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Jaxea kuemeli Bachmayer, 1954 (Malacostraca, Gebiidea, Laomediidae) from the Middle Miocene of Tunjice Hills (central Slovenia)

Rak deseteronožec *Jaxea kuemeli* Bachmayer, 1954 (Malacostraca, Gebiidea, Laomediidae) iz srednjemiocenskih plasti Tunjiškega gričevja

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Abstract

In the present paper we report on several new specimens of *Jaxea kuemeli* Bachmayer, 1954 from the Middle Miocene laminated sandstones from Košiše in Tunjice Hills. New and well-preserved material from shallow water environment of Laško Formation allows the re-evaluation of *Jaxea* cheliped morphology. The report enhances our knowledge of the variability of tooth formula in the cheliped of *Jaxea kuemeli* and opens questions about interspecific variations connected to temporal or ecological factors. We also discuss the environmental preferences of the species which is so far known exclusively from the Paratethys Sea.

Izvleček

V pričujočem članku poročamo o novih primerkih deseteronožca vrste *Jaxea kuemeli* Bachmayer, 1954 iz srednjemiocenskih plasti nahajališča Košiše v Tunjiškem gričevju. Novi in dobro ohranjeni primerki, iz plitvovodnih plasti Laške formacije, omogočajo primerjavo morfologije škarnikov vrste *Jaxea kuemeli*. Opis novih primerkov razširja naše poznavanje razlik v zobni formuli škarnikov predstavljene vrste in odpira vprašanja o možni variabilnosti znotraj le-te, ki so lahko posledica časovnih ali okoljskih dejavnikov. V članku med drugim opredeljujemo tudi okoljske preference vrste, ki je do sedaj poznana le iz območja Paratetide.

Introduction

Miocene decapod crustaceans from Slovenia have been the subject of studies since the 19th century (Bittner, 1884; Glaessner, 1928). Recently, a renewed interest has brought a number of publications from this area describing various decapod assemblages (Mikuž, 2003, 2010; Mikuž & Pavšič, 2003; Hyžný & Gašparič, 2014; Gašparič & Halásová, 2015; Gašparič & Hyžný, 2015; Gašparič & Ossó, 2016; Gašparič & Križnar, 2017). In this respect, the decapod fauna of the Tunjice Hills is yet undescribed, despite the fact that over 300 specimens belonging to at least 10 species were collected in recent years by local collectors (Gašparič & Brajković, 2016). Among the taxa identified in the preliminary report by Gašparič and Brajković (2016), there is also *Jaxea kuemeli* Bachmayer, 1954, a known laomediid shrimp from the Miocene strata deposited in the ancient Paratethys Sea (Rögl, 1998; Popov et al., 2004; Harzhauser & Piller, 2007). The species was previously reported from the Lower Miocene deep-water sediments of Činžat on the northern slope of the Pohorje mountain range in north-

east Slovenia (Gašparič & Hyžný, 2015), but remains largely understudied. Herein we aim for a more detailed report on *J. kuemeli* from the Tunjice Hills, where sediments deposited in a shallow-water environment are exposed.

Geological and stratigraphical settings

The area of the Tunjice Hills has been known for its wealth of fossil remains since the 19th century. In 1882 a well-known naturalists and local priest Simon Robič started collecting fossils and sent them to palaeontologists from the Natural History Museum in Vienna. Among these were also the first specimens of a brachyuran crab Cancer carniolicus Bittner, 1884, currently treated as Tasadia Müller in Janssen & Müller, 1984 (Schweitzer et al. 2010).

Here presented specimens of *Jaxea kuemeli* were recovered from the Middle Miocene (Badenian) sandstones and sandy limestone exposed in a road cut along the local road from Kamnik to Tunjice some 3 km northwest of the town of Kamnik near the village of Košiše (fig. 1).

The Tunjice Hills belong to the westernmost part of the Tunjice Syncline of the Sava Folds (Placer, 1999, 2008). In the south it borders with Triassic rocks of Trojane anticline and in the north to Teharje anticline and Menina mountain massif, both consisting of Triassic Dachstein limestone (Premru, 1983). The total thickness of the Miocene beds is estimated to approximately 1000 m (Žalohar & Zevnik, 2006).

The stratigraphic sequence of the Tunjice Hills starts with the Early Miocene (Burdigalian) Govce Formation. These strata consist of alternating conglomerates, sandstones, and fine-grained marls, as well as clays with lenses of sand and sandstones. Sediments of the Govce Fm. were deposited in a near-shore environment with variable terrestrial and marine influence (Vrabec, 2000) with the total thickness of 350 to 450 m (Premru, 1983). Marine fauna retrieved from marls also indicates near-coastal environment with common wood remains drilled by teredinid bivalves, carbonized pine cones, and rich mollusc fauna (Žalohar & Zevnik, 1998). Remains of decapod crustaceans are rare in the Govce Fm. and so far the only finds are a handful of specimens of *Retropluma slovenica* Gašparič & Hyžný, 2014 from sandy beds of this formation (Gašparič & Križnar, 2017).

Sediments of the Govce Fm. are discordantly overlapped by Middle Miocene (Langhian; Badenian) beds of the Laško Formation, which are exposed at Košiše locality discussed herein. The Laško Fm. consists of mudstones, sandstones, and limestone (Rijavec & Pleničar, 1979). Cyclic alterations of retrogradational sequences re-

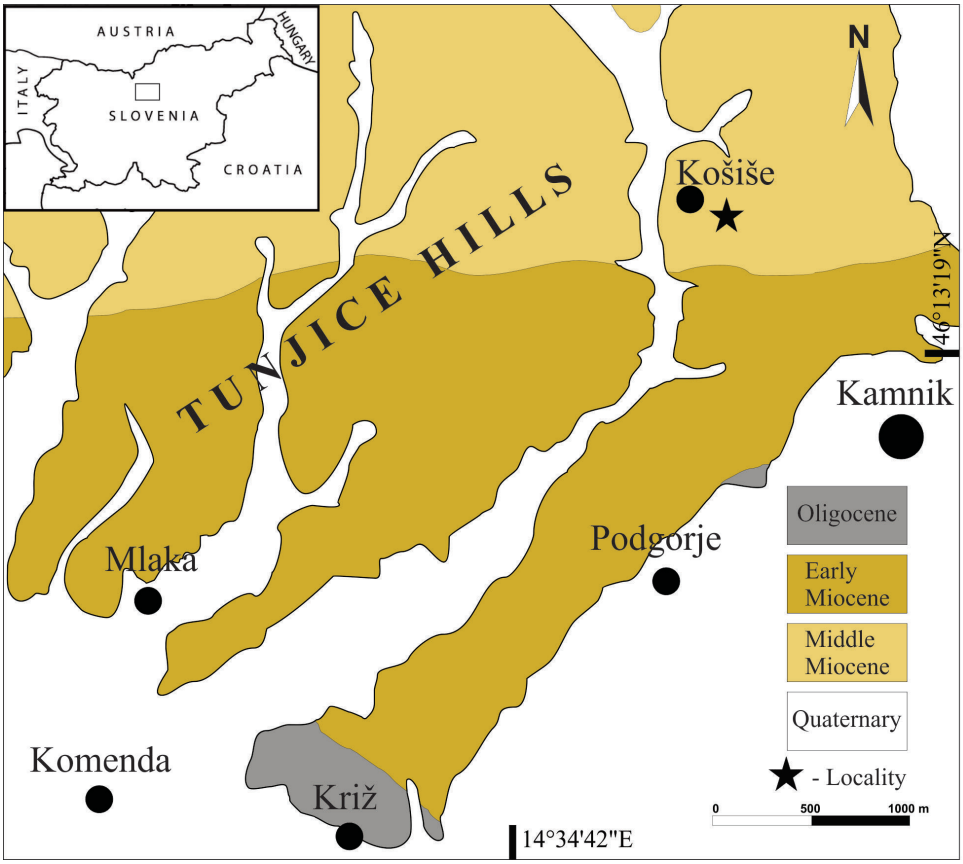


Fig. 1. Simplified geological map of Tunjice Hills, showing locality Košiše (modified after Gašparič & Križnar, 2017).

flect a rise in sea level or rapid subsidence of the terrain. Similarly to the underlying beds of the Govce Fm., sediments of the Laško Fm. were deposited in the shallow infralittoral environment (Vrabec et al., 2014). Sandstones and sandy limestone of the Laško Fm. are famous for their fossil molluscs (Mikuž & Pavšič, 2000) with commonly found and well-preserved bivalves belonging to genera *Glossus, Corbula, Anadara, Lucinoma, Thracia, Tellina, Cardium, Acanthocardia, Lutraria, Mytilus, Panopea,* and *Ostrea*, as well as gastropod genera *Xenophora, Trochus, Conus, Ancilla, Turritella, Lunatia,* and *Hinia* (Žalohar & Zevnik, 2006). Besides the mollusc fauna, rare whale remains represented by isolated vertebrae were also described (Gašparič & Križnar, 2014). Beds of the Laško Fm. also exhibit greater decapod diversity, with *Tasadia carniolica* as the dominant species (Mikuž & Pavšič, 2003), associated with frequent specimens of *Jaxea kuemeli* Bachmayer, 1954 (documented in detail further below) and rarer burrowing ghost shrimp *Calliax michelottii* (A. Milne Edwards, 1860) (Hyžný & Gašparič, 2014). In the upper part of the Laško Fm. increasing terrestrial influence is documented at the transition into the Serravallian (Sarmatian) Dol Formation (Vrabec et al., 2014). The fossil fauna of this formation indicates a fully marine environment (Horvat, 2003). Uppermost parts of the Dol Fm. suggest renewed shallowing of the environment, fresh-water influx, and periodic tectonic isolations of the Tunjice Basin (Žalohar & Hitij, 2014).

Material and methods

In total 30 specimens of *Jaxea kuemeli* from Košiše locality have been examined. Specimens were prepared using manual or pneumatic needle and studied under stereomicroscope Leica EZ4D. All specimens were measured, photographed using digital cameras Nikon Coolpix P340 and A900, and documented using computer graphic programmes (CoreDRAW X5, Adobe Photoshop CC). The material is deposited as a part of the "R. Gašparič Collection" in the Slovenian Museum of Natural History, Ljubljana, Slovenia (RGA/SMNH).

Systematics

The higher classification used herein follows De Grave et al. (2009).

Infraorder Gebiidea de Saint Laurent, 1979

Family Laomediidae Borradaile, 1903

Genus *Jaxea* Nardo, 1847

Type species. *Jaxea nocturna* Nardo, 1847, by original designation.

Diagnosis: Small firm exoskeleton, linea thalassinica straight anteroposteriorly, distinct and well developed (fig. 2). Abdominal segments approximately of same length, abdominal pleura 2-6 with minute serrations. Telson longer than wide, longitudinal dorsal ridges present, posterior border convex, median spine absent. Chelae equal and greatly developed, pereiopods P2-5 slender, simple. (After Ngoc- Ho, 2003; characters with low fossilization potential were omitted.)

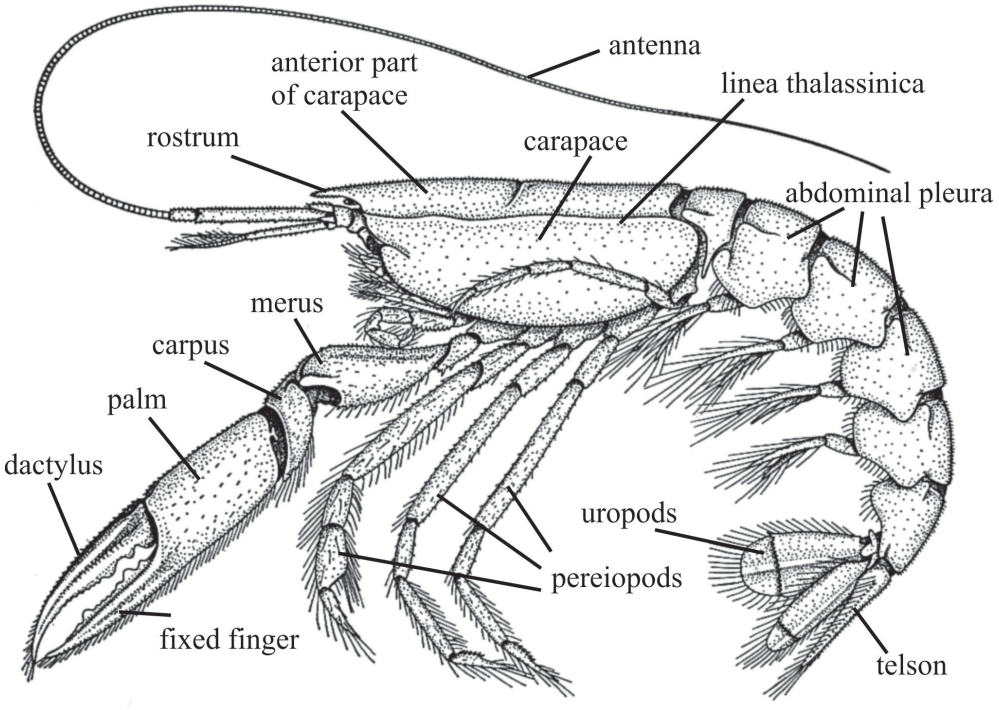


Fig. 2. Descriptive terminology used in the text showing basic morphology of *Jaxea novazealandiae* Wear & Yaldwyn, 1966 (modified after Wear & Yaldwyn, 1966).

Remarks: The genus *Jaxea* is represented by two extant species (known from adults), *Jaxea nocturna* Nardo, 1847 and *Jaxea novaezealandiae* Wear & Yaldwyn, 1966. *Jaxea nocturna* is represented also in the fossil record of the Mediterranean; well preserved remains have been reported from the Lower Pliocene of Italy (Delle Cave, 1988) and Spain (Mayoral et al., 1998; Garassino et al., 2009). *Jaxea kuemeli* Bachmayer, 1954 is known exclusively from the Miocene of Central Paratethys (Hyžný, 2011; Hyžný & Zorn, 2016).

Jaxea kuemeli Bachmayer, 1954

(Plate 1. A–G)

1954 *Jaxea kümeli* Bachmayer; p. 64, Pl. 1, Figs. 1–2.

1984a *Jaxea kuemeli* Bachmayer; Müller; p. 49.

1993 *Jaxea kuemeli* Bachmayer; Müller; p. 5.

1998 *Jaxea küumeli* Bachmayer; Mayoral et al.; p. 508.

1998 *Jaxea kuemeli* Bachmayer; Müller; p. 9.

2011 *Jaxea kuemeli* Bachmayer; Hyžný; p. 176, Figs 2–6.

2015 *Jaxea kuemeli* Bachmayer; Gašparič & Hyžný; p. 147, Figs. 8–9.

2016 *Jaxea kuemeli* Bachmayer; Hyžný & Zorn; p. 139, Pl. 17, Figs. 3–5.

Diagnosis: Cylindrical carapace with triangular rostrum with denticulate lateral margins; *linea thalassinica* and cervical groove well defined, not crossing each other. Telson slightly longer than wide with median longitudinal groove and two pairs of longitudinal ridges. First pereiopods chelate, equal or subequal, well developed, approximately as long as the cephalothorax; ischium and merus with spinules on entire lower margin; carpus with small lower distal spine; propodus granulate. Pollex with three or four larger round teeth positioned proximally followed with several smaller teeth, or with several round same sized teeth; large median triangular tooth positioned more proximally, usually composed from several smaller teeth; distal half of the cutting edge with numerous small round teeth. Dactylus with two or three larger round teeth positioned proximally followed with a broad notch and large median tooth. Second to fifth pereiopods simple. (After Hyžný, 2011.)

Material: In total 30 specimens of *Jaxea kuemeli* were collected and studied. The majority of the sample (25 specimens) represent cheliped remains (RGA/SMNH 0683, 0684, 0685, 0686, 0743, 0744, 0758, 0759, 0765, 0774, 0783, 0794, 0796, 0797, 1070, 1082, 1085, 1086, 1099, 1161, 1182, 1185, 1189, 1193, 1426). Additionally, there are some specimens with cheliped associated with fragmentary remains of dorsal carapace, abdominal pleura and telson (RGA/SMNH 0704), partial dorsal carapaces (RGA/SMNH 0676, 0682, 0760) and cheliped with pereipods (RGA/SMNH 1161).

Locality: The specimens studied herein were recovered from grey to yellowish Middle Miocene (Langhian/Badenian) laminated sandstones of the Laško Formation exposed at the Košiše locality (Sava folds Basin, Slovenia). Laško Formation beds of this locality consist of grey siltstones with concretions, interbedded with laminated grey to yellowish sandstones, overlain by poorly sorted bioturbated yellowish sandstones and sandstones with *Lithothamnium* fragments.

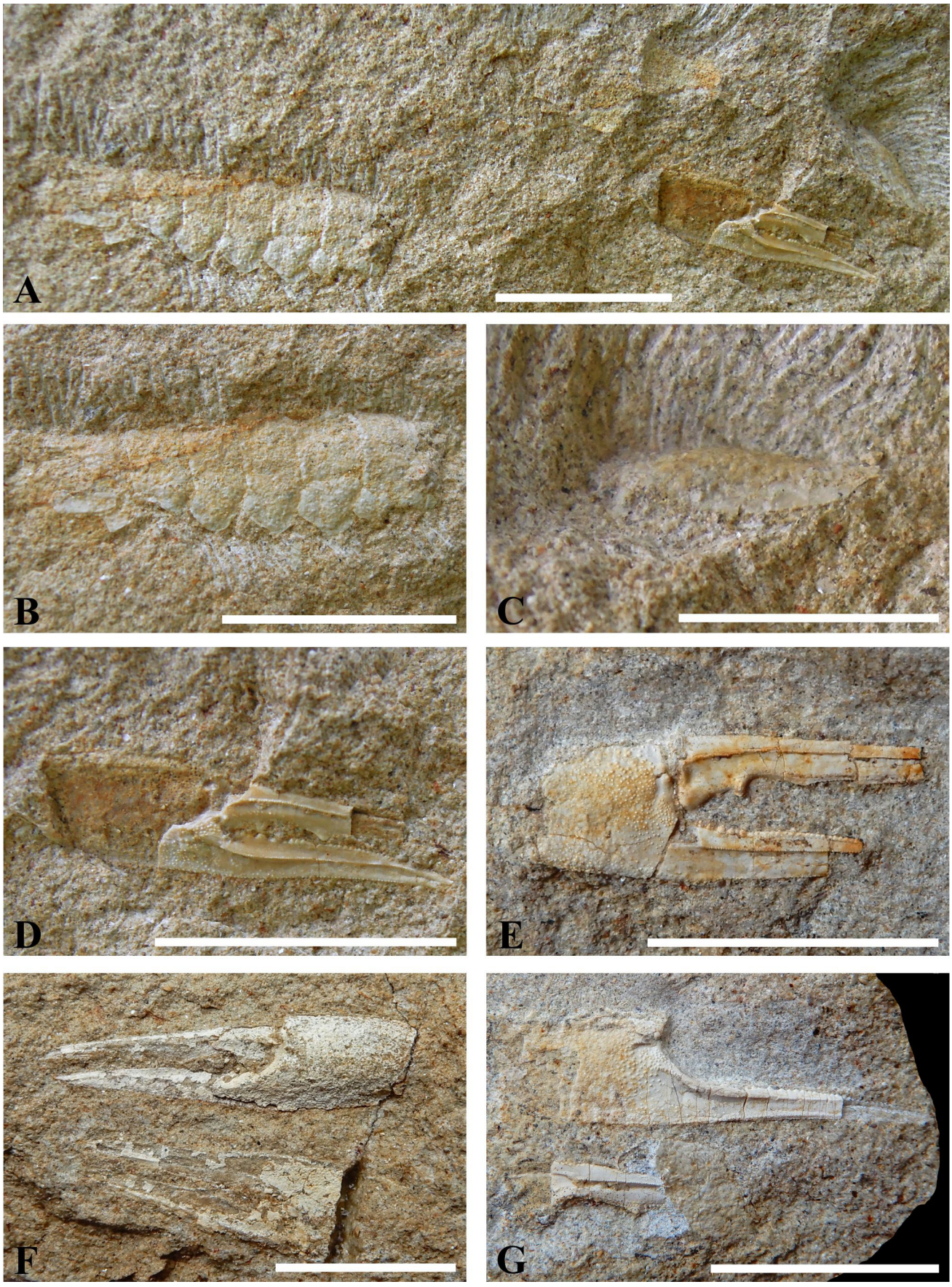
Laminated sandstones are more likely to contain macrofaunal fossil remains, including decapods, than other variations in lithology. Remains of *Jaxea kuemeli* were collected exclusively from bedding planes of grey to yellowish laminated sandstones.

Description: Dorsal carapace cylindrical, smooth and weekly calcified, with short, triangular rostrum (Pl. 1A, C). Abdomen well developed, abdominal pleurae 2-6 approximately of same

PLATE 1

Jaxea kuemeli Bachmayer, 1954. A–D RGA/SMNH 0704;
A - cheliped with scattered remains of dorsal carapace and abdomen;
B – close-up of abdomen with abdominal pleurae and fragmented telson;
C – close-up of anterior part of dorsal carapace with rostrum;
D - close-up of cheliped;
E - RGA/SMNH 0743, isolated cheliped, exhibiting strong tooth on dactylus;
F –RGA/SMNH 1193, chelipeds of fragmented specimen;
G –RGA/SMNH 1099, propodus, with occlusal margin of fixed finger.
All scale bars are 10 mm, except 1C scale bar is 5 mm.

PLATE 1



length, rounded, margins covered with minute spines, posterolateral margins concave. Telson longer than wide, posterior margin convex, dorsal surface with median longitudinal groove and two pairs of longitudinal ridges. Uropods equal in length to telson, with rounded posterior margin. Abdomen and telson weakly ornamented with small granules (Pl. 1B).

First pereiopods chelate, marginally subequal, one chela more slender, other robust. Both chelae well developed and strongly calcified, equal in length to carapace and strongly granulated. Manus rectangular, slightly longer than high. Dactylus slightly longer than fixed finger. Occlusal margin of both fingers adorned with row of teeth. Fixed finger with three to five larger, rounded teeth positioned proximally in concave part of occlusal margin. These are followed by row several smaller teeth, gradually diminishing in size in distal half, here occlusal margin slightly convex (Pl. 1G). Dactylus with two round teeth positioned proximally, first a small round tooth, followed by distinct strong tooth, knob like and proximally curved. Continuing distally follows a broad, unadorned notch and a large triangular median tooth (Pl. 1E). Distal half of dactylus occlusal margin slightly concave and adorned with equally small rounded teeth as on fixed finger. Termination of both fingers curved together and pincers-like. Two longitudinal ridges on dactylus, one throughout the finger, second less distinct and only present in proximal half. Fixed finger with one longitudinal ridge through the whole finger length. Ridges as well as outside margins of fingers evenly ornamented with small, spine like teeth (Pl. 1D). Pereiopods P2–5 simple, flattened and slender.

Remarks: Although Müller (1984b, 1993, 1998) and Mayoral et al. (1998) considered *J. kuemeli* to be possibly conspecific with extant species *Jaxea nocturna* Nardo, 1847, Hyžný (2011) argued for distinction between both taxa. Hyžný re-examined the type material of Bachmayer (1954) and additional specimens from Lower to Middle Miocene of Austria, Slovakia, and Hungary, and concluded that morphology of chelipeds expressed in unique tooth formula warrants keeping both species as separate. A major distinctive character is the position of the large median tooth on the occlusal margin of the fixed finger. In *J. kuemeli* this is located proximally relative to the position of the median tooth on the dactylus and less distinct, while it is positioned distally in *J. nocturna* and pronounced (Hyžný, 2011, p. 180, fig. 3).

Based on the cheliped morphology, the material from Košiše can be assigned to *Jaxea kuemeli*. The material confirms slight heterochely in the species as already documented (but not explored in detail) by Hyžný (2011). Additional intraspecific variation in the nature of the tooth formula is presented as well. Some specimens from Košiše do not show observable median tooth on the fixed finger or exhibits a different position of large proximal teeth on dactylus and constant rows of small rounded teeth in a distal half of fingers. These variations may be connected with temporal or ecological factors; more research, however, is needed to address these issues properly.

Taphonomy: Specimens of *Jaxea kuemeli* collected at the locality Košiše exhibit varying degrees of preservation. Only strongly mineralized chelipeds are commonly found due to the fragile cuticle of the dorsal carapace, abdomen, and pereiopods. Chelipeds are frequently found in pairs (Pl. 1F) and, where carapace or abdomen remains are recognized, these are always associated with chelipeds (Pl. 1A). Despite the fact that *Jaxea* representatives are active burrowers (Dworschak, 2004), described fossil remains are exclusively found on bedding plane and not in bioturbations present in the sediment. This type of preservation suggests limited post-mortem transport and rapid burial of remains, which likely represent moults rather than corpses (Glaessner, 1969).

Palaeoecology and environment

Modern representatives of *Jaxea* are reported exclusively from muddy substrates or sandy mud (Wear & Yaldwyn, 1966; Ngoc-Ho, 2003). Similarly, fossil occurrences come from fine-grained siliciclastic sediments (Hyžný, 2011; Garassino et al., 2009; Gašparič & Hyžný, 2015). *Jaxea* is considered an infaunal burrower in near-shore, shallow facies, which is supported by the palaeoenvironment of the Košiše locality. Interestingly, another report of *Jaxea kuemeli* from Slovenia (Gašparič & Hyžný, 2015) comes from deep-water sediments of the Lower Miocene (Karpatian) of north-east Slovenia. It appears *Jaxea kuemeli* is reported either from shallow water association with *Tasadia carniolica* (Bitner, 1884) (Hyžný & Zorn, 2016), as is also the case in specimens described herein, or found in association with a brachyuran *Styrioplax exiguus* Glaessner, 1928 (Hyžný, 2011; Gašparič & Hyžný, 2015) that is reported from deeper water settings. As for bathymetric preferences

of modern *Jaxea*, it has been reported mainly from shallow-marine settings up to 100 m depth (Wear & Yaldwyn, 1966; Ngoc-Ho, 2003), although some occurrences are known from depth exceeding 400 m (Diez et al., 1994).

Conclusions

A number of specimens of a laomediid shrimp *Jaxea kuemeli* are reported from the Middle Miocene beds of the Laško Formation exposed in the Tunjice Hills, central Slovenia. The species was a dominant decapod taxon of the studied infaunal community, in co-occurrence with a crab *Tasadia carniolica*. Intraspecific variation in the nature of chelipeds has been observed in the studied material of *J. kuemeli*. The intraspecific variation of cheliped in the fossil *Jaxea* has not been evaluated yet; with the increasing number of specimens of this species from various localities, such study is now feasible. *Jaxea kuemeli* has been identified in decapod associations of both shallow as well as deep water environments, which is in accordance with the ecological preferences of modern representatives of *Jaxea*.

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