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First record of the portunid crab *Bathynectes muelleri* Ossó & Stalennuy, 2011 (Crustacea, Decapoda, Polybiidae) from the Early Miocene of Slovenia

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ABSTRACT
A fossil specimen of the portunoid crab genus *Bathynectes* Stimpson, 1871, is described from Early Miocene (Ottnangian-Karpatian) marls exposed at Meljski hrib, near Maribor, northeastern Slovenia. Based on dorsal carapace morphology, the material is referred to *Bathynectes muelleri* Ossó & Stalennuy, 2011, previously known only from Middle Miocene (Badenian) deposits of western Ukraine. This record represents the first occurrence of the species in the western part of Central Paratethys and extends its stratigraphic range into the Early Miocene. The co-occurrence of *B. muelleri* in both reefal and deep-water hemipelagic facies highlights significant bathymetric plasticity during the Miocene. The observed pattern aligns with a broader palaeoecological shift among portunoids and other decapod crustaceans toward deeper marine environments during the Neogene.

KEY WORDS
Decapoda,
Polybiidae,
Bathynectes,
Central Paratethys,
Miocene,
palaeoecology.

RÉSUMÉ
Première mention du crabe portunidé Bathynectes muelleri *Ossó & Stalennuy, 2011 (Crustacea, Decapoda, Polybiidae) dans le Miocène inférieur de Slovénie.*
Un spécimen fossile du crabe portunoïde du genre *Bathynectes* Stimpson, 1871, est décrit dans les marnes du Miocène inférieur (Ottnangien-Karpátien) affleurant à Meljski hrib, près de Maribor, dans le nord-est de la Slovénie. Sur la base de la morphologie du bouclier dorsal, le matériel est attribué à *Bathynectes muelleri* Ossó & Stalennuy, 2011, jusque-là connu uniquement dans les dépôts du Miocène moyen (Badénien) d'Ukraine occidentale. Cet enregistrement constitue la première mention de l'espèce dans la partie occidentale de la Paratéthys centrale et prolonge son intervalle stratigraphique jusqu'au Miocène inférieur. La présence concomitante de *B. muelleri* dans des faciès récifaux et hémipélagiques profonds met en évidence une plasticité bathymétrique marquée au cours du Miocène. Ce schéma s'aligne sur une tendance paléoécologique plus large observée chez les portunoïdes et d'autres crustacés décapodes, témoignant d'un déplacement progressif vers des environnements marins plus profonds au cours du Néogène.

MOTS CLÉS
Decapoda,
Polybiidae,
Bathynectes,
Paratéthys centrale,
Miocène,
paléoécologie.

INTRODUCTION

The genus *Bathynectes* Stimpson, 1871, comprises extant portunoid crabs (Brachyura: Polybiidae) that inhabit deepwater environments across the Atlantic Ocean and Indo-West Pacific. Modern representatives are predominantly found at outer shelf to bathyal depths, typically ranging between 200 and 2000 metres (Manning & Holthuis 1981; Abelló *et al.* 2001).

Despite the wide geographic range of the genus *Bathynectes* in the present day, the fossil record remains limited. To date, only two fossil occurrences have been documented. The first is *Bathynectes muelleri* Ossó & Stalennuy, 2011, from the Middle Miocene (Badenian) carbonate reef facies of the Maksymivka Quarry in western Ukraine. The second is *Bathynectes longipes* (Risso, 1816), an extant species, also recorded from Lower Pleistocene deep-water clay deposits in Tuscany, Italy (Baldanza *et al.* 2013).

Miocene deposits of northeastern Slovenia, particularly those exposed in the vicinity of Maribor and within the broader Mura Depression, have yielded a modest but informative assemblage of fossil decapod crustaceans (Hyžný *et al.* 2014; Gašparič & Halásová 2015; Gašparič *et al.* 2021; Gašparič *et al.* 2025). In this study, we report a new, stratigraphically older occurrence of *Bathynectes muelleri* from Lower Miocene (Ottnangian–Karpatian) marls of the Meljski hrib locality near Maribor, northeastern Slovenia.

GEOLOGICAL SETTING

A specimen of a portunoid crab was collected from yellowish marls exposed in a talus deposit at Meljski hrib, near Maribor, northeastern Slovenia (46°33'38"N, 15°40'33"E) (Fig. 1). This locality is known for yielding a diverse Miocene invertebrate fauna and fossil wood (Mikuž & Gašparič 2014). The fossiliferous succession is exposed in near-vertical cliffs up to 100 m in height. The sediments are assigned to the Early Miocene (Ottnangian-Karpatian) based on calcareous nannoplankton (Gašparič *et al.* 2021).

The lower portion of the sequence consists of dark grey siltstones and sandstones, poor in macrofossils. Gašparič & Halásová (2015) reported the crab *Styrioplax exiguus* (Glaessner, 1928), although the callianopsid ghost shrimp *Callianopsis jahringensis* (Glaessner, 1928) is more abundant (Gašparič *et al.* 2025). The upper sequence comprises indurated light grey marls with calcite-rich concretions, yielding deep-water bivalves, echinoids, and mass mortality assemblages of brittle stars and the lobster *Metanephrops serendipitus* Gašparič, Tshudy, Chan & Ćorić, 2023.

These sediments are part of the Slovenske gorice tectonic unit (Pavšič & Horvat 2009), deposited within the Mura Depression of the Central Paratethys (Fodor *et al.* 2002), a marine seaway linking the Mediterranean and Eastern Paratethys during the Miocene (Rögl 1999; Bartol *et al.* 2014). The regional stratigraphy spans from the Early Miocene (Karpatian) to the Middle Miocene (Sarmatian), primarily dated by foraminiferal and calcareous nannoplankton assemblages (Rijavec 1976; Bartol *et al.* 2013; Gašparič & Halásová 2015).

MATERIAL AND METHODS

The study is based on a single dorsal carapace specimen preserved in yellowish marl. Specimen RGA/SMNH 6949 is registered as part of the palaeontological collections of the Slovenian Museum of Natural History, Ljubljana.

Preparation was conducted under Leica SZ4 and EZ4D stereomicroscopes. Images were captured with a Nikon Z7II digital camera equipped with a Nikkor Z MC 50 mm f/2.8 lens. A latex cast was whitened using ammonium chloride sublimate for photographic contrast. Image stacks were processed in Helicon Focus and edited in Adobe Photoshop CS6.

ABBREVIATIONS
RGA/SMNH Museum of Natural History, Ljubljana, Slovenia (Palaeontological collection of the Institute for Palaeobiology and Evolution);
TKMP Regional Museum of Ternopil, Ukraine;
MGB Museu de Geologia de Barcelona, Catalonia.

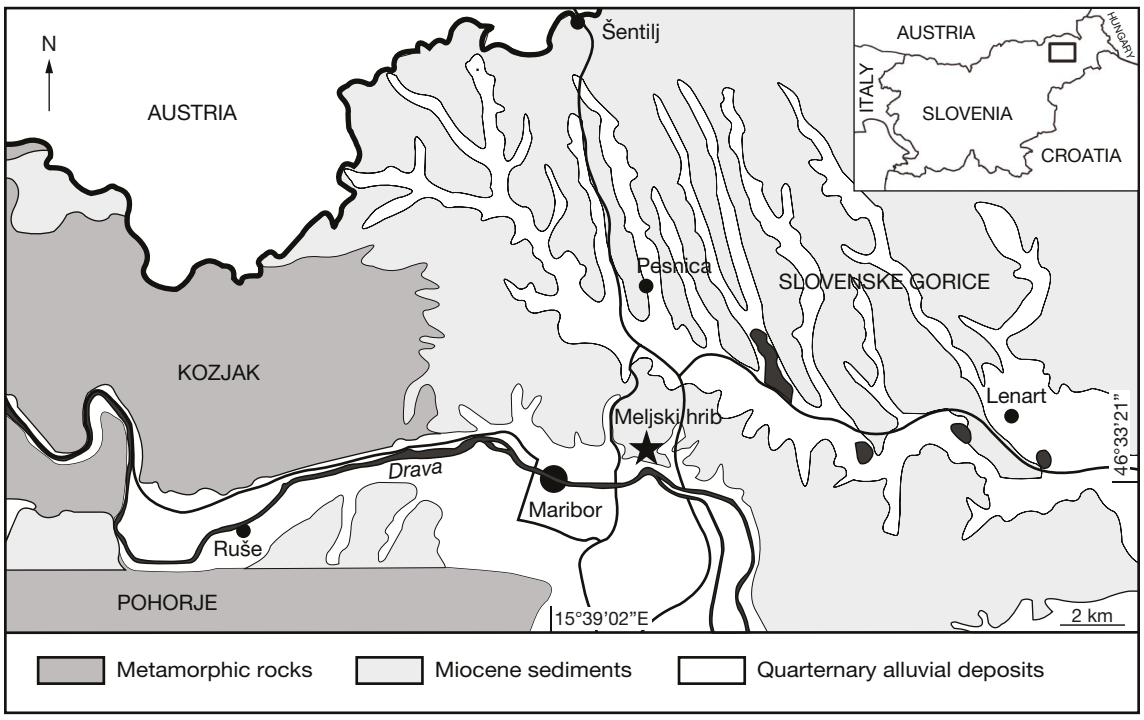


FIG. 1. — Simplified geological map of northeast Slovenia. The locality of Meljski hrib is marked with a star. Map by Rok Gašparič.

SYSTEMATIC PALAEONTOLOGY

Order DECAPODA Latreille, 1802
Infraorder BRACHYURA Latreille, 1802
Superfamily PORTUNOIDEA Rafinesque, 1815
Family POLYBIIDAE Paulson, 1875

REMARK

We consider Polybiidae as a full family in accordance with the latest works based in molecular phylogenies such as Wolfe *et al.* (2024).

Genus *Bathynectes* Stimpson, 1871

TYPE SPECIES. — *Bathynectes longispina* Stimpson, 1871, by subsequent designation.

REMARK

Characteristic morphological features of the genus include a moderately broad and subhexagonal carapace, distinct four-lobed front, spiny anterolateral teeth, and well-developed orbits. These traits distinguish *Bathynectes* from other polybiid genera (Zariquiey 1968; Poore & Ahyong 2023).

Bathynectes muelleri Ossó & Stalennuy, 2011 (Fig. 2A-F)

ORIGINAL DESCRIPTION. — Carapace subhexagonal, slightly wider than long; convex longitudinally, more at anterior third, relatively less convex in transverse section; maximum width at midlength of carapace; regions weakly defined; dorsal surface almost smooth. Dorsal regions weakly defined, epigastric and hepatic regions slightly swollen; protogastric, metagastric, epibranchial, and cardiac regions inflated. Branchial lobes inflated, laterally forming a low transverse ridge that connects epibranchial teeth across metagastric region. Front weakly four-lobed, outer lobes larger than inner lobes. Orbits small with two closed fissures on supraorbital margin; infraorbital margin visible in dorsal view. Anterolateral margin convex, with four teeth, excluding outer orbital tooth, first and second ones triangular, third and fourth teeth spiniform. Posterolateral margin slightly concave, smooth, converging posteriorly, with reentrant of fifth pereiopod well marked and almost parallel mesobranchial keel. Posterior carapace margin straight, rimmed, after Ossó & Stalennuy (2011: 41).

TYPE MATERIAL. — **Ukraine** • 2 specimens; Maksymivka quarry, ENE of Ternopil; Middle Miocene (Badenian); holotype: TKMP 1701 95840; paratype: MGB 59600.

ADDITIONAL MATERIAL EXAMINED. — **Slovenia** • 1 specimen; Meljski hrib, Maribor; Early Miocene (Ottnangian/Karpatian); RGA/SMNH 6949.
Ukraine • 4 specimens; Maksymivka quarry, ENE of Ternopil; Middle Miocene (Badenian); RGA/SMNH 1956, 1957, 2001, 2583.

MEASUREMENTS. — Carapace width (from the base of the epibranchial tooth [last anterolateral tooth]): 20 mm; length: 17 mm (estimated); orbito-frontal width: 7 mm.

LOCALITY AND AGE. — Meljski hrib, Maribor, Slovenia. Early Miocene (Ottnangian-Karpatian), calcareous nannoplankton zone NN4 (Martini 1971).

DISTRIBUTION. — Until now, known only from Middle Miocene (Badenian) of the type locality Maksymivka quarry, Ternopil, Ukraine.

DESCRIPTION

Carapace small, subhexagonal in outline, broader than long, with maximum width at the level of the epibranchial (fourth

and last anterolateral) tooth. Dorsal surface gently convex in longitudinal profile, strongly vaulted in the anterior third, and slightly convex in transverse section at mid-carapace. Surface finely granular overall, with coarser granules concentrated on elevated areas of the anterior protogastric lobes, epibranchial lobes, and cardiac region.

Frontal margin relatively broad, comprising approximately one-third of the total carapace width, weakly four-lobed; outer lobes twice as wide as the inner pair. Orbits well developed, bearing two closed fissures: one median and a second near the outer orbital tooth. The orbital margin features a small, blunt, triangular inner orbital tooth and a prominent, rounded outer orbital tooth.

Anterolateral margin broadly convex, bearing four distinct teeth (excluding the outer orbital tooth). The first tooth lies just posterior to the outer orbital tooth, is triangular, and directed anteriorly. The second and third teeth are progressively sharper, anteriorly curved, and spiniform; the third is separated from the second by a distinctly longer, U-shaped notch. The fourth tooth (epibranchial) is the most prominent, spiniform, directed laterally with its tip gently curved anteriad; it is approximately twice the length of the preceding teeth and densely granulated. Posterolateral margins slightly concave and converging posteriorly; remains of reentrant of the fifth pereiopod appear well-marked. Posterior margin not preserved.

Dorsal regions moderately defined; cervical and branchiocardiac grooves well marked. Two small epigastric swellings present at the base of the front; protogastric lobes large and inflated. Mesogastric process clearly delineated; hepatic region slightly swollen. Metagastric region inflated; urogastric region depressed. Metabranchial lobes inflated, forming part of the posterolateral carapace contour; mesobranchial region notably depressed. Urogastric region faintly defined by a short, narrow transverse inflation, below the two gastric pits. Cardiac region large, strongly inflated, bearing a short but distinct cardiac ridge. Intestinal region not preserved. A discontinuous epibranchial transverse ridge extends sinuously inward from the base of the last anterolateral (epibranchial) tooth toward the midline.

Remarks

The specimen closely resembles *Bathynectes muelleri* Ossó & Stalennuy, 2011, from the Middle Miocene of the Ukraine in overall carapace outline, general ornamentation, and region delineation. Both display a subhexagonal carapace, slightly broader than long, with maximum width at the level of the epibranchial tooth, and a moderately vaulted anterior region. The anterolateral margin in both bears four teeth, with the epibranchial tooth (fourth) being the most prominent, spiniform, and granulated, projecting laterally with a slight anterior curvature. The orbital configuration is also consistent, notably the presence of two closed orbital fissures, a rounded outer orbital tooth, and a triangular inner tooth, a key character state shared between the two.

Furthermore, the dorsal surface granulation pattern, with finer granules over most of the carapace and coarser granules localized on elevated regions (e.g., protogastric and epibranchial lobes), matches well with *B. muelleri* as described by Ossó & Stalennuy (2011).

Differences, such as the sharper, spiniform anterolateral teeth, more pronounced granulation of the epibranchial tooth and a more marked separation between the second and third anterolateral teeth via a U-shaped notch, are interpreted as intraspecific or possibly ontogenetic variations. Given the scarcity of fossil material for *B. muelleri*, these characters fall within the expected morphological range for the species.

The extant *Bathynectes longipes* Risso, 1816, the closest species to *B. muelleri*, differs from the present specimen in several key aspects. Notably, *B. longipes* possesses a proportionally narrower carapace, with a less vaulted anterior region and weaker granulation, particularly on the epibranchial and cardiac areas. The anterolateral teeth in *B. longipes* are generally less spiniform and more evenly spaced without the strongly granulated, elongated epibranchial tooth seen in the fossil species. The orbital margin in *B. longipes* tends to be less complex, often lacking a clearly defined triangular inner orbital tooth and only showing a single orbital fissure, or none at all in some populations.

The epibranchial transverse ridge, an important diagnostic feature in *Bathynectes*, is distinctly different between the extant *B. longipes* and the Middle Miocene *B. muelleri*. In extant species, the ridge is prominently developed, complete, sharply defined, and continuous between the epibranchial teeth, particularly acute in juvenile specimens. By contrast, *B. muelleri* exhibits a more subdued, swollen ridge that is interrupted medially at the level of the metagastric region, resulting in a sinuous and discontinuous expression of this structure.

Despite minor differences the material is confidently referred to *Bathynectes muelleri*, extending the known geographic and stratigraphic range of the species into the Early Miocene (Ottnangian–Karpatian) of the Central Paratethys.

DISCUSSION

The occurrence of *Bathynectes muelleri* in Early Miocene (Ottnangian-Karpatian) deposits of northeastern Slovenia extends the known stratigraphic and palaeogeographic range of the species beyond its original Middle Miocene (Badenian) type locality in western Ukraine. This new record demonstrates that *B. muelleri* has occupied a broader range of palaeoenvironments than previously recognized. While the Ukrainian specimens are associated with shallow marine reefal carbonates, the Slovenian material derives from hemipelagic marls indicative of lower shelf to upper bathyal settings. This disparity in depositional environments highlights the ecological flexibility of *B. muelleri* and suggests that it was capable of inhabiting both shallow and deeper marine habitats.

Such bathymetric versatility is significant in the context of the Neogene evolution of the genus *Bathynectes*, whose extant representatives predominantly inhabit deeper, bathyal environments (Manning & Holthuis 1981; Türkay 2001; Muñoz *et al.* 2024). In contrast to its congeners, which are

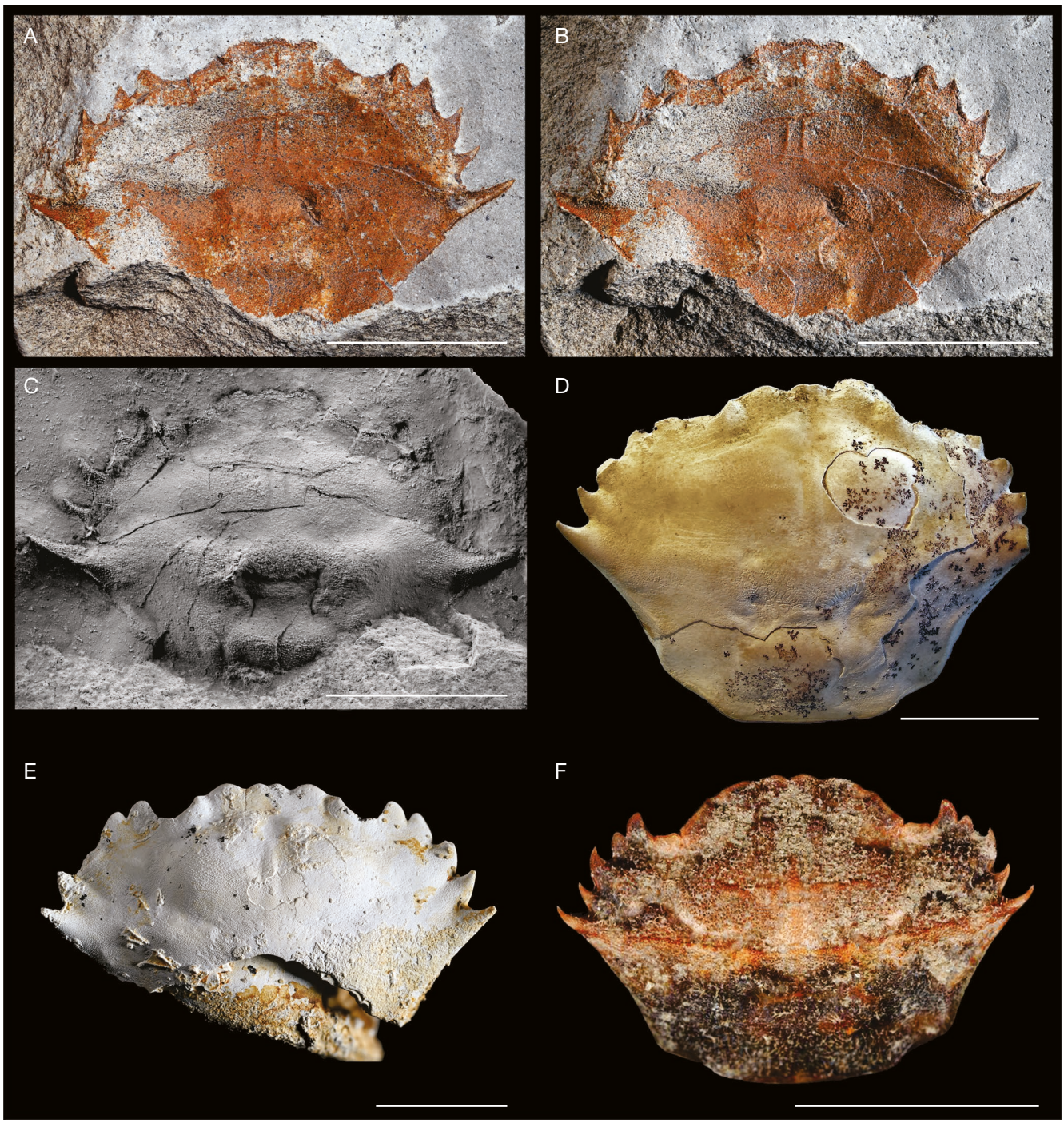


Fig. 2. — Dorsal carapaces of *Bathynectes* Stimpson, 1871: **A**-**E**, *Bathynectes muelleri* Ossó & Stalennuy, 2011; **F**, *Bathynectes longipes* (Risso, 1816); **A**, RGA/SMNH 6949 (Slovenia), directional lighting; **B**, RGA/SMNH 6949 (Slovenia), oblique lighting; **C**, RGA/SMNH 6949 (Slovenia), latex cast whitened with ammonium chloride; **D**, holotype specimen, TKMP 1701 95840 (Ukraine); **E**, RGA/SMNH 1957 Ukraine), oblique lighting; **F**, specimen caught off the coast of Cornwall, United Kingdom. Scale bars: 10.0 mm. Photos: A-E, Rok Gašparič; F, David Fenwick (Aphotomarine).

largely restricted to bathyal depths, *Bathynectes longipes* (Risso, 1816) represents an ecological outlier within the genus, as it occurs in the northeastern Atlantic and the Mediterranean, where it inhabits relatively shallow, rocky environments on the continental shelf (20-226 m) (Abelló *et al.* 2001). The fossil evidence presented herein supports a possible scenario of progressive ecological shift toward deeper marine settings, potentially driven by environmental change such as cooling trends, sea-level fluctuations, and loss of neritic habitats during the Neogene (Rögl 1999; Kováč *et al.* 2007).

The Slovenian specimen of *Bathynectes muelleri* thus represents a key data point for understanding the early history and habitat occupation of *Bathynectes* in the Central Paratethys. The discovery adds an additional polybiid

taxon to the regional faunal assemblage, highlighting the palaeoenvironmental heterogeneity of the Central Paratethys during the Early Miocene. Although the decapod fossil record from northeastern Slovenia remains incomplete, it underscores the biogeographic importance of the Slovenian Corridor as a faunal conduit between the Central Paratethys and the Mediterranean realm during Miocene marine transgressions.

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