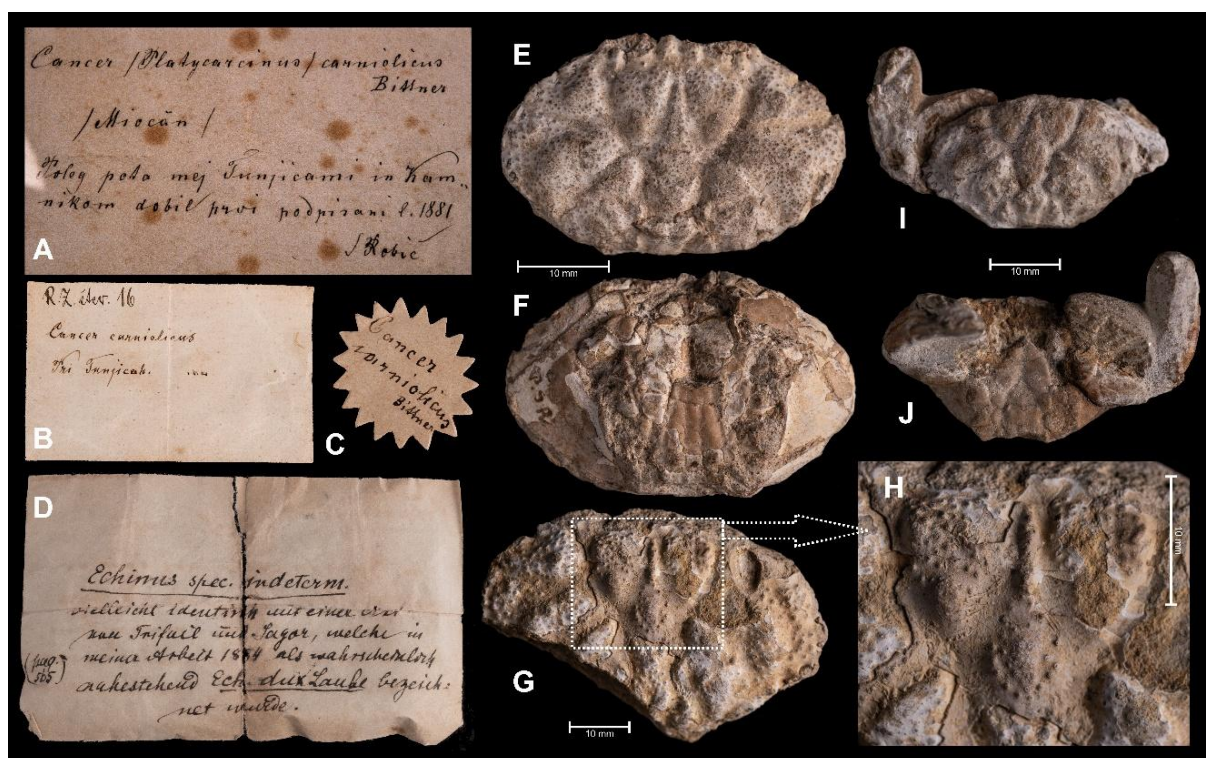


Figure 2. A, a label accompanied by a description of the fossil site and the year of discovery of *Tasadia carniolica* (Bittner, 1884), housed in the fossil collection of the Novo Mesto Gymnasium (photo courtesy of Vasja Mikuž). B-C, a label from Robič's paleontological-geological collection. D, a manuscript by Alexander Bittner on one of the labels. E-J, specimens (selected) of the carapace of *Tasadia carniolica* (Bittner, 1884), from the paleontological-geological collection of Simon Robič, housed in the Slovenian Museum of Natural History (Inv. No. SR-268 a-e, 5 specimens of carapace), photos Matija Križnar.

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Distribution of the Late Jurassic crabs (Brachyura) between Europe and Asia – palaeobiogeographical migration route riddle

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The widespread and rapid Callovian transgression in the whole European Peri-Tethyan epicratonic sea caused the origin of the Oxfordian cyanobacterial-sponge megafacies belt from Portugal to Romania and then Kimmeridgian coral-bearing facies (e.g., S Germany).

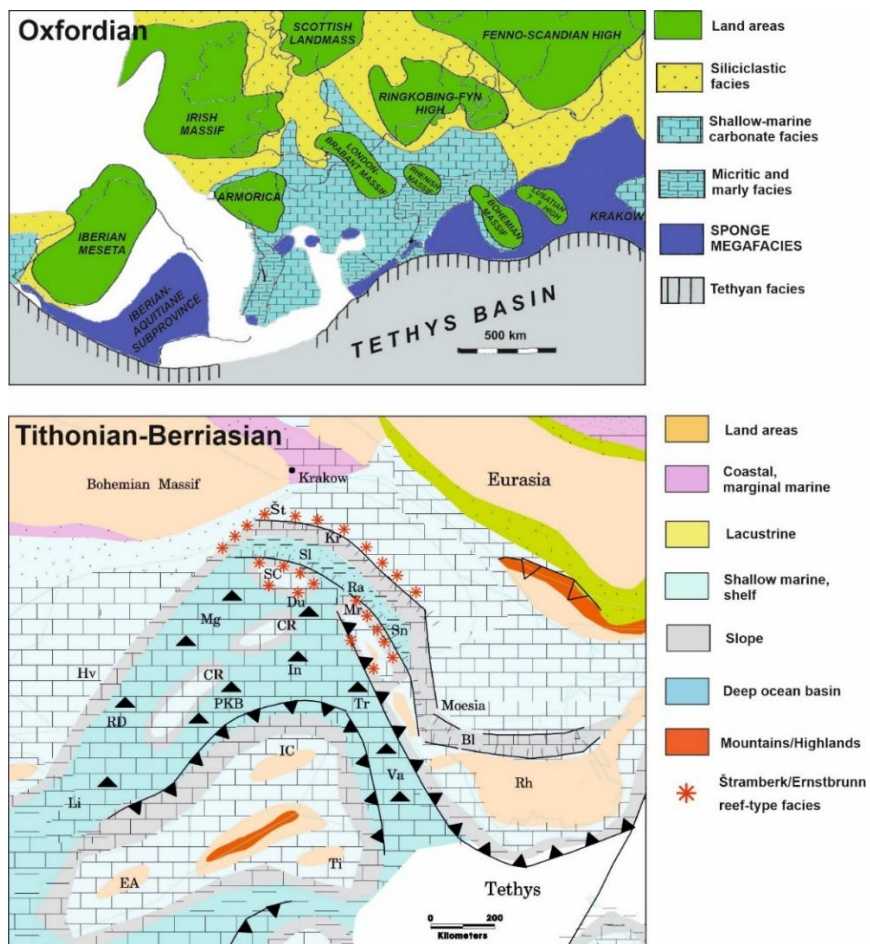


Figure 1. Palaeoenvironment and lithofacies during the Oxfordian of Europe (upper – after Matyja & Wierzbowski, 1995, simplified) and during the Tithonian-Berriasian of the circum-Carpathian area (lower) (modified from Golonka et al., 2006) with distribution of so-called Štramberk/Ernstbrunn-reef-type facies. Abbreviations: Bl – Balkan rift; CR – Czersztyn Ridge; Du – Dukla Basin; EA – Eastern Alps; Hv – Helvetic shelf; IC – Inner Carpathians; In – Inačovce-Kričovo zone; Kr – Kruhel Klippe; Li – Ligurian Ocean; Mg – Magura Basin; Mr – Marmarosh Massif; PKB – Pieniny Klippen Belt Basin; Ra – Rakhiv Basin; RD – Rheno-Danubian Basin; Rh – Rhodopes; SC – Silesian Ridge (Cordillera); SI – Silesian Basin; Sn – Sinaia Basin; St – Štramberk Klippe; Ti – Tisa plate; Tr – Transilvanian Ocean; Va – Vardar Ocean.

On the other hand, in the northernmost part of the Western Tethyan Carpathian basins the Tithonian-Berriasian coral reefs (so-called Štramberk/Ernstbrunn-reef-type limestones) flourished (Figure 1). In all these Late Jurassic facies crustaceans, including crabs, are common benthic representatives (e.g., Müller et al., 2000; Krobicki & Zatoń, 2008, 2016; Schweitzer & Feldmann, 2009a,b, 2010, 2011; Krobicki & Fraaije, 2017; Fraaije et al., 2019, 2020, 2022, 2023; Robins & Klompaker, 2019; Klompaker et al., 2020).

The explosion of the Late Jurassic crustaceans during the Brachyuran Oxfordian Explosion Event (*sensu* Krobicki & Zatoń, 2016) continued to Tithonian-Berriasian decapod-rich assemblages within European part of the Tethys Ocean. It resulted in the expansion of selected “European” taxa to the Late Jurassic environments of the Asian Eastern Tethys realm. A dozen or so years ago, new crab species were discovered in Japan (Karasawa & Kato, 2007; Kato et al., 2010) as the first fossil record of the Jurassic crabs from the circum-Pacific rim. They are mainly represented by species of *Goniodromites*, *Pithonoton* and *Planoprosopon* genera, which are common in European brachyuran assemblages as well, but their first occurrence in Europe is older (Middle Jurassic: Bajocian-Callovian) than in Asia (Late Jurassic: Oxfordian-Tithonian). These data indicate that the European Peri-Tethyan and Tethyan crab assemblages migrated into Asian Tethyan circum-Pacific realm during the Late Jurassic time (Kimmeridgian-Tithonian) (comp. Kato et al., 2010) but this migration route is still enigmatic (Figure 2) by the lack of faunas in between.

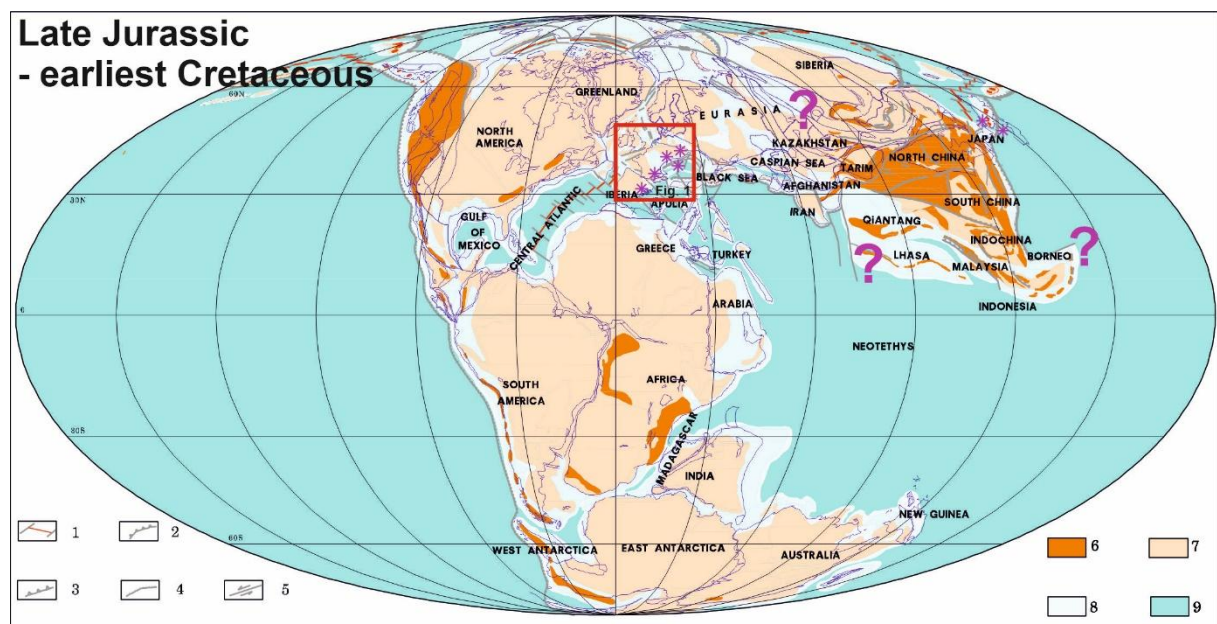


Figure 2. Global plate tectonic map with distribution of brachyurans (violet stars) and problematic migration route(s) (question marks). Explanations: 1 – oceanic spreading center and transform faults; 2 – subduction zone; 3 – thrust fault; 4 – normal fault; 5 – transform fault; 6 – mountains; 7 – landmass; 8 – shallow sea and slope; 9 – deep ocean basin (modified from Golonka, 2000).

Another problem is related to detailed knowledge on the palaeoenvironmental nature of host rocks in Japan, which are mainly clastics (sandstones, shales) (Karasawa & Kato, 2007; Kato et al., 2010), but in some cases unpublished data indicate that “shales” are in fact carbonates “closely associated with massive coralliferous reef limestones (*pers. comm. H. Karasawa*)” (Schweigert & Koppka, 2011, p. 12). The European fauna is connected with “reefs” and from palaeoenvironmental point of view it is important to exactly know what kind of rocks hosted Japanese specimens.

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Preliminary report of Neogene decapod fauna from Menorca (Balearic Islands, Western Mediterranean)

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Reports of fossil decapod crustaceans from the Neogene of Menorca Island are practically inexistent to date, despite the widely exposed fossiliferous Miocene outcrops in the Island. Only one catalog (Sánchez, 2004), some references in local press (Flores, 2008), a report of fossil remains, questionably attributed to crabs (Knight, 2024) or simply references to bioturbations, possibly caused by crustaceans (Pomar, 2001; Pomar et al., 2002, 2016), refer to fossil crabs in Menorca.

The geology of Menorca is defined by two regions: in the north by the Mesozoic and Paleozoic rocks of the Alpine fold belt horst-block of the Tramuntana region, and in the south, by the upper Miocene platforms of the Migjorn region (Bourrouilh, 1983). The Upper Miocene, where the decapods have been discovered, is represented mainly by the lower Tortonian sandstone and dolopackstone ramp deposits of the Lower Bar Unit, whereas the upper Tortonian and the lower Messinian, while present, have been largely removed by erosion (e.g. Pomar, 2012)

Remains of *Lobocarcinus' sismondai* (von Meyer, 1843) have been discovered recently *in situ* along the southern coast of the Menorca, in Tortonian sediments exposed in the coastal cliffs of Es Migjorn Gran municipality (Figure 1A). The generic and specific attribution of those remains is reliable in view of the observable features such as: carapace transversely ovate, wider than long, gently convex transversely and longitudinally; regions weakly marked, axial regions more elevated; front slightly raised and produced with three sharp triangular teeth the mesial one at lower level than the others; orbits small; and anterolateral margins widely convex with subrectangular trifid lobes, separated by closed fissures ending in a hole, as well as its narrow sternopleonal features (Figure 2A). Also, some specimens of this species have been located in the "Francesc d'Albranca" fossil collection of the Municipal Library of Es Migjorn Gran (Menorca) (Figure 1B). *Lobocarcinus' sismondai* is widely spread in the middle Miocene to middle Pliocene siliciclastic sediments of the circum-Mediterranean area, and even in the north Atlantic coast of Europe and the Central Paratethys (see Ossó et al., 2022, and references therein). *Lobocarcinus' sismondai* shows a dramatic similarity with the extant *Cancer bellianus* Johnson, 1861, and work is in progress to determine their relationships, and its possible return to its original placement as *Cancer sismondai* (see Charbonnier et al., 2024).

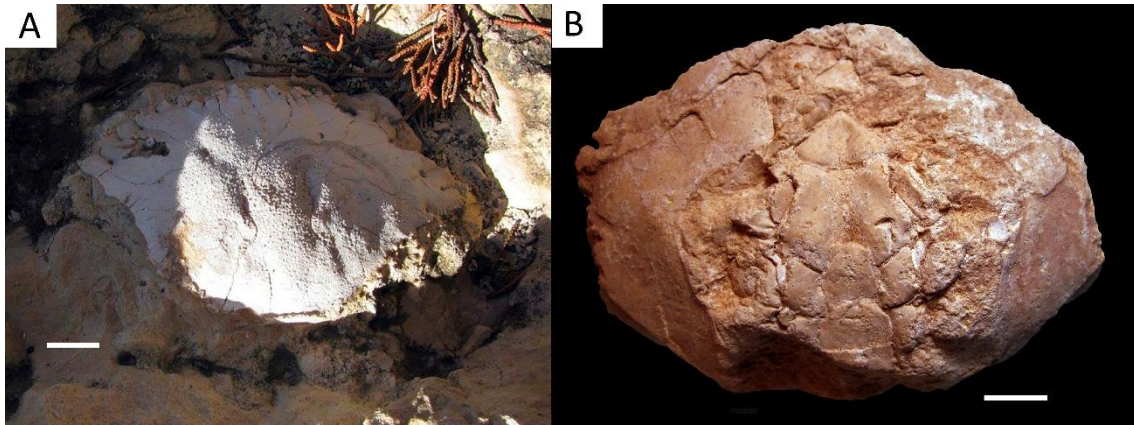


Figure 1. '*Lobocarcinus*' *sismondai* (von Meyer, 1843), from the lower Tortonian coastal rocks of Es Migjorn Gran municipality (Menorca island). A, specimen *in situ* in dorsal view. B, unnumbered specimen from the fossils collection Francesc d'Albranca, of the Municipal Library of es Migjorn Gran (Menorca), in ventral view, from unknown locality. Scale bar 10.0 mm.

Also, several *in situ* remains of another raninid decapod have been discovered in the Tortonian coastal rocks of Binissaida (southeastern Menorca). Although the remains, embedded in the rock, are sectioned tangentially by erosion, they retain enough of the profile shape and part of the cuticle to allow us to identify them reliably as raninid crabs, and in particular as *Ranina s.l.* (Figure 2A). Indeed, the ovate carapace outline and the observable spiny cuticle (Figure 2B) fits the morphology of some known Mediterranean Neogene raninids, such as *Ranina palmea* E. Sismonda, 1846, ?*R. pellattieroi* De Angeli & Beschin, 2011, or the Pleistocene *Tethiranina propinqua* (Ristori, 1891) (see Pasini & Garassino, 2018).

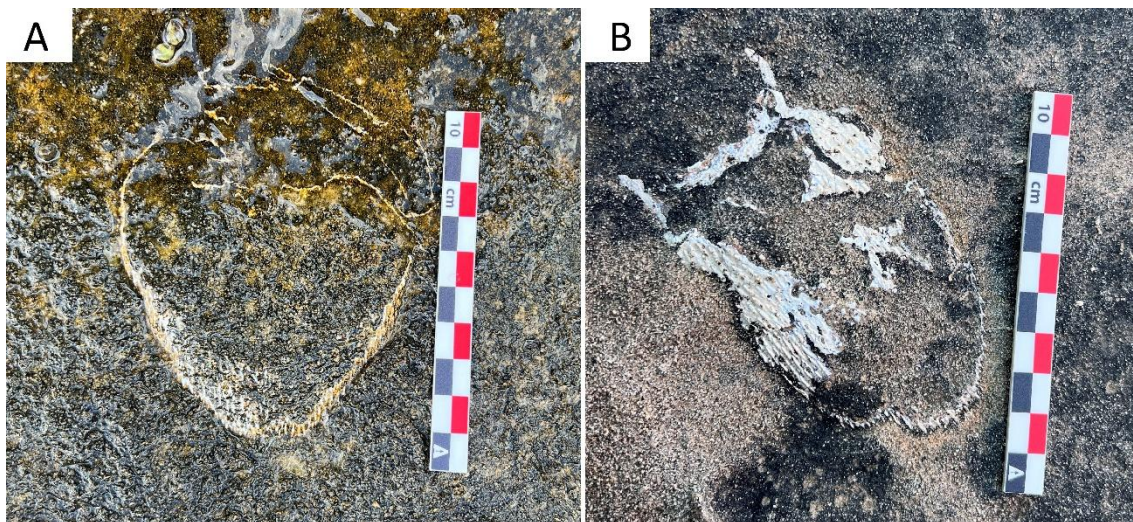


Figure 2. *In situ* specimens of raninid crabs from the lower Tortonian coastal rocks of Binissaida (southeastern Menorca). A, section of a specimen showing the typical shape of *Ranina s.l.* B, fragment of a carapace, showing the spiny cuticle typical of species of *Ranina s.l.*

These unexpected findings lead us to suggest that the richness of the Neogene decapods from the island of Menorca is yet to be discovered. Further field work, extraction of specimens after obtaining the required permit from the authorities, and review of old collections, will surely provide valuable additional information on the decapod faunas of the Neogene Mediterranean. The present note is the first formal report on fossil decapods of Menorca.

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Using quantitative morphology to compare adults and larvae of extant and fossil mantis shrimps

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Mantis shrimps, representatives of the group Stomatopoda, are predatory marine eucarid crustaceans. They are most common in tropical to subtropical regions like Southeast to East Asia or Australia (Ahyong, 1997; Piper, 2007). The fossil record of Stomatopoda is rather patchy, the oldest definitive representatives being known from the Carboniferous Bear Gulch Limestones, Montana, USA (c. 320 million years old). While the fossil record is rather long for the adult representatives, larvae are only known from much younger deposits, especially from the Jurassic Solnhofen limestones (c. 150 million years old) (Haug et al., 2008). Larvae of extant mantis shrimps mostly live as plankton in pelagic habitats. As adults they change to a benthic lifestyle, living in rock cavities, corals, or in self-built burrows in the mud (Ahyong, 1997; Piper, 2007). Due to their complex behaviour and their peculiar morphology and anatomy, extant mantis shrimps have received much attention in research, especially concerning their well-developed visual system or their raptorial appendages. Other morphological features exhibit a large diversity, like the shield and the telson, which are thus often used for species differentiation in the adult representatives. Consecutively, most research on mantis shrimp morphological diversity has focused on adult representatives. Only a few prior studies have addressed larval representatives of mantis shrimps. In this study, we quantitatively analysed three key features of numerous mantis shrimp species, including telson, shield, and major raptorial appendage. The analysed specimens comprised extant adults and larvae as well as those from the fossil record. Mantis shrimp larvae show a larger morphological diversity in the shield and the telson, most probably due to the relevance of these structures for surviving in the pelagic realm. In comparison, the adults display larger morphological diversity for the major raptorial appendages. Hence, ontogeny appears to have a strong influence on morphological diversity. The latter seems to be influenced by habitat shifts, both during individual development and over evolutionary time. The adult major raptorial appendages had a comparable morphology during the Palaeozoic as in adults today. The adult morphology of the raptorial appendages from the Mesozoic resembles that of larval representatives today. The reason could be the external ecological changes during the Mesozoic era. Telsons changed from a slimmer triangle form during the Palaeozoic to a broader square-shaped morphology today.

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The first known Cenozoic (Paleocene) galatheid from Alabama, USA

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North America has had few galatheoid occurrences identified within the fossil record, especially in comparison to the rich record across Europe. Fewer than 20 fossil galatheoid species are known from North America. The only named species from the southeastern portion of the US comes from Florida (the Pliocene *Petrolisthes myakkensis* Bishop & Portell, 1989). A yet to be officially described Eocene species is known from North Carolina (Frantescu, 2013), and Sohl (1964) listed a Late Cretaceous record of *?Galathea* sp. from Alabama based on a carapace and abdominal segments found in a drill core, but this specimen has not been located thus far. This paucity is at least in part due to the lack of recognition of these generally small anomurans.

Re-examination of historic localities with paleoenvironments that may have hosted decapods has recently yielded positive results in southern Alabama, USA. The Salt Mountain Limestone locality, so named because it abuts a Jurassic salt dome and was utilized as a salt source during the 19th and 20th centuries, extends across a large subsurface area. It is only known to crop out in one area at the surface along the Jackson Fault at the aptly named ‘Salt Mountain’ (Toulmin, 1940a; Bryan, 1991; Bryan et al., 1997; Kopaska-Merkel et al., 2013). It is a late Paleocene (late Selandian - early Thanetian), heavily altered and recrystallized muddy limestone with patchy sponge-dominated and coral-accessorized reef outcrops (Bryan et al., 1997). Large corals have been found – and preferentially removed by local collectors – from the limited surficial outcrop exposure (Toulmin, 1967, quoted in Bryan et al., 1997). Additional groups include echinoderms, annelids, bryozoans, sponges, brachiopods, foraminiferans, mollusks (primarily molds), ostracods, and algae (e.g., Toulmin, 1940a, 1940b, 1941; Bryan et al., 1997). Decapod crustaceans, a common element in extant and fossil reef environments, had not been reported in the literature, though Toulmin (1940a, p. 103) possibly referred to them when mentioning “crustacean fragments.” With this knowledge, a renewed effort was made to examine the outcrop recently. Close examination of these rocks in the upper (lower Thanetian) part of the section has yielded the first occurrence of a fossil galatheoid from the Cenozoic of Alabama, comprised of 10 carapace parts and assignable to a member of Galatheidae based upon the presence of transverse carapace ridges and a triangular rostrum with spines along the lateral margins.

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Wattendorf, the stratigraphically oldest Solnhofen-type Plattenkalk site in Germany and its decapod fauna

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Upper Jurassic Solnhofen-type deposits are among the best-known fossil conservation Lagerstätten worldwide. Most of these deposits are located in the southern and southeastern part of the Franconian Alb, where these limestones have been exploited since centuries for various commercial purposes. In older literature, these localities, especially those in the closer Solnhofen and Eichstätt areas, are often lumped as “Solnhofen Lithographic Limestones” or “Solnhofen Plattenkalks” and generally assigned to an Early Tithonian age. More recent studies of ammonite assemblages revealed that various localities have different stratigraphical ages (Schweigert, 2007; Tischlinger & Schweigert, 2020). The hitherto oldest-known fossiliferous Upper Jurassic Plattenkalk site, late Kimmeridgian (Pseudomutabilis Zone) in age, is located close to the village of Wattendorf in the northernmost part of the Franconian Alb, east of the town of Bamberg. This Plattenkalk is represented by a few up to decimetres-thick layers of laminated limestones within a series of bioturbated thicker-bedded mudstones. These limestone beds were deposited in a local depression between massive dolomitized reefal limestones. Both lithologies are exploited in an active quarry. Scientific excavations by a team of the Bamberg Natural History Museum and still ongoing excavations by amateur palaeontologists resulted in the discoveries of spectacular fossils, namely pterosaurs, marine crocodiles, sharks and coelacanths as well as fishes (e.g., Fürsich et al., 2007; Mäuser, 2015; Sachs et al., 2021; Martill et al., 2023). Besides the vertebrate remains and various mollusks (ammonites, belemnites, vampyromorph squids, bivalves, gastropods), a rich assemblage of arthropods came to light, of which only the iconic polychelid lobster *Soleryon schorri* is described in detail yet (Audo et al., 2014). The fossils are often preserved as moults or fragmentary remains of predation. Interactions between living crustaceans and the substrate have never been noticed. The decapod assemblage of Wattendorf comprises additional polychelid, erymid, glypheid and palinurid lobsters besides a variety of shrimps and other groups of crustaceans. The bulk of these fossils can be assigned to genera already described from younger deposits. At the specific level, however, morphometric and other differences are often noticeable, either as the result of evolutionary changes over time or environmental adaptations. In contrast to most younger Plattenkalk deposits in southern Germany, larger shrimps are mainly represented by the genera *Aeger* and *Bylgia*, whereas the otherwise common penaeid *Antrimpos* is extremely rare and still incompletely known from this site. Smaller-sized penaeid shrimps (e.g., *Dusa*, *Drobna*, *Buergerocaris*) and representatives of Caridea occur as well (e.g., *Alcmonacaris*, *Hefriga*). Ghost shrimps are represented by *Magila* sp. Despite the presence of shallow reefal environments in the near surroundings, neither

brachyurans nor anomurans have been recorded so far, whereas hermit crabs are represented by several isolated chelae.



Figure 1. Left: *Eryma veltheimii* Münster, 1839; right: *Aeger* cf. *insignis* Oppel, 1862. Upper Kimmeridgian Plattenkalk of Wattendorf near Bamberg, Germany (both specimens in private collection of M. & M. Wulf).

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Ecological guilds in Mesozoic Brachyura: a functional and macroevolutionary framework

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Recent study explores the emergence, diversification, and macro-evolutionary significance of ecological guilds within Mesozoic brachyuran crabs, offering a novel perspective on the functional morphology and palaeoecology of this diverse group. Building upon the classical guild concept as originally defined by Root (1967), and in a context of decapod crustaceans refined through the works of Schäfer (1954) and Glaessner (1980), an ecological classification of brachyuran crabs based on behavioural adaptations, morphological specialisations, and environmental interactions, can be proposed. This framework departs from narrow dietary classifications by incorporating full ecological resource use, thus allowing for a more integrative palaeobiological analysis.

Within this context, six principal brachyuran guilds are defined: walking, back-burying, burrowing, swimming, porter, and reef-dwelling guilds. Back-burying and swimming guilds are considered locomotion-driven innovations arising during the mid-Cretaceous in response to changing environmental conditions associated with the Mesozoic Marine Revolution (MMR). Through detailed analysis of morphological traits — including modifications to the carapace, pereopods, pleon, respiratory and reproductive structures — the origin and macroevolutionary trajectories of these guilds can be reconstructed. For instance, the back-burying guild reveals a shift away from carcinisation towards elongation and respiratory optimisation, while the swimming guild demonstrates multiple independent origins of analogous paddle-like appendages across both podotreme and eubrachyuran lineages.

These evolutionary innovations illustrate the adaptive significance of locomotory innovation in the context of ecological diversification and macroevolutionary success during the Mesozoic. By integrating palaeontological, functional, and ecological data, this framework provides a foundation for comparative studies across fossil decapod assemblages, offering new insights into the evolutionary ecology and palaeobiodiversity of Brachyura.

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A new decapod crustacean fauna from the Pliocene of Cyprus

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The Middle Miocene witnessed the closure of the connection between the Mediterranean Sea and the Indian Ocean (Bialik et al., 2019), to be followed by changes in the link with the Atlantic Ocean, which eventually led to the Messinian Salinity Crisis (MSC) (Bulian et al., 2021). During the MSC, the Mediterranean basin changed into a giant salty lake, and this had a great ecological impact on ecosystems in the Mediterranean Basin (Roveri et al., 2014). Numerous species disappeared as a result of high salinity levels, some (e.g. corals) going extinct (Agiadi et al., 2024). Following the MSC, the onset of the Pliocene was characterised by rapid marine reflooding of the Mediterranean Basin (Rouchy et al., 2001; Garcia-Castellanos et al., 2009). This, in turn, offered new opportunities for species to return to the Mediterranean, although it may have taken a few thousand years to (re-)establish ecosystems entirely (Agiadi et al., 2024).

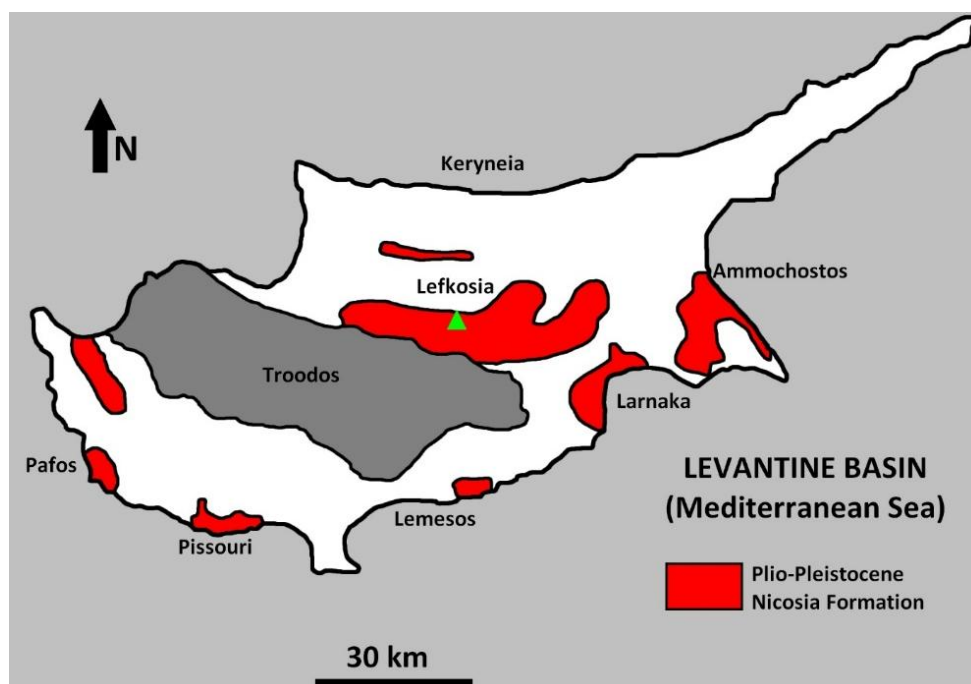


Figure 1. Map of Cyprus, showing the locality, indicated with a green triangle (adapted from Tsiolakis et al., 2019).

During the earliest Pliocene, strata assigned to the Nicosia Formation were laid down. This unit comprises a c. 750-m-thick sequence of marls, sands and chalks (Schirmer et al., 2010; Balmer et al., 2018). The type area of this formation is near Nicosia, but there are outcrops all over Cyprus (Tsiolakis et al., 2019). The decapod crustacean material presented in the present study was surface collected from the sandy facies of the Nicosia Formation, which crops out in the cliff into which the Panagia Chrysospiliotissa Church was hewn near Kato Deftera, to the south-east of Nicosia (Figures 1-2).

Numerous extant and extinct decapod crustaceans have been recorded from Cyprus to date (e.g. Heller, 1863; Lewinsohn & Holthuis, 1986; Fraaije, 2014; Wallaard et al., 2020, 2023; Wallaard, 2025). The aim of the present study is to further knowledge of Pliocene decapod crustaceans from the island and focus on changes in this group's biodiversity due to the impact of the MSC.



Figure 2. Leucosiid from the Pliocene of Cyprus.

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