

Taphonomy and diversity of Middle Miocene decapod crustaceans from the Novohrad-Nógrad Basin, Slovakia, with remarks on palaeobiography

Matúš Hyžný^{1,2}, Natália Hudáčková² & Štefan Szalma³

¹ Naturhistorisches Museum Wien, Geologisch-Paläontologische Abteilung, Burgring 7, 1010 Vienna, Austria; e-mail: hyzny.matus@gmail.com

² Department of Geology and Palaeontology, Faculty of Natural Sciences, Comenius University in Bratislava, Mlynská dolina, Ilkovičova 6, Bratislava 842 15, Slovakia; e-mail: hudackova@fns.uniba.sk

³ Plášťovce 87, 935 82, Slovakia; email: szalma.istvan7@gmail.com

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Abstract: Decapod crustacean assemblages from the Middle Miocene (lower 'Badenian'=Langhian) volcanoclastic Plášťovce Beds (Sebechleby Formation) in the Slovakian part of the Novohrad-Nógrad Basin comprise five species in five families (Callianassidae, Laomedidae, Munididae, Cancridae and Retroplumidae) and are dominated by the cancrid crab *Tasadia carniolica* (Bittner, 1884). *Munida* sp. constitutes the first record of this genus from Slovakia and the second from the European Neogene. Burrowing shrimp (*Jaxea kuemeli* Bachmayer, 1954) are associated with burrows tentatively attributed to this species. The occurrence of *Retropluma slovenica* Gašparič & Hyžný, 2014, previously recorded from the Lower Miocene of Slovenia, extends both the geographical distribution and stratigraphical range of the species. Differential decapod diversity at four localities in the Plášťovce area can be explained by collecting bias and palaeoenvironmental factors. The palaeosetting is interpreted as a muddy-bottom, nearshore zone with a water depth of approximately 100 m. Abundant articulated crabs suggest rapid burial. Third maxillipeds in open posture in some specimens may indicate respiratory stress of the animals, suggesting episodic events of rapid volcanoclastic flows responsible for killing crabs and promoting their preservation. Species composition of the decapod fauna of the Plášťovce Beds further strengthens similarities with Miocene faunas from the North Sea Basin.

Key words: Decapoda, Middle Miocene, Novohrad-Nógrad Basin, Sebechleby Formation, Plášťovce Member, volcanoclastics taphonomy

1. INTRODUCTION

Since the first half of the twentieth century (Dornay, 1913; Lőrenthey & Beurlen, 1929), fossil decapod crustaceans from Slovakia have only recently received renewed attention (Hyžný, 2010, 2011a–c, 2012, 2014; Hyžný & Schlögl, 2011; Hyžný & Hudáčková, 2012; Hyžný & Zágorský, 2012; Hyžný et al., 2011, 2014). A Middle Miocene decapod association from the Plášťovce Member (Sebechleby Formation) was briefly mentioned by Hyžný (2011a), but a detailed description of the shrimp *Jaxea kuemeli* Bachmayer, 1954 was provided in a separate paper (Hyžný, 2011b). However, so far, detailed descriptions of the entire decapod fauna were not available. The aims of the

present work are threefold; 1) to describe the fauna taxonomically; 2) to evaluate taphonomy and differential diversity of decapod crustaceans at several localities within the study area; 3) to discuss palaeobiogeographical relationships with coeval European decapod faunas.

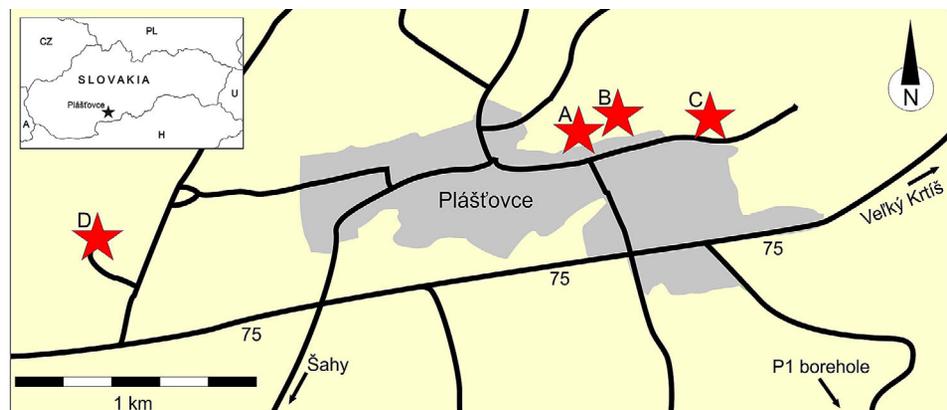


Fig. 1.: Localities (A–D) studied in the vicinity of Plášťovce.

2. GEOLOGICAL SETTING

Strata assigned to the Plášťovce Member extend over a fairly large area within the Slovakian part of the Novohrad-Nógrád Basin in the southern part of the country. At numerous places, these strata are exposed; however, decapod crustacean fossils are known only from a number of outcrops. Material from a total of four localities studied (Fig. 1) provides the basis for the present study; these are here referred to as Plášťovce A, B, C and D. The locality described by Sukatcheva et al. (2006) is the same as Plášťovce C here.

2.1 Sedimentology

The Plášťovce Member is part of the volcanoclastic sedimentary complex of the Sebechleby Formation (Konečný et al., 1983). Lithologically, it is composed of epiclastic volcanic sandstones, siltstones, fine-grained polymict conglomerates and tuffitic clays (Vass, 1971; Nagy, 1998). At the localities studied all lithologies typical of the Plášťovce Member are exposed, but differences in thickness and alteration of these types can be observed (Fig. 2) and stratification is relatively regular in bed development. On the basis of grain size alteration of clastic material, volcanoclastic sequences of the Plášťovce Member have been assigned to three main types (*sensu* Vass 1971), namely conglomerate-sandstone; conglomerate-sandstone-siltstone, and sandstone-siltstone. At the localities studied, type 1 is not present. The stratification conglomerate-sandstone-siltstone shows an irregular sequence development, i.e. bodies of respective lithology attain various thicknesses in different parts of the sections and may change laterally.

2.2 Localities studied

Plášťovce A (48°09'38.90"N, 18°59'2.16"E): Small outcrop situated on the southern slope of the Šípka Mts close to the Šípka State Nature Reserve, exposing approximately a 4-m-thick sequence of the volcano-sedimentary complex of the Plášťovce Member. In the lower part of the sequence, laminated tuffites are seen, with beds attaining up to 50 cm in thickness. At around 1.5 m from the bottom, a c. 40-cm-thick body of conglomerates overlies the tuffites; the contact is clearly erosional (Fig. 2A). Above the conglomerates follow approximately 30 cm of sandstone, the remainder of the sequence exposed being stratified tuffites.

A fauna of both whole and disintegrated crab exoskeletons was collected from fine-grained tuffites below the conglomerates.

Plášťovce B (48°09'39.53"N, 18°59'6.02"E): The locality is situated on the same slope as the previous (Plášťovce A), but approximately 200 m to the east. The outcrop is some 50 m in length and exposes approximately 20 metres in thickness. For the present study, a 12.5-m-thick section was sampled. The sequence includes two sets of typical stratification of type 2 (*sensu* Vass 1971), conglomerate-sandstone-siltstone. The contacts between sequences starting with conglomerates are erosional. A relatively regular vertical alteration of the same type is a common feature for the Plášťovce A and B sections.

At Plášťovce B, above the lower conglomeratic body, follow approximately 4 metres of massive epiclastic sandstones, with

bed thicknesses ranging from 10 to 50 cm. Grain size is finer in the upper part of the sequence, whereas in the lower part (at 5–6 m of the section) larger clasts occur in a much finer matrix. At the contact between sandstone and siltstone, soft-sediment deformation structures were observed (Fig. 2B; compare with Vass, 1971: p. 40, fig. 13). Tuffites consist of several beds, thickening upwards and becoming more massive and laminated. In the tuffites, abundant *Ophiomorpha* type trace fossils are preserved, composed of vertical shafts with a circular cross section (Fig. 2B) and horizontal tunnels. These traces are presumed to be of decapod origin (see below) and are filled with coarser material indicating that the burrow system was open when inhabited. Lamination is concentrated in the uppermost part of the tuffitic sequence, just below the erosional surface (erosion channel) at the contact with the conglomerates.

Decapod fossils are concentrated in finer-grained sediments. Isolated, poorly preserved carapace fragments and parts of appendages are present in epiclastic sandstones, whereas in finer-grained tuffites also near-complete crab exoskeletons are preserved. As far as species composition is concerned, Plášťovce B contains the richest decapod assemblage of all sections studied.

Plášťovce C (48°09'40.23"N, 18°59'22.19"E): Small outcrop (road cutting), situated approximately 400 m east of Plášťovce B, exposing a 4-m-thick sequence of bioturbated tuffites, alternating with beds of laminated tuffites (Fig. 2C). Bed thickness ranges between 10 and 40 cm. Plášťovce C roughly corresponds to section P3 of Sukatcheva et al. (2006). Decapod fossils include both near-complete and fragmentary crab exoskeletons.

Plášťovce D (48°09'22.91"N, 18°57'23.19"E): Section, located approximately 1 km west of the village of Plášťovce, exposed at a disused quarry. Nearly the entire sequence is composed of fine-grained, often laminated, massive tuffites of yellow to pinkish colour. In the lowermost part of the c. 10-m-thick sequence, there are two conspicuous sandstone beds, whereas the uppermost part of the sequence (c. 60 cm) is composed of conglomerates (Fig. 2D). An additional conspicuous sandstone bed occurs at 6.2 m of the sequence.

Decapod fossils were collected mostly from the interval between the sandstone beds, and comprise almost exclusively *Tasadia carniolica*, accompanied by *Gyrolithes*-like trace fossils.

2.3 Stratigraphy

The age of the Plášťovce Beds has traditionally been determined by approximation on the basis of lithostratigraphical schemes (Vass, 1971, 2002), i.e., early 'Badenian' (Langhian) to early late 'Badenian' (Langhian/Serravallian; *sensu* Kováč et al., 2007; Hohenegger et al., 2014). On the basis of foraminiferal assemblages from the Plášťovce 1 (P1) borehole core (located ca. 6 km SE of Plášťovce) and from localities nearby, the tuffitic rocks were assigned to the Upper Lagenide Zone (*sensu* Grill, 1941) or CPN7 Zone (*sensu* Cicha et al., 1975) in the lower part, and to the Spirorutilus carinatus Zone (*sensu* Grill, 1943) or CPN8 Zone (*sensu* Cicha et al., 1975) in the upper part of the sequence (Lehotayová, 1965). Samples from the P1 core (Lehotayová, 1965) at a depth of 47 m do not yield any foraminifera, while assemblages from depths between 59 and 52 m comprise both

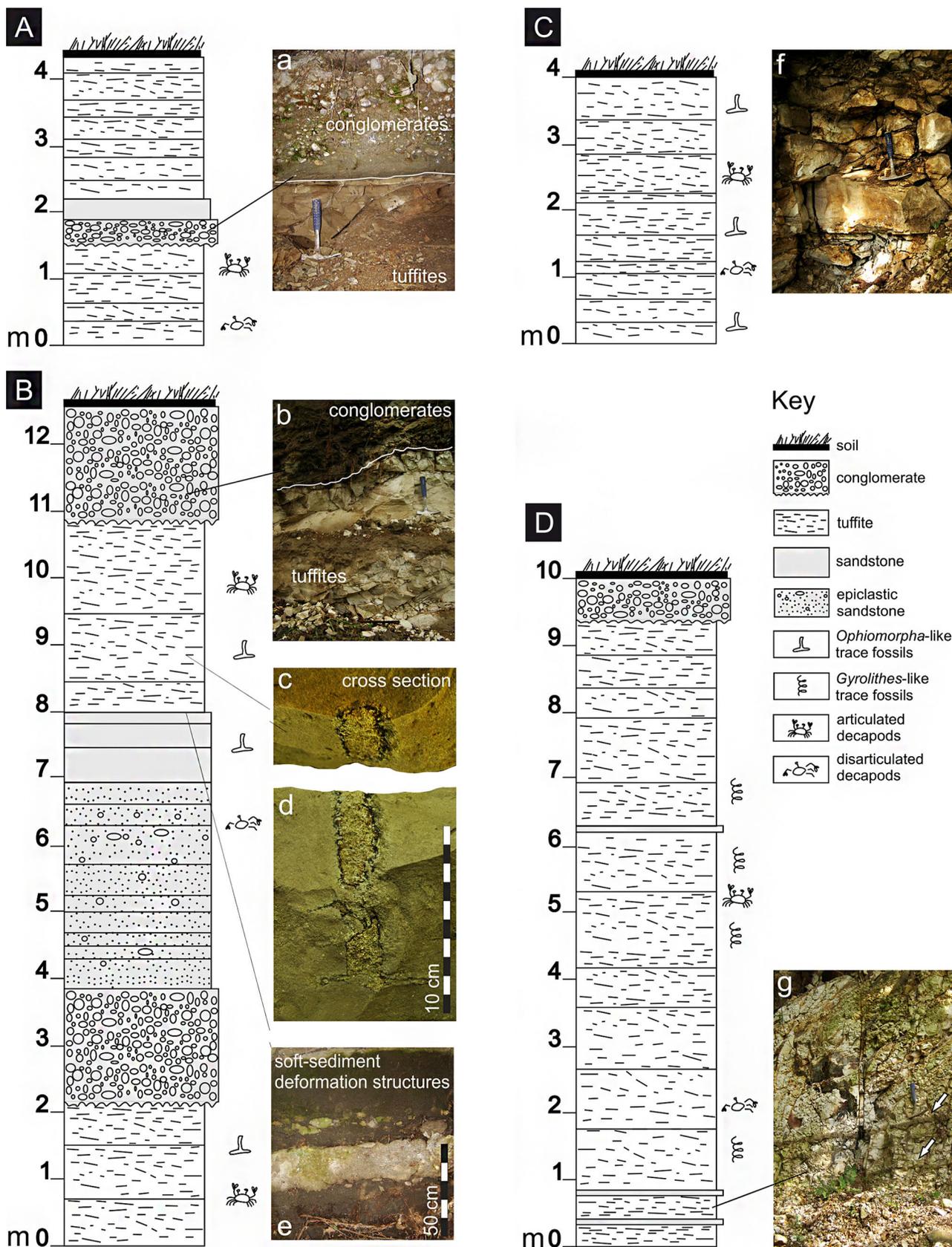


Fig. 2. Sections studied at Plášťovce. A – Plášťovce A; note the contact between tuffites and conglomerates (a); B – Plášťovce B; the contact between tuffites and conglomerates is erosional (b). Burrows include *Ophiomorpha*-like trace fossils (c–d); the contact between sandstones and tuffites often contains soft-sediment deformation structures (e); C – Plášťovce C; the section is strongly weathered (f); D – Plášťovce D; in the lowermost part of the section, there are two distinct sandstone beds (g).

planktonic and benthic species. The latter are characteristic of deeper, suboxic environments rich in nutrients, e.g. *Uvigerina brunensis* Karrer, 1877, *U. semiornata* d'Orbigny, 1846, *Fursenkoina schreibersiana* (Czjzek, 1848) and *Melonis pompilioides* (Fichtel & Moll, 1798). Unfortunately, no species counts (abundance) or semi-quantitative data are available.

New samples collected from Plášťovce A–D proved almost barren; only in some samples were moulds of foraminiferal tests (*Globigerina* sp., *Bulimina elongata* d'Orbigny, 1826, and *Nodosaria* sp.) found. Based on these, a detailed age assignment is impossible.

The Příbelce Member (exposed in the north-eastern part of the basin) has been considered by some workers (Vass, 1977, 2002: p. 172; Vass et al., 1979) to be coeval with the Plášťovce Member. Based on foraminifera, the age of the former was determined as early 'Badenian' (Langhian) (Vass, 1965; Zlinská & Šutovská, 1991). Sukatcheva et al. (2006) referred to these data in their claim for an early 'Badenian' date of the entire faunal assemblage of the Plášťovce Member exposed at the village of Plášťovce. Until more data become available, we adopt this view and assign an early 'Badenian' age to the strata studied.

3. MATERIAL AND METHODS

A total of 94 decapod specimens were collected from all lithofacies types, with the exception of epiclastic conglomerates that are barren of macrofossils. Preservation varies markedly depending

of lithofacies. In coarser-grained sediments decapod remains are fragmentary and poorly preserved, while in finer-grained sediments they are well preserved, often articulated and retaining ventral parts (Fig. 4E) or even antennae (Fig. 3A). The best-preserved material comes from fine-grained tuffites, usually just below the discordant base of epiclastic conglomerates.

Thirteen samples for micropalaeontological analysis were taken from sections studied, as well as from identical rock samples with preserved decapods. Rock samples were treated by traditional micropalaeontological methods for separating foraminiferal tests. For rock disintegration, the use of 5 per cent solution H_2O_2 was needed. After maceration, the sediment was sieved, using 0.071 and 0.9 mm mesh widths. Fractions 0.071 and 0.9 mm were kept and studied using stereoscopic binocular microscope. Residues and fossils collected are deposited at the Department of Geology and Palaeontology (KGP-MH), Comenius University at Bratislava, Slovakia.

Institutional abbreviations: KGP-MH – Department of Geology and Palaeontology, Comenius University, Bratislava, Slovakia; SNM-Z – Natural History Museum of Slovak National Museum, Bratislava, Slovakia.

4. SYSTEMATIC PALAEOLOGY

Remarks: The higher classification follows Ah Yong et al. (2010) and Schweitzer et al. (2010). Synonymy lists are as brief as possible, mentioning only taxonomically important works.

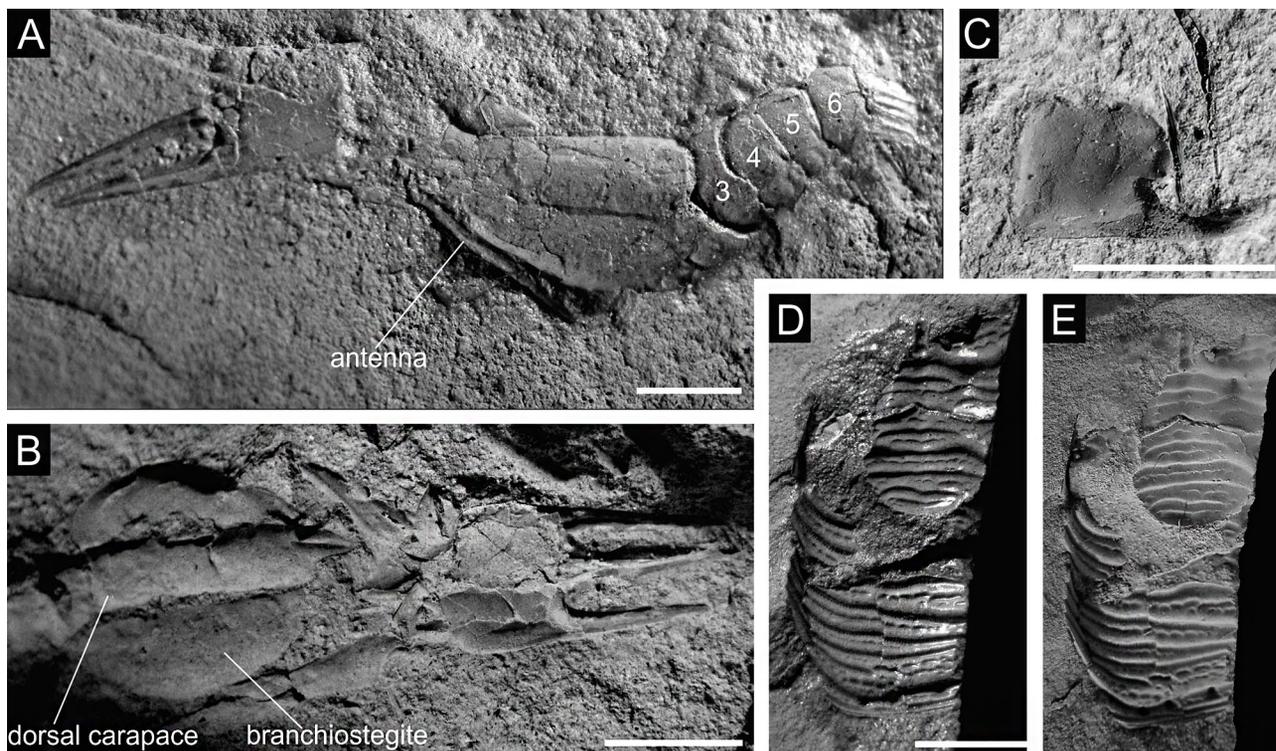


Fig. 3. Shrimp and squat lobsters of the Plášťovce Member; A – *Jaxea kuemeli* Bachmayer, 1954, near-complete specimen (SNM-Z 36891a), with abdomen partly covered with carapace (numbers indicate abdominal segments), its counterpart (SNM-Z 36891b) was illustrated by Hyžný (2011b: fig. 5C); B – *J. kuemeli*, cephalothorax retaining both chelipeds (SNM-Z 36892); C – *Callianassa* (s.l.) cf. *kerepesiensis* Müller, 1976, left major propodus (KGP-MH/PL068); D, E – *Munida* sp., partial carapace (KGP-MH/PL069), uncoated (D) and coated with ammonium chloride prior to photography. Scale bars equal 5 mm.

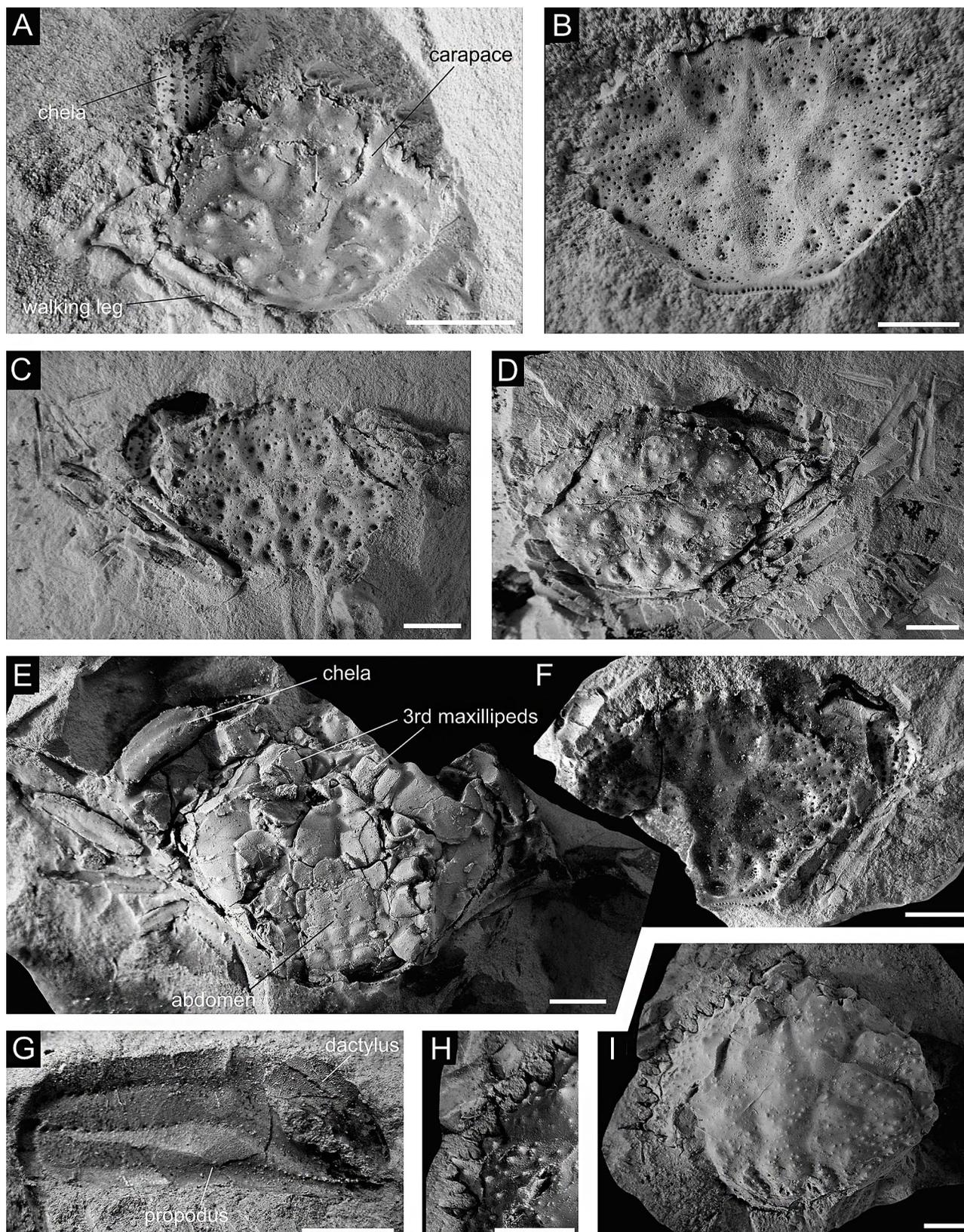


Fig. 4. Crabs of the Pláštovce Member: *Tasadia carniolica* (Bittner, 1884); A – carapace with associated chela and walking legs (KGP-MH/PL057); B – external mould of carapace showing numerous small tubercles among larger ones (KGP-MH/PL062); C, D – near-complete crab; note the different expression of preserved tubercles on external (C, KGP-MH/PL056) and internal moulds (D, KGP-MH/PL059); E – near-complete female specimen showing venter (KGP-MH/PL051). Note open third maxillipeds (Mxp3); F – external mould of carapace associated with appendages (KGP-MH/PL004); G – external mould of chela (propodus + dactylus); H – detail of anterolateral margin (SNM-Z 35790); I – internal mould of carapace (SNM-Z 35790). Specimens in B–E and I were coated with ammonium chloride prior to photography. Scale bars equal 5 mm.

Order Decapoda Latreille, 1802
 Infraorder Axiidea de Saint Laurent, 1979
 Family Callianassidae Dana, 1852

Genus *Callianassa* Leach, 1814

Type species: *Cancer (Astacus) subterraneus* Montagu, 1808, by original designation.

Remarks: In general, virtually any ghost shrimp fossil has been attributed to *Callianassa* in the past. As a result, numerous forms have been described under the collective name “*Callianassa*” (Schweitzer et al., 2010). These forms often do not correspond to the narrow definition of *Callianassa* as proposed by Manning & Felder (1991). This explains why subsequent authors have attempted to indicate clearly the collective nature of *Callianassa* when used in such a sense, e.g., *Callianassa sensu lato* (e.g., Karasawa, 2000, 2011; Hyžný et al., 2013).

***Callianassa* (s.l.) cf. kerepesiensis Müller, 1976**

Figure 3C

non 1976 *Callianassa kerepesiensis* Müller, p. 149, pl. 1, figs. 1-5

1979 *Callianassa kerepesiensis* Müller – Förster, p. 90, text-fig. 1; pl. 1, fig. 5

1984 *Callianassa cf. kerepesiensis* Müller – Müller, p. 52, pl. 7, figs. 1-2

Material: Pláštovce B: major propodus with articulated carpus (KGP-MH/PL067); Pláštovce D: isolated left major propodus (KGP-MH/PL068; Fig. 3C).

Description: Carpus higher than long, proximo-lower margin rounded. Manus approximately of equal length and height,

upper and lower margins parallel to each other, distal margin with well-developed notch above fixed finger. Fixed finger approximately of same length as manus, slender and curved upwards distally. Lateral surfaces smooth, without any tuberculation.

Remarks: The material is too fragmentary for a more detailed identification. However, the quadrate manus with a rather deep notch at the base of the fixed finger is reminiscent of some representatives of the subfamily Callianassinae, in particular *Trypaea* Dana, 1852, *Neotrypaea* Manning & Felder, 1991, *Nihonotrypaea* Manning & Tamaki, 1998 or *Paratrypaea* Komai & Tachikawa, 2007. The small size of the propodi (length of manus not exceeding 5 mm) may suggest attribution to *Paratrypaea* (see Dworschak, 2012), but in view of the fact that no major merus (usually considered of taxonomic importance, e.g., Manning & Felder, 1991) is available, we are reluctant to assign this poorly preserved material to any genus with confidence.

The shape of the propodus is strikingly similar to that of *Callianassa cf. kerepesiensis* from the upper ‘Badenian’ of the Budapest area, Hungary (Müller, 1984). Based on Förster (1979) and Müller (1984), *C. cf. kerepesiensis* differs from *C. kerepesiensis* in the nature of the fixed finger which possesses only a single rudimentary tooth instead of the two in the latter, although it is questionable whether this character can be considered taxonomically significant. Additionally, *C. cf. kerepesiensis* has an upper propodal margin which converges distally, which is not the case in *C. kerepesiensis*. A detailed revision of both taxa, with an assessment of intraspecific variation, is called for in order to clarify the status of *C. cf. kerepesiensis*.

Infraorder Gebiidea de Saint Laurent, 1979

Family Laomediidae Borradaile, 1903

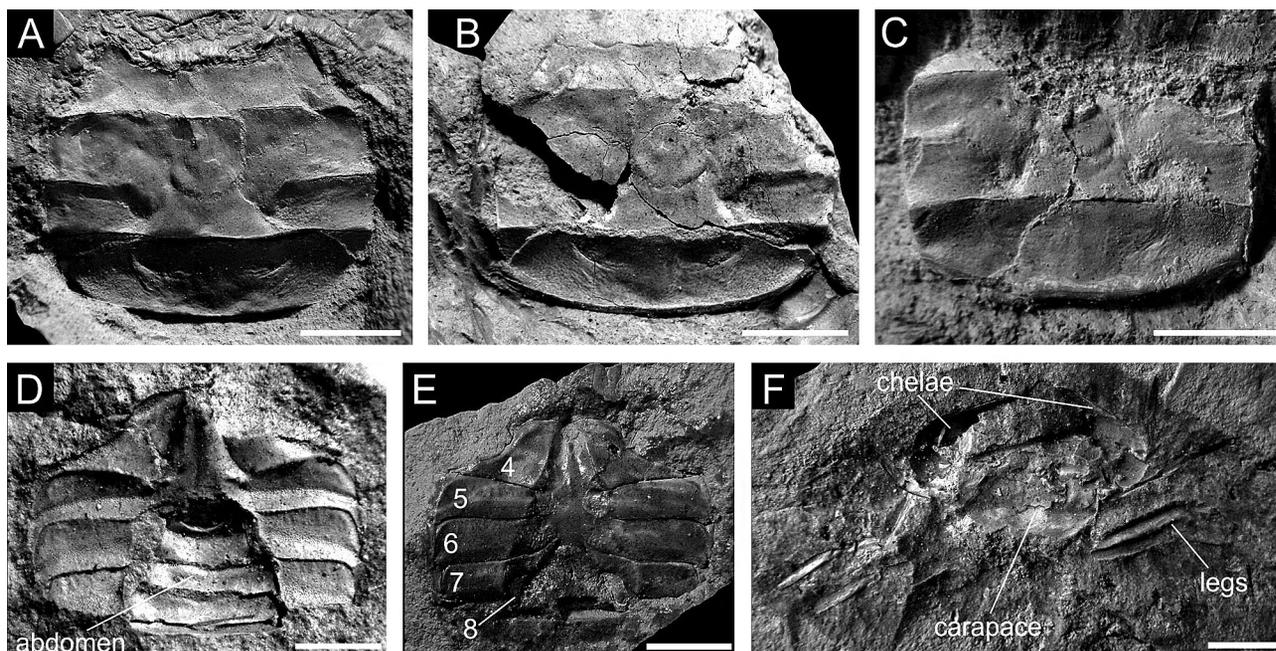


Fig. 5. Crabs of the Pláštovce Member: *Retropiuma slovenica* Gašparič & Hyžný, 2014; A, B – carapace (KGP-MH/PL063) preserved as external (A) and internal mould (B); C – incomplete carapace (KGP-MH/PL064); D, E – female venter (SNM-Z 35798) with preserved abdomen as external mould (D) and sternum as internal mould with numbered sternites (E); F – near-complete crab with damaged carapace (SNM-Z 35797). Scale bars equal 5 mm.

Genus *Jaxea* Nardo, 1847

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

Diagnosis: see Ngoc-Ho (2003: p. 501).

Jaxea kuemeli Bachmayer, 1954

Figures 3A–B

- *1954 *Jaxea kùmeli* Bachmayer, p. 64, pl. 1, figs. 1-2
- 1969 *Jaxea kuemeli* Bachmayer – Glaessner, p. R477, fig. 284.4a, b
- 1984 *Jaxea kuemeli* Bachmayer – Müller, p. 49
- 1998 *Jaxea kuemeli* Bachmayer – Müller, p. 9
- 2010 *Jaxea kuemeli* Bachmayer – Schweitzer et al., p. 41
- 2011a *Jaxea kuemeli* Bachmayer – Hyžný, p. 167, table 1
- 2011b *Jaxea kuemeli* Bachmayer – Hyžný, p. 176, figs. 2A-D, 3B, 5A-C, 6A-C, 7A-D
- 2015 *Jaxea kuemeli* Bachmayer – Gašparič & Hyžný, p. 9, figs. 8-9

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 pereopods 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 by several smaller teeth, or with several round, equal-sized teeth; large median triangular tooth positioned more proximally, usually composed of several smaller teeth; distal half of 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 pereopods simple (after Hyžný, 2011b).

Material: Plášťovce B: a near-complete specimen, including cephalothorax and abdomen (SNM-Z 36891a, b; Fig. 3A), another specimen consisting of cephalothorax with both chelipeds (SNM-Z 36892; Fig. 3B) and two isolated chelae (KGP-MH/PL065-066). Details of measurements of SNM-Z 36891-36892 can be found in Hyžný (2011b: table 2, fig. 4).

Remarks: Material from Plášťovce formed a part of the collection which served as a basis for the revision of *Jaxea kuemeli* by Hyžný (2011b), which is why a detailed description is not repeated here. Hyžný (2011b) also presented a detailed account of the differentiation between *J. kuemeli* and its extant congener from the Mediterranean, *J. nocturna*. The two species differ in cheliped morphology, in particular the dentition of fingers (Hyžný, 2011b: fig. 3). At Plášťovce B, *J. kuemeli* has been found in association with trace fossils interpreted as open burrows (see Discussion below).

Occurrence: *Jaxea kuemeli* is restricted to the Lower and Middle Miocene of Neogene basins in the Paratethys (Austria, Germany, Hungary, Slovakia and Slovenia; see Bachmayer, 1954; Hyžný, 2011b; Gašparič & Hyžný, 2015).

Infraorder Anomura MacLeay, 1838

Superfamily Galatheoidea Samouelle, 1819

Family Munididae Ah Yong, Baba, Macpherson & Poore, 2010

Genus *Munida* Leach, 1820

Type species: *Pagurus rugosus* Fabricius, 1775, by monotypy.

Diagnosis: Carapace rectangular or ovoid, longer than wide, rostrum flanked by one pair of supraorbital spines; two or three anterolateral spines; several small, lateral spines posterior to intersection of cervical groove with lateral margin; deep, arcuate cervical groove; transverse carapace ridges, ranging from simple and parallel to complex and bifurcating; and linear array of gastric spines paralleling frontal margin of carapace (after Schweitzer & Feldmann, 2000a: p. 154).

Munida sp.

Figures 3D–E

Material: Plášťovce C: a single incomplete dorsal carapace without rostrum (KGP/MH-PL069).

Description: Dorsal carapace incomplete, apparently longer than wide, broken along cervical groove; frontal margin (including rostrum), anterolateral margin and right half of carapace missing. Whole surface covered with transverse ridges; continuous ridges alternating with discontinuous ones forming scabrous ornamentation especially in posterior carapace portion. Epigastric regions with at least one pair of epigastric spines. Posterior carapace margin with three spines on its preserved half.

Remarks: The sole specimen available is too incomplete to be identified at the species level. Taxonomically important characters, e.g., rostrum, frontal and anterolateral margins, are not preserved. Assignment of the material to *Munida* is based on the presence of epigastric spines and discontinuous ridges, and should be considered tentative.

Franțescu (2014) recognised ten extinct species of the genus; however, none of these is known from the Neogene of Europe. The sole known occurrence is *Munida* sp. from the Upper Miocene of Denmark (Fraaije et al., 2005), which is based on two moderately preserved external moulds of abdominal somites. Thus, comparison with the Plášťovce material is not possible.

Infraorder Brachyura Linnaeus, 1758

Section Eubrachyura de Saint Laurent, 1980

Subsection Heterotremata Guinot, 1977

Superfamily Cancroidea Latreille, 1802

Family Cancridae Latreille, 1802

Subfamily Lobocarcininae Beurlen, 1930

Genus *Tasadia* Müller in Janssen & Müller, 1984 (? = *Glebocarcinus* Nations, 1975)

Type species: *Cancer carniolicus* Bittner, 1884, by monotypy.

Diagnosis: Carapace wider than long (L/W c. 0.60). Front not projected beyond orbits. Four or five frontal spines. Frontal orbital width/carapace width ratio c. 30 per cent; orbits small, shallow, directed forwards, with two fissures. Anterolateral margin convex, ornamented with eight or nine triangular spines,

with granules or spinelets, each separated to bases. Posterolateral margin nearly straight, granular, with several small spines. Posterior margin rimmed, nearly straight. Regions well defined, ornamented with closely spaced tubercles; regions defined by smooth, deep grooves.

Manus of chelipeds with at least four granular keels on outer surface; upper margin appearing to be ornamented with sharp spines; lower margin smooth. Fixed finger with two granular keels on outer surface. Dactylus with sharp granules on upper margin; at least one row of granules on outer surface (after Schweitzer & Feldmann, 2000b: p. 245).

Remarks: Müller *in* Janssen & Müller (1984) erected the genus to accommodate several Miocene species of *Cancer* now regarded to be synonymous (see the synonymy list below); thus, the genus is now monotypical (Schweitzer & Feldmann, 2000b). There has been some debate about the generic status of *Tasadia*. Karasawa (1990: p. 6) and Davie (1991: p. 509) expressed doubts over its distinct nature, but Schweitzer & Feldmann (2000b) opined for the reverse. It is interesting to note, that Müller himself (1998: p. 28) was uncertain if *Tasadia* represented a distinct genus and mentioned the possible synonymy with *Glebocarcinus* as had been suggested previously by Karasawa (1990). More comparative studies are needed to resolve this issue, but for the time being we concur with Schweitzer & Feldmann (2000b) in treating *Tasadia* as a “good” genus.

Tasadia carniolica (Bittner, 1884)

Figures 4A–I

- * 1884 *Cancer carniolicus* Bittner, p. 27, pl. 1, figs. 8–9
- 1893 *Cancer cf. illyricus* Bittner, p. 32
- 1897 *Cancer Szontaghii* Lörenthey, p. 159
- 1898 *Cancer Szontaghii* Lörenthey, p. 104
- 1904 *Cancer Bittneri* Toulou, p. 163, text-figs. 1–5
- 1928 *Cancer Bittneri* Toulou – Glaessner, p. 178
- 1929 *Cancer Bittneri* Toulou – Glaessner, p. 101
- 1929 *Cancer carniolicus* Bittner – Glaessner, p. 102
- 1929 *Cancer szontaghi* Lörenthey – Glaessner, p. 108
- 1929 *Atelecyclus carniolicus* (Bittner) – Lörenthey & Beurlen, p. 158, pl. 8, fig. 5
- 1929 *Atelecyclus szontaghi* (Lörenthey) – Lörenthey & Beurlen, p. 156, pl. 8, fig. 9a–b
- 1952 *Atelecyclus szontaghi vindobonensis* Bachmayer & Küpper, p. 201, figs. 1–2
- 1984 “*Cancer*” *szontaghii* Lörenthey – Müller, pp. 77, 112, pl. 59, figs. 1–5; pl. 60, figs. 1–2
- 1984 “*Cancer*” *szontaghii vindobonensis* (Bachmayer & Küpper) – Müller, pp. 78, 112
- 1984 “*Cancer*” *carniolicus* Bittner – Müller, pp. 78, 112
- 1984 “*Cancer*” *bittneri* Toulou – Müller, pp. 78, 112
- 1984 *Tasadia carniolica* (Bittner) – Müller *in* Janssen & Müller, p. 22, text-fig. 4a; pl. 4, fig. 3; pl. 5, figs. 1–2
- 2005 *Tasadia carniolica* (Bittner) – Fraaije et al., p. 57, pl. 1, figs. 7–9
- 2010 *Tasadia carniolica* (Bittner) – Schweitzer et al., p. 103
- 2011a *Tasadia carniolica* (Bittner) – Hyžný, p. 167, fig. 1C

Diagnosis: As for genus (see above).

Material: Plášťovce A: 22 specimens (KGP-MH/PL028-PL042, SNM-Z 35783, 35789–35794); Plášťovce B: 42 specimens (KGP-MH/PL001-PL027, PL062; SNM-Z 35775–35782, 35784–35788, 35795, 35796); Plášťovce C: 2 specimens (KGP-MH/PL043-PL044); Plášťovce D: 17 specimens (KGP-MH/PL045-PL061). The material is preserved in three different modes: 1) articulated specimens, i.e., carapace with appendages (Figs. 4A, C–F); 2) isolated carapaces (Figs. 4B, H–I); and 3) isolated appendage elements, usually chelae (Fig. 4G). More details on preservational aspects and taphonomical remarks are presented below. Carapace width varies between 1 and 4 cm.

Description: Carapace transversely ovate (*sensu* Ng 1998: fig. H), wider than long. Front with five spines, not projected beyond orbits. Fronto-orbital width/carapace width ratio about 30 per cent; orbits small, shallow, directed forwards, with two fissures. Anterolateral margin convex, ornamented with eight or nine triangular spines, with up to five spinelets (Fig. 4H), each separated to bases. Posterolateral margin nearly straight, granular, with four to five small spines. Posterior margin rimmed, nearly straight. Regions well defined by smooth, deep grooves. Entire carapace surface ornamented with densely spaced tubercles; each region with one to three large tubercles, usually positioned in the centre, smaller tubercles covering entire surface of the regions; tubercles on the posterior margin arranged in a continuous line. Protogastric regions with three large tubercles arranged in a triangle; mesogastric region with two large tubercles arranged longitudinally; metagastric region with a single large tubercle positioned in the centre; cardiac region with two large oval tubercles arranged in a transverse row; hepatic and epibranchial regions with a single large tubercle positioned in the centre; mesobranchial regions with two large tubercles; metabranchial regions with a single large tubercle. Sternum elongated longitudinally, with well-developed sutures between sternites. Manus of chelipeds with four granular keels on outer surface; upper margin ornamented with sharp spines; lower margin smooth. Fixed finger distinctly shorter than manus, with two granular keels on outer surface. Dactylus with sharp granules on upper margin. Occlusal surface of both fingers armed with simple teeth of the same shape; tips are usually darker in colour. Second to fifth pereopods with longitudinal granulated ridges on all elements.

Remarks: The material from Plášťovce is in all important aspects identical to *Tasadia carniolica* as described by Müller *in* Janssen & Müller (1984). Variation in the nature of ornamentation can mostly be ascribed to preservational aspects, i.e., whether the carapace is preserved as an internal or external mould (see Discussion). Otherwise, the entire assemblage is fairly homogeneous.

Occurrence: *Tasadia carniolica* is known from the Middle Miocene of Paratethyan Neogene basins of Austria, Hungary, Romania, Slovakia and Slovenia (Bittner 1884; Toulou, 1904; Müller, 1984, 1998; Mikuž, 2010; Hyžný, 2011a) and the Lower and Upper Miocene of the North Sea Basin (Belgium, Denmark, Germany, the Netherlands and Denmark; see Janssen & Müller, 1984; Fraaije et al., 2005; Van Bakel et al., 2006).

Superfamily Retroplumoidea Gill, 1894
Family Retroplumidae Gill, 1894

Genus *Retropluma* Gill, 1894

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

Diagnosis: Carapace flattened, subrectangular with three prominent transverse carinae; anterior and posterior carinae usually continuous across entire width of carapace. Front truncate, orbits exposed, rostrum narrow and single lobed. Anterolateral tooth large, triangular in outline; infraorbital tooth not spiniform; area between rostrum and anterolateral tooth with blunt granular projection. Eystalks ending at base of anterolateral tooth. Anterolateral margins strongly oblique. Chelipeds pincer-like, pereopods 2–4 long and slender, pereopod 5 diminutive due to reduced size of sternite 8 (emended from de Saint Laurent, 1989: p. 118).

***Retropluma slovenica* Gašparič & Hyžný, 2014**
Figures 5A–F

2011a *Retropluma borealis* Fraaije, Hansen & Hansen – Hyžný, p. 167, fig. 1F, table 1

2015 *Retropluma slovenica* Gašparič & Hyžný, p. 15, figs. 18–21

Diagnosis: Subrectangular carapace wider than long (W/L c. 1.20), well-developed anterolateral tooth, pointing slightly outwards. Rostrum curved downwards, of same length as anterolateral tooth, with concave sides and significantly wider at distal end. Ventrally positioned infraorbital tooth, closely followed and partly overlapping with anterolateral tooth. Dorsal carapace with three distinct transverse carinae, forming variably pronounced blunt teeth at contact with lateral carapace margin. Tooth on anterior carina border most pronounced (after Gašparič & Hyžný, 2015: p. 156).

Material: Plášťovce A: one near-complete individual with carapace and appendages (SNM-Z 35797: maximum carapace width 9.3 mm); Plášťovce B: three isolated carapaces (KGP-MH/PL063: maximum carapace width 17.7 mm; KGP-MH/PL064: maximum carapace width 15.2 mm; SNM-Z 35799: maximum carapace width 16.5 mm), sternum with abdomen (SNM-Z 35798).

Description: Carapace flat, transversely rectangular (*sensu* Ng, 1998: fig. B), wider than long ($W/L \sim 1.25$), with maximum width at level of median carina. Rostrum not preserved. Supraorbital margin wide with supraorbital tooth and distinct orbits. Single anterolateral tooth well developed, triangular in outline, pointing slightly outwards. Lateral and posterior margins slightly convex, with well-developed concave re-entrant for fifth pereopod. Carapace with three distinct transverse carinae, forming pronounced blunt teeth at contact with lateral carapace margin; anterior carina almost straight, continuously parallel to frontal margin; median carina strongly developed at flanks only, interrupted by gastric regions; posterior carina sinuous and well developed, convex laterally and slightly concave centrally at intersection with cardiac region. Frontal and lateral margins finely tuberculated.

Regions only moderately developed except urogastric and cardiac regions which are well defined. Metabranial regions with distinct, fine striation marks. Posterior margin rimmed. Female abdomen broadly triangular, narrowing distally, telson not preserved; pleonites with transverse ridges. Female sternum broad at sternites 5–7, sternite 8 reduced; sternites 5–7 with distinct transverse ridges. Chelipeds insufficiently preserved; walking legs long and slender.

Remarks: Based on a single carapace, the material from Plášťovce was identified by Hyžný (2011a) as *Retropluma borealis* Fraaije, Hansen & Hansen, 2005. Recently, a new species of *Retropluma* has been described from the Lower Miocene of Slovenia, *R. slovenica* Gašparič & Hyžný, 2014. Thorough comparison of additionally collected material with the newly described *Retropluma* has now demonstrated their conspecificity. *Retropluma slovenica* is morphologically close to *R. borealis* from the Upper Miocene of Denmark (Fraaije et al., 2005) and to *R. craverii* (Crema, 1895) from the Pliocene of Italy (De Angeli et al., 2011), however, it differs in a number of characters (discussed in detail by Gašparič & Hyžný, 2015). Importantly, a well-developed and tuberculate postorbital tooth with concave sides and strong projections at the junctions of carinae with lateral carapace margins are typical of *R. slovenica*; these are distinctly less well developed in *R. borealis* and *R. craverii*.

Occurrence: So far, *Retropluma slovenica* has been recorded solely from the Lower Miocene ('Karpatian') of the Slovenian part of the Styrian Basin (Gašparič & Hyžný, 2015). The present record is the second known; it extends both the geographical distribution of the species to the Slovakian part of the Novohrad-Nógrad Basin and the stratigraphical range into the Middle Miocene ('Badenian').

5. DISCUSSION

5.1 Palaeoenvironment

The Plášťovce Beds originated between the shoreface and offshore zones (Kováč et al., 1999). Deposition was controlled mainly by synsedimentary tectonics in the area and by volcanic activity (Vass, 1971). The basin was filled predominantly by volcanoclastic material derived from an active andesite stratovolcano situated to the north of the basin (Konečný et al., 1983).

In addition to decapod crustaceans, the faunal content of the Plášťovce Beds includes gastropods, plus infaunal, semi-infaunal and epifaunal bivalves (preserved often as internal moulds), and irregular echinoids (Sukatcheva et al., 2006). The presence of echinoids suggests a prevalence of stenohaline conditions. The muddy and/or fine sandy substrate was inhabited by burrowing shrimps, specifically "*Callianassa*" cf. *kerepesiensis* and *Jaxea kuemeli*. Extant members of *Jaxea* commonly inhabit muddy to sandy bottoms (Wear & Yaldwyn, 1966; Ngoc-Ho, 2003: p. 505). At Plášťovce B, relatively large fossil burrows (Fig. 2B) were observed in close proximity of remains of *J. kuemeli*. It is likely that their tracemaker was *Jaxea*, which constructs burrows with large galleries (Pervesler

& Dworschak, 1985; Pervesler & Hohenegger, 2006). Callianassids often construct burrows with tunnels and shafts which reflect the animal's size and chelae of "*Callianassa*" cf. *kerepesiensis* found are rather small. Consequently, it appears unlikely that they produced the burrow structures observed at Pláštovce B.

To date, *Jaxea* is known mainly from shallow-marine settings up to depths of 100 m (Wear & Yaldwyn, 1966; Ngoc-Ho, 2003), although it has been recorded from depths exceeding 400 m (Diez et al., 1994). In general, most specimens of European *Jaxea nocturna* were collected from the depths less than 100 m (Ngoc-Ho, 2003). Callianassids often inhabit the intertidal to subtidal zone (Dworschak, 2000; Dworschak et al., 2012). However, without proper generic assignment of "*Callianassa*" cf. *kerepesiensis*, it is difficult to compare its possible environmental preferences with its extant relatives.

Munida is a very speciose squat lobster genus that generally inhabits deep-water settings of several hundreds of metres, but among the numerous species there are some that have been recorded from depths not exceeding several tens of metres (Baba et al., 2008). The same is true for *Retropluma*, a typical inhabitant of deeper settings, with a bathymetric range of 70–450 m (de Saint Laurent, 1989; McLay, 2006). With regard to *Retropluma*, Artal et al. (2006) argued for adaptation to soft bottoms on inner and outer continental shelves, which is in accordance with depositional settings reflected by the Pláštovce localities. *Retropluma slovenica* from the Lower Miocene of Slovenia was recorded from settings interpreted to have been laid down in waters deeper than 125 m (Gašparič & Hyžný, 2015); a similar depth can be estimated for the palaeoenvironment at the Pláštovce localities.

The decapod associations studied are dominated by *Tasadia* (see below), which has no extant counterpart. Its closest relative today, morphologically speaking, is *Glebocarcinus* which inhabits a wide range of depths from 10 to 400 m (Nations, 1975) and which was identified in the Lower Miocene of Switzerland (Fraaije et al., 2010a). Based on the entire decapod fauna, the bathymetry of the Pláštovce Beds can be estimated to have been approximately 100 m, or deeper, which is in accordance with the bathymetric range of benthic foraminifera recorded by Lehoyová (1965) from the P1 borehole core.

Interestingly, Sukatcheva et al. (2006: p. 533) described a non-thermophilic caddisfly from the section here referred to as Pláštovce C. Those authors explained the presence of an adult caddisfly in a littoral marine setting as, "a result of fixation of its larvae in fresh water streams or rivers, coming from inland high elevations".

5.2 Differential diversity

The decapod fauna from the Pláštovce localities comprises five species in five families (Callianassidae, Laomeidiidae, Munididae, Cancridae and Retroplumidae). With a total of 82 specimens collected (87.2 per cent), *Tasadia carniolica* is a predominant species (Fig. 6A) and other taxa represent rather accessory elements. Species composition at the various localities differs (Fig. 6B), although *Tasadia* is predominant at every one of them. At

Pláštovce A two species were identified, with *Tasadia carniolica* accounting for 95.6 per cent of the association, the remainder being *Retropluma slovenica*. At Pláštovce B, the situation is different. Four species were identified here; in addition to *T. carniolica* (82.4 per cent), also *Callianassa* cf. *kerepesiensis* (2 per cent), *Jaxea kuemeli* (7.8 per cent) and *R. slovenica* (7.8 per cent) occur. Pláštovce C yielded only three specimens, of two taxa, *Munida* sp. (1) and *T. carniolica* (2). Because of the limited sample size, this locality was not included in further analysis (see Fig. 6B–C). At Pláštovce D, two species were identified; the dominant *T. carniolica* (94 per cent) is accompanied by *C. cf. kerepesiensis* (6 per cent).

This differential diversity at the Pláštovce localities can be explained as having been affected by two major factors:

Collecting bias: Pláštovce A and B are localities in close proximity, with comparable lithology. However, outcrop at Pláštovce B is significantly larger and more collecting time has been spent here. Collecting bias is clearly responsible for a different composition: 51 specimens were collected at Pláštovce B, and only 23 at Pláštovce A. Moreover, accessory taxa present at Pláštovce B include a total of 9 specimens, of which only a single individual of *C. cf. kerepesiensis* was found. Thus, one can speculate that further collecting at Pláštovce A should yield more taxa.

1. Environmental factors: It is possible that different microhabitats were present at the various localities. Pláštovce D differs from the others in having a more homogeneous lithology which affected also the preservation of the decapod fauna (Fig. 6C). Whereas sections at Pláštovce A, B and C contain *Ophiomorpha*-like trace fossils, at Pláštovce D these are replaced by *Gyrolithes*-like trace fossils that do not occur elsewhere, suggesting different substrate properties.

In general, Pláštovce A and B are close to each other geographically, lithologically and also faunally. Because of fewer specimens found, Pláštovce C is difficult to evaluate. However, the presence of *Munida* sp., which was not recorded at any other locality (despite extensive collecting at Pláštovce B), and the caddisfly recorded by Sukatcheva et al. (2006), may imply different depositional settings and palaeoenvironment. Finally, Pláštovce D, with its unique suite of trace fossils and absence of *Jaxea kuemeli*, points to a type of substrate not suitable for burrowers that constructed large galleries.

5.3 Taphonomy

In order to evaluate preservational aspects of the decapod fauna at the localities studied, specimens were divided into three groups:

Articulated specimens: any carapace with at least some walking legs and/or chela/chelae is considered to belong to this category.

Isolated carapace: no appendages retained.

Isolated appendage: either an isolated chela or element of other walking leg.

Based on this subdivision, Pláštovce A and B have a similar taphonomic pattern with approximately 23–25 per cent of articulated specimens, 33–35 per cent of isolated carapaces and 39–43 per cent of isolated appendages (Fig. 6C). Pláštovce D

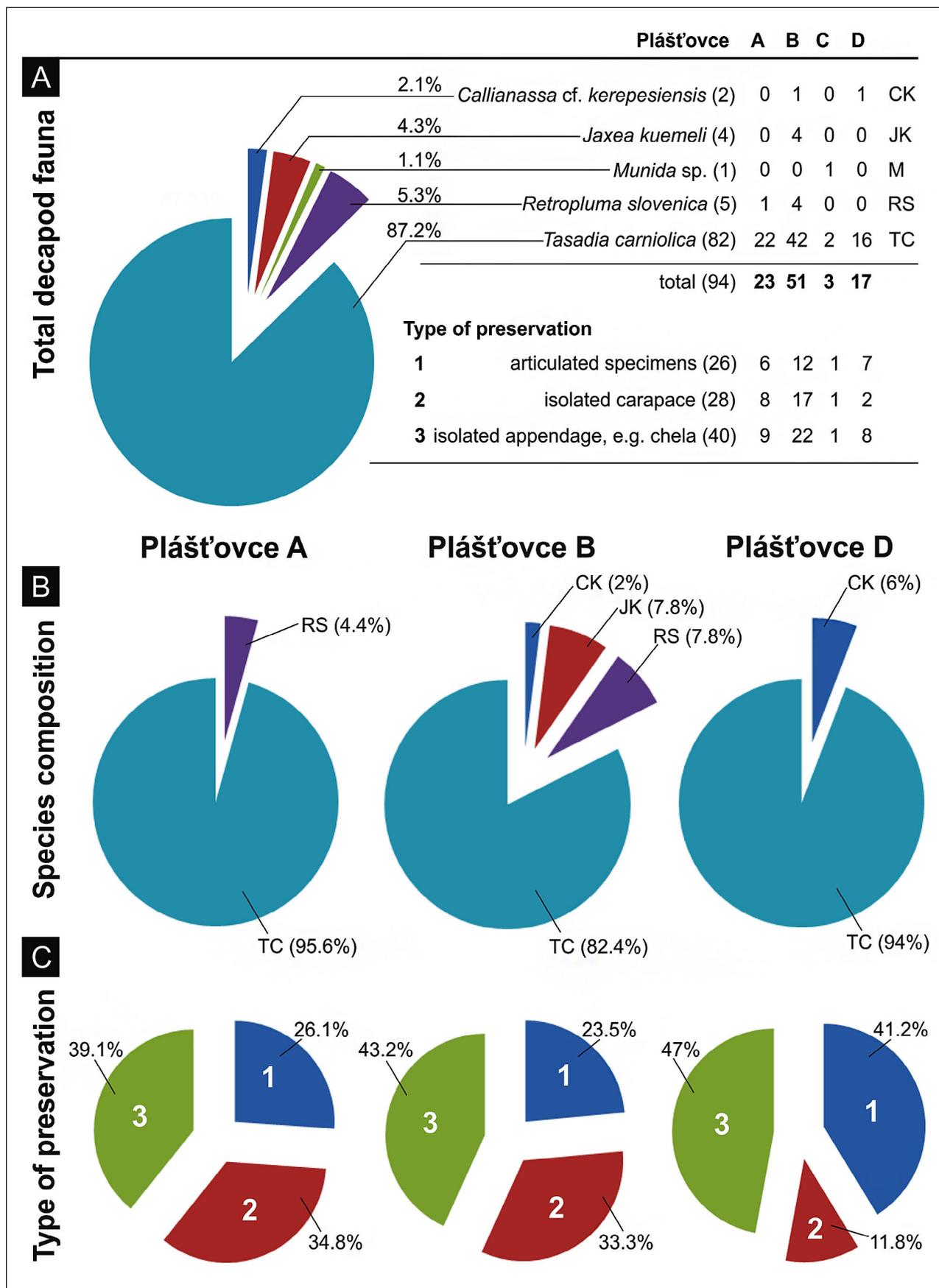


Fig. 6. Differential diversity and preservation of decapod crustacean fauna of the Plášťovce Member; A – species composition at all localities; B – species composition per locality (Plášťovce C is not included); C – type of preservation per locality (Plášťovce C is not included). See text for more details.

shows a different ratio; in excess of 40 per cent of all specimens are preserved articulated (Fig. 6C). This difference can be ascribed to the lithology which is much finer at Pláštovce D, lacking conglomerates and epiclastic sandstones (Fig. 2D).

Often the differentiation of moults from corpses is difficult in fossil decapod associations (Bishop, 1986). However, near-complete specimens of *Jaxea kuemeli* from Pláštovce B most likely represent moults, which can be deduced from the abdomen which is partly embedded under the carapace in one individual (Fig. 3A) and branchiostegites preserved in a single plane, together with the dorsal carapace in other specimen (Fig. 3B). The preservation of alleged moults might have been promoted by the moulting process of these shrimps that took place in burrows.

Specimens of *Tasadia carniolica* at Pláštovce do not always preserve the ventral side, but in case they do, their third maxillipeds usually are opened up (Fig. 4E). In such cases, all parts of the exoskeleton are in place, which suggests the animals to represent corpses. Third maxillipeds in a gaping posture may indicate respiratory distress (Warner, 1977) prior to death. This was reported for an assemblage of *Chaceon peruvianus* (d'Orbigny, 1842) from the Lower Miocene of Argentina (Crawford et al., 2008), that was interpreted to document preservation of rapidly buried crabs that had been suffocated by a cover of volcanic ash. Volcanic activity has already been suggested to have influenced deposition of the Pláštovce Beds (Vass, 1971), and thus episodic events of rapid volcanoclastic flows in the area could have killed crabs and been conducive to their preservation.

In general, rapid burial after very short or no *post-mortem* transport seems to be a rather characteristic feature of faunal elements of the Pláštovce Beds, as demonstrated also by two forewings of presumably a single individual of caddisfly (Sukatcheva et al., 2006) recorded from Pláštovce C.

Interestingly, nearly no cuticle is preserved in the decapod specimens studied. This probably is related to substrate geochemistry which caused dissolution of the cuticle after deposition and fossilisation. Decapods are preserved in two different ways, either as internal (Figs. 4A, D, I, 5B–C) or external moulds (Figs. 4B–C, F). In this respect it is important to note that ornamentation is strikingly different in these two modes, especially in *Tasadia carniolica*. While the external mould preserves all details of the original cuticular surface, the internal mould does not; thus, internal moulds do not preserve finer tuberculation. Taxonomic implications of this phenomenon have recently been discussed by Klompmaker et al. (2015; see also Waugh et al., 2009: fig. 2; Fraaije et al., 2013: p. 252).

5.4 Palaeobiogeography

The decapod fauna from the Pláštovce Beds can be compared directly with two European Miocene faunas. Fraaije et al. (2005) studied a Late Miocene assemblage from Gram, Denmark, dominated by *Chaceon miocenicus* Fraaije, Hansen & Hansen, 2005 and accompanied by *Nephrops*, *Munida*, *Tasadia* and *Retropluma*. The co-occurrence of the three last-named genera corresponds to that noted at Pláštovce herein. Recently, Gašparič & Hyžný (2015) described an Early Miocene fauna from Činžat, Slovenia,

dominated by *Retropluma slovenica* and *Styrioplax exiguus* (Glaessner, 1928) and accompanied by *Calliax*, *Lepidophthalmus*, *Jaxea* and *Neopilumnoplax*. The association of *R. slovenica* with *Jaxea kuemeli* is reminiscent of Pláštovce. All three faunas differ in many aspects, but they have one feature in common: the presence of the generally deep-water genus *Retropluma* which may be indicative not only of similar environmental conditions but also palaeobiogeographical relationships.

The assemblage from Činžat ('Karpatian') is slightly older than that of Pláštovce ('Badenian'), but both inhabited the Central Paratethys Sea. In fact, most of the 'Karpatian' and 'Badenian' decapod species from Slovenia (Gašparič & Hyžný, 2015: table 1) are present in roughly coeval strata in Austria or Slovakia (Müller, 1984, 1998; Hyžný, 2011a; Hyžný & Schlögl, 2011; Hyžný & Gašparič, 2014). Thus, faunal similarities between Pláštovce and Činžat do not come as a surprise. The affinity to decapod assemblages from Gram (Upper Miocene, Tortonian) can be explained differently. Since the birth of the Paratethys during the Oligocene, an intermittent seaway existed via the Rhine Graben (Martini, 1990; Berger et al., 2005) which connected the Paratethys with the North Sea; this came to an end during the Early Miocene. There was no seaway connection between the Central Paratethys and the North Sea during the Middle Miocene (e.g., Rögl, 1998; Harzhauser & Piller, 2007). During the Early and Middle Miocene, these two distinct biogeographic areas had some decapod genera (and even species) in common, as documented previously by several authors (Janssen & Müller, 1984; Fraaije et al., 2005, 2010b). The assemblage from Pláštovce adds further similarities which call for rigorous quantitative analysis in future.

6. CONCLUSIONS

On the basis of data presented herein, the following conclusions can be drawn:

1. Volcanoclastic sediments of the Middle Miocene Pláštovce Beds sampled at four localities in the Pláštovce area (Slovakian part of the Novohrad-Nógrad Basin) have yielded a decapod fauna dominated by *Tasadia carniolica* and accompanied by *Callianassa* (s. l.) cf. *kerepesiensis*, *Jaxea kuemeli*, *Munida* sp. and *Retropluma slovenica*.
2. Differential diversity at the localities studied can be explained by collecting bias and environmental factors. Based on a comparison with extant congeners or close relatives, the palaeoenvironment is interpreted as muddy-bottomed, near-shore zone at a depth of approximately 100 m.
3. Decapods are often preserved as near-complete, articulated specimens interpreted as moults (*J. kuemeli*) and corpses (*T. carniolica*). Third maxillipeds in open posture in some specimens of *T. carniolica* may indicate respiratory distress, suggestive of episodic events of volcanoclastic flows responsible for killing crabs and ensuring their preservation by rapid burial.
4. The species composition of the decapod fauna of the Pláštovce Beds further strengthens similarities with Miocene faunas of the North Sea Basin.

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