

# A new Early Cretaceous pylochelid hermit crab from Slovenia suggests that Trizochelinae (Decapoda, Paguroidea) may also be linked to the Mesozoic Marine Revolution<sup>†</sup>

Rok Gašparič,<sup>1,2</sup> René H.B. Fraaije,<sup>1</sup> John W.M. Jagt,<sup>3</sup> Barry W.M. van Bakel,<sup>4\*</sup> Tomaž Hitij,<sup>2,5</sup> and Jonathan J.W. Wallaard<sup>1</sup>

<sup>1</sup>Oertijdmuseum, Bosscheweg 80, 5283 WB Boxtel, the Netherlands <[rok.gasparic@gmail.com](mailto:rok.gasparic@gmail.com)>, <[directie@oertijdmuseum.nl](mailto:directie@oertijdmuseum.nl)>, <[curator@oertijdmuseum.nl](mailto:curator@oertijdmuseum.nl)>

<sup>2</sup>Institute for Palaeobiology and Evolution, Novi trg 59, 1241 Kamnik, Slovenia

<sup>3</sup>Natuurhistorisch Museum Maastricht, de Bosquetplein 6-7, 6211 KJ Maastricht, the Netherlands <[john.jagt@maastricht.nl](mailto:john.jagt@maastricht.nl)>

<sup>4</sup>Department of Earth Sciences, Faculty of Geosciences, Utrecht University, Budapestlaan 4, 3584 CD Utrecht, the Netherlands <[b.w.m.vanbakel@uu.nl](mailto:b.w.m.vanbakel@uu.nl)>

<sup>5</sup>University of Ljubljana, Faculty of Medicine, Vrazov trg 2, 1000 Ljubljana, Slovenia <[tomazhitij@gmail.com](mailto:tomazhitij@gmail.com)>

**Non-technical Summary.**—A newly discovered hermit crab species, *Cretatrizocheles rodfeldmanni*, has been identified in a limestone block from the Early Cretaceous period near Velika Strmica village in southeast Slovenia. This discovery contributes to our understanding of the Trizochelinae subfamily, which thrived in shallow-marine reef environments during the Late Jurassic and Early Cretaceous in Europe. These findings suggest a possible link between their past habitat preferences and the Mesozoic Marine Revolution, as they are now found exclusively in deep-marine settings.

**Abstract.**—A new pylochelid hermit crab, *Cretatrizocheles rodfeldmanni* new species, is recorded from a Lower Cretaceous (Aptian/Albian) olistolith reefal limestone block near the village of Velika Strmica, southeast Slovenia. It adds to the fossil record of the symmetrical pagurid subfamily Trizochelinae, whose members appear to have been successful inhabitants of shallow-marine reefal settings during at the least the Late Jurassic and Early Cretaceous across Europe. Given their exclusive occurrence in shallow-marine, reef-related facies of Mesozoic age and the present-day confinement to deep-marine settings, trizocheline paguroids may also illustrate the effect of the Mesozoic Marine Revolution.

UUID: <http://zoobank.org/b3f862ca-3b4d-44c1-911c-820af4426029>

## Introduction

Members of the family Pylochelidae Bate, 1888, commonly known as symmetrical hermit crabs, differ from all other marine paguroids in the presence of complete abdominal segmentation and paired appendages on each segment. Pylochelids do not usually inhabit gastropod shells but prefer decayed pieces of wood, stones, empty mollusk shells (mainly scaphopods, but also gastropods), serpulid worms, or living sponges (Forest, 1987b). Bathymetrically, the range of pylochelids varies from 30 to 1,570 m, but most representatives have been recorded from depths between 200 and 500 m (Forest, 1987a, b). Until Forest (1987b) published his seminal monograph, the importance of pylochelid paguroid faunas in tropical and subtropical deeper waters had been underestimated. One reason for this is that, because of their cryptic habitats, they were rarely collected (McLaughlin and Lemaitre, 2009).

Currently, pylochelids are assigned to four subfamilies: Parapylochelinae Forest, 1987 (Forest, 1987a); Pomatochelinae Stebbing, 1914; Pylochelinae Bate, 1888; and Trizochelinae Forest, 1987 (Forest, 1987a) (see e.g., Schweitzer et al., 2023). The last-named subfamily is by far the most speciose in present-day marine environments (e.g., McLaughlin and Lemaitre, 2009). To date, the genus *Trizocheles* accommodates 22 species (Komai, 2013; Komai and Chan, 2016), the majority of which are spongicoles (Forest et al., 2000).

Geographically, species of *Trizocheles* are generally limited to narrow areas (McLaughlin and Lemaitre, 2009), which is probably because their larvae are lecithotrophic, thus limiting their dispersal ability (Komai, 2013). As a general rule, the vertical range for each species of *Trizocheles* is also relatively narrow (120 m at the most); in other words, this genus appears to be the most stenobath of all pylochelid hermit crabs (Forest, 1987a).

Fossil representatives of this paguroid group are rare and poorly documented, which may be explained, at least in part, by their small size and unremarkable appearance. However,

\*Corresponding author

<sup>†</sup>Guest editor: Ovidiu Frantescu.

they are much more common than previously thought, as both recent work (Fraaije et al., 2012, 2019) and the new record described herein document.

### Locality and stratigraphy

Velika Strmica is situated approximately 10 km northwest of Novo mesto in southeast Slovenia (Fig. 1); structurally, the area belongs to the Dinarides (Placer, 2008). The stratigraphical succession exposed near Velika Strmica starts with Triassic, Jurassic, and Lower Cretaceous carbonates (Buser, 2009) deposited along the margin of the Dinaric Carbonate Platform (Vlahović et al., 2005). These platform carbonates are discordantly overlain either by upper Santonian to mid-Campanian marly limestones or by Campanian–Maastrichtian flysch-type deposits (Pleničar and Premru, 1977; Trotošek, 2002).

Lower Cretaceous (Aptian/Albian) carbonate olistolith blocks of reefal limestone are found embedded within the younger turbidite flysch series, west of the village of Velika Strmica.

The limestone olistolith measures approximately 2 m in diameter and consists of grainstone in its lower part, followed by sponge floatstone on the top (Gašparič and Gale, 2018). While grainstone is less rich with fossil remains, the floatstone facies contains a rich fauna with sponges, decapod crustaceans, corals, and brachiopods. Within the grainstone, clasts ranging between 0.1 and 1.3 mm represent 70% of the sample. The sediment is moderately well sorted. Fossils are represented by rare foraminifera, bryozoans, and brachiopods. Bryozoan colonies are fragmented and later abraded. Zooecia are filled with micrite. Most of the benthic foraminifera are fragmentary, whereas planktic forms are better preserved.

In the sponge floatstone, clasts larger than 2 mm represent 20–40% of the area. Sorting is very poor. Most of these are stromatoporoid and chaetetid sponges; corals and brachiopods are subordinate. Calcified sponges and corals are commonly encrusted by *Lithocodium*/*Pseudolithocodium*-like crusts, sessile foraminifera, serpulids, and red algae. Serpulids are also found within internal canals of sponges. Microborings are also very common on the outer surface of sponges and corals. Brachiopod shells are preserved with closed valves. Complete bivalve and gastropod shells are rarely preserved. Other grains include foraminifera, echinoderm ossicles, echinoid spines, fragmented bryozoans, and ostracods.

The present pylochelid paguroid originates from this olistolith, from which a diverse decapod crustacean fauna has previously been recorded (Gašparič and Gale, 2018; Gašparič et al., 2020, 2022). The olistolith has been dated as late Aptian to middle Albian on the basis of the presence of orbitolinid foraminifera, mainly the species *Mesorbitolina texana* (Roemer, 1849) (Gašparič et al., 2022).

### Material and methods

This study is based on a single anterior dorsal carapace (shield), registered as RGA/SMNH 4543 (part) and RGA/SMNH 4586 (counterpart) in the R. Gašparič Collection at the Institute of Palaeobiology and Evolution (Ljubljana, Slovenia). The specimen was collected by one of the authors (R.G.) in 2020 and prepared using fine needles under a Leica EZ 4D

stereomicroscope. Photographs were taken with a digital camera Nikon Z 7II with a Laowa 25 mm/f2.8 5x Ultra Macro lens. The photographs were subsequently stacked using the Helicon Focus 8 software to improve depth of field, and levels were adjusted in Adobe Photoshop CS6. For some photographs, the specimen was whitened with ammonium chloride sublimate before photography to enhance details of ornamentation.

*Repository and institutional abbreviation.*—RGA/SMNH—R. Gašparič Collection, part of the paleontological collections of the Natural History Museum of Ljubljana (Slovenia, SMNH).

### Systematic paleontology

Order Decapoda Latreille, 1802

Infraorder Anomura MacLeay, 1838

Superfamily Paguroidea Latreille, 1802

Family Pylochelidae Bate, 1888

Subfamily Trizochelinae Forest, 1987

Genus *Cretatrizocheles* Fraaije, Klompmaker, and Artal, 2012

*Type species.*—*Cretatrizocheles olazagutiensis* Fraaije, Klompmaker, and Artal, 2012 by original designation.

*Included species.*—In addition to the type species, *C. doerflensesis* Fraaije et al., 2019 and *C. rodfeldmanni* n. sp.

*Cretatrizocheles rodfeldmanni* new species

Figure 2

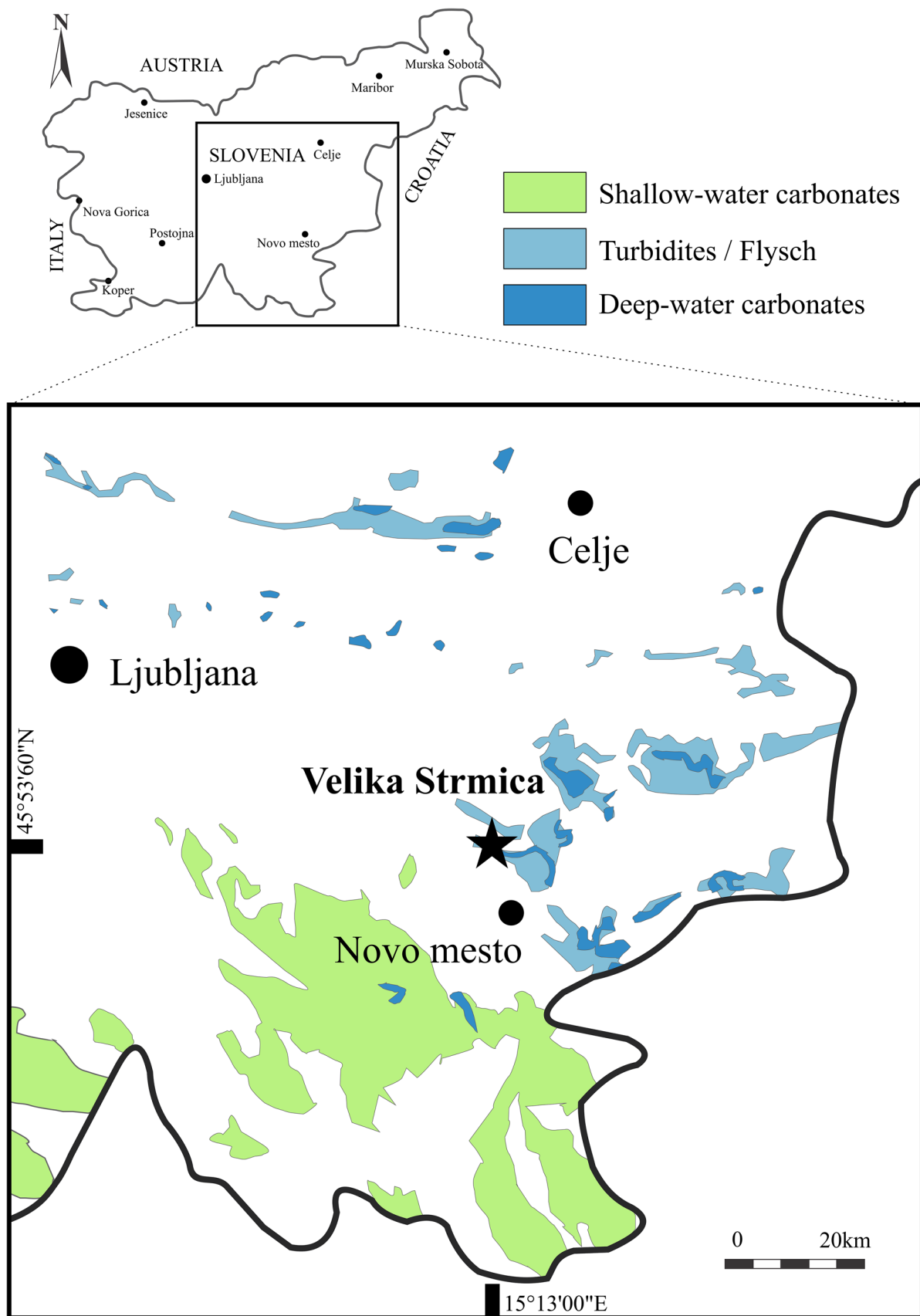
*Holotype.*—Holotype, and sole specimen known to date, is RGA/SMNH 4543 (part) and RGA/SMNH 4586 (counterpart). It is a well-preserved anterior dorsal carapace (shield).

*Diagnosis.*—Shield well calcified, nearly as long as wide. Prominent triangular rostrum considerably longer than post-ocular projection. Narrow, elongated massetic region. Globose keraial region. Prominent undulose post-rostral ridge. Short yet distinct central gastric groove. Posterior carapace not preserved.

*Occurrence.*—Known only from the type locality, late Aptian to middle Albian of Velika Strmica, Slovenia.

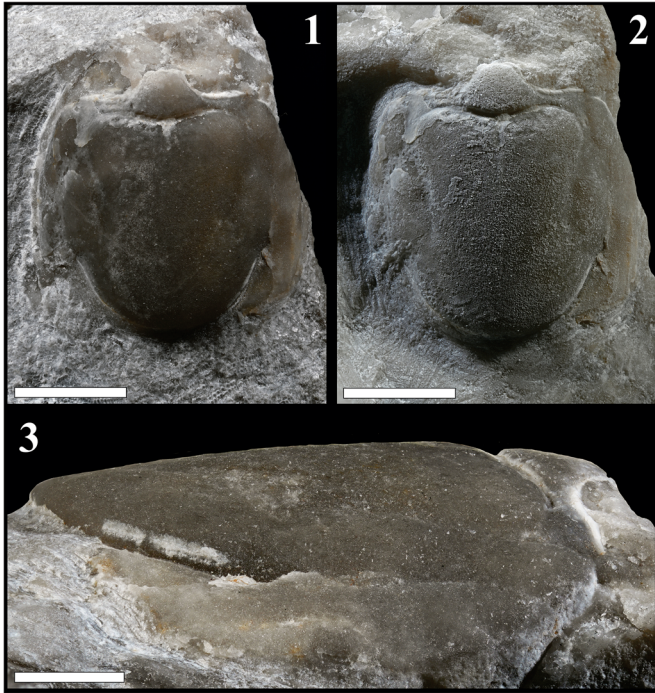
*Description.*—Shield smooth, strongly calcified, about as long as wide; prominent, broad-based, triangular rostrum, considerably longer than postocular and post-antennal projections. Short central gastric groove at posteriormost part of deep, concave, and undulose post-rostral ridge. Distinct lateral gastric grooves originating posterior to keraial region and effacing into subcircular lateral edges of post-rostral ridge. U-shaped cervical groove curving anteriorly toward thin and elongated massetic region. Posterior carapace, appendages, abdomen, and cuticle not preserved.

*Etymology.*—The specific epithet honors the paleontologist Dr. Rodney Feldmann in recognition of his considerable contributions to the crustacean paleontological record.



**Figure 1.** Simplified map of eastern Slovenia showing the locality of Velika Strmica (star) and the present-day position of Cretaceous outcrops across Slovenia (adapted after Buser, 2009).





**Figure 2.** Holotype (RGA/SMNH 4543) of *Cretatrizocheles rodfeldmanni* n. sp. from the upper Aptian–lower Albian of the Velika Strmica olistolith. (1) Dorsal shield; (2) ammonium chloride whitened dorsal shield; (3) lateral view of dorsal carapace. (1, 2) Scale bars = 2 mm; (3) scale bar = 1 mm.

**Remarks.**—Until now, the pylochelid paguroid genus *Cretatrizocheles* was known exclusively from Tithonian reefal limestones at Ernstbrunn (Austria; see Fraaije et al., 2019) and upper Albian reefal limestones in Navarra, northern Spain (Fraaije et al., 2012). *Cretatrizocheles rodfeldmanni* n. sp. is the third member of the genus to occur in reefal limestones, this time in Slovenia. The new species differs from the type species, *C. olazagutiensis*, in having a more pronounced and centrally concave post-rostral ridge that becomes more angular laterally and a longer central gastric groove. *Cretatrizocheles rodfeldmanni* differs from *C. doerflesensis* in having a broader, less elongate and more globose keraial region.

The only other fossil trizocheiline taxon recorded to date, *Cretatrizocheles doerflesensis* Fraaije et al., 2019, from Tithonian reefal limestones at Ernstbrunn (Austria) can be differentiated from *C. rodfeldmanni* in having a broader rostral base, a straight to centrally slightly convex post-rostral ridge, a longer central gastric ridge, and a narrower keraial region.

*Cretatrizocheles rodfeldmanni* is a significant addition to the fossil record of the symmetrical paguroid subfamily Trizocheilinae, whose members apparently were successful inhabitants of shallow-marine reefal settings during the Late Jurassic–Early Cretaceous in central and southwest Europe.

## Discussion

Although restricted to the Indo–West Pacific at present (Forest, 1987b), the genus *Trizocheles* is by far the most diverse taxon of pylochelid paguroids. There is a tendency among marine decapod crustaceans for species that have an advanced or highly abbreviated larval development to show more or less localized

distributions (e.g., Komai, 2013). This appears to be the case for species of *Trizocheles* because the majority have a restricted, endemic range (e.g., McLaughlin and Lemaitre, 2009; Komai 2013). In addition, they demonstrate a mutualistic relationship with thin-walled dictyonin hexactinellid sponges or with more massively built lithistid and haplosclerid demosponges (Forest, 1987b; McLaughlin and Lemaitre, 2009).

A spongicolous inquiline lifestyle, with lecithotrophic larvae, is highly beneficial in a shallow-marine, reef-like environments. In deep-marine settings, a planktotrophic development is generally more advantageous, as is a less closely knit inquiline way of life (Wisshak et al., 2009). It is quite possible that the possession of lecithotrophic larvae and a spongicolous inquiline lifestyle are relicts from the Mesozoic. The lack of appropriate abodes may have induced some species of *Trizocheles* to settle for various shells, mainly dentaliid scaphopods, but gastropod shells or serpulid tubes are occasionally chosen (Forest, 1987b).

Having been recovered exclusively from shallow-marine, reef-related facies of Middle and Late Mesozoic age and occurring nowadays only in deep-marine settings, suggests that the Trizocheilinae present yet another example of the effect of the Mesozoic Marine Revolution (e.g., Vermeij, 1977; Tackett, 2016), similar to stalked crinoids (Isocrinida), which, with a few exceptions, all migrated to deeper waters by the Late Cretaceous (Jagt, 1999; Hess, 2011; Gorzelak et al., 2012). The shift in the bathymetric range among sessile stalked crinoids during the Late Mesozoic, from shallow shelves to habitats further offshore, is likely a result of increased predation pressure in shallow waters (Oji, 1996).

Of note is that the cyrtocrinid crinoid *Proholopus holopiformis* (Remeš, 1902) has recently been recorded by Zamora and López Horgue (2022) from upper Albian strata (Albeniz unit), close to the locality that yielded *Cretatrizocheles olazagutiensis* in Navarra (western Pyrenees, Spain). This record ranks among the youngest occurrences of cyrtocrinids in shallow-marine environments before their migration into the deep sea as a result of the Mesozoic Marine Revolution.

Additional fieldwork and screening of collections for extinct pylochelids should clarify when these symmetrical hermit crabs also migrated from shallow- to deep-marine settings. We suggest this must have occurred in post-Albian times. To date, intensive fieldwork over years in the Maastrichtian type area (southeast Netherlands and northeast Belgium) by ourselves and in Eocene shallow-marine facies of northern Italy by our Italian colleagues has not yielded any trizocheiline paguroid remains.

## Acknowledgments

We thank the journal reviewers, G. Schweigert (Staatliches Museum für Naturkunde, Stuttgart, Germany) and F.A. Ferratges (Instituto Geológico y Minero de España, Zaragoza, Spain), for constructive comments on an earlier version of the manuscript.

## Declaration of competing interests

None of the authors received any specific grants from funding agencies in the public, commercial, or nonprofit sectors for the present study.

## References

- Bate, C.S., 1888, Report on the Crustacea Macrura collected by the H.M.S. Challenger during the years 1873–1876, in Report on the Scientific Results of the Voyage of H.M.S. Challenger During the Years 1873–76: Zoology, v. 24, 942 p.
- Buser, S., 2009, Geological map of Slovenia 1:250,000: Ljubljana, Geological Survey of Slovenia.
- Forest, J., 1987a, Les Pylochelidae ou «Pagures symétriques» (Crustacea Coenobitoidea), in Crosnier, A., ed., Résultats des Campagnes MUSORSTOM: Mémoires du Muséum national d'Histoire naturelle, v. 137, p. 1–254.
- Forest, J., 1987b, Ethology and distribution of Pylochelidae (Crustacea Decapoda Coenobitoidea): Bulletin of Marine Science, v. 41, p. 309–321.
- Forest, J., de Saint Laurent, M., McLaughlin, P.A., and Lemaitre, R., 2000, The marine fauna of New Zealand: Paguridea (Decapoda: Anomura) exclusive of the Lithodidae: NIWA Biodiversity Memoir, v. 114, p. 1–250.
- Fraaije, R.H.B., Klompmaker, A.A., and Artal, P., 2012, New species, genera and a family of hermit crabs (Crustacea, Anomura, Paguroidea) from a mid-Cretaceous reef of Navarra, northern Spain: Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, v. 263, p. 85–92, <https://doi.org/10.1127/0077-7749/2012/0213>.
- Fraaije, R.H.B., Robins, C., Van Bakel, B.W.M., Jagt, J.W.M., and Bachmayer, F., 2019, Paguroid anomurans from the Tithonian Erntbrunn Limestone, Austria—the most diverse extinct paguroid assemblage on record: Annalen des Naturhistorischen Museum in Wien, v. 121, p. 257–289.
- Gašparič, R., and Gale, L., 2018, A new Upper Jurassic decapod assemblage from a sponge reef olistolith from Velika Strmica, Slovenia, in Novak, M., and Rman, N., eds., 5. Slovenski Geološki Kongres, Do 5 milijard let z družbo 5.0, Velenje, 3.–5.10.2018: Velenje, Zbornik povzatkov, p. 41–42.
- Gašparič, R., Robins, C., and Gale, L., 2020, *Mesogalatheia ardua* sp. nov., a new species of squat lobster (Decapoda, Galatheidae) from the Upper Jurassic olistolith at Velika Strmica (Dolenjska, Slovenia): Geologija, v. 63, p. 29–38, <https://doi.org/10.5474/geologija.2020.003>.
- Gašparič, R., Van Bakel, B.W.M., Fraaije, R.H.B., and Jagt, J.W.M., 2022, First record of viaiid crabs (Decapoda, Brachyura) from the Lower Cretaceous of Slovenia, with the description of two new species: Cretaceous Research, v. 138, 105293, <https://doi.org/10.1016/j.cretres.2022.105293>.
- Gorzelak, P., Salamon, M.A., Trzysiok, D., Lach, R., and Baumiller, T.K., 2012, Predator-induced macroevolutionary trends in Mesozoic crinoids: Proceedings of the National Academy of Sciences of the United States of America, v. 109, p. 7005–7007, <https://doi.org/10.1073/pnas.1201573109>.
- Hess, H., 2011, Isocrinida, in Hess, H., and Messing, C.G., eds., Treatise on Invertebrate Paleontology, Part T, Echinodermata 2 (revised), Crinoidea, Volume 3: Lawrence, Kansas, The University of Kansas, Paleontological Institute, p. 42–69.
- Jagt, J.W.M., 1999, Late Cretaceous–Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium—part 2: crinoids: Scripta Geologica, v. 116, p. 59–255.
- Komai, T., 2013, Records of four species of the pylochelid hermit crab genus *Trizacheles* Forest, 1987 (Crustacea: Decapoda: Anomura) from the Sagami Sea and Izu Islands, central Japan, with descriptions of three new species: Natural History Research, v. 12, p. 91–112.
- Komai, T., and Chan, T.-Y., 2016, “Symmetrical” hermit crabs of the family Pylochelidae (Crustacea: Decapoda: Anomura) collected by the “BIOPAPUA” and “PAPUA NIUGINI” expeditions in the Papua New Guinea, with descriptions of two new species: Zootaxa, v. 4088, p. 301–328, <https://doi.org/10.11646/zootaxa.4088.3.1>.
- Latreille, P.A., 1802–1803, Histoire naturelle, générale et particulière des Crustacés et des Insectes, 3: Paris, F. Dufart, 468 p.
- MacLeay, W.S., 1838, On the brachyurous decapod Crustacea brought from the Cape by Dr. Smith, in Smith, A., Illustrations of the Annulosa of South Africa; being a portion of the objects of natural history chiefly collected during an expedition into the interior of South Africa, under the direction of Dr. Andrew Smith, in the years 1834, 1835. And 1836; fitted out by “The Cape of Good Hope Association for Exploring Central Africa”: London, Smith, Elder, and Co, p. 53–71.
- McLaughlin, P.A., and Lemaitre, R., 2009, A new classification for the Pylochelidae (Decapoda: Anomura: Paguroidea) and descriptions of new taxa: The Raffles Bulletin of Zoology, Suppl. 20, p. 159–231.
- Oji, T., 1996, Is predation intensity reduced with increasing depth? Evidence from the west Atlantic stalked crinoid *Endoxocrinus parrae* (Gervais) and implications for the Mesozoic Marine Revolution: Paleobiology, v. 22, p. 339–351, <https://doi.org/10.1017/S0094837300016328>.
- Placer, L., 2008, Principles of the tectonic subdivision of Slovenia: Geologija, v. 51, p. 205–217, <https://doi.org/10.5474/geologija.2008.021>.
- Pleničar, M., and Premru, U., 1977, Explanatory book for sheet Novo mesto, L 33-79, Basic Geological Map SFRY 1:100,000: Beograd, Federal Geological Survey, 61 p.
- Remeš, M., 1902, Nachträge zur Fauna von Stramberg, VI, Crinoiden-, Asteriden- und Echinoiden-Reste aus dem Weissen Kalkstein von Stramberg: Wien, Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients 14, 195.
- Roemer, C.F., 1849, Texas, mit besonderer Rücksicht auf deutsche Auswanderung und die physischen Verhältnisse des Landes nach eigener Beobachtung geschildert von Dr. Ferdinand Roemer: Bonn, Adolph Marcus, 464 p.
- Schweitzer, C.E., Feldmann, R.M., and Fraaije, R.H.B., 2023, Part R, Revised, Volume 1: Systematic Descriptions: Anomura (Gastrodoroidea, Lithodoidea, Lomisoidea, Paguroidea). Treatise Online, v. 173, <https://doi.org/10.17161/to.vi.21517>.
- Stebbing, T.R.R., 1914, South African Crustacea. Part VII: Annals of the South African Museum, v. 15, p. 1–55, pls LXV–LXXVI.
- Tackett, L.S., 2016, Late Triassic durophagy and the origin of the Mesozoic marine revolution: Palaios, v. 31, p. 122–124, <https://doi.org/10.2110/palo.2016.003>.
- Trotošek, S., 2002, Geological structure of the area north of Šmarješke Toplice [B.Sc. thesis]: Ljubljana, University of Ljubljana, 52 p. [in Slovenian]
- Vermeij, G.J., 1977, The Mesozoic marine revolution: evidence from snails, predators and grazers: Paleobiology, v. 3, p. 245–258.
- Vlahović, I., Tišljarić, J., Velić, I., and Matićec, D., 2005, Evolution of the Adriatic carbonate platform: palaeogeography, main events and depositional dynamics: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 220, p. 333–360, <https://doi.org/10.1016/j.palaeo.2005.01.011>.
- Wisshak, M., Neumann, C., Jakobsen, J., and Freiwald, A., 2009, The ‘living-fossil community’ of the cyrtocrinid *Cyathidium foresti* and the deep-sea oyster *Neopycnodonte zibrowii* (Azores Archipelago): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 271, p. 77–83, <https://doi.org/10.1016/j.palaeo.2008.09.015>.
- Zamora, S., and López-Horgue, M.A., 2022, A shallow-water cyrtocrinid crinoid (Articulata) from the upper Albian of the western Pyrenees, North Spain: Cretaceous Research, v. 134, 105161, <https://doi.org/10.1016/j.cretres.2022.105161>.

Accepted: 18 July 2024