

**Middle Miocene decapod crustacean assemblage
from the Tuzla Basin (Tušanj, Bosnia and Herzegovina),
with a description of two new species
and comparison with coeval faunas from Slovenia**

**Rok Gašparič, Matúš Hyžný, Gordana Jovanović,
Stjepan Čorić, and Sejfudin Vrabac**

ABSTRACT

A decapod assemblage consisting of three species is described from the upper Langhian (lower Badenian) of the Tuzla Basin in Bosnia and Herzegovina. The assemblage is dominated by *Retropluma minuta* sp. nov. (Brachyura, Retroplumidae) and accompanied by *Munidopsis salinaria* sp. nov. (Anomura, Galatheoidea) and *Portunus monspeliensis* A. Milne Edwards, 1860 (Brachyura, Portunidae). Based on the calcareous nannoplankton, the studied assemblage is assigned to the upper part of the NN5 Zone. The studied assemblage is considered to have inhabited a shallow, near-shore depositional setting, as suggested by the microfossil association. *Munidopsis*, *Portunus* and *Retropluma* have previously been reported from Slovenia, the area closest to the Tuzla Basin with known decapod fossils. Contrary to shallow-marine settings of the localities studied herein, *Munidopsis* and *Retropluma* from Slovenian localities are reported from deeper-marine settings. The occurrence of near-complete individuals of *Retropluma minuta* sp. nov. suggests a wider bathymetric range of the genus in its evolutionary past than it has today.

Rok Gašparič. Oertijdmuseum Boxtel, Bosscheweg 80, 5293 WB Boxtel, the Netherlands.
rok.gasparic@gmail.com

Matúš Hyžný. Department of Geology and Palaeontology, Faculty of Natural Sciences, Comenius University, Mlynská dolina G1, Ilkovičova 6, Bratislava 842 15, Slovakia; Geological-Paleontological Department, Natural History Museum Vienna, Burgring 7. A-1010 Vienna, Austria.
hyzny.matus@gmail.com

Gordana Jovanović. Natural History Museum Belgrade, Njegoševa 51, 11000 Belgrade, Serbia.
gordana.j@nhmbeo.rs

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Stjepan Ćorić. Geologische Bundesanstalt, Neulinggasse 38, 1030 Wien, Austria.
stjepan.coric@geologie.ac.at

Sejfudin Vrabac. Faculty of Mining, Geology and Civil Engineering Tuzla, Univerzitetska 2, 75000 Tuzla, Bosnia and Herzegovina. sejfudin.vrabac@untz.ba

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INTRODUCTION

Almost a century has passed since Glaessner's (1928) overview of Neogene decapods from what are now Austria and Slovenia, where he emphasised the need for studying fossil decapod associations in the neighbouring countries. At about the same time, a monograph on fossil decapods of the former Austro-Hungarian Empire was published (Lörentz and Beurlen, 1929). The beginning of modern research on fossil decapods from Austria is dated to the second half of the twentieth century with works of Bachmayer (e.g., Bachmayer, 1950, 1953, 1954, 1962; Bachmayer and Tollmann, 1953) and Müller (1984, 1998a, 1998b). Since the hallmark monograph on Badenian (= Langhian–early Serravallian) decapods by Müller (1984), the area once forming the Paratethys Sea (Rögl, 1998, 1999; Harzhauser et al., 2002, 2003) has received renewed attention at the beginning of the twenty-first century. A number of papers dedicated to Neogene decapod crustaceans of the northern part of the Pannonian Basin System include studies on taxonomy, taphonomy, biodiversity, and distribution (e.g., Hyžný and Müller, 2010; Hyžný and Schlögl, 2011; Hyžný et al., 2014, 2015, 2016; Hyžný, 2016). However, there is only limited information about fossil decapods from the southern part of the Pannonian Basin System (Mikuž, 2003; Gašparić and Hyžný, 2015; Gašparić and Ossó, 2016). This paper adds further data on Neogene decapod crustaceans of the latter area.

The earliest report of the Miocene fossil assemblage from the site Dolnja Tuzla in Bosnia and Herzegovina is that by Fuchs (1890), whereas Bittner (1892) reported briefly on a 'small unidentified crab' from the same locality. Later, Stevanović and Eremija (1960) reported several 'well-preserved impressions of crabs' in the marls of an immediate roof of a salt formation in Tušanj near Tuzla. This material has remained largely unstudied until recently. The present contribution aims to address this fossil decapod faunule in detail following a recent re-study of the material. The strati-

graphic age was determined with the microfossil assemblage analysis presented herein and discussion on palaeoenvironmental and palaeobiogeographic implications is also provided.

GEOLOGICAL SETTING

The studied area is located in the Tuzla Basin, in the north-eastern part of Bosnia (Figure 1), which is known for its rock-salt deposits. The Miocene infill, characterised by various lithologies, reaches a thickness of approximately 2300 m (Ćorić et al., 2007). The accessible exposures represent both siliciclastic and carbonate shallow-water sediments (Stevanović and Eremija, 1960). Middle Miocene (Badenian) sediments in the vicinity of the rock salt mine in Tuzla are exposed across a relatively large area with numerous fossil sites. Microfossil assemblages are dominated by foraminifers (Petrović, 1980; Vrabac and Mihajlović, 1990) and calcareous nannoplankton (Ćorić et al., 2007). Macrofossils are rare and consist of plant remains, foraminifera, pteropods, gastropods, bivalves, decapods, echinoids, and fish (Stevanović and Eremija, 1960; Vrabac, 1990).

Because of salt mine exploration and for understanding of its fossil content, the age of the sedimentary filling of the Tuzla Basin has been discussed for a long time. The sediments were assigned to the middle Miocene (Badenian) based on the study of basin lithostratigraphy and foraminifera (Petrović, 1959; Stevanović and Eremija, 1960; Jovanović, 1980; Soklić et al., 1980; Vrabac et al., 1990). According to the most recent study by Vrabac and Ćorić (2008), the salt formation was deposited during the middle Miocene (early Badenian) in a gulf of the Central Paratethys Sea. Exploratory drilling in the roof of the salt formation in the Tuzla Basin indicates the presence of strata of all three parts of the Badenian stage with overlying Sarmatian sediments (Vrabac et al., 2013). Based on calcareous nannoplankton, the age of the roof of the salt formation from the Tuzla Basin was assigned to the lower Badenian NN5 Zone *sensu* Martini (1971) (Ćorić et al., 2007).

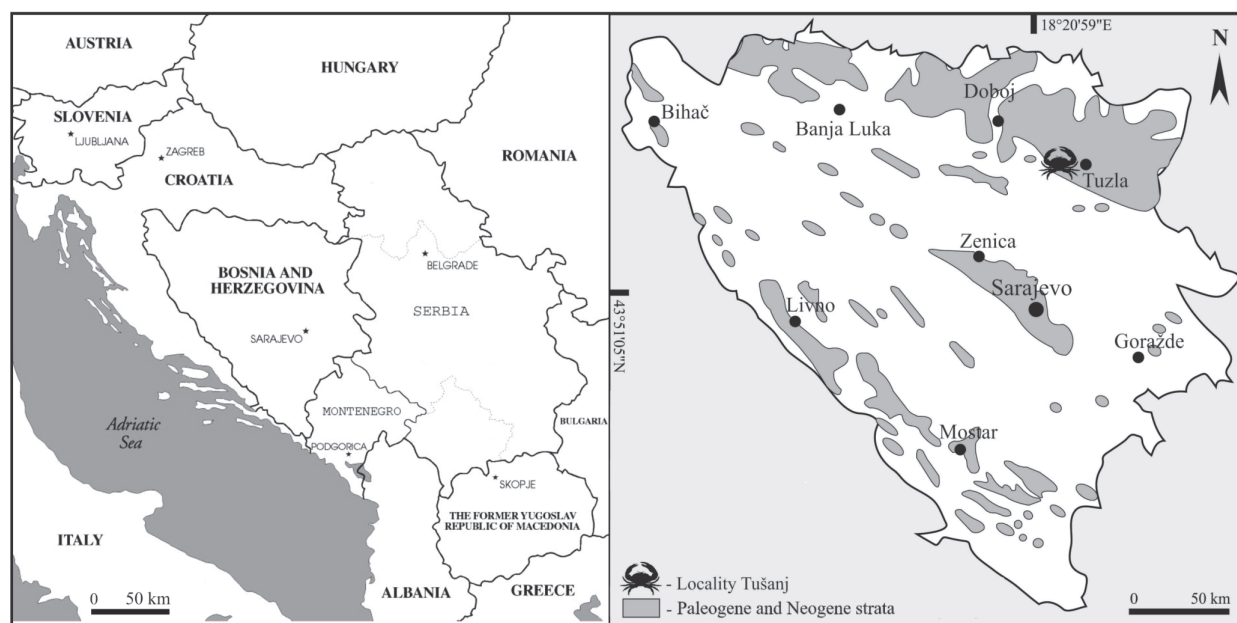


FIGURE 1. Simplified map of Bosnia and Herzegovina showing the fossiliferous locality Tušanj near Tuzla. The colour white represents pre-Cenozoic strata.

Decapod specimens described herein come from two localities in the Tuzla Basin: the ventilation shaft 'Tušanj-2' and the manhole in Simin Han at Dolnja Tuzla. The localities are positioned approximately 6 km from each other. At both sites, the presence of the roof of the salt formation is documented. Based on Bittner (1892), the initial exploratory salt shaft is dated to 1887; however, the ventilation shaft 'Tušanj-2', from which decapod specimens originate, was excavated in the second half of the twentieth century (1953–1967). The shaft 'Tušanj-2' is located approximately 30 m from the exploration borehole 'IB-1' with the GPS coordinates E 18°40'22" and N 44°32'57". The manhole to the salt mine in Simin Han at Dolnja Tuzla is located at E18°45'01" and N44°31'53".

It is possible to establish the boundaries between the salt formation and its immediate roof, which is located at a depth of 266 m (Vrabac and Mihajlović, 1990). The laminated and massive marls with a dominant foraminiferan assemblage of *Ammonia viennensis* (d'Orbigny, 1846) and *Nonion commune* (d'Orbigny, 1846) overlie the salt formation. The first appearance of the foraminifer *Uvigerina macrocarinata* Papp and Turnovský, 1953, indicates the beginning of the early Badenian in the Central Paratethys (Cicha et al., 1998), and is recorded at about 15 m above the salt formation (Vrabac et al., 2013). The total thickness of these marls is about 150 m. In the Tetima salt deposit, located 10 km northeast of the salt deposits in

Tušanj, *A. viennensis* (d'Orbigny, 1846) is documented only 3 m above the salt formation (Vrabac et al., 2013). In Tušanj, similarly to the deposit in Tetima, in the first 3 m following the salt formation foraminifera are extremely rare and planktic forms are dominant. From this information, as well as from the borehole 'IB-1' section, we conclude that the decapod specimens from the ventilation shaft in 'Tušanj-2' collected at a depth of 283 m belong to beds from the immediate proximity of the salt formation.

The investigated sediment from 'Tušanj-2' contained a rich association of calcareous nanofossils with *Sphenolithus heteromorphus* Deflandre, 1953. Accompanied nanofossils included *Braarudosphaera bigelowii* (Gran and Braarud, 1935) Deflandre, 1947; *Coccolithus pelagicus* (Wallich, 1877) Schiller, 1930; *Helicosphaera carteri* (Wallich, 1877) Kamptner, 1954; *H. walbersdorfensis* Müller, 1974; *Micrantholithus* sp.; *Reticulofenestra haqii* Backman, 1978; *R. minuta* Roth, 1970; *Rhabdosphaera sicca* (Stradner, 1963) Fuchs and Stradner, 1977; and *Sphenolithus moriformis* (Brönnimann and Stradner, 1960) Bramlette and Wilcoxon, 1967. Reworked Mesozoic specimens included *Watznaueria barnesi* (Black in Black and Barnes, 1959) Perch-Nielsen, 1968; and *W. fossacincta* (Black, 1971) Bown in Bown and Cooper, 1989.

Based on the absence of *Helicosphaera ampliaperita* Bramlette and Wilcoxon, 1967, the

sample can be attributed to the nannoplankton NN5 Zone sensu Martini (1971). The absence of *Helicospaera waltrans* Theodoridis, 1984 allows the assignment of the assemblage to the upper part of the NN5 Zone, which can be correlated with the upper part of the Langhian and the upper part of the lower Badenian (Kováč et al., 2007; Piller et al., 2007).

Foraminifers are very rare in the sample from 'Tušanj-2' and planktic forms dominate. Several taxa were identified, including *Globigerina bulloides* d'Orbigny, 1826, *Globigerina* sp., *Quinqueloculina* sp., *Cibicidoides* sp., and *Laevidentalina* sp.

MATERIAL AND METHODS

Eight decapod specimens were collected from the middle Miocene marls of Tušanj. Seven of them were recovered from the ventilation shaft of the salt mine at a depth of 283 m, whereas a single specimen originates from Dolnja Tuzla. After preparation with fine needles, the specimens were photographed, measured, and further documented using CorelDRAW X5, Adobe Photoshop CC, and Statistica. Photographs were taken with digital cameras Nikon D810 and Nikon Coolpix P7800 under low angle light source conditions. We observed morphological details and measured specimens under stereomicroscope Leica EZ-4D. Because of a delicate nature of the studied specimens they were not whitened prior to photography.

Sieved material from the 'Tušanj-2' shaft with granulation 0.1–0.8 mm was used for determination of foraminifera. Samples were analysed by stereomicroscope Technical Carl Zeiss Jena with up to x100 magnification.

Repositories

Material studied herein. Specimens PS-02–08 are a part of the Petar Stevanović Collection housed in the Natural History Museum in Belgrade (Serbia). The specimen GBA 1892/005/0001 is housed in the collections of the Geological Survey in Vienna (Austria).

Comparative material. *Retropluma minuta* sp. nov. described herein was compared with several fossil *Retropluma* species. The material of these taxa is deposited in the following institutions: MCZ, Museo Civico "G. Zannato" di Montecchio Maggione, Italy; MSM, Midtsønderjyllands Museum at Gram, Denmark; MSNM, Museo Civico di Storia Naturale di Milano, Italy; RGA/SMNH, Slovenian Museum of Natural History, Ljubljana, Slovenia.

Abbreviations

Parameters measured: L, carapace length excluding rostrum; LR, total carapace length including rostrum; LG, length of gastric region; LP, length of pleon; WM, maximum carapace width; WA, total width of anterior margin; OW, fronto-orbital width; WP, width of pleon. All measurements are in millimetres.

SYSTEMATIC PALAEONTOLOGY

Order DECAPODA Latreille, 1802

Infraorder ANOMURA MacLeay, 1838

Superfamily GALATHEOIDEA Samouelle, 1819

Family MUNIDOPSIDAE Ortmann, 1898

Genus MUNIDOPSIS Whiteaves, 1874

Type species. *Munidopsis curvirostra* Whiteaves, 1874, by monotypy.

Remarks. *Munidopsis* is one of the most speciose decapod genera and includes more than 220 species (Macpherson and Baba, 2011). It is highly diverse morphologically, which led some scholars to recognise several subgenera in the genus (for details see Ahyong et al., 2011 and Robins et al., 2013). Indeed, phylogenetic studies based both on molecular and morphological data clearly show that *Munidopsis* as currently understood is not monophyletic (Ahyong et al., 2011; Bracken-Grisom et al., 2013). Despite its speciose nature, the genus has a poor fossil record consisting of only a handful of taxa (Hyžný et al., 2014). For a discussion on differentiation of *Munidopsis* from other exclusively fossil genera, a reference is made to Robins et al. (2013) and references therein.

Munidopsis salinaria sp. nov.

Figure 2.1–2.2

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Diagnosis. Carapace with well-defined hepatic, epigastric, mesogastric, epibranchial and cardiac regions; epigastric regions circular; rostrum styliform, keeled; carapace surface covered with parallel striae, striae forming longer ridges in mesogastric region and posterior part of carapace.

Etymology. The species epithet refers to the circumstances of the type specimen discovery which was recovered from the exploratory shaft of a salt mine. Latin fem. adj. *salinaria*, belonging to salt-works.

Holotype. GBA 1892/005/0001—isolated, slightly compressed carapace.

Measurements. L = 6.1; LR = 8.1; LG = 2.5; WM = 6.6; WA = 4.2; WM/L = 1.08.

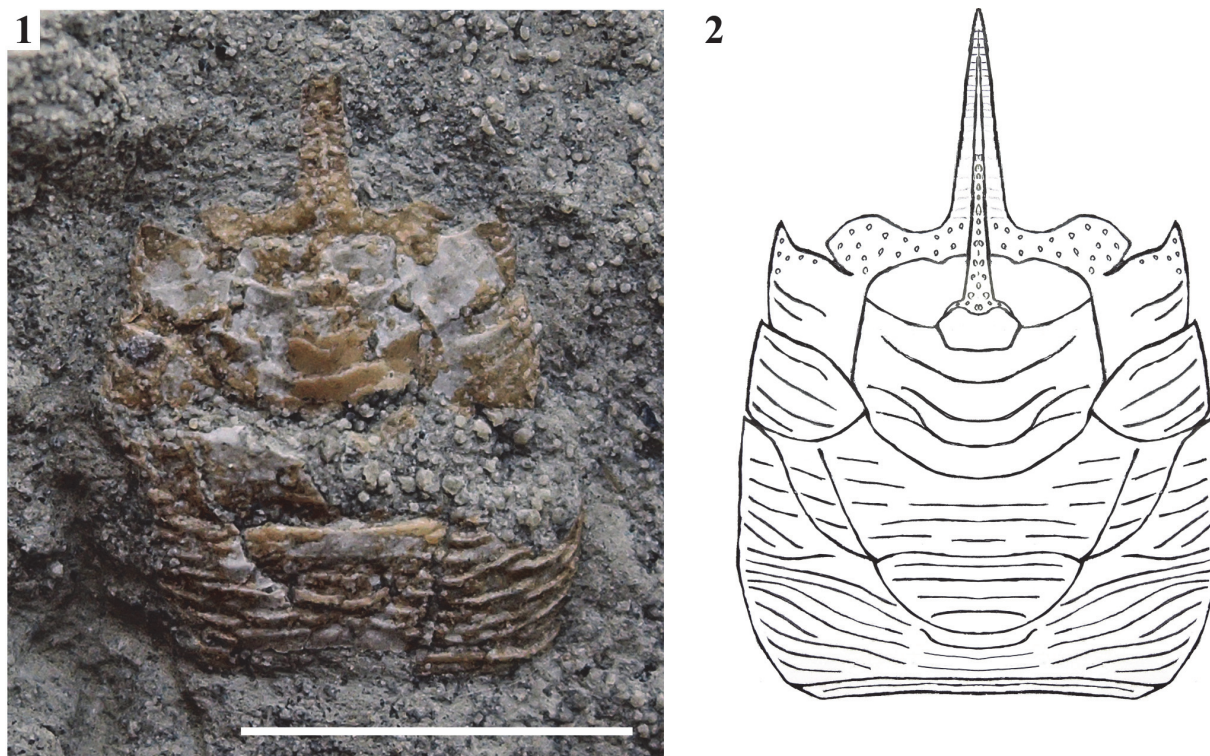


FIGURE 2. *Munidopsis salinaria* sp. nov., holotype (GBA 1892/005/0001) showing an incomplete isolated dorsal carapace (1) and its schematic reconstruction (2). Scale bar equals 10 mm.

Description. Carapace subsquare (length excluding rostrum/width is ~ 1); moderately convex transversely. Rostrum styliform, keeled; tip broken. Anterior margin sinuous. Lateral margins slightly convex, with two spines. Grooves well-developed. Circumgastric groove strong; slightly V-shaped in posteriormost part; hepatic and epibranchial branches distinct. Epigastric, hepatic, epibranchial, and cardiac regions well defined. Regions slightly inflated. Hepatic region quadrate with one anterolateral spine epigastric regions circular and inflated. Area of metagastric region not well preserved. Cardiac region broad, U-shaped posteriorly, straight posteriorly. Carapace ornamented with short to moderately long parallel transverse striae, striae forming transverse, squamous ridges in mesogastric and posterior portions of carapace. Posterior margin strongly rimmed, seemingly straight, not well preserved. Ventral surface and appendages not preserved.

Remarks. The only known specimen represents an incomplete dorsal carapace, broken at about mid-length; thus, the area of the metagastric region and posterior carapace margin cannot be described properly. Nevertheless, the specimen is complete enough to allow direct comparison with known fossil and extant congeners. From the area

once covered by the Paratethys Sea, two additional species of *Munidopsis* are known (Hyžný et al., 2014). *Munidopsis lieskovensis* Hyžný and Schlögl, 2011, from the lower Miocene (Karpatian) of the Slovak part of the Vienna Basin, differs in having a narrower cardiac region and rather uniform carapace ornamentation. *Munidopsis salinaria* sp. nov. possesses strong squamous ridges on the posterior portions of the carapace; in this respect, it is close to *Munidopsis palmuelleri* Hyžný, Gašparič, Robins and Schlögl, 2014, from the middle Miocene (lower Badenian) of northern Slovenia. However, *M. palmuelleri* differs from the new species by its proportionally longer carapace, not well-marked cardiac region, and unkeeled rostrum. In general, the new species shares some characters with *M. lieskovensis* (keeled rostrum, circular epigastric regions) and other characters with *M. palmuelleri* (strong squamous ridges on posterior portions of the carapace). *Munidopsis salinaria* sp. nov. appears to be intermediate between the two taxa mentioned and, therefore, is considered a close relative of both discussed species. This is not surprising given both the geographic proximity of the known occurrences and stratigraphic overlap of all three taxa.

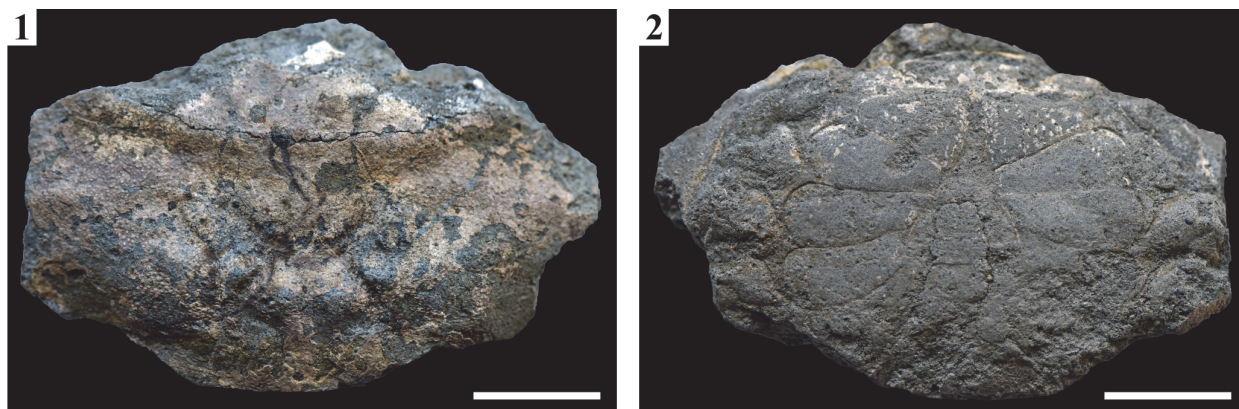


FIGURE 3. *Portunus monspeliensis* A. Milne Edwards, 1860, a male individual (PS-8) in dorsal (1) and ventral (2) views. Scale bar equals 10 mm.

Munidopsis salinaria sp. nov. differs also from its fossil congeners from more distant parts of the world. *Munidopsis scabrosa* Feldmann and Wilson, 1988, from the upper Eocene of Antarctica, and *M. foersteri* Feldmann, Tshudy and Thomson, 1993 from the Upper Cretaceous (Campanian) of Antarctica have a rounded base of the circumgastric groove, which seems to be slightly V-shaped in *M. salinaria* sp. nov. Moreover, *M. foersteri* has a pyriform carapace and the rostrum is nearly as long as the carapace (Feldmann et al., 1993), quite unlike many other munidopsids (Ahyong et al., 2011, figure 1). In fact, accommodation of *M. foersteri* within the family Chirostylidae would be more appropriate, for which the pyriform carapace with much elongated rostrum is typical (Baba et al., 2008, figure 1). *Munidopsis scabrosa* has scabrose ornamentation directed forwards; that of *M. salinaria* sp. nov. is much more ridge-like.

From extant congeners, *Munidopsis salinaria* sp. nov. with its arrangement of carapace regions is similar to the *Bathyankestrytes* group sensu Ahyong et al. (2011) represented by, e.g., *M. (B.) levis* Alcock and Anderson, 1894. The combination of the characters present in *M. salinaria* sp. nov., however, is unique and warrants an erection of a new species.

Occurrence. The species is known only from its type locality, i.e., Dolnja Tuzla in Bosnia and Herzegovina.

Infraorder BRACHYURA Latreille, 1802
Superfamily PORTUNOIDEA Rafinesque, 1815
Family PORTUNIDAE Rafinesque, 1815
Subfamily PORTUNINAE Rafinesque, 1815
Genus PORTUNUS Weber, 1795

Type species. *Cancer pelagicus* Linnaeus, 1758, by subsequent designation of Rathbun (1926).

Remarks. There are more than 40 exclusively fossil species of *Portunus* reported worldwide (Schweitzer et al., 2010); it must, however, be noted that subgenera are not commonly recognized in the palaeontological practice. As noted by Karsawa et al. (2008) and Spiridonov et al. (2014), the subgenera as recognized by Davie (2002) and Ng et al. (2008) appear to be not closely related, but rather represent distinct clades. In this respect, the fossil record of *Portunus* sensu lato is in need of revision.

Portunus is a common element in Neogene decapod assemblages, including those reported from the circum-Mediterranean area (Müller, 1984; Gašparič and Ossó, 2016; Díaz-Medina et al., 2018).

Portunus monspeliensis A. Milne Edwards, 1860
Figure 3.1-3.2

- 1860 *Neptunus monspeliensis* A. Milne Edwards, p. 232, pl. 4, fig. 1, pl. 5, fig. 1.
- 1860 *Neptunus granulatus* A. Milne Edwards, p. 241, pl. 3, fig. 1, pl. 7, fig. 2.
- 1929 *Neptunus granulatus* A. Milne Edwards; Lörentz and Beurlen, p. 188, pl. 13, figs. 3–4, pl. 14, figs. 1–4.
- 1956 *Neptunus granulatus* A. Milne Edwards; Comaschi Caria, p. 284, 288, pl. 1, figs. 1–7, pl. 2, figs. 1–6, pl. 3, figs. 1–2.
- 1968 *Neptunus granulatus* A. Milne Edwards; Stancu and Andreescu, p. 466, pl. 7, fig. 85.
- 1984 *Portunus monspeliensis* (A. Milne Edwards); Müller, p. 79, pl. 62, figs. 1–2.
- 1991 *Portunus monspeliensis* (A. Milne Edwards); Marras and Ventura, p. 108, pl. 1, figs. 1–4, pl. 2, figs. 1, 4, pl. 3, figs. 1–3.
- 1993 *Portunus monspeliensis* (A. Milne Edwards); Müller, p. 14–15, pl. 6, fig. G, pl. 7, fig. A.

- 2003 *Portunus monspeliensis* (A. Milne Edwards); Mikuž, p. 187–199, p. 1, figs. 1–5, pl. 2, figs. 1–8.
- 2007 *Portunus monspeliensis* (A. Milne Edwards); Artal and Gilles, p. 8, pl. 1, fig. C.
- 2009 *Portunus monspeliensis* (A. Milne Edwards); Marangon and De Angeli, p. 5–10, figs. 2–4.
- 2016 *Portunus monspeliensis* (A. Milne Edwards); Gašparič and Ossó, p. 55–66, pl. 2, figs. A–H.
- 2018 *Portunus monspeliensis* (A. Milne Edwards); Díaz-Medina, Ossó and Hyžný, p. 133, figs. 3A–E. (abbreviated synonymy)

Material. Single partially preserved carapace of a male individual, with preserved sternum and pleon (PS-08).

Measurements. L = 30.5; OW = 27.8; MW = 56.4 (estimated value); L/MW = 0.54.

Description. Carapace hexagonal, incomplete, and heavily weathered, with relative carapace measurements of approximately 1.85 times wider than long. Front protruding and slightly downturned. Fronto-orbital and anterolateral margins poorly preserved. Posterolateral margin presumably straight with concave depression in the last third of its length. Posterior margin broad.

Dorsal carapace surface covered densely by small granules, cuticle not preserved in its entirety. Carapace regions faintly defined; protogastric regions as semi-circular lobes with indistinct transverse ridge; mesogastric and metagastric regions trapezoid in outline and separated by faint transverse ridge. Cardiac region well-defined, pentagonal, somewhat swollen with central depression running longitudinally. Intestinal region faint and circular. Epibranchial region wide, separated from mesobranchial region by arcuate transverse ridge. Cervical groove distinct. Branchiocardiac groove well marked, along sides of cardiac region.

Thoracic sternum broad, oval, widening posteriorly, widest at thoracic sternite 6, with straight to slightly concave sutures between respective sternites. Thoracic sternites 1–2 not preserved, sternites 3–4 fused in trapezoidal plate, axial sulcus reaching anterior margin of sternite 3, transverse ridge in sternite 4 medially interrupted; sternites 5–7 transversely elongated, distally rounded; sternite 6 the longest; sternite 7 shorter than sternite 6; sternite 8 not recognizable; sternites 5–7 expanded laterally into episternites. Pleon broadly subtriangular; pleonites 1–4 not preserved, pleonites 5–6 similarly long; telson subtriangular, poorly preserved.

Remarks. Despite the poor preservation of the studied specimen, it is attributed herein to *Portunus monspeliensis* based on the broadly hexagonal carapace outline, the presence of protogastric

keels, and the characteristic sternum (Müller, 1984, pl. 62, figures 1–2; Marangon and De Angeli, 2009, figures 2–4; Gašparič and Ossó, 2016, pl. 1, figures A–H). *Portunus monspeliensis* is among the most widespread Miocene brachyuran crabs of the circum-Mediterranean area (Lőrentthey and Beurlen, 1929; Gašparič and Ossó, 2016; Díaz-Medina et al., 2018). This report represents the first occurrence of *P. monspeliensis* from the southern Pannonian Basin of the Central Paratethys.

Superfamily RETROPLUMOIDEA Gill, 1894

Family RETROPLUMIDAE Gill, 1894

Genus RETROPLUMA Gill, 1894

Type species. *Archaeoplax notopus* Alcock and Anderson, 1894, by monotypy.

Remarks. All species of *Retropluma* share a set of characteristic carapace features, including a flattened carapace with a more or less quadrangular outline and distinct transverse carinae, a truncate front, exposed orbits, a narrow single-lobed rostrum, pincer-shaped chelipeds, long slender pereopods (P2–P4), and a reduced setose fifth pereopod (P5) (McLay, 2006). The fossil species of *Retropluma* differ in their carapace width to length ratio, dorsal ornamentation, the position of anterolateral teeth, and the shape of the rostrum (Artal et al., 2006; Gašparič and Hyžný, 2015). Other distinctive features such as relative size of ocular peduncles (de Saint Laurent, 1989) are usually not present in the fossil material.

Retropluma is known from the Miocene of Europe, including Slovenia (Gašparič and Hyžný, 2015; Gašparič and Križnar, 2017), Slovakia (Hyžný et al., 2015), and Denmark (Fraaije et al., 2005). The material described below is the first report of the genus from Bosnia.

Retropluma minuta sp. nov.

Figures 4.1–4.6, 5.1–5.4, 6

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Diagnosis. Carapace square in outline (W/L~1.0), with strong anterolateral tooth pointing slightly outwards. Rostrum rounded and spiny distally. Rounded, swollen bases of antennules extending over the sinuous anterior margin.

Etymology. The species epithet refers to its minute size for retroplumid crabs. The new species represents the smallest fossil representative of the genus described to date.

Holotype. The holotype (PS-03) consists of an articulated near-complete individual preserved in ventral aspect.

Paratypes. PS-02, near-complete and articulated male individual in ventral aspect with preserved

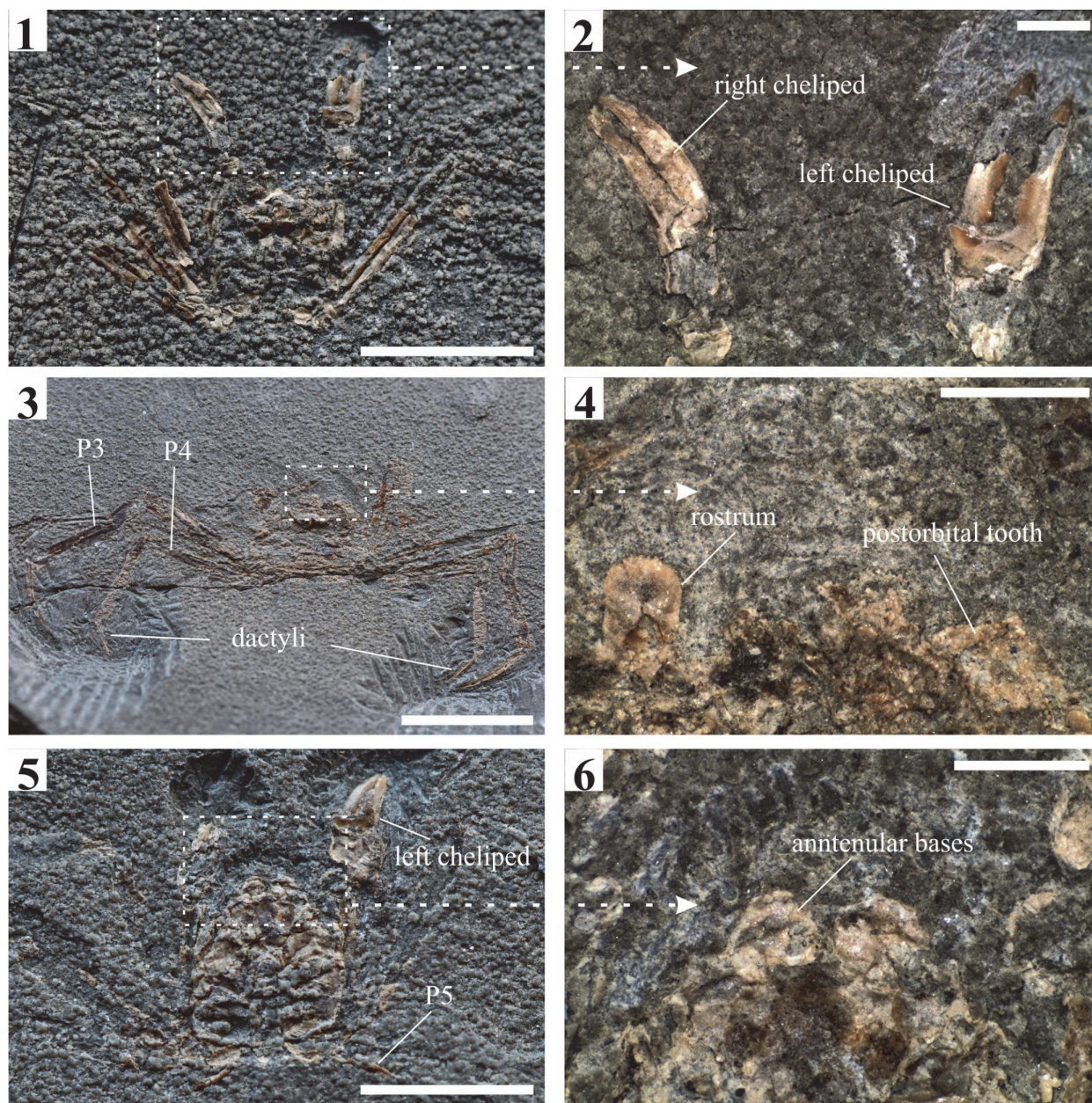


FIGURE 4. *Retropluma minuta* sp. nov. **1**, PS-3 (holotype), male individual. **2**, PS-3 (detailed view on chelipeds. **3**, PS-7 (paratype), female individual. **4**, PS-7, detailed view on rostrum. **5**, PS-4 (paratype), male individual. **6**, PS-4, detailed view on antennular bases. Scale bars in 1, 3, and 5 equal 5 mm, scale bars in 2, 4, and 6 equal 1 mm. P3–P5 = pereopods 3–5.

anterior; PS-04, near-complete and articulated male in ventral aspect with preserved bases of antennules; PS-06, near-complete and articulated female in ventral aspect with pleon and fifth pereopods; PS-07, near-complete and articulated individual in ventral aspect with preserved front including rostrum.

Measurements. PS-02: L = 3.9; LP = 2.6; WM = 3.8; WA = 2.1; WP = 1.0; WM/L = 0.97. PS-03: L = 4.1; LP = 2.6; WM = 3.8; WA = 2.6; WP = 1.0; WM/

L = 0.98. PS-04: L = 3.9; LP = 2.3; WM = 3.7; WA = 2.4; WP = 1.0; WM/L = 0.95. PS-05: L = 6.7 (estimated value); WM = 6.9 (estimated value); WM/L = 1.03. PS-06: L = 6.1; LP = 3.6; WM = 6.1; WP = 2.3; WM/L = 1.00. PS-07: L = 7.1; LP = 4.5; WM = 7.5; WA = 5.6 (estimated value); WP = 2.0; WM/L = 1.03.

Description. Carapace subsquare (WM/L = 0.97–1.03). Rostrum bent slightly downward, rounded and spiny distally. Supraorbital margin sinuous,

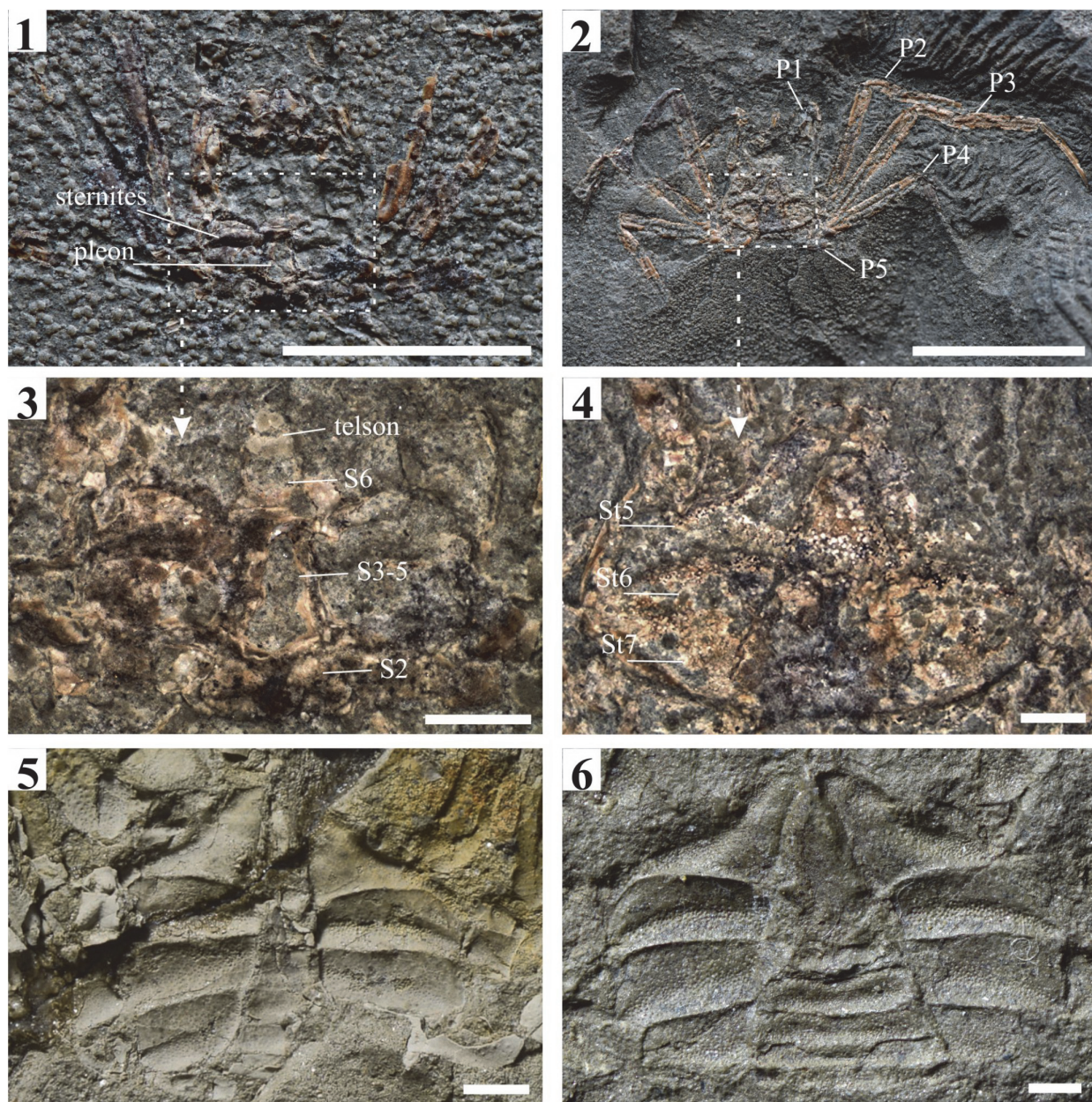


FIGURE 5. *Retropluma minuta* sp. nov. (1–4) and *Retropluma slovenica* Gašparič and Hyžný, 2014 (5, 6). 1, PS-2 (paratype), male individual. 2, PS-6 (paratype), female individual. 3, PS-6, detailed view on male pleon. 4, PS-7, detailed view on female pleon. 5, CNZ-660, male individual. 6, CNZ-275, female individual. Scale bars in 1 and 2 equal 5 mm, scale bars in 3–6 equal 1 mm. P1–P5 = pereopods 1–5; S2–S6 = pleonal somites 2–6; St5–St7 = thoracic sternites 5–7.

with indistinct supraorbital tooth and reduced orbits. Postorbital tooth strong and triangular, pointed forwards. Rounded, swollen bases of antennules extending over the anterior margin and filling entire orbital area beneath the rostrum. Anterolateral margin straight till anterior carina. Lateral and posterolateral margins slightly convex. Posterior margin strong and rimmed, with weakly developed re-entrant for fifth pereopods (P5).

Morphological characters of dorsal carapace only partially preserved. Three transverse carinae discernible on lateral portions of carapace. Carinae forming ridges at intersection with lateral margin. Carapace widest mid-length at median carina. Surface of thoracic sternites pitted and finely granulate, with enlarged granules laterally and on ridges.

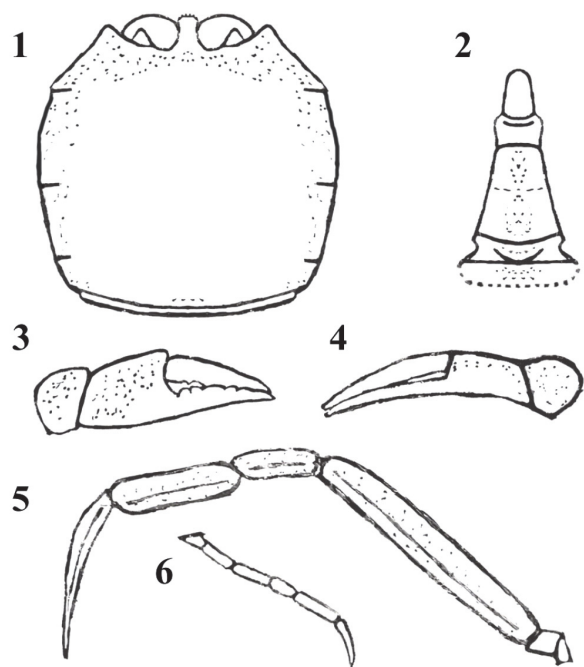


FIGURE 6. *Retropluma minuta* sp. nov., schematic reconstruction. 1, Carapace in dorsal view (blank area represents not preserved portion). 2, Male pleon (pleonal somite 1 is not preserved). 3, Left cheliped (P1). 4, Right cheliped (P1). 5, Longest pereopod (P3). 6, Shortest pereopod (P5), conjectural.

Female pleon broadly triangular, with straight margins, narrowing anteriorly, somites becoming narrower and longer anteriorly, telson longer than wide and terminally rounded. Male pleon narrower than that of female. Somite 2 wide, with strong sinuous transverse ridge. Posterior margin straight, anterior margin strongly concave. Lateral margins almost triangular. Male pleon widest at transverse ridge of somite 2. Somites 3–5 fused, sutures 3/4 and 4/5 visible. Lateral margins of fused 3–5 segment straight, narrowing distally. Somite 6 longer than wide, with sinuous lateral margins, convex posteriorly and concave anteriorly, posterolateral corners bluntly rounded. Distinct transverse ridge in anterior part of somite 6, anterior margin with telson slightly convex and centrally rimmed. Telson narrow and long, with rounded termination. Female sternal plate in outline more round than that of male, sternites 5–7 long, convex and ridged. Sternite 8 reduced and covered by pleon.

Chelipeds (P1) long, slender and distinctly unequal. Right cheliped slender, propodus and dactylus curved, narrowing distally, both fingers long and forceps-like, lateral surfaces without ornamentation. Occlusal margin of right cheliped fingers straight and unarmed. Left cheliped noticeably

more robust than right cheliped. Fingers stouter, both with several large blunt teeth. Carpus and merus stout and adorned with tubercles. P2–P4 achelate, much longer than chelipeds, P3 longest, surface finely granulose and flattened, with central groove running along the whole length, ending in long blade-like dactyli. P5 strongly reduced and thin, length about one third of P3.

Remarks. The studied material consists of six articulated specimens preserved in ventral aspect. Original cuticle, although preserved, is covered by coarse mineral grains which obliterate finer details. Although dorsal carapace features are incomplete, there are enough distinguishing characters to warrant the erection of a new species. *Retropluma minuta* sp. nov. differs from its fossil congeners, i.e., *Retropluma borealis* Fraaije, Hansen and Hansen, 2005; *R. craverii* (Crema, 1895); *R. eocenica* Vía Boada, 1959; and *R. slovenica* Gašparič and Hyžný, 2014, not only by its minute size, but more importantly, by a distinctly square carapace outline, and the smallest width to length ratio (Figure 7; for raw data see Appendix 1). *Retropluma gallica* Artal, Van Bakel and Castillo, 2006, was not included in the comparison because of lack of sufficient data (i.e., available carapace measurements). Additionally, *Retropluma minuta* sp. nov. is characterised by a sinuous anterior margin with reduced orbits and enlarged, rounded bases of antennules and a unique male pleon with strong ridge on somite 2.

Of the previously described fossil representatives of *Retropluma*, *R. minuta* sp. nov. is similar to *Retropluma slovenica* (Figure 5.5–5.6) from the early Miocene of Slovenia (Gašparič and Hyžný, 2015) and the middle Miocene of Slovakia (Hyžný et al., 2015). The new species differs from *R. slovenica* in having a subsquare carapace ($WM/L = 0.98–1.03$) whereas it is wider in *R. slovenica* ($WM/L = 1.24$), and having a smaller rounded and spinous rostrum. On the anterior margin of *R. minuta* sp. nov. are visible greatly enlarged rounded bases of antennules (present also among extant species, e.g., McLay, 2006, figure 3A) and reduced ocular orbits, unlike the specimens of *R. slovenica*. Additionally, *R. minuta* sp. nov. displays a uniquely developed and strongly ridged male pleonal somite 2 and possesses distinctly unequal chelipeds, with a much stronger left cheliped (preserved in three studied specimens) with a dentate occlusal margin, whereas the chelipeds in *R. slovenica* are of subequal size with left cheliped being somewhat slenderer. Pereiopods 2–4 are longer compared to carapace size in *R. minuta* sp. nov. and the blade-like

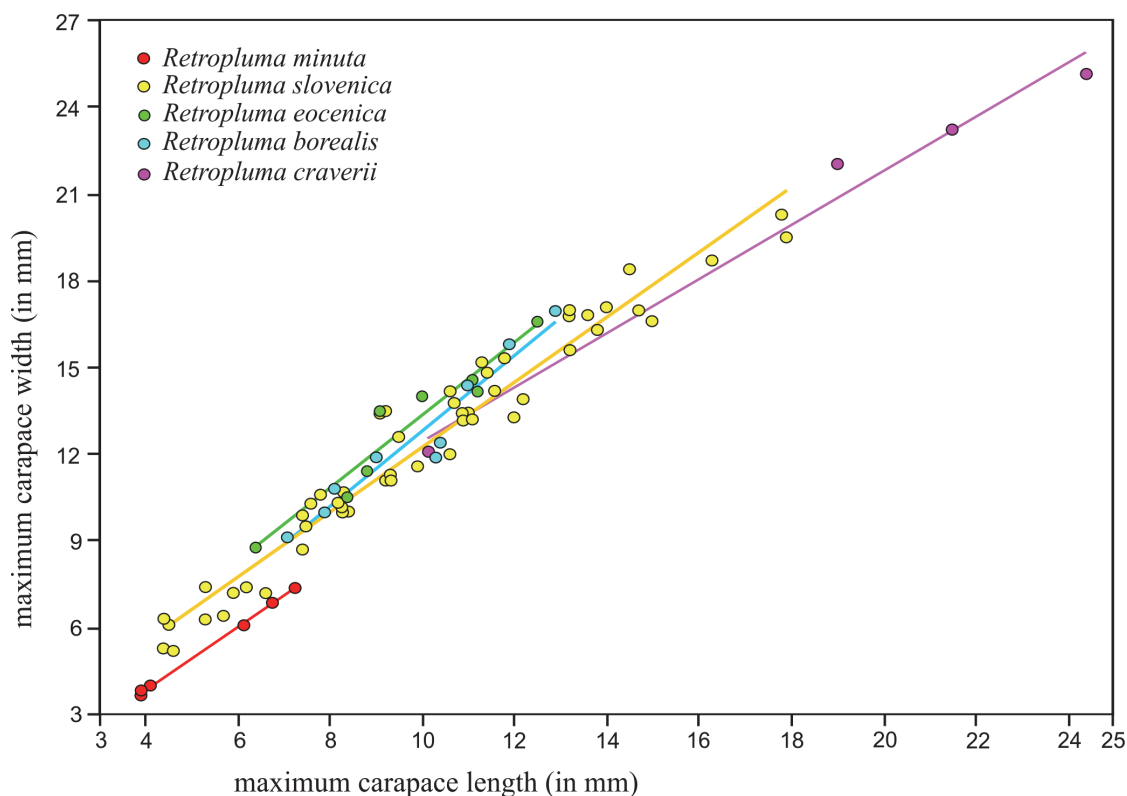


FIGURE 7. Graph showing the ratio between the maximum carapace width and carapace length of fossil *Retropluma* species. The regression line is based on the ordinary least squares linear model.

dactyli are also markedly longer. *Retropluma minuta* sp. nov. also has a more convex posterior margin than *R. slovenica*.

Retropluma is represented by seven extant species, mostly from the Indo-Pacific region (Gašparič and Hyžný, 2015, table 4). *Retropluma minuta* sp. nov. resembles closely the extant *Retropluma laurentae* McLay, 2006, in general outline of the carapace, possession of a small rounded rostrum, a forward pointing triangular postorbital tooth and swollen, rounded bases of antennules. The carapace outline of *R. minuta* sp. nov. is sub-square, whereas it is rectangular in *R. laurentae* and the anterior margin of *R. minuta* sp. nov. is more sinuous with noticeable supraorbital tooth.

Occurrence. The species is known only from its type locality, i.e., the ventilation shaft of the salt mine Tušanj-2, Bosnia and Herzegovina.

DISCUSSION

Decapod Taphonomy

Decapod crustaceans have a relatively low fossilisation potential in comparison to more calcified mollusc shells (Kidwell and Flessa, 1995; Stempien, 2005). Consequently, decapods are

subject to rapid decomposition, and the fragile exoskeleton is often fragmented before burial takes place (Plotnick et al., 1988; Stempien, 2005; Krause et al., 2011; Klompmaker et al., 2017).

All examined specimens of *Retropluma minuta* sp. nov. are preserved in ventral aspect. Their relaxed position (appendages aligned along the carapace sides and chelipeds closed; cf. Bishop, 1986, p. 331) suggests that they represent corpses, which indicates that the retroplumid specimens are autochthonous. No carapace displacement could be observed, which is otherwise characteristic for preservation of crab moults, in which the pleon is not connected to the carapace anymore (Schäfer, 1972; Bishop, 1986). However, the moulted carapace may flip back (Schäfer, 1972), especially in a low-energy environment, so the resulting remains are impossible to distinguish from the corpse. Thus, we cannot say for sure whether the specimens represent corpses or moults. Whatever the real nature of the specimens, the preservation of delicate appendages still attached to the crab body does not suggest post-mortem transport.

Studied decapod specimens from the Tuzla Basin show two basic modes of preservation. The

squat lobster *Munidopsis* and the brachyuran crab *Portunus* are preserved as isolated carapaces without appendages, whereas retroplumid crabs are complete and virtually intact. This observation has further implications: retroplumid crabs are to be considered autochthonous, whereas isolated carapace of *Munidopsis* and insufficiently preserved specimen of *Portunus monspeliensis* might have been transported prior to final burial. However, such transport had to be rather short; otherwise fragile carapaces would not be preserved at all.

Environment Preferences of Decapods

Although the squat lobster *Munidopsis* is considered a typical deep-water genus (Macpherson, 2007), squat lobsters in general inhabit a wide range of habitats from the intertidal zone to bathyal depths (Baba et al., 2008) and are a common element of benthic communities on coral reefs or rocky and muddy bottoms (Lowrich and Thiel, 2011). Moreover, there are fossil representatives of *Munidopsis* reported from shallow marine settings (Feldmann and Wilson, 1988; Feldmann et al., 1993).

Many extant portunids, such as *Portunus pelagicus* (Linnaeus, 1758), are found in the Indo-Pacific waters and even in the eastern margin of the Mediterranean Sea (Lai et al., 2010). Judging from the lithologies (sandstones and sandy limestones interbedded with marls) bearing fossils of *Portunus monspeliensis* (Gašparič and Ossó, 2016), and comparing to extant *P. pelagicus* (Chande and Mgaya, 2003; Kunsook et al., 2014), it can be concluded that *P. monspeliensis* inhabited a wide range of habitats, but preferred sublittoral algal and sea grass meadows on both sandy and muddy substrate. Based on the cluster analysis, Müller (1984, table 4) estimated the bathymetry of sedimentary settings with abundant *Portunus* remains as deposited in a shallow marine environment with 20–30 m water depth.

Extant representatives of *Retropluma* preferentially inhabit muddy or sandy bottoms at a depth of 70 to 450 m (de Saint Laurent, 1989; McLay, 2006; see also Gašparič and Hyžný, 2015, table 4), where they spend most of the time buried in soft substrate (Ahyong, 2008). *Retropluma slovenica* from the early Miocene of Slovenia was recorded from settings interpreted to have been deposited in waters deeper than 125 m (Gašparič and Hyžný, 2015), and a similar depth was estimated for the palaeoenvironment at the middle Miocene locality

of Slovakia where *R. slovenica* was also found (Hyžný et al., 2015).

Palaeoenvironment and Bathymetry

The middle Miocene transgression occurred in the area of what is now northern Bosnia and Herzegovina during the early Badenian, having its base at 14.91 Ma (Čorić et al., 2009; Pezelj et al., 2013; see also Kováč et al., 2017a, 2017b) as a result of the increase in global sea level. The gastropod *Sveltia* cf. *dertovaricosa* (Sacco, 1894) and the pteropod *Vaginella austriaca*, Kittl, 1886, were found in the ventilation shaft 'Tušanj-2' at 283 m depth, together with the decapod remains and internal moulds of cancellariid snails. The mollusc assemblage suggests fully marine settings. The foraminiferal assemblages of 'Tušanj-2' indicate that the investigated marls of Tušanj were deposited in very shallow sublittoral settings with the water depth not exceeding 10 m. For comparison, numerous miliolid foraminifers inhabit the Gulf of Florida today, in association with nonionids and rotalid foraminifera, at depths of up to 3 m (Moore, 1957). *Quinqueloculina* with *Ammonia* are characteristic for shallow inner shelf settings (Haq and Boersma, 1998). Similarly, the absence of discoasters and the dominance of *Reticulofenestra minuta*, *Helicosphaera carteri*, and *Coccolithus pelagicus* in the nannoplankton assemblage point to a nutrient-rich, shallow-marine environment (Čorić et al., 2009).

Interestingly, the investigated decapod assemblage from the Tuzla Basin consists of taxa not commonly found in shallow-marine settings. Besides *Portunus*, a typical inhabitant of shallow waters, there are also specimens of *Retropluma*. The occurrence of articulated specimens of the latter genus in sublittoral settings is rather surprising. Although some Eocene retroplumoids have been reported from shallow-marine settings (Beschinn et al., 1996; Khodaverdi et al., 2016), these taxa represent genera other than *Retropluma*, whereas Eocene representatives of *Retropluma* are known from outer-shelf habitats (Artal et al., 2006).

Comparison with Miocene Decapod Assemblages from Slovenia

Paratethyan decapod faunas are rather homogeneous across respective basins (Hyžný, 2016); in fact, the Paratethys has been shown to represent a compact area without further biogeographic fragmentation (Harzhauser et al., 2002, 2003). Thus, not surprisingly, the decapod assemblage from the Tuzla Basin of Bosnia and Herze-

TABLE 1. Palaeoenvironmental preferences of congeners from the roughly coeval decapod assemblages from Slovenia.

Taxon	<i>Retropluma slovenica</i> Gašparič and Hyžný, 2014	<i>Munidopsis palmuelleri</i> Hyžný et al., 2014	<i>Portunus monspeliensis</i> A. Milne Edwards, 1860
Localities	Činžat (NE Slovenia), Tunjice (Central Slovenia)	Košaki (NE Slovenia)	Šentilj (NE Slovenia), Kozje (E Slovenia), Brežice (E Slovenia)
Age	latest Burdigalian (Karpatian)	Langhian (early Badenian)	Langhian–early Serravallian (Badenian)
Lithology	micaceous siltstones, sandy siltstones	clayey marls	calcareous sandstone
Bathymetry	epibathyal	epibathyal	sublittoral
Preservation	fully articulated	disarticulated	disarticulated
Substrate	muddy bottom	muddy bottom	sandy or seagrass bottom
Ecology	benthic infaunal	benthic epifaunal	benthic/pelagic

govina described herein is very close taxonomically to decapod associations from the geographically proximal area of Slovenia. All three genera, *Munidopsis*, *Portunus*, and *Retropluma*, have been previously reported from Slovenian early and middle Miocene localities (Hyžný et al., 2014; Gašparič and Hyžný, 2015; Gašparič and Ossó, 2016). There are, however, distinct differences in the inferred palaeoenvironment of localities with respective decapod taxa (Table 1). Although in all cases muddy sea bottoms with predominantly siliciclastic depositional settings were documented, the water depth apparently was not similar. Whereas *Retropluma slovenica* and *Munidopsis palmuelleri* are considered to derive from a deep water environment (Hyžný et al., 2014; Gašparič and Hyžný, 2015), the association from the Tuzla Basin dominated by *Retropluma minuta* sp. nov. occurred in a shallow-water, nutrient rich palaeoenvironment.

CONCLUSIONS

A fossil decapod assemblage consisting of three species is described from the upper Langhian (lower Badenian) of the Tuzla Basin. The occurrence is the first formal report of fossil decapod crustaceans from Bosnia and Herzegovina. The decapod assemblage is dominated by *Retropluma minuta* sp. nov. (Brachyura, Retroplumidae) and accompanied by *Munidopsis salinaria* sp. nov. (Anomura, Galatheoidea) and *Portunus mon-*

speliensis (Brachyura, Portunidae). Based on the microfossil association, the studied assemblage is considered to have once inhabited a shallow, near-shore depositional setting. The occurrence of near-complete individuals of *Retropluma* in the Miocene shallow-marine settings of the Tuzla Basin suggests wider bathymetric range of the genus than it displays today. All three genera reported from the Tuzla Basin, namely *Munidopsis*, *Portunus* and *Retropluma*, have previously been reported from Slovenia, the most proximal area with known decapod fossils to that of the Tuzla Basin in Bosnia and Herzegovina. Contrary to shallow-marine settings of the localities of the Tuzla Basin, *Munidopsis* and *Retropluma* from Slovenian localities are reported from deeper-marine settings.

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APPENDIX 1.

Measurements of *Retropluma* spp. used for construction of graph shown in Figure 7.

taxon	repository number	locality	reference	carapace max. length (including rostrum) in mm	carapace max. width in mm	carapace width/ carapace length
<i>Retropluma slovenica</i>	RGA/SMNH 173	Činžat, Slovenia	Gašparič and Hyžný (2015)	4.6	5.2	1.13
<i>Retropluma slovenica</i>	RGA/SMNH 267	Činžat, Slovenia	Gašparič and Hyžný (2015)	11.1	13.2	1.19
<i>Retropluma slovenica</i>	RGA/SMNH 270 and 290	Činžat, Slovenia	Gašparič and Hyžný (2015)	13.2	16.8	1.27
<i>Retropluma slovenica</i>	RGA/SMNH 318 and 319	Činžat, Slovenia	Gašparič and Hyžný (2015)	15.0	16.6	1.11
<i>Retropluma slovenica</i>	RGA/SMNH 320	Činžat, Slovenia	Gašparič and Hyžný (2015)	13.6	16.8	1.24
<i>Retropluma slovenica</i>	RGA/SMNH 554 and 559	Činžat, Slovenia	Gašparič and Hyžný (2015)	11.3	15.2	1.35
<i>Retropluma slovenica</i>	RGA/SMNH 555 and 556	Činžat, Slovenia	Gašparič and Hyžný (2015)	14.7	17.0	1.16
<i>Retropluma slovenica</i>	RGA/SMNH 558 and 553	Činžat, Slovenia	Gašparič and Hyžný (2015)	12.2	13.9	1.14
<i>Retropluma slovenica</i>	RGA/SMNH 642 and 619	Činžat, Slovenia	Gašparič and Hyžný (2015)	10.6	12.0	1.13
<i>Retropluma slovenica</i>	RGA/SMNH 656	Činžat, Slovenia	Gašparič and Hyžný (2015)	6.2	7.4	1.19
<i>Retropluma slovenica</i>	RGA/SMNH 657	Činžat, Slovenia	Gašparič and Hyžný (2015)	5.3	7.4	1.40
<i>Retropluma slovenica</i>	RGA/SMNH 658 and 659	Činžat, Slovenia	Gašparič and Hyžný (2015)	13.2	15.6	1.18
<i>Retropluma slovenica</i>	RGA/SMNH 662	Činžat, Slovenia	Gašparič and Hyžný (2015)	11.6	14.2	1.22
<i>Retropluma slovenica</i>	RGA/SMNH 663	Činžat, Slovenia	Gašparič and Hyžný (2015)	10.7	13.8	1.29
<i>Retropluma slovenica</i>	RGA/SMNH 673 and 674	Činžat, Slovenia	Gašparič and Hyžný (2015)	13.2	17.0	1.29
<i>Retropluma slovenica</i>	RGA/SMNH 705	Činžat, Slovenia	Gašparič and Hyžný (2015)	13.8	16.3	1.18
<i>Retropluma slovenica</i>	RGA/SMNH 707	Činžat, Slovenia	Gašparič and Hyžný (2015)	17.9	19.5	1.09
<i>Retropluma slovenica</i>	RGA/SMNH 710	Činžat, Slovenia	Gašparič and Hyžný (2015)	12.0	13.3	1.11
<i>Retropluma slovenica</i>	RGA/SMNH 724	Činžat, Slovenia	Gašparič and Hyžný (2015)	8.2	10.3	1.26
<i>Retropluma slovenica</i>	RGA/SMNH 735	Činžat, Slovenia	Gašparič and Hyžný (2015)	14.0	17.1	1.22
<i>Retropluma slovenica</i>	RGA/SMNH 1142 and 1143	Činžat, Slovenia	Gašparič and Hyžný (2015)	7.8	10.6	1.36
<i>Retropluma slovenica</i>	RGA/SMNH 1203	Činžat, Slovenia	Gašparič and Hyžný (2015)	9.3	11.1	1.19
<i>Retropluma slovenica</i>	RGA/SMNH 1208 and 1207	Činžat, Slovenia	Gašparič and Hyžný (2015)	5.9	7.2	1.22
<i>Retropluma slovenica</i>	RGA/SMNH 1216	Činžat, Slovenia	Gašparič and Hyžný (2015)	5.7	6.4	1.12
<i>Retropluma slovenica</i>	RGA/SMNH 139	Činžat, Slovenia	Gašparič and Hyžný (2015)	8.3	10.7	1.29
<i>Retropluma slovenica</i>	RGA/SMNH 145	Činžat, Slovenia	Gašparič and Hyžný (2015)	9.2	11.1	1.21
<i>Retropluma slovenica</i>	RGA/SMNH 275	Činžat, Slovenia	Gašparič and Hyžný (2015)	9.9	11.6	1.17
<i>Retropluma slovenica</i>	RGA/SMNH 287	Činžat, Slovenia	Gašparič and Hyžný (2015)	8.3	10.0	1.20
<i>Retropluma slovenica</i>	RGA/SMNH 322	Činžat, Slovenia	Gašparič and Hyžný (2015)	11.8	15.3	1.30
<i>Retropluma slovenica</i>	RGA/SMNH 548	Činžat, Slovenia	Gašparič and Hyžný (2015)	11.4	14.8	1.30
<i>Retropluma slovenica</i>	RGA/SMNH 549	Činžat, Slovenia	Gašparič and Hyžný (2015)	4.5	6.1	1.36
<i>Retropluma slovenica</i>	RGA/SMNH 557	Činžat, Slovenia	Gašparič and Hyžný (2015)	7.6	10.3	1.36
<i>Retropluma slovenica</i>	RGA/SMNH 561	Činžat, Slovenia	Gašparič and Hyžný (2015)	9.3	11.3	1.22
<i>Retropluma slovenica</i>	RGA/SMNH 564	Činžat, Slovenia	Gašparič and Hyžný (2015)	8.3	10.1	1.22
<i>Retropluma slovenica</i>	RGA/SMNH 631	Činžat, Slovenia	Gašparič and Hyžný (2015)	9.1	13.4	1.47
<i>Retropluma slovenica</i>	RGA/SMNH 633	Činžat, Slovenia	Gašparič and Hyžný (2015)	9.2	13.5	1.47
<i>Retropluma slovenica</i>	RGA/SMNH 641	Činžat, Slovenia	Gašparič and Hyžný (2015)	9.5	12.6	1.33
<i>Retropluma slovenica</i>	RGA/SMNH 646	Činžat, Slovenia	Gašparič and Hyžný (2015)	6.6	7.2	1.09
<i>Retropluma slovenica</i>	RGA/SMNH 655	Činžat, Slovenia	Gašparič and Hyžný (2015)	7.4	8.7	1.18
<i>Retropluma slovenica</i>	RGA/SMNH 660	Činžat, Slovenia	Gašparič and Hyžný (2015)	8.4	10.0	1.19
<i>Retropluma slovenica</i>	RGA/SMNH 664	Činžat, Slovenia	Gašparič and Hyžný (2015)	4.4	5.3	1.20
<i>Retropluma slovenica</i>	RGA/SMNH 672	Činžat, Slovenia	Gašparič and Hyžný (2015)	7.5	9.5	1.27
<i>Retropluma slovenica</i>	RGA/SMNH 725	Činžat, Slovenia	Gašparič and Hyžný (2015)	11.0	13.4	1.22

taxon	repository number	locality	reference	carapace max. length (including rostrum) in mm	carapace max. width in mm	carapace width/ carapace length
<i>Retropluma slovenica</i>	RGA/SMNH 732	Činžat, Slovenia	Gašparič and Hyžný (2015)	16.3	18.7	1.15
<i>Retropluma slovenica</i>	RGA/SMNH 886 and 887	Činžat, Slovenia	Gašparič and Hyžný (2015)	10.9	13.2	1.21
<i>Retropluma slovenica</i>	RGA/SMNH 890	Činžat, Slovenia	Gašparič and Hyžný (2015)	7.4	9.9	1.34
<i>Retropluma slovenica</i>	RGA/SMNH 1206	Činžat, Slovenia	Gašparič and Hyžný (2015)	5.3	6.3	1.19
<i>Retropluma slovenica</i>	RGA/SMNH 1209	Činžat, Slovenia	Gašparič and Hyžný (2015)	10.6	14.2	1.34
<i>Retropluma slovenica</i>	RGA/SMNH 1212	Činžat, Slovenia	Gašparič and Hyžný (2015)	4.4	6.3	1.43
<i>Retropluma slovenica</i>	RGA/SMNH 1213	Činžat, Slovenia	Gašparič and Hyžný (2015)	4.5	6.1	1.36
<i>Retropluma craverii</i>	RGA/SMNH 1316	Castellarano, Italy	De Angeli et al. (2011)	19.0	22.0	1.16
<i>Retropluma craverii</i>	RGA/SMNH 1315	Castellarano, Italy	De Angeli et al. (2011)	21.5	23.2	1.08
<i>Retropluma craverii</i>	RGA/SMNH 1313	Castellarano, Italy	De Angeli et al. (2011)	24.4	25.1	1.03
<i>Retropluma craverii</i>	RGA/SMNH 1317	Castellarano, Italy	De Angeli et al. (2011)	10.1	12.1	1.20
<i>Retropluma eocenica</i>	MCZ 1467	Nogarole Vincentino, Italy	Beschin et al. (1996)	8.4	10.5	1.25
<i>Retropluma eocenica</i>	MCZ 1469	Nogarole Vincentino, Italy	Beschin et al. (1996)	8.8	11.4	1.30
<i>Retropluma eocenica</i>	MCZ 1470	Nogarole Vincentino, Italy	Beschin et al. (1996)	9.1	13.5	1.48
<i>Retropluma eocenica</i>	MCZ 1474	Arzignano, Italy	Beschin et al. (1996)	10.0	14.0	1.40
<i>Retropluma eocenica</i>	MCZ 1473	Nogarole Vincentino, Italy	Beschin et al. (1996)	11.2	14.2	1.27
<i>Retropluma eocenica</i>	MCZ 1471	Nogarole Vincentino, Italy	Beschin et al. (1996)	11.1	14.6	1.32
<i>Retropluma eocenica</i>	MCZ 1478	Nogarole Vincentino, Italy	Beschin et al. (1996)	12.5	16.6	1.33
<i>Retropluma cf. eocenica</i>	MSNMI26238	Ponzone, Italy	Larghi (2003)	6.4	8.8	1.38
<i>Retropluma borealis</i>	MSM 1577	Gram, Denmark	Fraaije et al. (2005)	12.9	17.0	1.32
<i>Retropluma borealis</i>	MSM 1454	Gram, Denmark	Fraaije et al. (2005)	11.9	15.8	1.33
<i>Retropluma borealis</i>	MSM 1580	Gram, Denmark	Fraaije et al. (2005)	8.1	10.8	1.34
<i>Retropluma borealis</i>	MSM 1581	Gram, Denmark	Fraaije et al. (2005)	10.3	11.9	1.15
<i>Retropluma borealis</i>	MSM 1582	Gram, Denmark	Fraaije et al. (2005)	11.0	14.4	1.31
<i>Retropluma borealis</i>	MSM 1593/1	Gram, Denmark	Fraaije et al. (2005)	10.4	12.4	1.20
<i>Retropluma borealis</i>	MSM 1593/5	Gram, Denmark	Fraaije et al. (2005)	7.9	10.0	1.26
<i>Retropluma borealis</i>	MSM 1593/8	Gram, Denmark	Fraaije et al. (2005)	9.0	11.9	1.32
<i>Retropluma borealis</i>	MSM 1593/10	Gram, Denmark	Fraaije et al. (2005)	7.1	9.1	1.29
<i>Retropluma slovenica</i>	RGA/SMNH 1500 and 1501	Kamnik/Rakovnik, Slovenia	Gašparič and Križnar (2017)	14.5	18.4	1.27
<i>Retropluma slovenica</i>	RGA/SMNH 1502 and 1503	Kamnik/Rakovnik, Slovenia	Gašparič and Križnar (2017)	10.9	13.4	1.23
<i>Retropluma slovenica</i>	RGA/SMNH 1504 and 1505	Kamnik/Rakovnik, Slovenia	Gašparič and Križnar (2017)	17.8	20.3	1.14
<i>Retropluma minuta</i>	PS-2	Tušanj, Bosnia and Herzegovina	this paper	3.9	3.8	0.97
<i>Retropluma minuta</i>	PS-3	Tušanj, Bosnia and Herzegovina	this paper	4.1	4.0	0.98
<i>Retropluma minuta</i>	PS-4	Tušanj, Bosnia and Herzegovina	this paper	3.9	3.7	0.95
<i>Retropluma minuta</i>	PS-5	Tušanj, Bosnia and Herzegovina	this paper	6.7	6.9	1.03
<i>Retropluma minuta</i>	PS-6	Tušanj, Bosnia and Herzegovina	this paper	6.1	6.1	1.00
<i>Retropluma minuta</i>	PS-7	Tušanj, Bosnia and Herzegovina	this paper	7.2	7.4	1.03