



New reports of decapod *Portunus monspeliensis* A. Milne Edwards, 1860 from Miocene beds of eastern Slovenia with notes on palaeoecology and palaeobiogeography

Nove najdbe rakovice *Portunus monspeliensis* A. Milne Edwards, 1860 iz miocenskih plasti vzhodne Slovenije z opisom paleookolja in njihove paleogeografske razširjenosti

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Abstract

In the present paper we report on several new occurrences of decapod *Portunus monspeliensis* A. Milne Edwards, 1860 from Miocene beds of eastern Slovenia, *i. e.* from the already known locality Šentilj in the northeastern Štajerska region and additional new localities in the Kozjansko and Dolenjska regions. These new reported occurrences of *P. monspeliensis* from the Middle Miocene (Badenian) strata of eastern Slovenia improve our knowledge of this otherwise widespread decapod crustacean. Additionally, we also re-evaluate the environmental preferences of the species and its wider palaeobiogeographical distribution during the Miocene in the Mediterranean, Atlantic and Paratethys Seas.

Izvleček

V pričujočem članku poročamo o novih primerkih rakovic vrste *Portunus monspeliensis* A. Milne Edwards, 1860 iz miocenskih plasti v vzhodni Sloveniji, in sicer iz že znanega najdišča pri Šentilju v severovzhodnem delu Štajerske in iz novih nahajališč iz območja Kozjanskega in Dolenjske. Nove najdbe iz miocenskih plasti vzhodne Slovenije dopolnjujejo naše poznavanje vrste *P. monspeliensis*. Med drugim v članku na novo opredeljujemo okoljske preference te vrste in njeno širšo paleobiogeografsko razširjenost v obdobju miocena na območju Sredozemskega morja, Atlantskega oceana in Paratetide.

Introduction

The portunid crab *Portunus monspeliensis* A. Milne Edwards, 1860 has a widespread distribution during the Miocene period. The species has been reported from the Mediterranean, the Paratethys as well as from Atlantic coastal waters. It is known from Miocene sediments of Austria, France, Hungary, Italy, Malta, Portugal, Spain, Slovenia, Egypt and the Sinai Peninsula (MILNE EDWARDS, 1860; RISTORI, 1888; GLAESSNER, 1928, 1933; LÖRENTHEY & BEURLEN, 1929; VIA, 1932; MÜLLER, 1979, 1984, 1993; MIKUŽ, 2003; GATT, 2006).

The remains of *P. monspeliensis* are one of the most abundant Miocene crabs and almost always represent the dominant decapod species in the strata where they occur. They are almost exclusively found in siliciclastic sediments such as sandstones and calcarenites, and their state of preservation is mostly not good. Due to their size, they are usually compressed, fractured and lacking exocuticle. Only recently illustrated specimens from the marly limestone of the middle Miocene Sardinia (MARANGON & DE ANGELI, 2009) are exceptionally well preserved and provide better insight on the species morphology of the dorsal carapace.

Despite the widespread distribution and common occurrence, this fossil portunid species has not received relevant scientific attention in the last decades. In the 19th and in the beginning of the 20th century several authors (VIA, 1923; VEIGA FERREIRA, 1954; PHILIPPE & SECRETAN, 1971) have reported the European specimens under different, synonymous, names: *Lupa hastata* LINNAEUS, 1767; *Neptunus convexus* RISTORI, 1888; and *Neptunus granulatus* A. Milne Edwards, 1860. Beside these recognized synonyms of *P. monspeliensis*, there are currently over 40 valid fossil species of genus *Portunus* WEBER, 1795 (KARASAWA et al., 2008), and many of them were described only from single poorly preserved specimens or chelae. Although even a superficial investigation of the fossil representatives of the genus shows great morphological variations, descriptions of fossil species usually illustrate carapaces lacking cuticle, severally fragmented specimens, and descriptions of isolated chelipeds. As it has already been pointed out by KARASAWA and co-authors (2008) a re-evaluation and revision of all fossil species of *Portunus* would be welcome, but that is out of the scope of the present paper.

The only known occurrence of fossil remains of *P. monspeliensis* from the Miocene strata of Slovenia so far is the report of 27 fragments of this decapod (five carapaces) from Badenian sandstones of Šentilj (MIKUŽ, 2003). Interestingly, KRIŽNAR (2014) also presents a historical report of donations of a fossil crab specimen to the Nature History Museum in Vienna in 1850. The original report of this donation was published in the Leibacher Zeitung newspaper on the 21st of February 1853 and details the donations done in 1850 as: “Der hochwertige Herr Primus Remiz, Cooperator in Grossdolina, welcher Herrn Freyer bei seinen geognostischen Wanderungen ein Paar Tage zu begleiten die Gefälligkeit hatte, verehrte dem Museum eine fossile Krabbe, welche er in Tschatesch am nördlichen Bügel nächst der Strasse ob der Post gefunden hat. Eine ausgezeichnete Stelle und reiche Fundgrube zur Zussammlung von fossilen Muscheln, Schneckenschalen usw... Herr Vincenz Kollar, Kustos der vereinigten k. k. Hof-Naturalien-Cabinete, wirkli Mitglied der Kaiserliche Academie der Wissenschaften zu Wien, hatte die Gewogenheit, oberwähnten Krebsen zu bestimmen, mit den Worten: “Dieser Krebs gehört zu der recenten Gattung *Lupa*, stimmt in Größe und den Verhältnissen der einzelnen Theile mit *Lupa dicantha* Latreille und Milne Edwards überein, und scheint zunächst mit *Lupa spinimana* Milne Edwards verwandt. Auf jeden Fall nähert sich diese Art den Formen, welche an den amerikanischen Küsten vorkommen”.

The cited passage in German, illustrates the finding of a fossil crab by Mr. Primož Remic in today's town Čatež (on the hill north of the Post) in eastern Slovenia, who sent it to the curator Mr. Vincenz Kollar from the Nature History Museum in Vienna. Mr. Kollar determined it as belonging

to the genus *Lupa* (junior objective synonym of *Portunus*) and closely resembling extant species *Lupa dicantha* or *Lupa spinimana*. This historical specimen can no longer be located, but likely represents the first documented find of the crab *Portunus monspeliensis* and the first recognized find of a fossil decapod crustacean in Slovenia.

Geology and stratigraphy of the localities

The newly presented specimens originate from various localities of the former Central Paratethys Sea that covered the eastern part of Slovenia in the Miocene period (Fig. 1). The following localities yielded new material of this widespread decapod crustacean:

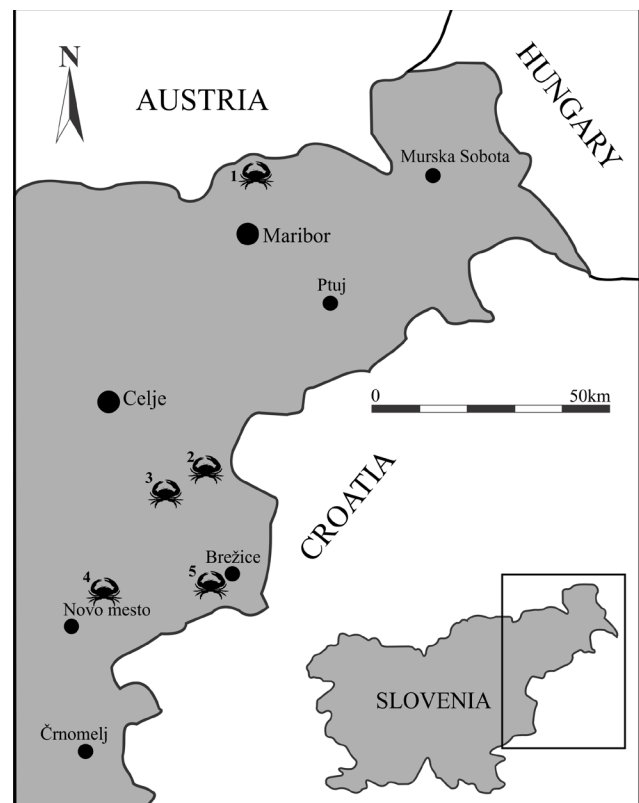


Fig. 1. Simplified geographical map of East Slovenia showing all known occurrences of decapod *Portunus monspeliensis* A. Milne Edwards, 1860. 1 – Štrihovec / Šentilj, 2 – Gruška / Kozje, 3 – Trebče / Bistrica ob Sotli, 4 – Dolnja Stara vas, 5 – Šentvid / Čatež.)

1. Štrihovec / Šentilj

Štrihovec was until recently the only known locality with fossil remains of *P. monspeliensis* from the Slovenian territory (MIKUŽ, 2003). Štrihovec is situated near Šentilj, a town in northeast Slovenia, bordering on Austria. The fossil bearing layers were accessible in the years 1995/1996, when middle Miocene (Badenian) sandstone, marl, and lithothamnium limestone were exposed during construction works for the new highway.

A rich association of macrofossils was collected by amateur collectors and described in the following years (MIKUŽ 1997, 1998, 2003, 2008; MIKUŽ & MITROVIĆ-PETROVIČ, 2001). The represented

fossil taxons include brachiopods, pectinid bivalve fauna, clypeasteroid echinoderms, octocorals, nautiloids, and crabs.

2. Gruška / Kozje

One decapod crab specimen was recovered from the Gruška jama locality near the town of Kozje in eastern Slovenia, close to border of Croatia. The Middle Miocene (Badenian) strata exposed here are comprised of sandstone and lithothamnium limestone (ANIČIĆ & JURIŠA, 1985), where macrofossils are rare. Sporadic finds from this locality comprise mostly poorly preserved bivalves with dissolved shells and rare echinoderms (MIKUŽ, 2010).

3. Trebče / Bistrica ob Sotli

This specimen was retrieved from a road cut on local road from Trebče towards Podsreda in eastern Slovenia, in the Kozjansko region. The crab was collected in yellowish calcareous sandstone of Middle Miocene (Badenian) age. There is also an outcrop of coarser clastic rocks, i. e. conglomerates with rhodoid spheres located close by (ANIČIĆ et al., 2002).

4. Dolnja Stara vas

A construction site behind the gasoline station in Dolnja Stara vas near Škocjan na Dolenjskem was opened in the early 2000s, which exposed a long outcrop of Middle Miocene (Badenian) strata (MIKUŽ & HORVAT, 1998). The lithologies at outcrop vary from breccia, sandstone, biocalcarenes and lithothamnium limestone. A rich macro fauna,

comprising mostly of bivalve species with rare gastropods and cirripeds was described from the sandstones and calcarenites (MIKUŽ & PETRIČ, 2008), from which we also collected a specimen of the *P. monspeliensis*.

5. Šentvid / Čatež

Grey to yellowish sandstones and calcarenites interbedded with grey siltstone are exposed along the slopes of hill St. Vid, south of Brežice in eastern Slovenia. Similarly to the wider surrounding area this lithology is part of the middle Miocene (Badenian) Čatež formation sequence (RIŽNAR et al., 2002). So far only sporadic finds of echinoderm fragments and indeterminable bivalves are reported from these beds. The crab specimens are surprisingly common in the yellowish calcarenites in this locality.

Material and methods

We describe 25 new specimens of *Portunus monspeliensis* that were not yet presented. One articulated specimen in the collection of Mr. Damjan Zupančič (Inv. No. DZ3135) from the locality Štrihovec, a single carapace from the locality Gruška (Inv. No. RGA/SMNH 1988), a complete carapace from the locality Trebče (Inv. No. RGA/SMNH 0586), one partial carapace from the locality Dolnja Stara vas (Inv. No. RGA/SMNH 1885) and 21 specimens from the collection of Mrs. Natalija Grdovič from the locality Šentvid near Čatež. These later include seven well-preserved, almost complete carapace (Inv. Nos.: NG118, 123,

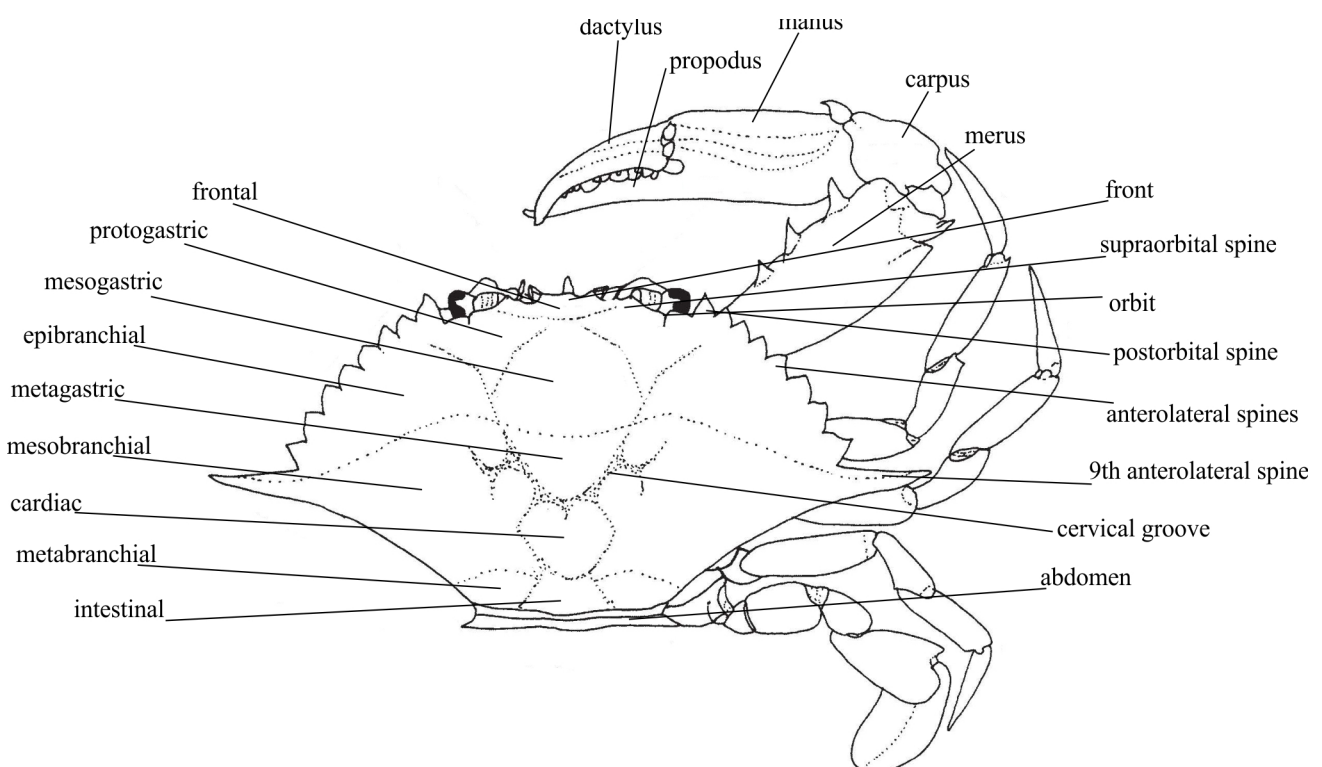


Fig. 2. Descriptive terminology used in the text showing dorsal morphology of portunid crab (modified after LAI et al., 2010).

124, 132, 133, 137, 138), thirteen partial carapace remains (Inv. Nos.: NG94, 117, 119, 120, 121, 122, 125, 127, 129, 130, 136, 141, 147), and one specimen of left propodus (Inv. No. NG128). All specimens were analysed and compared to other remains of the species *Portunus monspeliensis* from Štrihovec, Slovenia (Inv. No.: SMNH 1939, 1940, 1941, 1942, 1943, 1962), Austria (Inv. No.: RGA/SMNH 0837, 0838, 0963, 1031, 1036, 1037, 1109, 1123, 1339, 1340, 1341, 1344, 1345, 1438, 1477, 1479, 1480, 1484, 1911), and from Catalonia and Portugal (AO collection, Inv. No.: C-040/1, C-040/2, C-040/3, C-040/3, C-040/4, C-040/5, C-040/6). Specimens from the Mediterranean of Italy and France were analysed using data from references. All specimens were photographed, measured and studied using computer graphic programmes (CorelDRAW X5, Adobe Photoshop CC). Photographs were taken with digital camera Nikon Coolpix P340.

Abbreviations: SMNH - Slovenian Museum of Natural History, Ljubljana, Slovenia; RGA/SMNH - Slovenian Museum of Natural History, Ljubljana, Slovenia (R. Gašparič Collection); AO - Àlex Ossó fossil crab collection, Tarragona, Catalonia; DZ - Damjan Zupančič private collection, Maribor, Slovenia; NG - Natalija Grdovič private collection, Brežice, Slovenia.

Systematic description

The systematics used herein follows KARASAWA et al., 2008.

Subsection Heterotremata Guinot, 1977

Superfamily Portunoidea Rafinesque, 1815

Family Portunidae Rafinesque, 1815

Subfamily Portuninae Rafinesque, 1815

Genus *Portunus* Weber, 1795

Type species. *Cancer pelagicus* Linnaeus, 1758.

Diagnosis: Carapace much wider than long; carapace regions moderately developed; six frontal spines including inner-orbital spines which are usually present; orbit with two closed supraorbital fissures; nine anterolateral spines including outer-orbital spine; chelae keeled; male abdomen triangular with somites 3–5 fused. (after SCHWEITZER et al, 2006)

Portunus monspeliensis (A. Milne Edwards, 1860)
(Plate 1. A–G, Plate 2. A–G)

- 1860 *Neptunus monspeliensis* A. Milne Edwards; p. 232
- 1860 *Neptunus monspeliensis* A. Milne Edwards; Pl. 4 (fig. 1), Pl. 5 (fig. 1)
- 1860 *Neptunus granulatus* A. Milne Edwards; p. 241, Pl. 3 (fig. 1), Pl. 7 (fig. 2)
- 1888 *Neptunus granulatus* A. Milne Edwards - RISTORI; p. 215, Pl. 4 (figs. 5–11)
- 1893 *Neptunus* *cfr.* *granulatus* A. Milne Edwards - BITTNER; p. 11
- 1897 *Neptunus* *cfr.* *granulatus* A. Milne Edwards - LÖRENTHEY; p. 159
- 1898 *Neptunus* *cfr.* *granulatus* A. Milne Edwards - LÖRENTHEY; p. 110, 153, Pl. 9 (figs. 2, 3)
- 1909 *Neptunus granulatus* A. Milne Edwards - LÖRENTHEY; p. 242, Pl. 2 (figs. 1, 2)
- 1929 *Neptunus granulatus* A. Milne Edwards - LÖRENTHEY & Beurlen; p. 188, Pl. 13 (figs. 3, 4), Pl. 14 (figs. 1, 4)
- 1950 *Neptunus granulatus* A. Milne Edwards - COMASCHI CARIA; p. 324, Pl. 1
- 1956 *Neptunus granulatus* A. Milne Edwards - COMASCHI CARIA; p. 284, 288, P. 1 (figs. 1–7), Pl. 2 (figs. 1–6), Pl. 3 (figs. 1, 2)
- 1968 *Neptunus granulatus* A. Milne Edwards - STANCU & ANDREESCU; p. 466, Pl. 7 (fig. 85)
- 1979 *Portunus granulatus* A. Milne Edwards - FÖRSTER; p. 94
- 1979 *Portunus monspeliensis* (A. Milne Edwards) - MÜLLER; p. 274, 280, 288, Pl. 18
- 1984 *Portunus monspeliensis* (A. Milne Edwards) - MÜLLER; p. 79, Pl. 62 (figs. 1, 2)
- 1991 *Portunus monspeliensis* (A. Milne Edwards) - MARRAS & VENTURA; p. 108, Pl. 1 (figs. 1–4), Pl. 2 (figs. 1, 4), Pl. 3 (figs. 1–3)
- 1992 *Portunus granulatus* A. Milne Edwards - DE ANGELI & MARANGON; p. 176
- 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, Pl. 1 (figs. 1–5), Pl. 2 (figs. 1–8)
- 2007 *Portunus monspeliensis* (A. Milne Edwards) - MARANGON & DE ANGELI; p. 70–72, Pl. 1 (figs. A–H)

PLATE 1

Portunus monspeliensis A. Milne Edwards, 1860.

A – RGA/SMNH 1885, partial dorsal carapace;

B – RGA/SMNH 1885, partial ventral side with abdomen (male);

C – RGA/SMNH 0586, dorsal carapace;

D – RGA/SMNH 0586, partial ventral side with abdomen (male);

E – RGA/SMNH 1988, dorsal carapace;

F – DZ3135, fragmented dorsal carapace with an associated chelipeds;

G – DZ3135, right cheliped;

H – DZ3135, left cheliped.

All scale bars are 10 mm.

PLATE 1



Description: The specimens have a medium sized hexagonal carapace, significantly wider than long (width/length ratio is about 1.75, greater in bigger individuals, up to 1.85); greatest width at the last (ninth) anterolateral spine (Tab. 1). The carapace is slightly convex in the cross section and its dorsal surface is densely covered by small granules. The front is protruding and slightly downturned, approx. 20 % of maximum carapace width, with axial notch; two forward directed short spines on either side and followed by a distinctive sharp, outward pointing, inner orbital spine. Fronto-orbital margin about 50 % of maximum carapace width. Orbits wider than front, forward directed; supraorbital margin sinuous, incised by two closed fissures, one medially and other near the outer orbital tooth. Anterolateral margin long and slightly convex with nine anterolateral spines, first spine (outer orbital) directed forward and strong, with subsequent seven subtrigonal spines each somewhat smaller and outwards directed; ninth anterolateral spine prominent, the largest and laterally directed at almost a right angle to the vertical axis; in younger specimens steeper angle with regards to anterior margin. Posterolateral margin straight with concave depression (re-entrant of fifth pereopod) in the last third of its length. Posterior margin slightly concave and rimmed, broad, width approx. 75 % of the fronto-orbital margin width.

Carapace regions faintly defined; protogastric region semi-circular lobes with transverse ridge; mesogastric and metogastric regions are trapezoid shaped and separated by faint transverse ridge; mesogastric process long, ending behind frontal axial notch. Cardiac region well-defined, pentagonal, anterior borders straight, posterior borders concave, whole region somewhat swollen with longitudinally running central depression. Intestinal region faint and circular. Hepatic region flat and triangular. Epibranchial region wide, forming arcuate transverse ridge from largest anterolateral spine to mesogastric region, separating the epibranchial and

mesobranchial regions. Cervical groove distinct. Branchiocardiac grooves well marked, along sides of cardiac region.

Thoracic sternum broad, oval, widening posteriorly, widest at 6 thoracic sternite, with straight to slightly concave sutures between sternites. Thoracic sternites 1–2 not preserved, sternites 3–4 fused in a trapezoidal plate, axial sulcus reaching the 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 reduced, subtrigonal; sternites 5–7 form laterally expanded episternites. Suture 2 complete; suture 3/4 distinct; sutures 4/5 to 7/8 laterally complete.

Male abdomen subtriangular with straight converging margins, abdominal somite 1 and 2 narrow and wide, only somite 2 is observable from the ventral side with a concave notch on the distal end where it interlocks with thoracic sternite 8; abdominal somites 3–5 fused in a wide, subtrapezoidal plate with slightly concave lateral margins, somite 3 widest, transversely keeled; somite 6 trapezoidal, longer than somites 3–5 with convex lateral margins; male telson subtriangular approximately as high as wide. Female abdomen much wider, about half the carapace width, semi-circular; somites 1 and 2 narrow and wide; somites 3–5 rectangular in shape with convex lateral margins; somite 6 wider posteriorly, with sinuous lateral margin, posteriorly convex and anteriorly concave, telson roundly triangular.

Merus of the third maxillipeds subrectangular and elongated. Chelipeds subequal with elongated merus; carpus short, palm rectangular and elongated, with three longitudinal ridges on outer surface. Fixed finger is triangular and elongated, as long as palm. Occlusal margin of chelae heterodontic with a clear knobstick molariform tooth in the right chela, followed by a series of tuberos teeth.

Table 1. Comparison of dimensions of new specimens of *Portunus monspeliensis* A. Milne Edwards, 1860.

Species	Specimen No.	Carapace width (in mm)	Front width (in mm)	Fronto-orbital width (in mm)	Posterior width (in mm)	Carapace length (in mm)
<i>Portunus monspeliensis</i>	RGA/SMNH0586	87.0	16.0	45.5	34.0	50.5
<i>Portunus monspeliensis</i>	RGA/SMNH1988	60.2	12.7	28.0	21.4	32.9
<i>Portunus monspeliensis</i>	DZ3135	99.0	17.4	49.6	40.2	53.5
<i>Portunus monspeliensis</i>	NG118	77.4	14.6	40.9	34.4	42.2
<i>Portunus monspeliensis</i>	NG123	33.4	7.2	18.4	12.1	19.2
<i>Portunus monspeliensis</i>	NG124	50.8	10.5	28.9	18.2	29.6
<i>Portunus monspeliensis</i>	NG132	66.1	11.6	33.3	23.2	36.1
<i>Portunus monspeliensis</i>	NG133	74.8	14.5	40.2	29.2	41.8
<i>Portunus monspeliensis</i>	NG137	76.7	14.4	38.2	33.2	43.5
<i>Portunus monspeliensis</i>	NG138	32.1	6.8	17.4	12.5	19.0

Palaeoecology and environment

As indicated in the geological setting of most of the aforementioned works and personal observations of the authors, specimens of *Portunus monspeliensis* are recovered from typical Miocene siliciclastic sediments. *Portunus monspeliensis* is almost exclusively collected from sandstone and sandy limestone that is interbedded with marl. These lithologies represent a variety of sublittoral facies comprising from inshore to offshore waters (COMASCHI CARIA, 1956; MARANGON & DE ANGELI, 2009), or from estuarine and even lagoon or brackish environments with a sandy, muddy, or sea grass bottom (NICHOLS, 2009).

Portunus monspeliensis may be considered a euryhalin species given the high salinity fluctuation existent in the different observed ecosystems it inhabits (MÜLLER, 1993). Many of the extant portunids, such as *Portunus pelagicus*, are found in the Indo-Pacific waters and even in the oriental margin of the Mediterranean Sea and share similar ecological preferences and habitats as well as clear morphological similarities with species *P. monspeliensis* (LAI et al., 2010). From this it can be inferred that other aspects of their biology and ecology, such as predation or swimming capacities, may be similar as well. Both species have similar nearly homochealic claws with a clear knobstick molariform tooth in the

right chela and followed by tuberosus teeth or a series of conical teeth (Pl. 1,F) which indicate the capacity of chelae for crushing and cutting its prey (SPIRIDONOV et al., 2014). Accordingly, *P. monspeliensis* must have been, similarly as *Portunus pelagicus*, an opportunistic predator and scavenger, depending on the availability of prey. The majority of its diet would consist of teleost fish, molluscs, crustaceans, polychaetes, and substrate debris (KUNSOOK et al., 2014). Judging by the shared paddle-like form of the fifth pereopod in *Portunus monspeliensis*, it is supposed that the species was an active swimmer, remaining buried in the sediment during inactivity, analogous to the extant *P. pelagicus*.

When evaluating the depositional settings that bear fossils of *Portunus monspeliensis*, it can be concluded from comparison with extant *P. pelagicus* and fossil bearing lithologies, that they inhabited a wide range of habitats, but preferred sublittoral algal and sea grass meadows on both sandy and muddy substrata (KUNSOOK et al., 2014; CHANDE & MGAYA, 2003). The choice of habitat, ranging from shallow inshore waters to deeper offshore waters, would most likely also vary with age, sex, and season (SVANE & HOOPER, 2004). In addition to the above mentioned similarities with the extant *Portunus pelagicus* which may share its habitat with genus *Scylla* De Haan, 1833 and

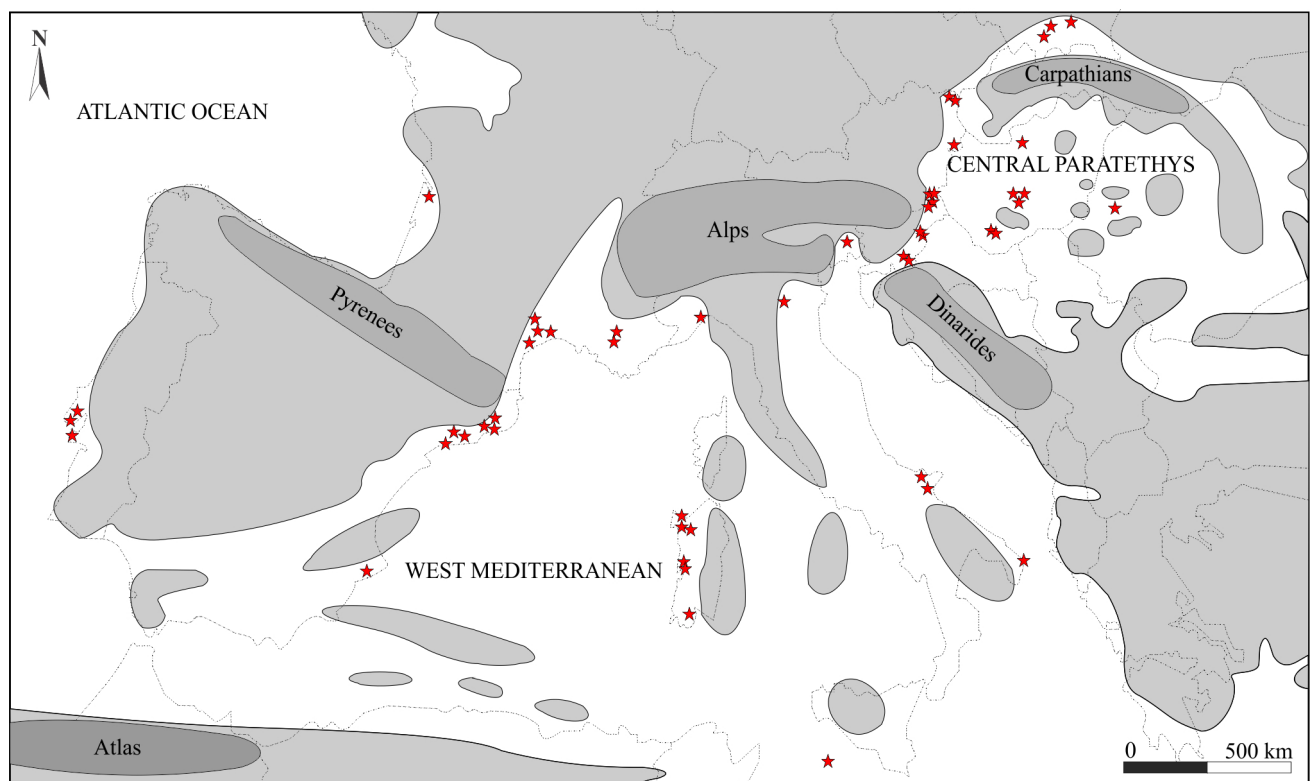


Fig. 3. Distribution of *Portunus monspeliensis* A. Milne Edwards, 1860 in the Central Paratethys, Mediterranean and Atlantic Ocean, during the middle Miocene, projected onto the Recent geographical map of Europe (modified after ПОРОВ et al., 2004). White areas represent respective Miocene basins, grey areas represent land masses, stars represent known localities of *Portunus monspeliensis*.

with other portunids (CHANDE & MGAYA, 2003), *P. monspeliensis* species frequently occurs with less common Miocene portunids such as *Scylla* and *Necronectes* Milne-Edwards, 1881 (Via, 1932; Veiga Ferreira, 1954; Müller, 1993 and AO pers. obs.).

Palaeobiogeography

True portunids first appeared in the Middle-Late Eocene period according to the present fossil record (Ossó, 2016). The *Portunus monspeliensis* species appears to be a derived taxon from the robust stock of true portunids that dwelt in the western margin of the Tethys during the Middle-Late Eocene and Oligocene, and inhabited coasts with siliciclastic sediments that originated from the Alpine Orogeny and filled the Mediterranean and Central Paratethys basins during the Miocene period. Strikingly, we have no fossil records of *P. monspeliensis* from the Miocene of the Balearic Islands (J. Juárez, pers. comm.) nor in the extensive Miocene deposits of the Betic Strait (I. Bajo, pers. comm.), which would seem a natural migration path from the Mediterranean to the Atlantic coast in Portugal during the middle Miocene.

Portunus monspeliensis was widely distributed along the Paratethys, the Mediterranean and the southern Atlantic coast of the Iberian Peninsula during the Miocene. Interestingly the reported distribution of *P. monspeliensis* in Paratethys is heavily dominated in the Central and Western Paratethys (Fig. 3), near the hypothetical Slovenian Corridor, connecting the Central Paratethys and the Mediterranean (BARTOL et al., 2014). Further fossil species of *Portunus* were present either eastward in the Indo-Pacific waters or westward in the Caribbean waters. Different species of *Portunus* have so far been reported in Miocene outcrops in Iran (GLAESSNER, 1928; HEIDARI et al., 2012; YAZDI et al., 2013), India (RALTE et al., 2009; TIWARI & VEGA, 2014), Pakistan and Burma (SATSANGI & PARIDA, 1980), Malaysia (COLLINS et al., 2003), Indonesia (VAN STRAELEN, 1924), Taiwan (HU, 1984), and Fiji (RATHBUN, 1945). The genus was first recorded in Japan only from strata that date to the Pliocene period (KARASAWA & NOBUHARA, 2008).

Concurrently, the genus *Portunus* is also present westward during the Miocene, *i. e.* in the Caribbean and in the Central and South America waters, for example in Cuba (SCHWEITZER et al., 2006), Haiti and Dominican Republic (RATHBUN, 1919; 1920 & 1923), in the southeast of the US of America (RATHBUN, 1935; PORTELL, 2004), Mexico (VEGA et al., 1999; 2009), Costa Rica and Panama (TODD & COLLINS, 2005; COLLINS et al., 2009), and Brazil (BRITO, 1972; MARTINS NETO, 2001).

Conclusions

In the present paper, we described 25 new specimens of *Portunus monspeliensis* A. Milne Edwards, 1860 from Middle Miocene beds of eastern Slovenia from four new localities. The newly presented diversity and richness of *P. monspeliensis* in sublittoral siliciclastic lithologies of eastern Slovenia confirms the presence of Middle Miocene Slovenian Corridor, connecting the Central Paratethys and the Mediterranean Sea.

Considering the near shore facies and lithologies of new localities from eastern Slovenia *P. monspeliensis* must have been a euryhalin species, similar to some extant portunids. This widespread decapod crustacean usually has a dominant role in the ecosystems it shares with less common portunids such as *Scylla* and *Necronectes*.

The described material shows that the fossil record of *P. monspeliensis* in Slovenia is much more robust than previously thought. New localities in eastern Slovenia are important data points on palaeobiogeographical map of Middle Miocene, which illustrate the possible seaway connection between Paratethys and Mediterranean.

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PLATE 2

Portunus monspeliensis A. Milne Edwards, 1860.

A – NG137, dorsal carapace;

B – NG133, dorsal carapace;

C – NG124, dorsal carapace;

D – NG124, ventral side with abdomen (male);

E – NG132, dorsal carapace;

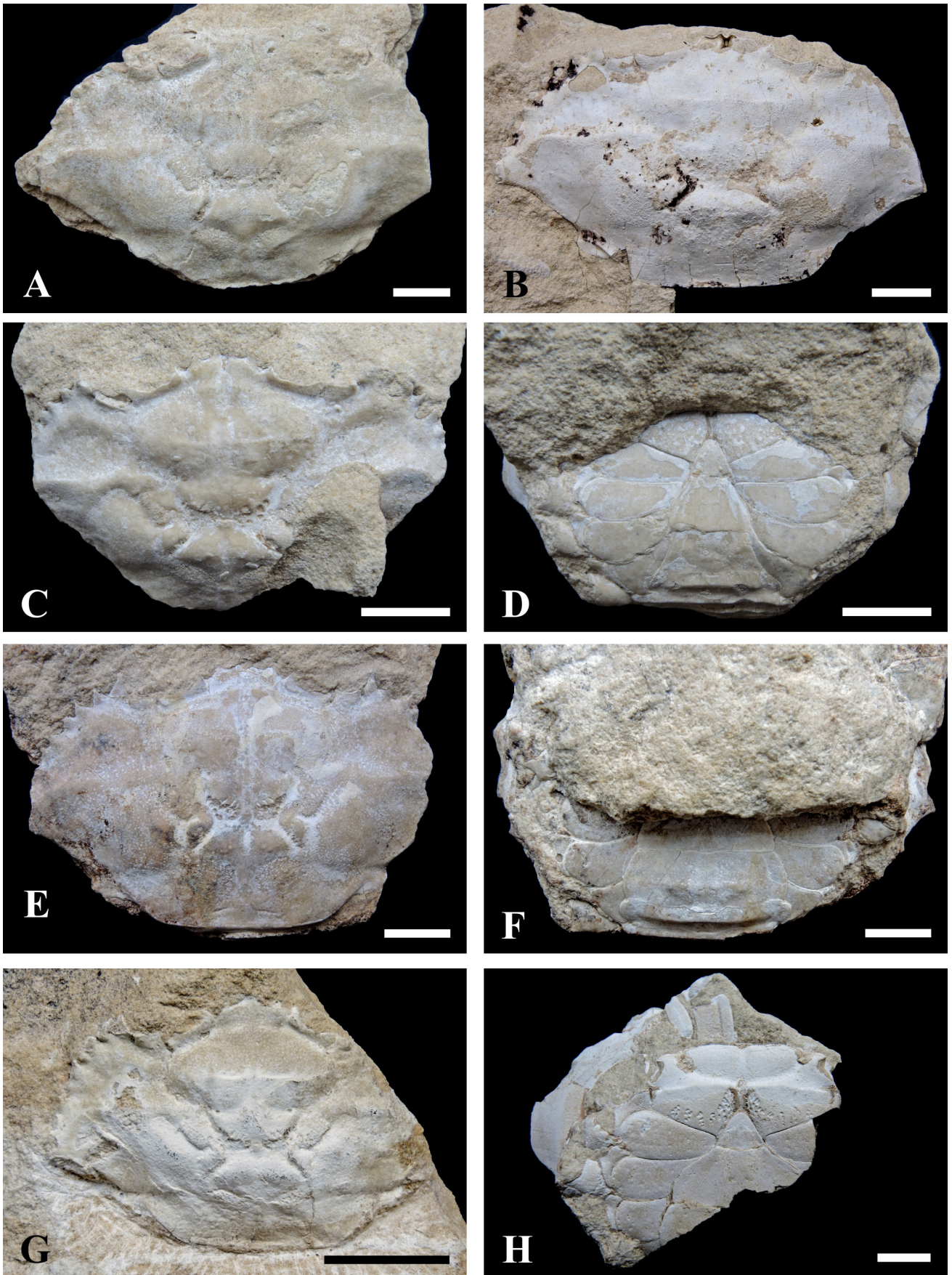
F – NG132, ventral side with abdomen (female);

G – NG123, dorsal carapace;

H – NG141, partial ventral side with abdomen (female).

All scale bars are 10 mm.

PLATE 2



References

- ANIČIĆ B. & JURIŠA, M. 1985: Osnovna geološka karta SFRJ 1:100.000, List Rogatec, L33-68. Zvezni geološki zavod Beograd.
- ANIČIĆ, B., OGORELEC, B., KRALJ, P. & MIŠIĆ, M. 2002: Lithology of Tertiary beds in Kozjansko, Eastern Slovenia. *Geologija*, 45/1: 213–246, doi:10.5474/geologija.2002.017.
- BARTOL, M., MIKUŽ, V. & HORVAT, A. 2014: Palaeontological evidence of communication between the Central Paratethys and the Mediterranean in the late Badenian/early Serravallian. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 394: 144–157.
- BITTNER, A. 1893: Decapoden des pannonischen Tertiärs. *Sitzungsberichte der kaiserlichen Akademie der Wissenschaften in Wien*, 102/II: 10–37.
- BRITO, I. M. 1972: Contribuição ao conhecimento dos crustáceos decápodes da Formação Pirabas. II – *Brachyura Ocypodidae*. *Anais da Academia Brasileira de Ciências*, 44/1: 95–98.
- COLLINS, J. S. H., LEE, C. & NOAD, J. 2003: Miocene and Pleistocene crabs (Crustacea, Decapoda) from Sabah and Sarawak. *Journal of Systematic Palaeontology*, 1/3: 187–226.
- COLLINS, J. S. H., PORTELL, R. W. & DONOVAN, S. K. 2009: Decapod crustaceans from the Neogene of the Caribbean: diversity, distribution and prospectus. *Scripta Geologica* 138: 55–111.
- COMASCHI CARIA, I. 1950: Crostacei Decapodi nel Miocene (Elveziano) di Bosa in Sardegna. *Rendiconto del Seminario della Facoltà di Scienze dell'Università di Cagliari*, 20/3–4: 324–327.
- COMASCHI CARIA, I. 1956: I Crostacei miocenici della Sardegna. *Bollettino del Servizio Geologico d'Italia*, 78/1–2: 283–290.
- CHANDE, A. I. & MGAYA, Y. D. 2003: The Fishery of *Portunus pelagicus* and Species Diversity of Portunid Crabs along the Coast of Dar es Salaam, Tanzania. *Western Indian Ocean. J. Mar. Sci.*, 2/1: 75–84.
- DE ANGELI, A. & MARANGON, S. 1992: *Necronectes schafferi* Glaessner nel Miocene della Sardegna, Italia. *Lavori Società Veneziana di Scienze Naturali*, 17: 175–182.
- FÖRSTER, R. 1979: Decapod crustaceans from the middle Miocene (Badenian) deposits of southern Poland. *Acta Geologica Polonica*, 29: 89–106.
- GATT, M. 2006: Il-Ġeoloġija u l-Paleontoloġija tal-Gżejjer Maltin. *Pubblikazzjonijiet Indipendenza*, Malta: 264 p.
- GLAESSNER, M. F. 1928: Die Dekapodenfauna des Österreichischen Jungtertiärs. *Jahrbuch der Geologischen Bundesanstalt*, 78: 161–219.
- GLAESSNER, M. F. 1933: New Tertiary crabs in the collection of the British Museum. *Annals and Magazine of Natural History*, 10/12: 1–28.
- GUINOT, D. 1977: Proposition pour une nouvelle classification des Crustacés Décapodes Brachyours. *Comptes Rendus Hebdomadaires de Séances de l'Académie des Sciences, Paris*, series D 285: 1049–1052.
- HEIDARI, A., FELDMANN, R. M. & MOUSSAVI-HARAMI, R. 2012: Miocene decapod crustacean from the Guri Member of the Mishan Formation, Bandar-Abbas, Southern Iran. *Bulletin of the Mizunami Fossil Museum*, 38: 1–7.
- HU, C.H. 1981: Studies on crab fossils from Neogene Formations of northern Taiwan. *Proceedings of the Geological Society of China*, 23: 29–36.
- KARASAWA, H., SCHWEITZER, C. E. & FELDMANN, R. M. 2008: Revision of *Portunoidea Rafinesque*, 1815 (Decapoda: Brachyura) with emphasis on the fossil genera and families. *Journal of Crustacean Biology* 28/1: 82–127.
- KARASAWA, H. & NOBUHARA, T. 2008: Decapoda and Isopoda (Crustacea) from the Pliocene Shimajiri Group in the Miyako-jima Island, Ryukyus, Japan. *Bulletin of the Mizunami Fossil Museum*, 34: 23–30.
- KRIŽNAR, M. 2014: O kremenovih kristalnih Simona Robiča in fosilnem raku iz Dolenjske. *Društvene novičke, Društvo prijateljev mineralov in fosilov Slovenije*, 16: 16.
- KUNSOOK, C., GAJASENI, N. & PAPHAVASIT, N. 2014: The Feeding Ecology of the Blue Swimming Crab, *Portunus pelagicus* (Linnaeus, 1758), at Kung Krabaen Bay, Chanthaburi Province, Thailand. *Tropical Life Sciences Research*, 25/1: 13–27.
- LAI, J. C. Y., NG, P. K. L. & DAVIE, P. J. F. 2010: A Revision of the *Portunus pelagicus* (Linnaeus, 1758) species complex (Crustacea: Brachyura: Portunidae), with the recognition of four species. *Raffles Bulletin of Zoology*, 58/2: 199–237.
- LINNAEUS, C. VON 1761: *Fauna Suecica sistens Animalia Sueciae Regni: Mammalia, Aves, Amphibia, Pisces, Insecta, Vermes. Distributa per classes et ordines, genera et species, cum differentiis specierum, synonymis auctorum, nominibus incolarum, locis natalium, descriptionibus Insectorum*. Editio altera, auctior. *Stockholmiae*: 578 p.
- LÖRENTHEY, E. 1897: Adatok Magyarország harmadkorú rák- faunájához. *Math. Termész. Értesítő*, 15: 149–169.
- LÖRENTHEY, E. 1898: Beiträge zur Decapodenfauna der ungarischen Tertiärs. *Természetrizsi Füzetek*, 21: 1–133.
- LÖRENTHEY, E. 1909. Beiträge zur tertiären Dekapodenfauna Sardinien. *Mathematische und Naturwissenschaftliche Berichte aus Ungarn*, 24: 202–259.
- LÖRENTHEY, E. & BEURLIN, K. 1929: Die fossilen Dekapoden der Länder der ungarischen Krone. *Geologica Hungarica, Series Palaeontologica*, 3: 1–420.
- MARANGON, S. & DE ANGELI, A. 2007: Preservation of some specimens of *Portunus monspeliensis* (Milne Edwards, 1860) from the Miocene of Sardinia (Italy). In GARASSINO, A., FELDMANN, R. M. & TERUZZI, G. (eds.): 3rd Symposium on Mesozoic and Cenozoic Decapod Crustaceans. *Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, XXXV/II: 70–72.

- MARRAS, G. & VENTURA, G. 1991: Crostacei decapodi del Miocene di Sassari (Sardegna nord occidentale). *Bollettino della Società Sarda di Scienze Naturali*, 28: 105–119.
- MARTINS NETO, R. G. 2001: Review of some Crustacea (Isopoda and Decapoda) from Brazilian deposits (Paleozoic, Mesozoic and Cenozoic) with descriptions of new taxa. *Acta Geologica Leopoldensia*, 24(52/53): 237–254.
- MIKUŽ, V. 1997: Turrids (Neogastropoda) from Middle Miocene Badenian beds of Slovenia. *Geologija*, 40: 65–101, doi:10.5474/geologija.1997.002.
- MIKUŽ, V. 1998: Middle Miocene Pectinids from vicinity of Šentilj (NE Slovenia). *Razprave IV. razreda SAZU*, 39/3: 81–135.
- MIKUŽ, V. 2003: The Miocene crabs from vicinity Šentilj in Slovenske Gorice, Slovenia. *Razprave IV. Razreda SAZU*, 44: 187–199.
- MIKUŽ, V. 2008: The gorgonacean coral remains (Octocorallia) from the Middle Miocene beds near Šentilj in Slovenske gorice, NE Slovenia. *Razprave IV. Razreda SAZU*, 49/2: 79–93.
- MIKUŽ, V. 2010: The largest corona of fossil sea urchin in Slovenia. *Geologija*, 53/2: 153–164, doi:10.5474/geologija.2010.013.
- MIKUŽ, V. & HORVAT, A. 1998: Pen shells from Badenian beds at Dolnja Stara vas near Škocjan and at Gorenja vas near Šmarjeta in Lower Carniola (Slovenia). *Razprave IV. razreda SAZU*, 39/4: 137–197.
- MIKUŽ, V. & MITROVIĆ-PETROVIĆ, J. 2001: Miocene sea urchins from surroundings Šentilj in Slovenske gorice, NE Slovenia, Clypeasteridae. *Razprave IV. razreda SAZU*, 42/1: 47–77.
- MIKUŽ, V. & PETRIČ-ŠKEDELJ, J. 2008: Interesting and rare find of a Middle Miocene snail in Lower Carniola, SE Slovenia. *Razprave IV. razreda SAZU*, 49/2: 37–49.
- MILNE EDWARDS, A. 1860: Histoire des Crustacés podophthalmiques fossiles et Monographie des Décapodes Macroures de la famille des Thalassinens. *Annales des Sciences Naturelles*, 4e série, 14: 129–357.
- MILNE EDWARDS, A. 1881: Note sur quelques crustacés fossiles des environs de Biarritz. *Annales des Sciences géologiques*: 11, 1–8.
- MÜLLER, P. 1979: The Indo-West-Pacific character of the Badenian Decapod Crustaceans of the Paratethys. *Annales Géologiques des Pays Helléniques*, 2: 865–869.
- MÜLLER, P. 1984: Decapod Crustacea of the Badenian. *Geologica Hungarica, Series Palaeontologica*, 42: 3–317.
- MÜLLER, P. 1993: Neogene Decapod Crustaceans from Catalonia. *Scripta Musei Geologici Seminarii Barcinonensis*, 225: 30 p.
- NICHOLS, G. 2009: *Sedimentology and Stratigraphy*. Blackwell Science Ltd., London: 335 p.
- Ossó, À. 2016: *Eogeryon elegius* n. gen. and n. sp. (Decapoda: Eubrachyura: Portunoidea), one of the oldest modern crabs from the late Cenomanian of the Iberian Peninsula. *Boletín de la Sociedad Geológica Mexicana*, 68/2: 231–246.
- PHILIPPE, M. & SECRETAN, S. 1971: Crustacés décapodes du Burdigalien des Courennes (Vaucluse). *Annales de Paléontologie*, 57: 117–134.
- POPOV, S. V., RÖGL, F., ROZANOV, A. Y., STEININGER, F. F., SHCHERBA, I. G. & KOVÁČ, M. 2004: Lithological paleogeographic maps of Paratethys. 10 Maps Late Eocene to Pliocene. *Courier Forschungsinstitut Senckenberg*, 250: 1–46.
- PORTELL, R. W. 2004: Eocene, Oligocene, and Miocene decapod crustaceans. *Florida Fossil Invertebrates*, 5: 1–28.
- RAFINESQUE, C. S. 1815: *Analyse de la nature, ou tableau de l'univers et des corps organisés*. J. Barravecchia, Palermo: 224 p.
- RALTE, V. Z., LALCHAWIMAWII, J., MALSAWMA, J. & TIWARI, R. P. 2009: Decapod fossils from the Bhuban Formation, Surma Group, Aizawl, Mizoram. *Earth Science India*, 2/III: 196–210.
- RATHBUN, M. J. 1919: West Indian Tertiary decapod crustaceans. In: VAUGHAN, T. W. (ed.): *Contributions to the Geology and Paleontology of the West Indies*. Carnegie Institution of Washington Publication, 291: 159–184.
- RATHBUN, M. J. 1920: Additions to the West Indian Tertiary decapod crustaceans. *Proceedings of the United States National Museum*, 58: 381–384.
- RATHBUN, M. J. 1923: Fossil crabs from the Republic of Haiti. *Proceedings of the Biological Society of Washington*, 63: 1–6.
- RATHBUN, M. J. 1935: Fossil Crustacea of the Atlantic and Gulf Coastal Plain. *Geological Society of America Special Papers*, 2: 1–160.
- RATHBUN, M. J. 1945: Decapod Crustacea. In: LADD, H. S. & HOFFMEISTER, J. E. (eds.): *Geology of Lau, Fiji*. Bernice Pauahi Bishop Museum Bulletin, 181: 373–383.
- RISTORI, G. 1888: Alcuni Crostacei del Miocene medio italiano. *Atti della Società Toscana di Scienze Naturali*, 9: 212–219.
- RIZNAR, I., MILETIĆ, D., VERBIĆ, T. & HORVAT, A. 2002: Middle Miocene sediments on the northern part of Gorjanci between Čatež and Kostanjevica (SE Slovenia). *Geologija*, 45/2: 531–536, doi:10.5474/geologija.2002.060.
- SATSANGI, P. P. & PARIDA, K. 1980: A new fossil crab from Garo Hills, Meghalaya. *Journal Geological Society of India*, 21: 302–305.
- SCHWEITZER, C. E., ITURRALDE-VINENT, M., HETLER, J. L. & VÉLEZ-JUARBE, J. 2006: Oligocene and Miocene decapods (Thalassinidea and Brachyura) from the Caribbean. *Annals of Carnegie Museum*, 75/2: 111–136.
- SPIRIDONOV, V. A., NERETINA, T. V. & SCHEPETOV, D. 2014: Morphological characterization and molecular phylogeny of Portunoidea Rafinesque, 1815 (Crustacea Brachyura): Implications for understanding evolution of swimming capacity and revision of the family-level classification. *Zoologischer Anzeiger*, 253: 404–429.
- STANCU, I. & ANDREESCU, E. 1968: Fauna tortoniana din regiunea Rugi-Delinsti (Bazanul Caransebesului). *Studii si Cercetari de Geol. Geofiz. Geogr. ser. Geol.* 2: 455–471.

- SVANE, I. & HOOPER, G. 2004: Blue Swimmer Crab (*Portunus pelagicus*). Fishery Assessment Report to PIRSA for the Blue Crab Fishery Management Committee, Aquatic Sciences Publication RD03/0274, Australia: 56 p.
- TIWARI, R. P. & VEGA, F. J. 2014: The Records of Miocene Crabs (Crustacea: Decapoda) from India. Special publication of the Palaeontological Society of India, 5: 183–188.
- TODD, J. A. & COLLINS, J. S. H. 2006: Neogene and Quaternary crabs (Crustacea, Decapoda) collected from Costa Rica and Panama by members of the Panama Paleontology Project. Bulletin of the Mizunami Fossil Museum, 32: 53–85.
- VAN STRAELEN, V. 1924: *Portunus brouweri*, portunien nouveau du Tertiaire de l'Île Célèbes. Jaarboek van het Mijnwezen en Ned-Oost Indie, 52: 168–171.
- VEGA, F. J., FELDMANN, R. M., VILLALOBOS-HIRIART, J. L. & GIO-ARGÍEZ, R. 1999: A new decapod fauna from the Miocene Tuxpan Formation, eastern Mexico. Journal of Paleontology, 73: 407–413.
- VEGA, F. J., NYBORG, T., COUTIÑO, M. A., SOLÉ, J. & HERNÁNDEZ-MONZÓN, O. 2009: Neogene Crustacea from southeastern Mexico. Bulletin of the Mizunami Fossil Museum, 35: 51–69.
- VEIGA FERREIRA, O. 1954: Malacostraceos do Mioceno Marinho de Portugal. Commission du Service Geologique du Portugal, 35: 5–23.
- VIA, L. 1932: Els crancs fòssils del Terciari de Catalunya. Butlletí de la Institució Catalana d'Història Natural, 32/4: 131–146.
- WEBER, F. 1795: Nomenclator entomologicus secundum entomologiam systematicam ill. Fabricii, adjectis speciebus recens detectis et varietatibus. Bohn, C. E. Hamburg/London: 171 p.
- YAZDI, M., BAHRAMI, A., ABBASI, P., SADEGHI, R. & VEGA, F. J. 2013: Miocene brachyuran Crustacea from Konar-Takhteh and Ahram sections, southwestern Iran. Boletín de la Sociedad Geológica Mexicana, 65/2: 225–233.