

# Diversity and distribution patterns of the Oligocene and Miocene decapod crustaceans (Crustacea: Malacostraca) of the Western and Central Paratethys

MATÚŠ HYŽNÝ

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

(Manuscript received June 17, 2015; accepted in revised form September 22, 2016)

**Abstract:** Decapod associations have been significant components of marine habitats throughout the Cenozoic when the major diversification of the group occurred. In this respect, the circum-Mediterranean area is of particular interest due to its complex palaeogeographic history. During the Oligo-Miocene, it was divided in two major areas, Mediterranean and Paratethys. Decapod crustaceans from the Paratethys Sea have been reported in the literature since the 19<sup>th</sup> century, but only recent research advances allow evaluation of the diversity and distribution patterns of the group. Altogether 176 species-level taxa have been identified from the Oligocene and Miocene of the Western and Central Paratethys. Using the three-dimensional NMDS analysis, the composition of decapod crustacean faunas of the Paratethys shows significant differences through time. The Ottnangian and Karpatian decapod associations were similar to each other both taxonomically and in the mode of preservation, and they differed taxonomically from the Badenian ones. The Early Badenian assemblages also differed taxonomically from the Late Badenian ones. The time factor, including speciation, immigration from other provinces and/or (local or global) extinction, can explain temporal differences among assemblages within the same environment. High decapod diversity during the Badenian was correlated with the presence of reefal settings. The Badenian was the time with the highest decapod diversity, which can, however, be a consequence of undersampling of other time slices. Whereas the Ottnangian and Karpatian decapod assemblages are preserved virtually exclusively in the siliciclastic “Schlier”-type facies that originated in non-reefal offshore environments, carbonate sedimentation and the presence of reefal environments during the Badenian in the Central Paratethys promoted thriving of more diverse reef-associated assemblages. In general, Paratethyan decapods exhibited homogeneous distribution during the Oligo-Miocene among the basins in the Paratethys. Based on the co-occurrence of certain decapod species, migration between the Paratethys and the North Sea during the Early Miocene probably occurred via the Rhine Graben. At larger spatial scales, our results suggest that the circum-Mediterranean marine decapod taxa migrated in an easterly direction during the Oligocene and/or Miocene, establishing present-day decapod communities in the Indo-West Pacific.

**Key words:** Decapod crustaceans, Cenozoic, Paratethys, Mediterranean, palaeobiogeography.

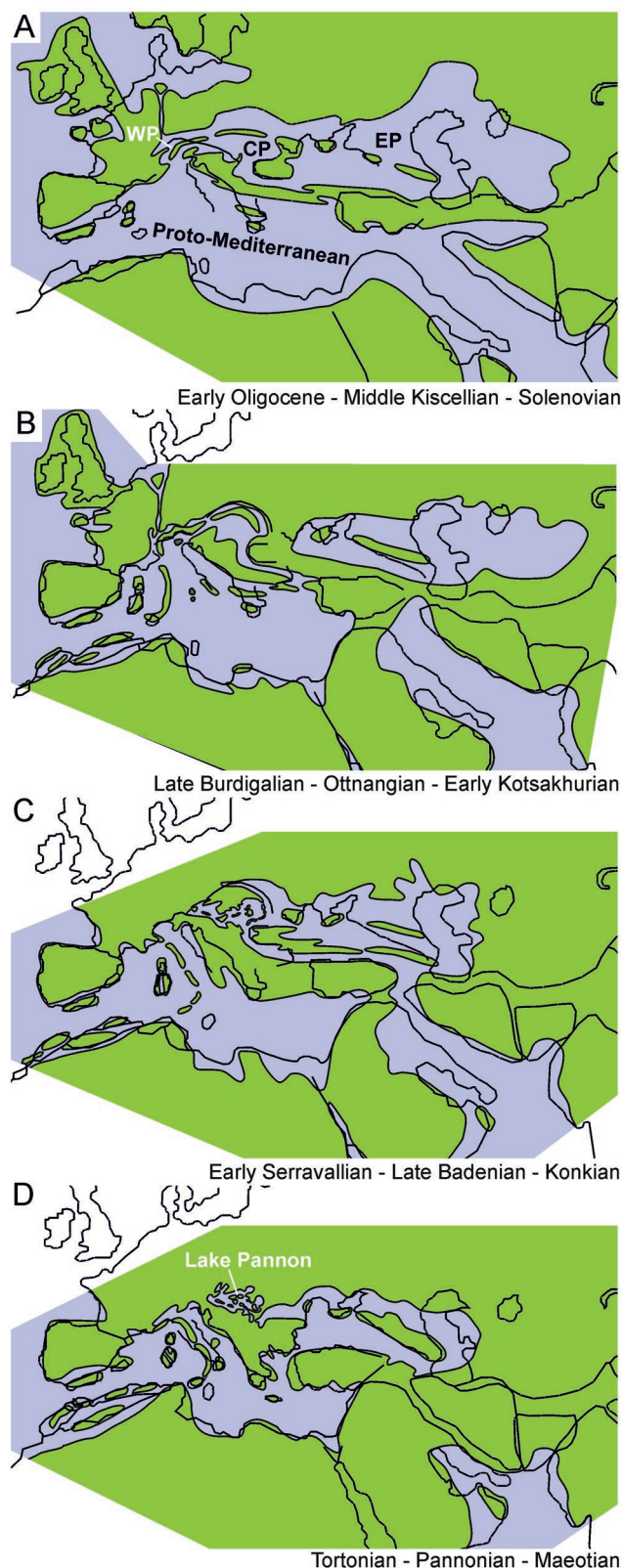
## Introduction

Decapod associations have been significant components of marine habitats since the Mesozoic, with ever-increasing importance throughout Palaeogene and Neogene (Glaessner 1969; Schweitzer 2001; Feldmann & Schweitzer 2006; Klompaker et al. 2013) until today (Noël et al. 2014). Decapods have planktonic larvae (Martin 2014a) and some of them are active swimmers, so their dispersal and migration can be very quick (Por 1986). Previously, Müller (1979a) argued that brachyuran decapods are “among the best zoogeographical indicators” because their migration is fast, many forms can penetrate straits and channels of abnormal salinity and the duration of their pelagic larval stage is well defined. Today, the state of knowledge of European Cenozoic decapods seems to be robust enough to use them for palaeobiogeographical studies (Hyžný 2015).

During the Eocene the collision of the African continent with the European plate initiated the Alpine orogeny, which resulted in the break-up of the Tethyan Realm into two different

palaeogeographical areas: circum-Mediterranean in the south and Paratethys in the north (Rögl & Steininger 1983; Rögl 1998). An increase in biogeographical differentiation can be observed during the Oligocene and Miocene (e.g., Harzhauser et al. 2002; Harzhauser & Piller 2007). From the Oligocene onward, the northern domain became a large network of inland seas intermittently connected to the Mediterranean, the Atlantic and also to the Indo-Pacific (Rögl & Steininger 1983; Rögl 1998, 1999; Popov et al. 2004; Harzhauser & Piller 2007; Harzhauser et al. 2007; Kroh 2007; Reuter et al. 2009; Bartol et al. 2014; Fig. 1). For enclosed or semi-enclosed basins, seaways are very important because they are the only means of communication with other basins. Variations in the opening of the seaways were apparently responsible for changes in temperature, salinity and exchange flows (Popov et al. 2004; Báldi 2006; Moissette et al. 2006; Karami et al. 2011). Seaways and landbridges discriminate the northern domain into Western, Central and Eastern Paratethys.

Migration patterns between Paratethys and adjacent areas of the Western Tethys have been previously investigated



**Fig. 1.** Changing palaeogeography of the circum-Mediterranean area. Selected time slices include: **A** — Early Oligocene (ca. 30 Ma); **B** — Early Miocene (ca. 17.5 Ma); **C** — Middle Miocene (ca. 13 Ma); **D** — Late Miocene (ca. 8 Ma). Maps modified from Rögl (1999). CP, EP, WP=Central, Eastern and Western Paratethys, respectively.

using foraminifers (Báldi 2006), bryozoans (Moisette et al. 2006), brachiopods (Kocsis et al. 2012), gastropods (Harzhauser et al. 2002, 2003, 2007), bivalves (Studencka et al. 1998; Harzhauser et al. 2003, 2007, 2008), and echinoderms (Kroh & Harzhauser 1999; Harzhauser et al. 2007). To test these patterns with decapod crustaceans, a database has been compiled including all previously published Oligocene and Miocene decapod occurrences and newly gathered data from unpublished material deposited in institutional collections.

The goals of the present contribution are: 1) to evaluate the previous research on decapod crustaceans of the Western and Central Paratethys; 2) to summarize the present knowledge of decapod associations from the Oligocene and Miocene by listing all respective species-level taxa and discussing their occurrences; 3) to discuss factors influencing temporal and spatial changes of the decapod species richness, using multivariate analyses; and 4) to outline distribution patterns of decapod crustaceans during the Oligo-Miocene.

### Study area: Western and Central Paratethys

The studied area comprises basins once belonging to Western and/or Central Paratethys as indicated in Fig. 2. The Western Paratethys covered the area of Switzerland, southern Germany and western Austria. The Central Paratethys covered the area from the present-day Austria to Poland, Ukraine and Romania – it includes the Eastern Alpine-Carpathian Foreland basins (from Lower Austria to Moldova) and the area of the Pannonian Basin System itself formed first during the Early/Middle Miocene.

The geographic separation of the Mediterranean and the Paratethys seas resulted in a biogeographic differentiation (Harzhauser et al. 2002; Harzhauser & Piller 2007) and necessitated the establishment of a regional stratigraphic scheme (Piller et al. 2007). The definition of the regional stages is based solely on fossil contents (assemblage and abundance zones). Correlation with Mediterranean/Global chronostratigraphy is based mainly on calcareous nannoplankton, planktonic and larger benthic foraminifers (Piller et al. 2007). All stages are bounded by sea level lowstands coinciding with 3<sup>rd</sup> order sea level cycles and can be correlated with the sea level curve of Haq et al. (1988) and sequence stratigraphic cycles of Hardenbol et al. (1998). Important summaries of the Oligocene and Miocene Central Paratethys stratigraphy and palaeogeography include works by Rögl (1998, 1999), Kováč et al. (2003, 2007, 2016), Popov et al. (2004, 2006), Piller et al. (2007) and Harzhauser & Piller (2007).

### Material and methods

The synopsis of all occurrences of Oligocene and Miocene decapod crustaceans is based on two types of sources: 1) specimens and/or taxa examined personally by me and/or in cooperation with other colleagues; and 2) specimens and/or



**Fig. 2.** Neogene basins of the Western and Central Paratethys analysed in this study. White colour represents the extent of exposed strata of respective basins. CFB = Carpathian Foreland Basin, DB = Danube Basin, GHB = Great Hungarian Basin, HZB = Hrvatsko-Zagorje Basin, MB = Mura Basin, NAFB = North Alpine Foreland Basin, NNB = Novohrad-Nógrad Basin, StB = Styrian Basin, TcB = Transcarpathian Basin, TsB = Transylvanian Basin, VB = Vienna Basin.

taxa mentioned in the literature only and still waiting for re-examination. The material examined personally includes previously published occurrences as well as still unpublished collection material. A combination of 10 basins (North Alpine Foreland Basin=NAFB; Vienna Basin=VB; Styrian Basin=StB; Hrvatsko Zagorje, Slovenian and Mura basins=HZB, SIB, MB; Danube Basin=DB; Great Hungarian Basin=GHB; Novohrad-Nógrad Basin=NNB; Transcarpathian Basin=TcB; Transylvanian Basin=TsB; Carpathian Foreland Basin=CFB) and 6 (sub)stages (Ottungian, Karpatian, Early Badenian, Middle Badenian, Late Badenian, Early Sarmatian) defines 21 samples. Not all (sub)stages are represented in every basin. Altogether 176 species-level taxa have been identified. Their stratigraphic range and geographical distribution in the Paratethys is indicated in Table 1.

In the analyses of temporal changes in the species composition (i.e., presence-absence), pre-Karpatian, Sarmatian (two samples) and samples with less than three species were removed from the compositional matrix (modified Table 1). The three-dimensional non-metric multidimensional scaling (NMDS) and cluster analysis have been performed using freeware PAST (Hammer et al., 2001). In addition, decapod associations from reefal and non-reefal settings were analysed separately. Reefal taxa are defined here as taxa occurring exclusively in reefal settings. The Jaccard index was used to quantify dissimilarity among analysed associations. Because most decapod occurrences come from non-quantitative samples, statistical comparison of species abundances was not possible.

Major collections of the Miocene and Oligocene fossil decapod crustaceans, which formed the basis of the database, are housed in several European institutions. All of them

except the Polish Academy of Sciences Museum of the Earth in Warsaw were visited and studied first-hand. Abbreviations of the repository institutions: GBA — Geological Survey in Vienna, Austria; HNHM — Hungarian Natural History Museum in Budapest, Hungary; KGP-MH — Department of Geology and Palaeontology, Comenius University in Bratislava, Slovakia; MFGI — Hungarian Geological and Geophysical Survey in Budapest, Hungary; MTM — Mátra Museum in Gyöngyös, Hungary; MZ — Polish Academy of Sciences Museum of the Earth in Warsaw, Poland; NHMW — Geological-palaeontological Department, Natural History Museum in Vienna, Austria; RGA/SMNH — “Rok Gašparič palaeontological collection”, Slovenian Museum of Natural History in Ljubljana, Slovenia; SNM-Z — Natural History Museum of the Slovak National Museum in Bratislava, Slovakia; UMJGP — Universalmuseum Joanneum in Graz, Austria. In the following text, regional Paratethyan stages are largely used. For correlation with the Mediterranean scale, see Fig. 3.

## Results

### *Decapod associations basin by basin*

Decapod crustaceans from the area once covered by the Paratethys Sea have been reported in the literature since the 19<sup>th</sup> century. The first papers were dedicated to sporadic findings of mainly Middle Miocene taxa. Among the first scholars studying Paratethyan decapods were August Reuss (\*1811–†1873), Alexander Bittner (\*1850–†1902) and Paul Brocchi (\*1838–†1898). Subsequently, in the first half of the 20<sup>th</sup> century, Imre (Emmerich) Lőrenthey (\*1867–†1917; see

**Table 1:** List of the Western and Central Paratethys decapod species with occurrence within the studied basins (codes for basins used as in Fig. 1 and the text). Freshwater taxa are not included. Asterisk (\*) indicates the species exhibiting extra-Paratethyan distribution. Exclamation (!) indicates the species living until today. Abbreviations (taxonomy) used: AL=Albuneidae, AN=Anomura, AX=Axiidea, BR=Brachyura, CA=Callianassidae, CAL=Calappoidea, CAN=Cancroidea, CAR=Carpilioidea, CT=Ctenochelidae, DOR=Dorripoidea, DRO=Dromioidea, GA=Galatheaidea, GE=Gebiidea, GON=Goneplacoidea, GRA=Grapsoidea, LA=Laomeidiidae, LEU=Leucosioidea, MAJ=Majoidea, PAL=Palicoidea, PAR=Parthenopoidea, PG=Paguroidea, PIL=Pilumnoidea, POR=Portunoidea, RAN=Raninoidea, RET=Retroplumoidea, TH=Thomassiniidae, UP=Upogebiidae, XAN=Xanthoidea.

		Taxon (species)	Kiscellian/ Rupelian	Egerian/ Chatthian	Eggenburgian	Ottmangian/ Helvetian	Karpatian	E. Badenian	M. Badenian	L. Badenian	E. Sarmatian
1	GE/UP	<i>Upogebia scabra</i> Müller, 1974b								GHB	
2	GE/LA	<i>Jaxea kuemeli</i> Bachmayer, 1954				NAFB	NNB, StB	NNB, StB	VB		
3	AX/CA	* <i>Callianassa</i> <i>almerai</i> Müller, 1993						StB			
4	AX/CA	<i>Callianassa</i> <i>ferox</i> Bittner, 1893	TsB								
5	AX/CA	<i>Callianassa</i> <i>jahringensis</i> Glaessner, 1928					StB				
6	AX/CA	<i>Callianassa</i> <i>kerepesiensis</i> Müller, 1976						NNB		GHB	
7	AX/CA	* <i>Callianassa</i> cf. <i>kerepesiensis</i> Müller, 1976						CFB, NNB		GHB	
8	AX/CA	<i>Callianassa</i> <i>norica</i> Glaessner, 1928						StB			
9	AX/CA	<i>Callianassa</i> <i>oroszyi</i> (Bachmayer, 1954)								VB	
10	AX/CA	<i>Callianassa</i> <i>rapax</i> Bittner, 1893	TsB								
11	AX/CA	<i>Callianassa</i> <i>roztoczensis</i> Müller, 1996								CFB, GHB	
12	AX/CA	<i>Callianassa</i> <i>simplex</i> Bittner, 1893	TsB								
13	AX/CA	<i>Callianassa</i> <i>velox</i> Bittner, 1893	TsB								
14	AX/CA	<i>Callianassa</i> <i>vorax</i> Bittner, 1893	TsB								
15	AX/CA	* <i>Calliax michelottii</i> (A. Milne Edwards, 1860)		NAFB		NAFB	StB	NNB, StB		DB	
16	AX/CA	<i>Eucalliax pseudorakosensis</i> (Lörenthey in Lörenthey & Beurlen, 1929)					DB	NNB	TsB	GHB, VB	VB
17	AX/CA	* <i>Calliaxina chalmasii</i> (Brocchi, 1883)							VB	GHB	VB
18	AX/CA	<i>Callichirus bertalani</i> Hyžný & Müller, 2010a						DB			
19	AX/CA	<i>Neocallichirus brocchii</i> (Lörenthey, 1897)								GHB	VB
20	AX/CA	<i>Balsscallichirus florianus</i> (Glaessner, 1928)		GHB			StB, VB	StB	VB		
21	AX/CA	* <i>Balsscallichirus sismondai</i> (A. Milne Edwards, 1860)						StB			
22	AX/CA	* <i>Glypturus munieri</i> (Brocchi, 1883)						DB, StB	VB	DB, GHB, VB	
23	AX/CA	<i>Lepidophthalmus crateriferus</i> (Lörenthey in Lörenthey & Beurlen, 1929)	GHB								
24	AX/CA	<i>Lepidophthalmus paratethyensis</i> Gašparič & Hyžný, 2014					StB				
25	AX/CT	* <i>Ctenocheles rupeliensis</i> (Beurlen, 1939)	GHB								
26	AX/CT	<i>Callianopsis marianae</i> Hyžný & Schlögl, 2011					VB				
27	AX/TH	<i>Crosniera schweitzeriae</i> Hyžný & Schlögl, 2011					VB				
28	AN/PG	<i>Anapagurus carinatus</i> Harvey, 1998								GHB	
29	AN/PG	<i>Anapagurus miocenicus</i> Müller, 1978						StB		GHB	
30	AN/PG	<i>Ciliopagurus substriatiformis</i> (Lörenthey in Lörenthey & Beurlen, 1929)							VB	GHB, VB	
31	AN/PG	! <i>Dardanus arrosor</i> (Herbst, 1796)						DB			
32	AN/PG	* <i>Dardanus hungaricus</i> (Lörenthey in Lörenthey & Beurlen, 1929)						CFB, DB, NNB, StB	VB	GHB	



Table 1 (continuation):

		Taxon (species)	Kiscellian/ Rupelian	Egerian/ Chattian	Eggenburgian	Ottomanian/ Helvetian	Karpatian	E. Badenian	M. Badenian	L. Badenian	E. Sarmatian
33	AN/PG	<i>Diogenes cf. pugilator</i> (Roux, 1828)								GHB	
34	AN/PG	<i>Diogenes matrensis</i> Müller, 1984a						NNB			
35	AN/PG	<i>Paguristes cserhatensis</i> Müller, 1984a						NNB			
36	AN/PG	<i>Pagurus concavus</i> Müller, 1978								GHB	
37	AN/PG	<i>Pagurus rakosensis</i> Müller, 1978							VB	CFB, GHB	
38	AN/PG	<i>Pagurus retznensis</i> Collins, 2014						StB			
39	AN/PG	<i>Pagurus tuberculosus</i> Harvey, 1998								GHB	
40	AN/PG	<i>Pagurus turcus</i> Müller, 1984a						DB			
41	AN/PG	* <i>Petrochirus priscus</i> (Brocchi, 1883)						StB	TsB	GHB, VB	
42	AN/PG	<i>Pylopagurus corallinus</i> Müller, 1996						CFB, NNB	VB		
43	AN/PG	<i>Pylopagurus leganyii</i> Müller, 1984a						NNB			
44	AN/GA	<i>Agononida cerovensensis</i> Hyžný & Schlögl, 2011					VB				
45	AN/GA	<i>Galathea weinfurteri</i> Bachmayer, 1950						CFB, GHB	CFB, VB	CFB, VB	
46	AN/GA	<i>Munidopsis lieskovensis</i> Hyžný & Schlögl, 2011					VB				
47	AN/GA	<i>Munidopsis palmuelleri</i> Hyžný, Gašparič, Robins & Schlögl, 2014						StB			
48	AN/GA	<i>Petrolisthes haydni</i> Müller, 1984a						StB	VB	CFB	
49	AN/GA	<i>Petrolisthes magnus</i> Müller, 1984a							VB	CFB, GHB	
50	AN/GA	* <i>Pisidia kokayi</i> (Müller, 1974a)						NNB	VB	GHB	
51	AN/GA	* <i>Pisidia viai</i> Müller, 1984b						DB, StB			
52	AN/GA	<i>Pisidia</i> aff. <i>viai</i> Müller, 1984b						CFB			
53	AN/GA	<i>Pisidia?</i> <i>subnodosa</i> Collins, 2014						StB			
54	AN/AL	<i>Albunea asymmetrica</i> Müller, 1978								GHB	
55	BR/DRO	<i>Dromia evae</i> Collins, 2014						StB			
56	BR/DRO	* <i>Dromia neogenica</i> Müller, 1978							VB	CFB, GHB	
57	BR/DRO	<i>Dynomene emiliae</i> Müller, 1979b						CFB, DB	VB	CFB	
58	BR/DRO	<i>Kerepesia viai</i> Müller, 1976						StB		GHB	
59	BR/DRO	<i>Kromititis koberi</i> (Bachmayer & Tollmann, 1953)						CFB, DB, StB	VB		
60	BR/DRO	<i>Lucanthonisia eotvoesi</i> (Müller, 1975a)								CFB, GHB	
61	BR/DOR	<i>Dorippe fankhauseri</i> Studer, 1892				NAFB					
62	BR/DOR	<i>Dorippe margaretha</i> Lörenthey in Lörenthey & Beurlen, 1929								GHB	
63	BR/DOR	<i>Dorippe ornatissima</i> Müller, 2006								GHB	
64	BR/DOR	<i>Neodorippe carpathica</i> (Förster, 1979a)						CFB			
65	BR/DOR	<i>Ethusa octospinosa</i> Müller, 2006								GHB	
66	BR/RAN	<i>Lyreidus hungaricus</i> Beurlen, 1939	GHB								
67	BR/RAN	<i>Ranidina rosaliae</i> Bittner, 1893						CFB, VB			
68	BR/CAL	<i>Calappa heberti</i> Brocchi, 1883								GHB, VB	VB

Table 1 (continuation):

		Taxon (species)	Kiscellian/ Rupelian	Egerian/ Chatthian	Eggenburgian	Ottományian/ Helvetian	Karpatian	E. Badenian	M. Badenian	L. Badenian	E. Sarmatian
69	BR/CAL	* <i>Calappa praelata</i> Lörenthey in Lörenthey & Beurlen, 1929						CFB, DB, NNB, StB, VB	CFB, VB		
70	BR/CAL	<i>Calappilia matzkei</i> (Bachmayer, 1962)							VB		
71	BR/CAL	<i>Calappilia tridentata</i> (Beurlen, 1939)	GHB								
72	BR/CAL	<i>Mursia harnicari</i> Hyžný & Schlögl, 2011					VB				
73	BR/CAL	* <i>Mursia lienharti</i> (Bachmayer, 1962)							VB	GHB, VB	
74	BR/CAL	<i>Osachila tiechei</i> (Studer, 1898)				NAFB					
75	BR/CAL	<i>Szaboa inermis</i> (Brocchi, 1883)								GHB	VB
76	BR/CAN	<i>Cancer illyricus</i> Bittner, 1883								HZB	
77	BR/CAN	<i>Cancer styriacus</i> Bittner, 1884					VB	StB		CFB, VB	
78	BR/CAN	<i>Corystites latifrons</i> (Lörenthey in Lörenthey & Beurlen, 1929)								GHB	
79	BR/CAN	<i>Glebocarcinus helveticus</i> Fraaije, Menkveld-Gfeller, van Bakel & Jagt, 2010				NAFB					
80	BR/CAN	* <i>Lobocarcinus sismondai</i> von Meyer, 1843							VB		
81	BR/CAN	<i>Lobocarcinus</i> aff. <i>sismondai</i> von Meyer, 1843						StB			
82	BR/CAN	<i>Microdium nodulosum</i> Reuss, 1867							CFB		
83	BR/CAN	<i>Miocyclus bulgaricus</i> Müller, 1979b								CFB	
84	BR/CAN	* <i>Tasadia carniolica</i> (Bittner, 1884)						NNB, VB	GHB, VB	SIB, VB	VB
85	BR/CAR	* <i>Eocarpilius antiquus</i> (Glaessner, 1928)						CFB	VB	VB	
86	BR/GON	<i>Coeloma macoveii</i> Lăzărescu, 1959		TsB							
87	BR/GON	<i>Coeloma egerense</i> Lörenthey in Lörenthey & Beurlen, 1929		GHB							
88	BR/GON	* <i>Goneplax gulderi</i> Bachmayer, 1953c					StB		VB	CFB	
89	BR/GON	<i>Goneplax?</i> <i>carnuntinus</i> (Bachmayer, 1953b)								VB	
90	BR/GON	<i>Mioplax socialis</i> Bittner, 1884									CFB, HZB, StB, TcB
91	BR/GON	<i>Neopilumnoplax pohorjensis</i> Gašparič & Hyžný, 2014					StB				
92	BR/GON	<i>Styrioplax exiguus</i> (Glaessner, 1928)					NNB, StB	StB			
93	BR/LEU	<i>Andorina elegans</i> Lörenthey, 1901								GHB	
94	BR/LEU	<i>Ebalia hungarica</i> Müller, 1974a								GHB	
95	BR/LEU	<i>Ebalia oersi</i> Müller, 1978								GHB	
96	BR/LEU	<i>Ebalia vanstraeleni</i> Bachmayer, 1953b								VB	
97	BR/LEU	<i>Myra emarginata</i> Glaessner, 1928						StB			
98	BR/LEU	<i>Palaeomyra globulosa</i> (Müller, 1975a)						DB		GHB	
99	BR/LEU	<i>Palaeomyra strouhali</i> (Bachmayer, 1953a)				NAFB					
100	BR/MAJ	<i>Achaeus magnus</i> Müller, 1978								GHB	
101	BR/MAJ	<i>Hyas meridionalis</i> Glaessner, 1928						StB			
102	BR/MAJ	* <i>Maja biaensis</i> Lörenthey in Lörenthey & Beurlen, 1929						DB	VB	CFB, GHB	
103	BR/MAJ	<i>Micippa hungarica</i> (Lörenthey in Lörenthey & Beurlen, 1929)							VB	GHB, VB	
104	BR/MAJ	<i>Pisa oroszyi</i> (Bachmayer, 1953b)								CFB, VB	

Table 1 (continuation):

		Taxon (species)	Kiscellian / Rupelian	Egerian / Chattian	Eggenburgian	Ottományian / Helvetian	Karpatian	E. Badenian	M. Badenian	L. Badenian	E. Sarmatian
105	BR/MAJ	* <i>Schizophrys visegradensis</i> Müller, 1984a						DB	VB		
106	BR/PAL	<i>Crossotonotus diosdensis</i> Müller, 1984a								GHB	
107	BR/PAL	<i>Palicus hungaricus</i> Müller, 2006								GHB	
108	BR/PAR	<i>Parthenope szaboi</i> Müller, 1974b								GHB, VB	
109	BR/PAR	<i>Parthenope tetenyensis</i> Müller, 1984a							VB	GHB	
110	BR/PIL	<i>Actumnus telegdii</i> (Müller, 1974b)								CFB, GHB	
111	BR/PIL	<i>Glabropilumnus fossatus</i> Müller, 1996						CFB, DB			
112	BR/PIL	<i>Glabropilumnus nitidus</i> Collins, 2014						StB			
113	BR/PIL	<i>Pilumnopeus paratethyensis</i> Müller, 1984a								GHB	
114	BR/PIL	<i>Pilumnopeus tetenyensis</i> Müller, 1984a								GHB	
115	BR/PIL	<i>Pilumnus mediterraneus</i> (Lőrenthey, 1897)						CFB, NNB	VB	CFB, GHB	
116	BR/PIL	<i>Pilumnus</i> aff. <i>mediterraneus</i> (Lőrenthey, 1897)						StB			
117	BR/POR	<i>Bathynectes muelleri</i> Ossó & Stalenny, 2011								CFB	
118	BR/POR	! <i>Carupa</i> cf. <i>tenuipes</i> Dana, 1852						DB			
119	BR/POR	<i>Chaceon heimertingensis</i> (Bachmayer & Wagner, 1957)		NAFB							
120	BR/POR	<i>Charybdis fragilis</i> (Müller, 1978)						StB	VB	GHB	
121	BR/POR	<i>Charybdis mathiasi</i> Müller, 1984a							VB	GHB	
122	BR/POR	* <i>Geryon</i> cf. <i>latifrons</i> Van Straelen, 1937								GHB	
123	BR/POR	<i>Liocarcinus kuehni</i> (Bachmayer, 1953b)								GHB, VB	
124	BR/POR	<i>Liocarcinus oligocaenicus</i> (Paučá, 1929)	CF, TsB	GHB							
125	BR/POR	<i>Liocarcinus oroszyi</i> (Bachmayer, 1953b)								VB	
126	BR/POR	<i>Liocarcinus ottományensis</i> (Bachmayer, 1953a)				NAFB					
127	BR/POR	<i>Liocarcinus praeaeuatus</i> Müller, 1996								CFB, GHB	
128	BR/POR	<i>Liocarcinus rakensis</i> (Lőrenthey in Lőrenthey & Beurlen, 1929)						NNB	TsB, VB	CFB, GHB	
129	BR/POR	<i>Liocarcinus</i> aff. <i>rakensis</i> (Lőrenthey in Lőrenthey & Beurlen, 1929)						StB			
130	BR/POR	<i>Lissocarcinus szoeraenyiae</i> (Müller, 1974b)								GHB	
131	BR/POR	<i>Macropipus gruneri</i> Bachmayer & Rutsch, 1962				NAFB					
132	BR/POR	<i>Miopipus pygmeus</i> (Brocchi, 1883)								GHB	
133	BR/POR	<i>Mioxaiva psammophila</i> Müller, 1978								GHB	
134	BR/POR	<i>Necronektes schafferi</i> Glaessner, 1928					VB	StB, VB		GHB	
135	BR/POR	<i>Pirimela loerentheyi</i> (Müller, 1974a)								GHB	
136	BR/POR	<i>Portumnus tricarinatus</i> (Lőrenthey in Lőrenthey & Beurlen, 1929)								GHB	
137	BR/POR	<i>Portunus kisslingi</i> Studer, 1892				NAFB					
138	BR/POR	<i>Portunus krambergeri</i> Bittner, 1893		HZB							
139	BR/POR	<i>Portunus miocaenicus</i> Müller, 1984a								GHB	
140	BR/POR	* <i>Portunus monspeliensis</i> (A. Milne Edwards, 1860)						NNB, StB	VB	GHB	
141	BR/POR	<i>Portunus muelleri</i> Collins, 2014						StB			
142	BR/POR	<i>Portunus neogenicus</i> Müller, 1978								GHB	

Table 1 (continuation):

		Taxon (species)	Kiscellian/ Rupelian	Egerian/ Chatthian	Eggenburgian	Ottományian/ Helvetian	Karpatian	E. Badenian	M. Badenian	L. Badenian	E. Sarmatian
143	BR/POR	<i>Portunus radobojanus</i> (Bittner, 1884)									HZB
144	BR/POR	<i>Portunus stenaspis</i> (Bittner, 1884)									HZB
145	BR/POR	* <i>Portunus viai</i> Secretan in Philippe & Secretan, 1971			GHB						
146	BR/POR	<i>Rakosia carupoides</i> Müller, 1984a							VB	CFB, GHB	
147	BR/POR	<i>Rakosia rectifrons</i> Müller, 1996						CFB			
148	BR/POR	<i>Scylla molassica</i> Studer, 1898				NAFB					
149	BR/POR	* <i>Scylla michelini</i> A. Milne Edwards, 1860					StB				
150	BR/POR	<i>Trachypirimela grippi</i> (Müller, 1974b)									GHB
151	BR/POR	<i>Xaiva bachmayeri</i> Müller, 1984a									GHB
152	BR/RET	* <i>Loerenthopluma lata</i> Beschin, Busulini, De Angeli & Tessier, 1996	GHB								
153	BR/RET	<i>Retropluma slovenica</i> Gašparič & Hyžný, 2014					StB	NNB			
154	BR/XAN	* <i>Actaea turcocampestris</i> Müller, 1984a						DB, StB, VB	VB		
155	BR/XAN	* <i>Daira speciosa</i> (Reuss, 1871)						DB, StB, VB	VB	CFB, GHB	
156	BR/XAN	<i>Eomaldivia friebeli</i> Collins, 2014						StB			
157	BR/XAN	* <i>Etisus evamuelleriae</i> Hyžný, Van Bakel & Guinot, 2014						DB	VB		
158	BR/XAN	<i>Glyphithyreus sulcatus</i> (Beurlen, 1939)	GHB								
159	BR/XAN	<i>Haydnella steingeri</i> Müller, 1984a						CFB, DB, StB	VB		
160	BR/XAN	<i>Chlorodiella juglans</i> Müller, 1984a						StB		CFB, GHB	
161	BR/XAN	<i>Chlorodiella loczyi</i> Müller, 1984a						StB		GHB	
162	BR/XAN	<i>Chlorodiella mediterranea</i> (Lörenthey in Lörenthey & Beurlen, 1929)						CFB, DB, StB	VB	GHB	
163	BR/XAN	* <i>Chlorodiella tetenyensis</i> Müller, 1984a						StB		CFB, GHB	
164	BR/XAN	<i>Jonesius planus</i> (Müller, 1996)						CFB	VB		
165	BR/XAN	<i>Panopeus wronai</i> Müller, 1984a						StB	VB	CFB	
166	BR/XAN	<i>Pilodius vulgaris</i> (Glaessner, 1928)						DB	VB	GHB	
167	BR/XAN	<i>Trapezia glaessneri</i> Müller, 1975b						DB			
168	BR/XAN	* <i>Xantho moldavicus</i> (Yanakevich, 1977)						StB	VB	CFB, GHB, VB	
169	BR/GRA	<i>Asthenognathus rakosensis</i> Müller, 2006									GHB
170	BR/GRA	<i>Brachynotus februaryi</i> Müller, 1974a									GHB
171	BR/GRA	<i>Metopograpsus badenis</i> Müller, 2006									GHB
172	BR/GRA	<i>Metopograpsus traxleri</i> Müller, 1998					VB				
173	BR/GRA	<i>Pachygrapsus hungaricus</i> Müller, 1974a							VB	CFB, GHB	
174	BR/OCY	* <i>Macrophthalmus aquensis</i> A. Milne Edwards & Brocchi, 1879					VB	CFB, StB			
175	BR/OCY	<i>Paracleistostoma miocaenica</i> Müller, 1998					VB				
176	BR/OCY	<i>Tritodynamia miocaenica</i> Müller, 2006									GHB
		<b>Total number of species</b>	<b>12</b>	<b>7</b>	<b>1</b>	<b>10</b>	<b>21</b>	<b>73</b>	<b>46</b>	<b>90</b>	<b>9</b>



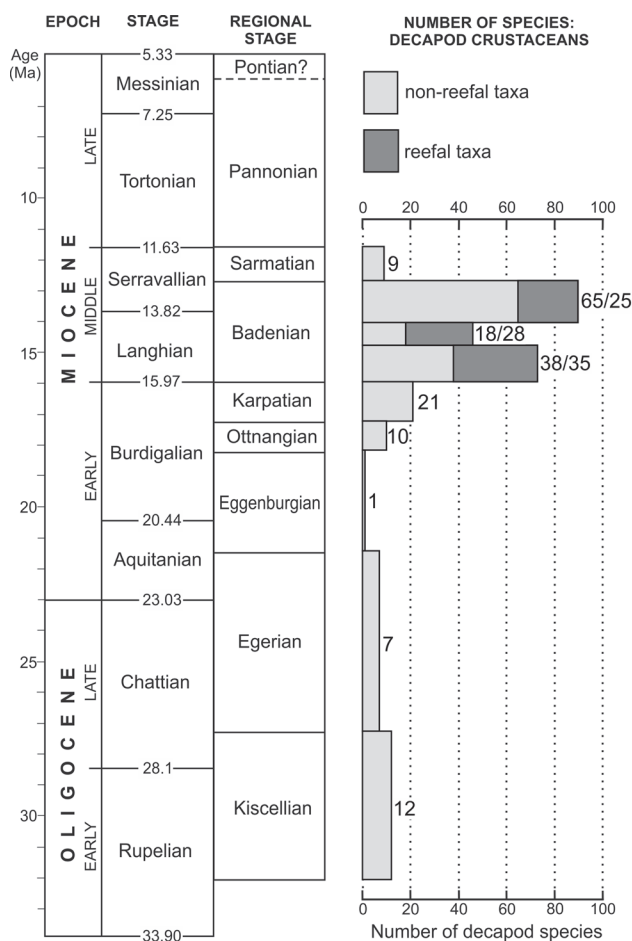
Müller 1987), Karl Beurlen (\*1901–†1985) and Martin F. Glaessner (\*1906–†1989; see Küpper 1991) contributed to the study of fossil decapod crustaceans with several milestone works (Lörenthey & Beurlen 1929; Glaessner 1929, 1969). In the second half of the 20<sup>th</sup> century Friedrich Bachmayer (\*1913–†1989; see Kollmann & Zapfe 1979), Reinhard Förster (\*1935–†1987; see Herm 1987) and Pál Müller (\*1935–†2015; see Hyžný et al. 2014a, 2015a) published numerous papers focused (mostly) on Neogene decapods of the Western and Central Paratethys.

All decapod species (excluding freshwater taxa) reported from the respective area are listed in Table 1. Proportions of decapod species per stage and basin are shown in Figs. 3 and 4, respectively.

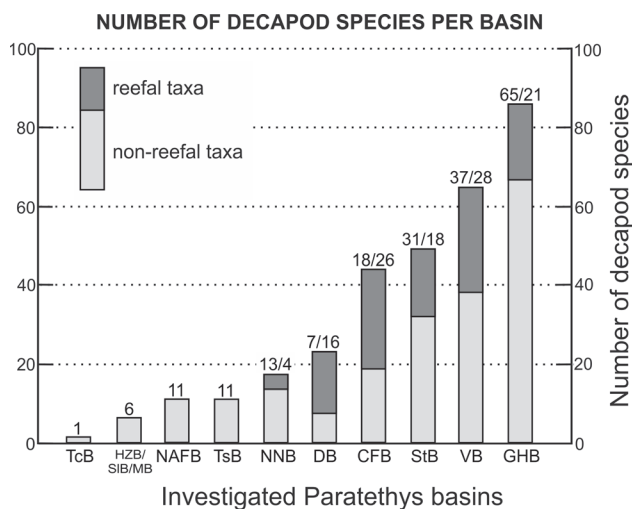
**North Alpine Foreland Basin:** From the Oligocene (Chattian) of Bavaria, Germany, Bachmayer & Wagner (1957) recorded a single occurrence of *Chaceon heimertingensis* (Bachmayer & Wagner, 1957). From the Oligo-Miocene (Chattian-Aquitanian) of Bavaria, Barthelt (1989) mentioned claws attributed to *Callianassa* sp. More decapod associations are known from the Molasse Zone of Switzerland; Fröhlicher (1951) reported on portunid crabs from the Oligocene strata, whereas Studer (1892, 1898) and Bachmayer & Rutsch (1962) described several taxa from the Miocene “Meeresmolasse”. Fraaije et al. (2010a) briefly reviewed all Lower Miocene decapod crustaceans from the type area of the Helvetian stage in the Bern area (Switzerland), including one new species, *Glebocarcinus helveticus* Fraaije, Menkveld-Gfeller, van Bakel & Jagt, 2010. Bachmayer (1953a, 1982) reported several brachyuran species from the Ottnangian strata of Ottnang and Limberg, respectively. Hyžný (2011a) reported *Jaxea kuemeli* Bachmayer, 1954 from the same site. All decapod taxa known from the Ottnangian strata of Austria and Germany have been revised by Hyžný et al. (2015b).

**Vienna Basin and its satellite basins:** The Miocene deposits of the Vienna Basin and its satellite basins have yielded many decapod crustacean remains; altogether 65 species were identified in this basin (Fig. 4). A decapod fauna from the Karpatian of the Korneuburg Basin was described by Glaessner (1924, 1928), Müller (1998) and Hyžný (2016). Hyžný & Schlögl (2011) described roughly coeval association from the northern Vienna Basin. Most decapod remains of the Vienna Basin are of Badenian age and were described by many authors (Reuss 1859; Von Reuss 1871; Bittner 1877; Toulou 1904; Glaessner 1928; Bachmayer 1950, 1953b, c, 1954, 1962; Bachmayer & Küpper 1952; Bachmayer & Tollmann 1953; Müller 1984a). The localities were summarized by Müller (1984a).

**Styrian Basin:** Decapod crustaceans from the Miocene deposits of the Austrian part of the Styrian Basin were reported by Glaessner (1928), Schoupe (1949), Flügel (1986) and Friebe (1987, 1990). Badenian reef-associated



**Fig. 3.** Decapod crustacean species diversity of the Central and Western Paratethys per stage. Oligo-Miocene stages correlated to regional chronostratigraphy of the Central Paratethys are adapted from Piller et al. (2007). Absolute ages are based on the International Chronostratigraphic Chart ([www.stratigraphy.org](http://www.stratigraphy.org)).



**Fig. 4.** Proportion of the studied decapod taxa per basin. Basin abbreviations used as in Fig. 1.

decapod fauna of the quarry in Retznei (Reuter & Piller 2011; Reuter et al. 2012) has been described by Collins (2014); Hyžný (2011b) reported from the same locality ghost shrimps preserved *in situ* within the burrow structures. Several ghost shrimps and few brachyurans were described from the Karpatian sediments cropping out at localities close to Austria/Slovenia border (Glaessner 1928). From the Slovenian part of the Styrian Basin Miocene decapod faunas were reported by Glaessner (1928), Mikuž (2003a), Gašparič & Hyžný (2014) and Gašparič & Halásová (2015).

**Hrvatsko Zagorje, Slovenian and Mura basins:** Sporadic finds of the Oligocene and Miocene decapods from the Slovenian Basin were reported by Bittner (1884), Mikuž (2003b, 2010), Mikuž & Pavšič (2003), and Križnar (2009). Decapod faunas from the Karpatian of the Mura Basin were described by Glaessner (1928). Miocene decapods from the Hrvatsko Zagorje Basin (Croatia) were reported by Bittner (1884, 1893); Bittner (1893) described *Achelous krambergeri* (now treated as *Portunus*) from the Egerian of Varaždin and Bittner (1884) described a small decapod fauna from the Badenian of Radoboj.

**Danube Basin:** Müller (1984a) described several localities in the Hungarian part of the Danube Basin (Börzsöny near Visegrád) with Badenian decapod remains. Hyžný & Müller (2010a) described additional ghost shrimps from the area close to Lake Balaton. Little is known about the decapods from the Slovak part of the basin; Špinar et al. (1965) illustrated few specimens of *Calliax michelottii* (A. Milne Edwards, 1860) (see also Hyžný & Gašparič 2014) and *Goneplax* sp. from boreholes near Želiezovce village.

**Great Hungarian Basin:** Oligo-Miocene strata (and its “predecessor”, namely the Hungarian Palaeogene Basin) have yielded 86 species of decapods (Fig. 4). Concerning decapod crustaceans, this basin is the most sampled area of the Central Paratethys. A deep-water decapod crustacean fauna was described by Beurlen (1939) and partly re-described by Hyžný & Dulai (2014) in the Lower Oligocene Kiscell Clay Formation. A rare find of *Loerenthopluma lata* Beschin, Busulini, De Angeli & Tessier, 1996 from the Oligocene Mány Formation was reported by Hyžný & Müller (2010b). From the Upper Oligocene (Egerian) of Eger a new crab species *Coeloma egerense* was described by Lörenthey in Lörenthey & Beurlen (1929). The Middle Miocene (Badenian) decapod faunas were extensively documented by Brocchi (1883), Bittner (1893), Lörenthey (1897, 1898a,b,c, 1904a,b, 1911, 1913), Lörenthey & Beurlen (1929) and Müller (1974a, b, 1975a,b, 1976, 1978, 1984a, 2006). Localities in the Budapest area are in this respect the classical ones (for details see Müller 1984a).

**Novohrad-Nógrad Basin:** Few decapod remains of *Jaxea kuemeli* and *Styrioplax exiguus* are known from the Karpatian of the Hungarian part of the basin (Álsoszuha 1 borehole;

see Hyžný 2011a; Hyžný & Schlögl 2011). Müller (1984a) described several sites with Badenian decapod remains in the Hungarian part of the basin; a decapod fauna from the Badenian of the Slovak part of the basin (locality Plášťovce) was described by Hyžný et al. (2015c).

**Transcarpathian Basin:** Hyžný & Ledvák (2014) and Hyžný et al. (2016) reported on the occurrence of *Mioplax socialis* Bittner, 1884 from the Sarmatian of the Slovak part of the basin. No other decapod occurrences from TcB are known to date.

**Transylvanian Basin:** Bittner (1893) described small decapod faunas from the Oligocene Mera Beds and the Miocene of the vicinity of Cluj (Klausenberg). Lăzărescu (1959) described *Coeloma macoveii* Lăzărescu, 1959 from the Chattian (Early Egerian) of Romania, although Schweitzer et al. (2009: 11) stated the Miocene age of the species.

**Carpathian Foreland Basin:** Oligocene crabs were described by Paucă (1929), Jaroš (1939) and Jerzmańska (1967) from Romanian, Moravian and Polish parts of the Silesian-Krosno Belt, respectively. This belt belonged to the Silesian-Krosno domain *sensu* Kováč et al. (2016), a predecessor of the Carpathian Foredeep. Reuss (1867), Förster (1979a, b), Müller (1984a, 1996) and Górká (2002) described Badenian decapod associations from several localities situated in the Polish part of the Carpathian Foreland Basin. A Late Badenian reef-associated decapod fauna of the Medobory Hills (Ukraine) has been reported by Radwański et al. (2006), Ossó & Stalennuy (2011) and Górká et al. (2012).

**Freshwater decapods:** Fossil freshwater decapods are in general rare. Only few occurrences are known from the Oligo-Miocene strata of the studied area. Houša (1956) and Zázvorka (1956) reported on freshwater shrimps from Czech Republic and Klaus & Gross (2010) provided a comprehensive synopsis of the fossil freshwater crabs of Europe, including those from the North Alpine Foreland Basin and Pannonian Basin System.

### Analyses

**Species richness per stage:** The Badenian was the time of the highest decapod diversity: 90, 73, and 46 species were recorded from the Late Badenian (B3), Early Badenian (B1) and Middle Badenian (B2), respectively. Large percentages of the Badenian taxa, namely 47.9 % (B1), 60.9 % (B2) and 27.8 %, (B3), are known from reefal settings only (Fig. 3). The smallest diversity was recorded from the Eggenburgian and Egerian, with only 1 and 7 recorded decapod species, respectively. The species richness of the Ottnangian and Sarmatian is similarly low, with ten and nine species, respectively.

**Species richness per basin:** The Great Hungarian Basin, Vienna Basin, Styrian Basin, and Carpathian Foreland Basin were relatively well-sampled with 86, 65, 49, and 44 species, respectively (Fig. 4). Relatively high diversity was observed always in the basins with the presence of reefal settings. Low species richness (<12) was recorded in the basins with no reefal settings. From the Transcarpathian Basin, a single species was recorded.

**NMDS and cluster analyses:** Decapod associations of five time slices were analysed (NMDS, Jaccard index): Ottnangian (O), Karpatian (K), Early Badenian (B1), Middle Badenian (B2) and Late Badenian (B3). Ottnangian and Karpatian assemblages do not overlap with the Badenian ones. Early Badenian assemblages were always separated from the Late Badenian ones without any overlap (Fig. 5). Decapod taxa restricted to reefal settings analysed separately (NMDS, Jaccard index) show distinct pattern with associations from all three substages separated from each other (Fig. 6A). Cluster analysis (Jaccard index), however, did not resolve the associations of respective substages so unambiguously (Fig. 6B). Interestingly, the Middle Badenian association of the Vienna Basin (B2-VB) was clustered together with the Early Badenian association of the Danube Basin (B1-DB), and the Early Badenian association of the Styrian Basin (B1-StB) was clustered together with the Late Badenian associations (B3-GHB, B3-CFB).

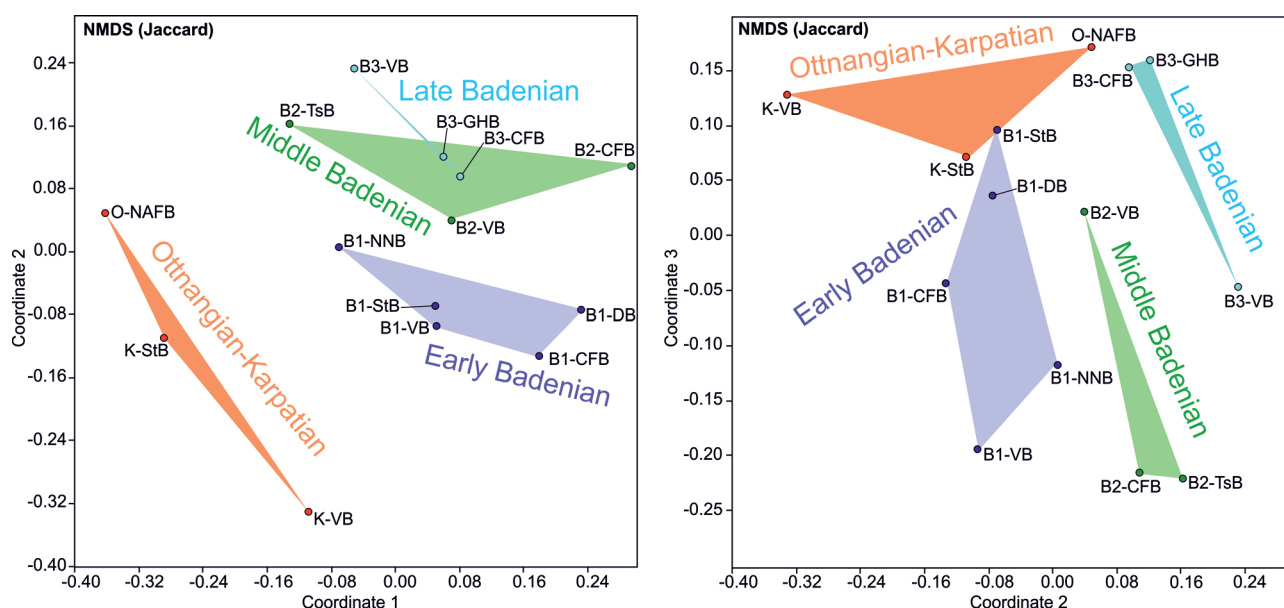
The NMDS analysis (Jaccard index) of non-reefal taxa resolved the Ottnangian and Karpatian associations as distinct from all Badenian ones (Fig. 7). All Early Badenian associations were clearly separated from the Late Badenian ones.

## Discussion

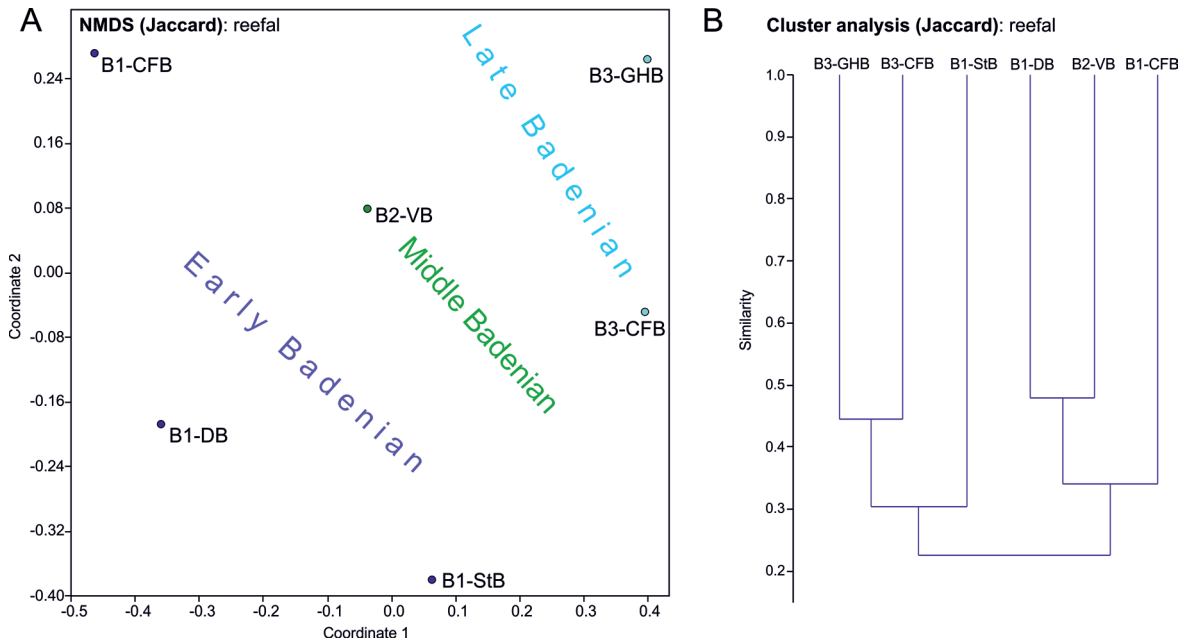
### Collection bias

A sampling-standardized comparison of decapod species richness across the basins and/or time intervals is not possible because some basins and stages are under-represented in the analysed matrix due to uneven sampling effort, outcrop availability, facies distribution and preservation potential of decapod crustaceans. For example, there are only 12, 7 and 1 decapod species recorded from the Kiscellian, Egerian and Eggenburgian, respectively (Fig. 3). The time span of these three stages is longer than the time span of the Ottnangian, Karpatian, Badenian and Sarmatian taken together, and the smaller diversity of decapod species recorded in these three stages is probably related to much smaller collection efforts.

More than 60 decapod species were recorded both from the Great Hungarian Basin and the Vienna Basin. Although reefal settings in these areas yielded numerous decapod taxa (Fig. 4), there is at least one more factor contributing to the observed pattern of species richness. Two cities, Budapest and Vienna, with a long tradition in fossil decapod research (see above), are located in the respective basins, presumably owing to the over-sampling in comparison with other areas. Moreover, the presence of numerous outcrops with the Badenian strata in the vicinity of Budapest and Vienna contributed to preferential focus of the scholars on these strata. Thus, the high decapod species diversity in the Late Badenian of the Great Hungarian Basin is partially influenced by the scientific contributions of Imre Lörenthey and Pál Müller, whereas high diversity of decapod crustaceans in the Vienna Basin owes much to the efforts of Friedrich Bachmayer (see above).



**Fig. 5.** NMDS plots of decapod associations of the Western and Central Paratethys using the Jaccard index (stress: 0.195). Labelled points represent all decapod species per stage and basin. For comments see text. Age abbreviations: O=Ottnangian, K=Karpatian, B1=Early Badenian, B2=Middle Badenian, B3=Late Badenian. Basin abbreviations used as in Fig. 1.



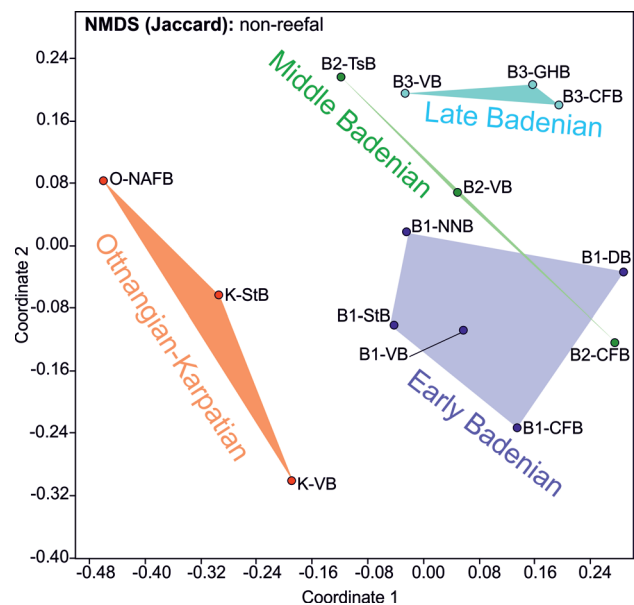
**Fig. 6.** NMDS plot (A) and dendrogram of the cluster analysis (B) of reef-associated decapod associations of the Western and Central Paratethys using the Jaccard index (stress: 0.113). For comments see text. Age abbreviations: B1=Early Badenian, B2=Middle Badenian, B3=Late Badenian. Basin abbreviations used as in Fig. 1.

Additionally, as stated by Müller (1979a), decapod fossils “need a careful collecting and preparing process and they are not very abundant”.

#### Preservation aspects

Preservation potential of decapod crustaceans is relatively low compared with molluscs, a major group often used for investigation of migration patterns (Studencka et al. 1998; Harzhauser et al. 2002, 2003, 2007, 2008). Bodies of decapod crustaceans are the subject of quick decomposition and the fragile exoskeleton is often fragmented before burial takes place (Schäfer 1951; Plotnick 1986; Plotnick et al. 1988; Stempien 2005; Mutel et al. 2008). Ideal conditions for preservation of complete decapod bodies include a calm depositional setting coupled with a quick burial without subsequent physical disturbance or biotic reworking (Müller et al. 2000). Dysoxic and anoxic conditions in the Oligocene menilites yielded near-complete body fossils of decapods (Paučá 1929; Jerzmańska 1967; Jaroš 1939; Bieńkowska-Wasiluk 2010). However, they are flattened, and superimposed body parts are difficult to interpret. Moreover, these occurrences have so far received virtually no or limited taxonomic or taphonomic attention (Glaessner 1965). Thus, it is not surprising that the observed species richness of the Oligocene Paratethyan crabs is rather low (Fig. 3).

The Miocene fine-grained siliciclastic facies (“Schlier”-type and “Tegel”-type facies) often yielded near-complete decapod specimens. This is the case of the Ottnangian (Bachmayer 1982; Hyžný et al. 2016), Karpatian (Hyžný & Schlögl 2011; Gašparič & Hyžný 2015) and some Badenian strata (e.g., Bittner 1884). Fine-grained volcanoclastics may



**Fig. 7.** NMDS plot of non-reefal decapod associations of the Western and Central Paratethys using the Jaccard index (stress: 0.267). For comments see text. Age abbreviations: O=Ottnangian, K=Karpatian, B1=Early Badenian, B2=Middle Badenian, B3=Late Badenian. Basin abbreviations used as in Fig. 1.

promote preservation of complete decapod body fossils as is the case of the locality Plášťovce (NNB) reported by Hyžný et al. (2015c). Coarser-grained facies (silici- or volcanoclastic) yielded mostly isolated cheliped fingers and fragmentary carapaces, which, however, can be successfully taxonomically evaluated if thorough comparison with extant taxa is made (e.g., Müller 1984a; Hyžný & Klompaker 2015).



Reefs have an uneven surface and contain a lot of cavities and micro-lagoons, protected from currents and washout. Decapod crustaceans are usually preserved in such places, preferentially in the cavities or pockets *sensu* Müller (2004). Thus, even fragile decapod remains tend to be preserved and have potential to be taxonomically evaluated. It can be concluded that relatively high species diversity observed across stages (Fig. 3) and basins (Fig. 4) is partly dependent on the occurrence of reefal settings.

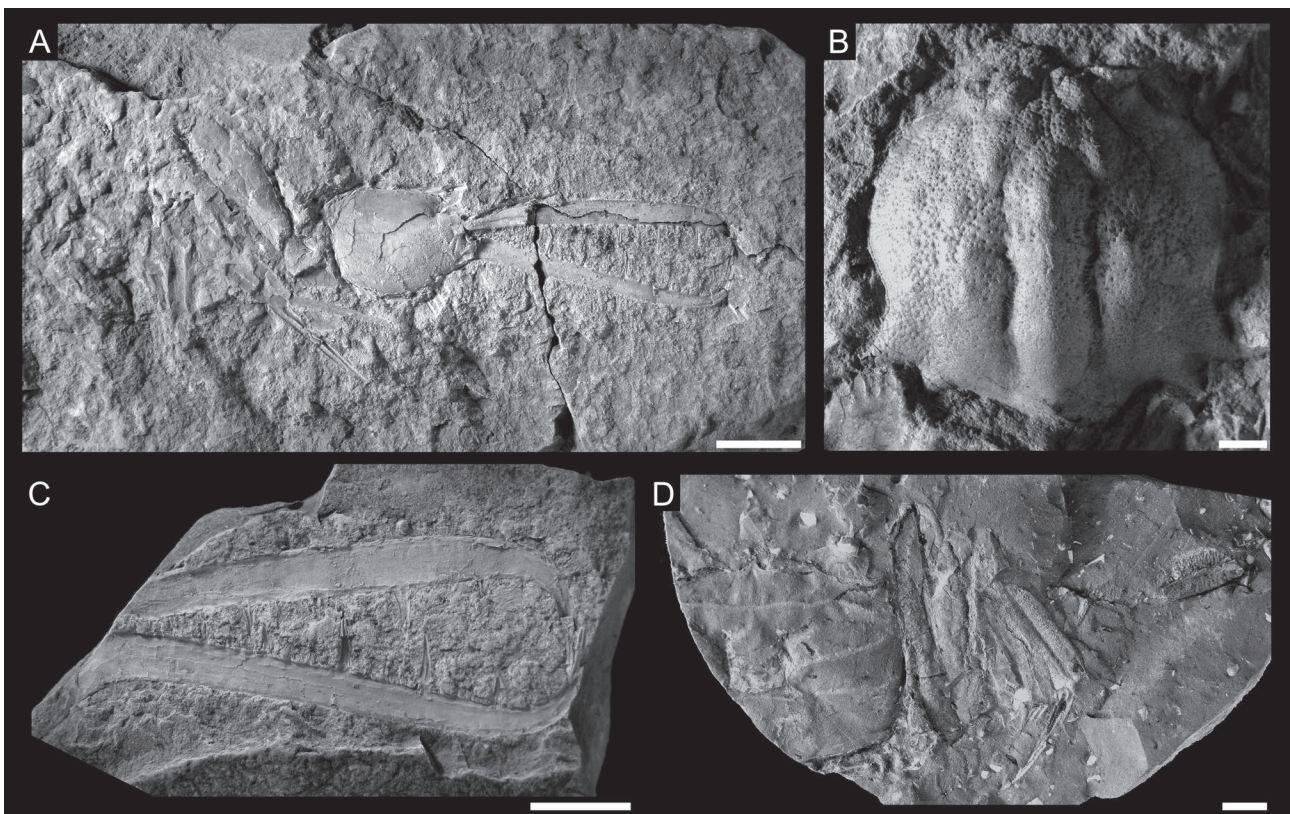
#### *Temporal patterns in the regional species richness*

**Oligocene:** At the beginning of the Oligocene, the Central Paratethys was separated from the Mediterranean (Fig. 1A). Individual basins in the Central Paratethys gained a character of a semi-closed sea (Kováč et al. 2016). They were characterized by primarily estuarine water circulation pattern with recurrent episodes of stagnation (Popov et al. 2004). As a consequence, accumulations of dysoxic to anoxic sediments were predominant during the Oligocene and Early Miocene in the entire Paratethys (Popov et al. 2004; Kováč et al. 2016). In the deeper part of the Palaeogene Hungarian Basin, laminated black shales were deposited in the anoxic environment represented by the Tard Clay (Báldi 1984) and

Schöneck (Schulz et al. 2005) formations. The Kiscell Clay Formation, conformably overlying these sediments, contains a decapod association dominated by *Ctenocheles rupeliensis* (Beurlen, 1939) (Beurlen 1939; Hyžný & Dulai 2014; Fig. 8A, C). From the menilite-type strata of the Carpathian Foreland Basin near-complete decapod exoskeletons were reported by Paučá (1929), Jaroš (1939), Jerzmańska (1967) and Bienkowska-Wasiluk (2010).

The Transylvanian Basin was a part of the Apuseni shelf and it was probably connected with the Fore-Rhodopian Basin of the Tethyan Realm (Popov et al. 2004). In the shallow part of the Transylvanian Basin, sandy-calcareous sedimentation took place typified with the Hoia and Mera beds (Popov et al. 2004). From the Mera Beds numerous ghost shrimps remains were reported by Bittner (1893).

During the Middle Kiscellian-Solenovian (Late Rupelian), the entire Paratethys was characterized by brackish salinities and endemic biota (e.g., Popov et al. 2004; Melinte-Dobrinescu & Brustur 2008). From this time interval, no Paratethyan decapod crustaceans are known. In the Late Oligocene the marine regime was re-established. Marine connections existed towards the North Sea Basin and the North Italy Basin via the Slovenian Corridor (Báldi 1986). *Calliax michelottii* is documented in the Oligocene of the



**Fig. 8.** Selected decapod crustaceans from the Oligocene of the Central Paratethys. **A** — *Ctenocheles rupeliensis* (Beurlen, 1939), lectotype HNHM M.59.4696a. **B** — *Calappilia tridentata* (Beurlen, 1939), syntype HNHM M.59.4679. **C** — *Ctenocheles rupeliensis*, HNHM.M.59.4696. **D** — *Loerenthopluma lata* Beschin, Busulini, De Angeli & Tessier, 1996, HNHM.M.2010.1.1. Specimens in A–C are from Óbuda in Budapest (Hungary), specimen in D comes from the borehole Má 115 at Mány (Hungary). Scale bar equals 5 mm. All specimens except B were covered with ammonium chloride prior to photography.



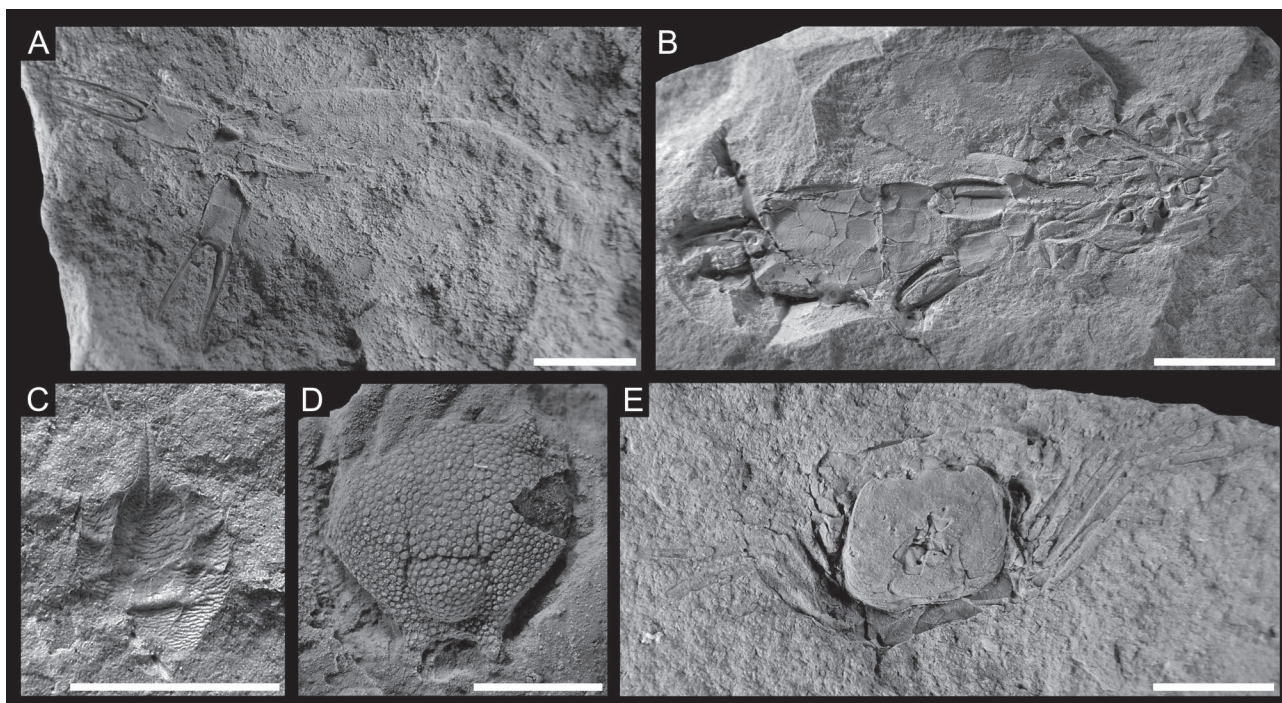
Northern Lower Miocene of Austria and Slovenia and the Middle Miocene of Hungary, Slovakia and Slovenia (Hyžný & Gašparič 2014). This species probably used both seaways for its spreading. In general, only several decapod species are known from the Oligocene of the Paratethys (Fig. 3), owing to the limited exposure of the Oligocene strata and relatively few published studies on the Oligocene decapods from the studied area.

**Early Miocene:** Most of the Early Miocene deep-water environments were characterized by clayey sedimentation under dysoxic to anoxic conditions. In the Central Paratethys, the Eggenburgian is characterized by a transgression with fully marine conditions as a consequence of an open connection to the Mediterranean via the Pre-Alpine passage (Sztano 1994). During the Ottnangian, the Alpine Trough was open (Grunert et al. 2012) and a shallow connection existed between the Western Paratethys and the North Sea (Martini 1990) (Fig. 1B). In the Central Paratethys, strong Atlantic influences are observed (Rögl 1999). From the Early Ottnangian of the North Alpine Foreland Basin decapod associations dominated by *Calliax michelottii*, *Jaxea kuemeli* (Fig. 9A) and *Liocarcinus ottmangensis* (Bachmayer, 1953a) have been reported (Hyžný et al. 2015b). By the end of the Ottnangian a strong regression occurred in the Alpine Foredeep and this Ottnangian crisis is reflected in brackish water settings with the endemic *Rzehakia* fauna (Steininger 1973).

From the Ottnangian (=Helvetian), 10 species were recorded (Studer 1892, 1898; Bachmayer & Rutsch 1962; Fraaije et al. 2010a; Hyžný et al. 2015b). This relatively low number probably represents an underestimation influenced mainly by collection bias. Fine, siliciclastic sedimentation typical for this stage promotes preservation of near-complete decapod bodies as exemplified by a mud shrimp *J. kuemeli* (Fig. 9A) and a ghost shrimp *C. michelottii* (Hyžný et al. 2015b: fig. 5).

In the Karpatian, the marine realm was restricted to the north-western Pannonian Basin System and the Carpathian Foreland Basin (Rögl 1999; Mandić et al. 2012). Typical components of the deep-water habitats (below 200 m) with muddy bottom are ghost shrimp *Callianopsis* de Saint Laurent, 1973 (Fig. 9B), squat lobster *Munidopsis* Whiteaves, 1874 (Hyžný et al. 2014b; Fig. 9C) and brachyuran *Styrioplax* Glaessner, 1969. *Styrioplax exiguus* (Fig. 9E) is known from the Karpatian of the Slovak part of the Vienna Basin (Hyžný & Schlögl 2011) and Austrian and Slovenian parts of the Styrian Basin (Glaessner 1928; Gašparič & Hyžný 2014; Gašparič & Halásová 2015).

In contrast to undersampled Ottnangian stage, 21 decapod species were recorded from the Karpatian alone (Fig. 3). This comparatively higher species richness is a result of recent efforts to document decapod associations from the Vienna and Styrian basins (Hyžný & Schlögl 2011; Gašparič & Hyžný 2015). As taken together, the Ottnangian and



**Fig. 9.** Selected decapod crustaceans from the Early Miocene of the Western and Central Paratethys. **A** — *Jaxea kuemeli* Bachmayer, 1954, NHMW 2009/0150/0001. **B** — *Callianopsis mariana* Hyžný & Schlögl, 2011, KGP-MH CL-011. **C** — *Munidopsis lieskovensis* Hyžný & Schlögl, 2011, KGP-MH CE-005. **D** — *Palaeomyra strouhali* (Bachmayer, 1953), holotype NHMW 1953/0051/0001. **E** — *Styrioplax exiguus* (Glaessner, 1928), holotype UMJGP-5453. Specimens in A and D come from Ottnang (Austria), B and C are from Cerová-Lieskové (Slovakia), and E comes from St. Egidí (Slovenia). Scale bar equals 5 mm. All specimens except C were covered with ammonium chloride prior to photography.

Karpatian decapod associations are close to each other not only taxonomically (Figs. 5, 7) but also in the mode of preservation which is a direct consequence of the prevalent siliciclastic sedimentation during both stages.

**Middle Miocene:** In the Central Paratethys, sand-free calcareous clays (“Tegel facies”) were the most abundant facies in the Early and Middle Badenian. For this facies, the most typical decapod species is *Tasadia carniolica* (Bittner, 1884) (Fig. 10I) which occurs throughout the entire Central Paratethys. The Early Badenian is characterized by an exceptionally rich warm water fauna (Harzhauser & Piller 2007), including foraminifers, red algae, ostracods, sea urchins, molluscs, corals, and decapods. Müller (1984a, 1996) and Collins (2014) reported occurrences of reef-associated decapod faunas from the Early Badenian of Hungary, Poland and Austria, respectively; typical representatives are *Petrolisthes haydni* Müller, 1984a; *Kromtitis koberi* (Bachmayer & Tollmann, 1953); *Chlorodiella mediterranea* (Lörenthey in Lörenthey & Beurlen, 1929) (Fig. 10K); and *Daira speciosa* (Reuss, 1871) (Fig. 10J). Nearly a half (47.9 %) of all Early Badenian decapod species are strictly reef-associated (Fig. 3). An even higher proportion (60.9 %) of the reefal taxa were recorded from the Middle Badenian. One of the best examples of the Middle Badenian coral patch-reefs inhabited by decapods is the Fenk quarry in the south-eastern Vienna Basin (Bachmayer & Tollmann 1953; Riegl & Piller 2000; Müller, 1984a; Hyžný et al. 2014c). Virtually all Middle Badenian reefal decapod taxa were recorded from this single locality.

During the Late Badenian, a new transgression began. The East Slovakian Basin was connected with the Transylvanian Basin via the Transcarpathian depression and all these basins were connected with the central Pannonian area (Rögl 1998, 1999; Popov et al. 2004; Fig. 1C). Thriving reef-associated decapod assemblages are known from the coral settings of the Great Hungarian Basin (Müller 1984a) and algal-vermetid reefs of the Carpathian Foreland Basin (Radwański et al. 2006; Studencka & Jasionowski 2011; Górká et al. 2012). The Late Badenian is still characterized by a warm water fauna but the overall diversity slightly decreases due to the onset of the Miocene Climate Transition (Studencka et al. 1998; Kováč et al. 2007; Harzhauser & Piller 2007). The drop in diversity affects both corals and reef-associated decapod faunas (Müller 1984a: table 2; Fig. 2). In general, however, Late Badenian is the time of greatest decapod diversity of the entire Oligo-Miocene of the Central Paratethys (Fig. 3), partly owing to the collection efforts of Pál Müller (see above)

The Early Badenian and Late Badenian decapod associations do not overlap in NMDS ordination (Figs. 5–7). Taxonomic differences between decapod associations of these two substages were already demonstrated by Müller (1984a). Middle Badenian faunas in general are taxonomically much closer to the Early Badenian ones; this pattern can be observed in the results of all analyses (Figs. 5–7).

At the Badenian/Sarmatian boundary, the fossil composition changed abruptly and stenohaline groups disappeared (Harzhauser & Piller 2007; Studencka & Jasionowski 2011). One of the latest marine decapod associations of the Vienna Basin is documented from the lowermost Sarmatian strata of the Devínska Kobyla hill (Hyžný 2012; Hyžný & Hudáčková 2012; Hyžný et al. 2012), dominated by ghost shrimps which are able to tolerate salinity fluctuations.

In the Sarmatian, the open oceanic connections ceased and the entire Paratethys was inhabited by homogeneous euryhaline biota, most of which were endemic to the region (Rögl 1998, 1999; Popov et al. 2004). Salinity had regionally specific composition and ranged from slightly brackish in the earliest Sarmatian (Studencka & Jasionowski 2011) to hypersaline in the Late Sarmatian (Piller & Harzhauser 2005). One of the Paratethyan endemites was probably also *Mioplax socialis* Bittner, 1884, a crab reported from the Badenian strata of Croatia (Bittner 1884) and the Lower Sarmatian strata of Austria (Glaessner 1928) and Slovakia (Hyžný & Ledvák 2014; Hyžný et al. 2016). The euryhaline preferences of this crab have been demonstrated by Hyžný et al. (2016). This crab is the only decapod species recorded from the studied localities from the Sarmatian age suggesting it was one of the latest marine crabs of the Central Paratethys.

**Late Miocene:** The Upper Miocene deposits with documented fauna reflect the existence of a large, long-lived brackish to freshwater Lake Pannon inside the Carpathian arch (Fig. 1D) which was separated from the Central Paratethys at the Sarmatian/Pannonian boundary (Magyar et al. 1999; Harzhauser & Piller 2007). During that time a shallow brackish-lacustrine deposition was typical for the Vienna Basin (Kováč et al. 2004, 2005; Magyar et al. 1999; Harzhauser et al. 2004). From these deposits fossil burrow systems attributed to callianassid ghost shrimps were reported (Hyžný et al. 2015d; Fig. 11H). Later, the Vienna and Danube basins were filled with deltaic deposits prograding from the northwest and northeast (Magyar et al. 2007). From isolated marginal lakes in the west remains of freshwater crabs were reported (Bachmayer & Pretzmann 1971; Fordinál 1994; Fordinál & Nagy 1997; Klaus & Gross 2010; Fig. 11A–G). In the Mediterranean reef-associated decapod faunas still flourished (Müller 1984b; Gatt & De Angeli 2010).

#### **Reefal versus non-reefal taxa**

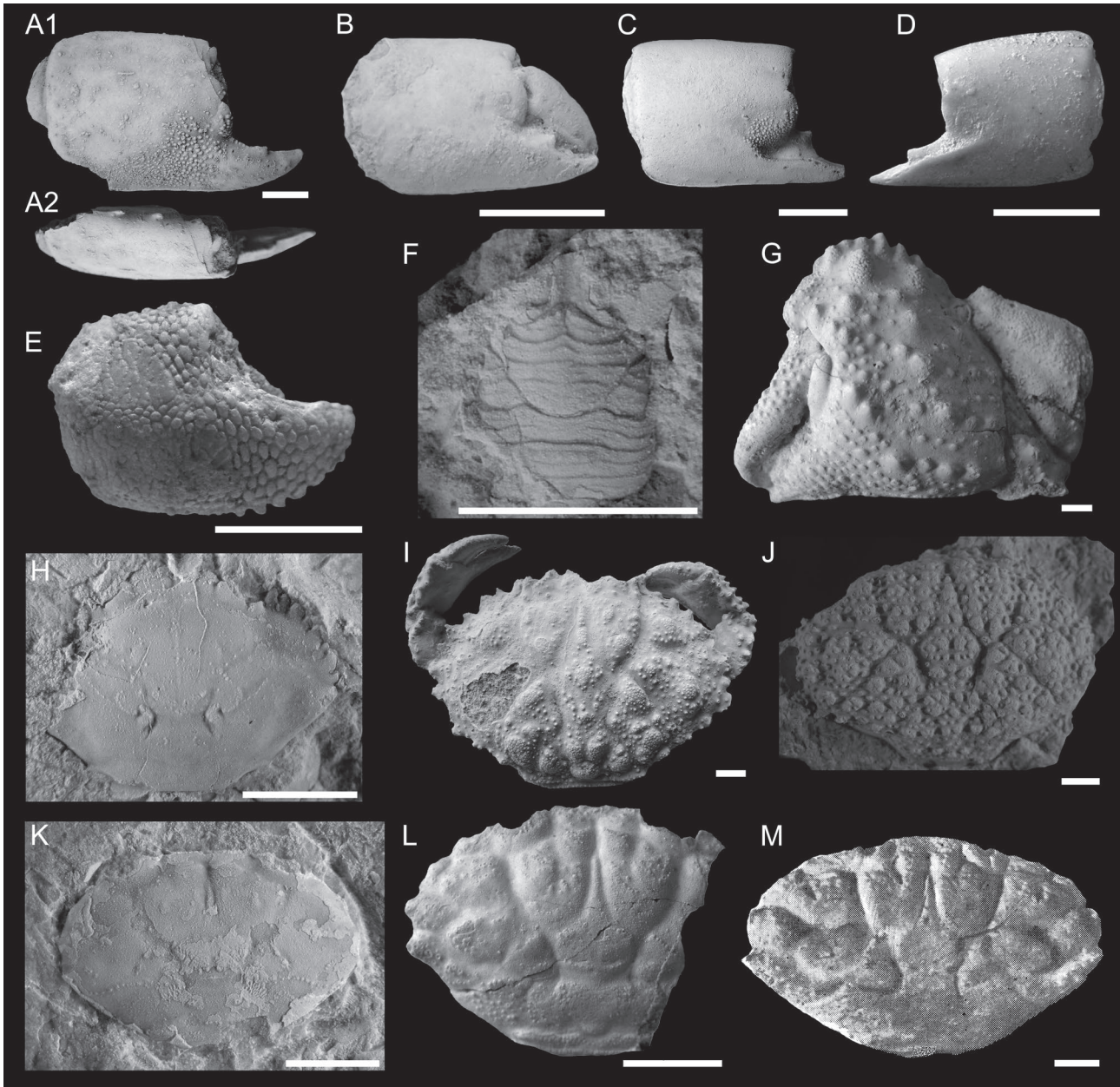
Ottangian and Karpatian assemblages differ from the Badenian ones (Fig. 5). The main contributing factor is the type of sedimentation and the availability and extent of reef habitats. Whereas Ottangian and Karpatian decapod assemblages are preserved virtually exclusively in the “Schlier”-type facies, carbonate sedimentation during the Badenian and the presence of reefal environments at that time in the Central Paratethys (Pisera 1996) promoted thriving of more diverse reef-associated assemblages. As a consequence, the assemblages from individual basins group in the NMDS



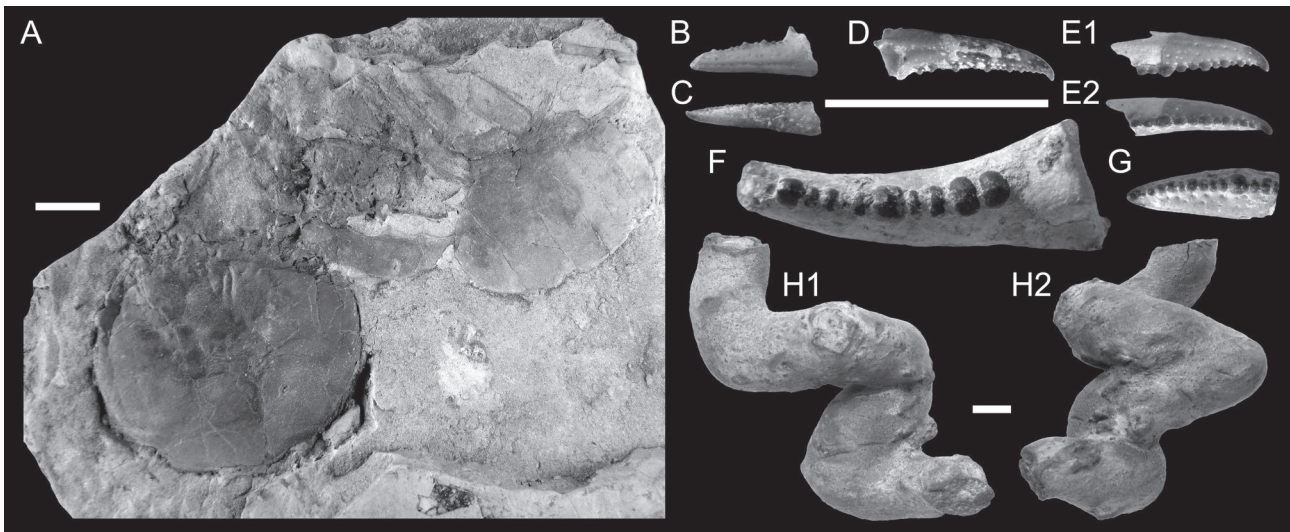
analysis not according to their spatial proximity but according to age. Interestingly, not only Ottnangian-Karpatian assemblages were distinct from Badenian ones, but Badenian associations were further subdivided into three distinct

groupings, each for the substages Early, Middle and Late Badenian (best observable in reefal taxa as shown in Fig. 6).

A great abundance of reefal decapod taxa in the Early and Middle Badenian is connected to the widespread reefal



**Fig. 10.** Selected decapod crustaceans from the Middle Miocene of the Central Paratethys. **A** — *Glypturus munieri* (Brocchi, 1883), MFGI M.2355; Rákos, Hungary. **B** — *Eucalliax pseudorakosensis* (Lőrenthey in Lőrenthey & Beurlen, 1929), syntype MFGI M.20; Felménes, Romania. **C** — *Calliastina chalmasii* (Brocchi, 1883), minor chela, MFGI M.21 (holotype of *Callianassa rakosensis* Lőrenthey, 1897); Rákos, Hungary. **D** — *Calliastina chalmasii*, major chela, HHNM PAL 2011.33; Rákos, Hungary. **E** — *Pylopagurus leganyi* Müller, 1984a, holotype HHNM 62 3253; Sámsonháza, Hungary. **F** — *Galathea weinfurteri* Bachmayer, 1850, NHMW 2013/0580/0014; Deutsch-Altenburg, Austria. **G** — *Calappa heberti* Brocchi, 1883, MFGI M.2379; Rákos, Hungary. **H** — *Rakosia carupoides* Müller, 1984a, NHMW 2015/0052/0007; Gross-Höflein, Austria. **I** — *Tasadia carniolica* (Bittner, 1884), MFGI M.35 (holotype of *Cancer szontaghii* Lőrenthey, 1897); Tasádfő, Romania. **J** — *Daira speciosa* (von Reuss, 1871), NHMW 1896/93; Gamlitz, Austria. **K** — *Chlorodiella mediterranea* (Lőrenthey in Lőrenthey & Beurlen, 1929), NHMW 2015/0056/0294; Gross-Höflein, Austria. **L** — *Pilodius vulgaris* (Glaessner, 1928), holotype NHMW 1927/0001/0002; Rauchstallbrunngraben, Austria. **M** — *Xantho moldavicus* (Janakevich, 1977), Shepteban, Moldova; digitalized copy of Janakevich (1969: pl., fig. 6). Scale bar equals 5 mm. All specimens except E, J and M were covered with ammonium chloride prior to photography.



**Fig. 11.** Selected decapod crustaceans from the Late Miocene of the Central Paratethys. **A** — *Potamon proavitum* Glaessner, 1928, holotype UMJGP 5828 from Andritz, Austria. **B–G** — *Potamon hegauense* Klaus & Gross, 2010, isolated fingers (KGP-MH uncatalogued) from borehole PiD-1, Slovakia (Danube Basin). **H** — Fragment of larger complex burrow system *Egbellichnus jordidegiberti* Hyžný, Šimo & Starek, 2015 (paratype SNM-Z 37738) attributed to callianassid ghost shrimp (Hyžný et al. 2015d). Scale bar equals 10 mm.

settings at that time (Pisera 1996). These settings included coral patch reefs and coral carpets (Riegl & Piller 2000; Reuter & Piller 2011), and algal-vermetid reefs (Radwański et al. 2006; Górká et al. 2012). Diverse coral-associated decapod associations are known from the Lower Badenian strata of the Styrian, Great Hungarian and Carpathian Foreland basins (B1-StB, B1-GHB, B1-CFB), the Middle Badenian strata of the Vienna Basin (B2-VB) and the Upper Badenian strata of the Great Hungarian Basin (B3-GHB). Decapods associated with algal-vermetid reefs were reported from the Upper Badenian strata of the Carpathian Foreland Basin (B3-CFB).

#### **Palaeobiogeographical implications**

**Biogeographical homogeneity of Paratethys:** The planktotrophic larval mode in most anomurans and brachyurans plays a major role in their dispersal pattern (Gurney 1942; Moore & McCormick 1969; Harvey et al. 2002, 2014; Martin 2014b). They passively drift in ocean currents promoting high dispersal potential with larval development having a great impact on their latitudinal diversity gradients (Fernández et al. 2009). This is in striking contrast with peracaridans (e.g., isopods and amphipods) exhibiting direct development (Harvey et al. 2002; Boyko & Wolff 2014; Wolff 2014) and consequently restricted dispersal, lower connectivity and higher potential for isolation. In addition, some decapods are active swimmers, so the dispersal and migration of decapods can be very quick (Por 1986). Decapods as palaeobiogeographical indicators were successfully used in the Northern Pacific Ocean (Schweitzer 2001) and in the Southern Hemisphere (Feldmann & Schweitzer 2006). Migration pathways reconstructed in these studies match those observed for molluscs with planktotrophic larval mode earlier. In this study, the spatial patterns in decapod composition rather demonstrate

biogeographical homogeneity of the Paratethys, with sedimentological and palaeoenvironmental conditions being the major factors influencing distribution of specific taxa. Already Müller (1984a: 102) recognized that Early, Middle and Late Badenian reef-associated decapod faunas differ from each other and proposed several “decapod zones” based on them. The present results (Fig. 6) corroborate his findings. The conclusion about the biogeographical homogeneity of the Paratethyan decapod associations has already been demonstrated for the Miocene molluscs (Studencka et al. 1998; Mandić & Steininger 2003) and echinoderms (Kroh 2007). Rapid dispersal of decapod crustaceans as discussed above promoted their homogeneous distribution in the Paratethys.

#### **Interactions between Mediterranean and Paratethys:**

Previous studies indicate that an alternating anti-estuarine and estuarine circulation regulated the Middle Miocene faunal exchange between these two provinces (Báldi 2006: foraminifers; Moissette et al. 2006: bryozoans; Harzhauser et al. 2003: molluscs; Kroh & Harzhauser 1999: echinoderms). For the Early and Middle Badenian, an anti-estuarine (lagoonal) circulation is assumed, permitting an easier incursion of Mediterranean species into the Paratethys, but hindering the Paratethyan endemics from entering the Mediterranean. In the Late Badenian, the circulation reversed to estuarine type, which is connected with the cooler period (Báldi 2006). As demonstrated by Karami et al. (2011), the Paratethys was more responsive to climate change after closure of the marine seaways than the Mediterranean. Moreover, the palaeobiogeographic domain formed by the Mediterranean and the Paratethys was relatively homogeneous during the Middle Miocene and the similarities with the Atlantic were smaller (Kroh & Harzhauser 1999; Harzhauser et al. 2003; Moissette et al. 2006). If this scenario applies to decapod



crustaceans, it will imply that the Middle Miocene Mediterranean and Paratethys decapod assemblages as taken together were relatively homogeneous.

Gatt & De Angeli (2010: text-fig. 11) compared coral-associated decapod species from the Middle Miocene (Badenian) of the Paratethys with the association from the Late Miocene (Messinian) of Malta (Mediterranean): seven species out of 19 taxa recorded from Malta are shared with the Paratethys, whereas similarities are even greater on the genus level (Müller 1993; Gatt & De Angeli 2010). Based on similarities in decapod faunas and comparison with migration patterns of other groups, Gatt & De Angeli (2010) suggested the migration of taxa between the Mediterranean and the Paratethys during the Langhian. Assuming that the Early and Middle Badenian exchange flow was controlled by anti-estuarine circulation (Báldi 2006; Moissette et al. 2006), the reefal decapod taxa from the Lower and Middle Badenian strata of the Paratethys are migrants from the Mediterranean. However, after the reversal in circulation to estuarine type, the newly evolved Paratethyan species could migrate back to the Mediterranean. Thus, the Late Miocene reefal decapod associations could represent (at least partly) descendants of the Paratethyan migrants.

**Paratethys vs. North Sea:** Miocene decapod faunas of the North Sea share numerous genera (and even species) with the Central Paratethys assemblages. For instance Janssen & Müller (1984) and Polkowsky (2014) reported a crab *Tasadia carniolica* from the Miocene of Belgium and northern Germany, respectively; the species is common in the Middle Miocene sediments of Austria, Slovakia, Slovenia and even Romania (Müller 1984a; Hyžný 2011c). Similarly, Fraaije et al. (2010b) reported another crab, *Dromia neogenica* Müller, 1978, from the Miocene and Pliocene of the southern North Sea Basin documenting a link between that basin and the Central Paratethys and coeval levels in North Africa (Algeria); all these areas share some decapod species. Hyžný & Gašparič (2014) reviewed all occurrences of a ghost shrimp *Calliax michelottii* including those from the Oligocene of northern Germany and the Miocene of Austria, Hungary, Slovakia and Slovenia representing another example of connection between the North Sea Basin and the Paratethys. Clearly, these faunal similarities between the discussed areas are not an artefact of poor systematics. It is thus reasonable to assume the migration of decapods sometimes during the Early Miocene via the Rhine Graben (Martini 1990; Berger et al. 2005) because no seaway connection existed between the Central Paratethys and the North Sea during the Middle Miocene (e.g. Rögl 1998; Harzhauser & Piller 2007). Based on the proposed estuarine circulation pattern during the Oligocene and Early Miocene (Popov et al. 2004), it is likely that decapods originated in the Paratethys and migrated into the Atlantic (North Sea).

**Decapods exterminated by the Messinian salinity crisis?** At the end of the Miocene, the Messinian salinity crisis took

place in the Mediterranean basins, thereby also affecting the Paratethys. This event left marine faunas severely impoverished (Hsü et al. 1978; Harzhauser et al. 2002; Krijgsman et al. 2010; Roveri et al. 2014). Decapod taxa probably responded differently to the Messinian salinity crisis. For instance, callianassid genera such as *Glypturus* and *Neocallinurus* Sakai, 1988, which today are bound to the subtropics and tropics (e.g. Dworschak & Ott 1993; Felder 2001; Dworschak 2004), did not survive in the modern Mediterranean. On the other hand, the callianassid genera *Calliaxina* Ngoc-Ho, 2003 and *Calliax* de Saint Laurent, 1973 are still present in the Mediterranean today (Ngoc-Ho 2003), which apparently is a consequence of different ecological requirements of various ghost shrimp taxa.

**A Tethyan origin of Indo-West Pacific faunas?** The similarities between decapod faunas of the Badenian of the Central Paratethys and today's Indo-West Pacific led Müller (1979a, 1984a) to suggest that Tethyan faunas have their origin in the Indo-West Pacific. However, he noted that reverse may also be true (Müller 1979a: 868). The present state of knowledge of the fossil record suggests migration of Tethyan marine faunas in an easterly direction during the Oligocene and/or Miocene. This migration led to a major shift towards the West Pacific as a centre of diversity, as documented for molluscs and ophiuroids (Harzhauser et al. 2007, 2008; see also Renema et al. 2008). Apparently, decapod crustaceans of the Tethyan stock took the same migratory routes as demonstrated by Schweitzer (2001), Hyžný (2011a) and Hyžný & Müller (2012). The fossil record of a mud shrimp *Jaxea Nardo, 1847* suggests its origin in the Tethys before the Early Miocene. Its descendant lineage is represented by the extant *Jaxea novaezealandiae* Wear & Yaldwyn, 1966 (Hyžný 2011a) living in the Western Pacific. The same scenario can be postulated for a ghost shrimp *Glypturus* Stimpson, 1866 with its fossil record extending into the Middle Eocene of Spain and Italy (Hyžný & Müller 2012; Beschin et al. 2012) and subsequent migration both westwards into the Western Atlantic and eastward into the Indo-West Pacific (Hyžný & Müller 2012; Hyžný et al. 2013).

## Conclusions

Only a limited number of decapod species are known from the Oligocene of the Paratethys, owing to the limited exposure of the Oligocene strata and relatively few published studies on the Oligocene decapods from the studied area.

Whereas Ottnangian and Karpatian decapod assemblages are preserved virtually exclusively in the "Schlier"-type facies, carbonate sedimentation during the Badenian and the presence of reefal environments at that time in the Central Paratethys promoted thriving of more diverse reef-associated assemblages.

In all analyses, Early Badenian decapod associations were resolved as taxonomically distinct from the Late Badenian ones.



The Late Badenian was recognized as the time of greatest decapod diversity of the entire Oligo-Miocene of the Central Paratethys, partly owing to collection efforts of Pál Müller.

Decapod crustaceans of the Paratethys exhibited relatively homogeneous distribution. The time factor, including speciation and extinction, can explain differences among assemblages from the same environment (reefs) but different times.

Based on the distribution of the decapod taxa in the Paratethys and adjacent areas, several working hypotheses on palaeobiogeographical patterns are presented for further testing: a) the Miocene Paratethyan decapod assemblages have their origin in the Mediterranean with increasing rate of endemites due to anti-estuarine migration pattern; b) in the Miocene the North Sea shared some species with the Paratethys suggesting migration via the Rhine Graben into the Paratethys; c) during the Oligocene and/or Miocene decapods migrated in an easterly direction, thus, contributing to the modern diversity in the Indo-West Pacific Region.

**Acknowledgements:** Access to the collections was provided by Emese Bodor and Klára Palotás (MFGI), Alfréd Dulai (HNHM), Rok Gašparič (RGA/SMNH), Martin Gross (UMJGP), Oleg Mandić (NHMW), Barbara Zahradníková (SNM-Z), and Irene Zorn (GBA). Klement Fordinál (Geological Institute of Dionýz Štúr, Bratislava) provided material from the borehole PiD-1. Mathias Harzhauser, Andreas Kroh and Oleg Mandić (all NHMW) are thanked for constructive comments on the earlier draft of the manuscript. Oleg Mandić helped with palaeogeographical maps. Thomas Neubauer (NHMW) and Natália Hudáčková (KGP) are thanked for help with the NMDS analysis. The manuscript benefited from the constructive criticism of an associate editor Adam Tomašových and reviewers Barbara Studencka and Rafał Nawrot. The research has been supported by the Austrian Science Fund (FWF; Lise Meitner Program M 1544-B25), VEGA 02/0136/15 and the Slovak Research and Development Agency under contracts no. APVV-0099-11 and APVV-0436-12.

## References

- Bachmayer F. 1950: Neue Dekapoden aus dem österreichischen Tertiär. *Ann. Naturhist. Mus. Wien* 57, 133–140.
- Bachmayer F. 1953a: Zwei neue Crustaceen-Arten aus dem Helvet-Schlier von Ottmang (Oberösterreich). *Ann. Naturhist. Mus. Wien* 59, 137–140.
- Bachmayer F. 1953b: Die Dekapodenfauna des tortonischen Leithakalkes von Deutsch-Altenburg (Niederösterreich). *Mitt. Geol. Ges. Wien* 44 (for 1951), 237–262.
- Bachmayer F. 1953c: *Goneplax gulderi*, eine neue Crustaceen-Species aus dem tortonischen Tegel des Wiener-Beckens. *Paläont. Z.* 27, 143–145.
- Bachmayer F. 1954: Zwei bemerkenswerte Crustaceen-Funde aus dem Jungtertiär des Wiener Beckens. *Sitzungsber. österr. Akad. Wiss., math.-naturwiss. Kl. I* 163, 63–70.
- Bachmayer F. 1962: Die Calappiden (Crustacea, Decapoda) aus den tortonischen Ablagerungen des Wiener Beckens. *Ann. Naturhist. Mus. Wien* 65, 39–46.
- Bachmayer F. 1982: Funde von fossilen Krabben aus den Diatomeenschiefern (Miozän, Ottmangien) von Limberg, Niederösterreich. *Anz. Österr. Akad. Wiss., math.-naturwiss. Kl.* 1982, 2, 21–24.
- Bachmayer F. & Küpper K. 1952: Eine bemerkenswerte Krabbe aus dem Badener Tegel (Torton) von Soos im Wiener Becken. *Verh. Geol. Bundesanst.* 1952, 1–6.
- Bachmayer F. & Pretzmann G. 1971: Krebsreste aus den altploziänen Süßwasserablagerungen des Eichkogels bei Mödling, Niederösterreich. *Ann. Naturhist. Mus. Wien* 75, 283–291.
- Bachmayer F. & Tollmann A. 1953: Die Crustaceen-Fauna aus dem tortonischen Leithakalk (Steinbrüche der Firma Fenk) bei Groß-Höflein im Burgenland. *Kober-Festschrift 1953, Skizzen zum Anlaß des 70. Geburtstages von Prof. Dr. L. Kober, Universität Wien, Gesellschaftsbuchdruckerei Brüder Hollinek, Wien*, 308–314.
- Bachmayer F. & Rutsch R.F. 1962: Brachyurenfunde (Crustacea) aus der miozänen Meeresmolasse der Schweiz. *Eclogae Geol. Helv.* 55, 675–682, pls. 1–3.
- Bachmayer F. & Wagner R. 1957: *Geryon heimertingensis* n. sp., eine Krabbe aus dem Chattien der Erdölbohrung Heimertingen (bayerische Vorlandmolasse). *Paläont. Z.* 31, 99–102.
- Báldi K. 2006: Paleocyanography and climate of the Badenian (Middle Miocene, 16.4–13.0 Ma) in the Central Paratethys based on foraminifera and stable isotope ( $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$ ) evidence. *Int. J. Earth Sci. (Geol. Rundsch.)* 95, 119–142.
- Báldi T. 1984: The Terminal Eocene and Early Oligocene events and separation of an anoxic, cold Paratethys. *Eclogae Geol. Helv.* 77, 1–27.
- Báldi T. 1986: Mid-Tertiary stratigraphy and paleogeographic evolution of Hungary. *Akadémiai Kiadó, Budapest*, 1–201.
- Barthelt D. 1989: Faziesanalyse und Untersuchung der Sedimentationsmechanismen in der Unteren Brackwasser-Molasse Oberbayerns. *Münchner Geowiss. Abh. (A)* 17, 1–118.
- Bartol M., Mikuž V. & Horvat A. 2014: Palaeontological evidence of communication between the Central Paratethys and the Mediterranean in the late Badenian/early Serravalian. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 394, 144–157.
- Berger J.-P., Reichenbacher B., Becker D., Grimm M., Grimm K., Picot L., Storni A., Pirkenseer C., Derer Ch. & Schaefer A. 2005: Paleogeography of the Upper Rhine Graben (URG) and the Swiss Molasse Basin (SMB) from Eocene to Pliocene. *Int. J. Earth Sci. (Geol. Rundsch.)* 94, 697–710.
- Beschin C., Busulini A., De Angeli A. & Tessier G. 1996: *Retroplumoidea* (Crustacea, Decapoda) in the Tertiary of the Vicenza area (N. Italy). *Lavori — Soc. Ven. Sc. Nat.* 21, 83–102 (in Italian, with English abstract).
- Beschin C., De Angeli A., Checchi A. & Zarantonello G. 2012: Eocene crustaceans of Grola near Spagnago of Cornedo Vicentino (Vicenza, northern Italy) (Decapoda, Stomatopoda, Isopoda). *Museo di Archeologia e Scienze Naturali “G. Zanato”, Montecchio Maggiore, Vicenza*, 1–100 (in Italian, with English abstract).
- Beurlen K. 1939: Neue Dekapoden-Krebse aus dem ungarischen Tertiär. *Paläont. Z.* 21, 135–161.
- Bieńkowska-Wasiluk M. 2010: Taphonomy of Oligocene teleost fishes from the Outer Carpathians of Poland. *Acta Geol. Pol.* 60, 479–533.
- Bittner A. 1877: Über *Phymatocarcinus speciosus* Reuss. *Sitzungsber. kaiserl. Akad. Wiss. Wien I* 75, 435–447.
- Bittner A. 1884: Beiträge zur Kenntniss Tertiärer Brachyuren-Faunen. *Denkschr. kaiserl. Akad. Wiss. math.-naturwiss. Kl.* 48, 15–30.
- Bittner A. 1893: Decapoden des pannonischen Tertiärs. *Sitzungsber.*

- kaiserl. Akad. Wiss. Wien 102, 10–37.
- Boyko Ch.B. & Wolff C. 2014: Isopoda and Tanaidacea. In: Martin J., Olesen J. & Høeg J. (Eds.): Atlas of Crustacean Larvae. *The Johns Hopkins University Press*, 210–215.
- Brocchi P. 1883: Notes sur les Crustacés fossiles des terres tertiaires de la Hongrie. *Ann. Sci. Géol.* 14, 1–8.
- Collins J.S. 2014: Middle Miocene “Badenian” (Langhian) decapod crustaceans from the Retznei quarry, Styrian Basin, Austria. *Bull. Mizunami Fossil Museum* 40, 29–50.
- de Saint Laurent M. 1973: Sur la systématique et la phylogénie des Thalassinidea: définition des familles des Callianassidae et des Upogebiidae et diagnose de cinq genres nouveaux (Crustacea Decapoda). *CR Acad. Sci. D Nat.* 277, 513–516.
- Delle-Cave L. 1988: *Jaxea* cf. *nocturna* (Crustacea, Decapoda, Anomura) from the Early Pliocene of Tuscany, Italy. *Boll. Soc. Paleontol. Ital.* 27, 3–10.
- Dworschak P.C. 2004: Biology of Mediterranean and Caribbean Thalassinidea (Decapoda). In: Tamaki A. (Ed.): Proceedings of the Symposium on “Ecology of large bioturbators in tidal flats and shallow sublittoral sediments - from individual behavior to their role as ecosystem engineers”. November 1-2, 2003, Nagasaki. *Nagasaki University*, 15–22.
- Dworschak P.C. & Ott J.A. 1993: Decapod burrows in mangrove-channel and back-reef environments at the Atlantic Barriers Reef, Belize. *Ichnos* 2, 277–290.
- Felder D.L. 2001: Diversity and ecological significance of deep-burrowing macrocrustaceans in coastal tropical waters of the Americas (Decapoda: Thalassinidea). *Interciência* 26, 440–449.
- Feldmann R.M. & Schweitzer C.E. 2006: Paleobiogeography of Southern Hemisphere decapod Crustacea. *J. Paleontol.* 80, 83–103.
- Fernández M., Astorga A., Navarrete S.A., Valdovinos C. & Marquet P.A. 2009: Deconstructing latitudinal species richness patterns in the ocean: does larval development hold the clue? *Ecol. Lett.* 12, 601–611.
- Flügel H.W. 1986: Ein neuer Fund von *Portunus monspeliensis* (A. Milne-Edwards) aus dem Badenium von Retznei (Stmk.). *Mitt. Naturwiss. Ver. Steiermark* 116, 91–96.
- Fordinál K. 1994: Upper Pannonian (Zone H) of the eastern margin of Považský Inovec. *Geol. práce* 99, 67–75 (in Slovak, with English abstract).
- Fordinál K. & Nagy A. 1997: Hlavina Member — marginal Upper Pannonian sediments of the Rišňovce depression. *Miner. Slovaca* 29, 401–406 (in Slovak, with English abstract).
- Förster R. 1979a: Decapod crustaceans from the Middle Miocene (Badenian) deposits of Southern Poland. *Acta Geol. Pol.* 29, 89–106.
- Förster R. 1979b: Decapod crustaceans from the Korytnica basin (Middle Miocene; Holy Cross Mountains, Central Poland). *Acta Geol. Pol.* 29, 253–268.
- Fraaije R.H.B., Menkveld-Gfeller U.E., Van Bakel B.W.M. & Jagt J.W.M. 2010a: Decapod crustaceans from the type area of the Helvetian Stage (lower Miocene) in the Bern area, Switzerland. *Bull. Mizunami Fossil Museum* 36, 1–11.
- Fraaije R.H.B., Van Bakel B.W.M. & Jagt J.W.M. 2010b: First record of *Dromia neogenica* Müller, 1979 (Decapoda, Brachyura, Dromiidae) from Neogene strata in the southern North Sea Basin. In: Fransen C.H.J.M., De Grave S. & Ng P.K.L. (Eds.): Lipke Bijdeley Holthuis memorial volume - Studies on Malacostraca. *Crustaceana Monogr.* 14, 231–240.
- Friebe G. 1987: Eine Krabben-Fauna aus dem Leithakalk (Badenien) von Wurzing bei Wildon, Steiermark. *Mitt. Naturwiss. Verein Steiermark* 117, 57–65.
- Friebe G. 1990: Lithostratigrafische Neugliederung und Sedimentologie der Ablagerungen des Badenium (Miozän) um die Mittelsteirische Schwelle (Steirisches Becken, Österreich). *Jahrb. Geol. Bundesanst.* 133, 223–257.
- Fröhlicher H. 1951: Brachyuren aus den stampischen Fischeschiefern des Entlebuch, Kt. Luzern. *Eclogae Geol. Helv.* 44, 358–359.
- Gašparič R. & Halásová E. 2015: New reports of crab *Styrioplax exiguus* Glaessner, 1928 (Decapoda, Brachyura) from Miocene beds near Maribor, Slovenia. *Geologija* 58, 201–212 (in Slovenian with English abstract).
- Gašparič R. & Hyžný M. 2015 (online 2014): An early Miocene deep-water decapod crustacean faunule from the Slovenian part of the Styrian Basin and its palaeoenvironmental and palaeobiogeographical significance. *Papers in Palaeontology* 1, 141–166.
- Gatt M. & De Angeli A. 2010: A new coral-associated decapod assemblage from the upper Miocene (Messinian) Upper Coralline Limestone of Malta (central Mediterranean). *Palaeontology* 53, 1315–1348.
- Glaessner M.F. 1924: Über eine neue miozäne Krabbe und die Brachiurenfauna des Wiener Beckens. *Verh. Geol. Bundesanst.* 1924/6, 109–118.
- Glaessner M.F. 1928: Die Dekapodenfauna des österreichischen Jungtertiärs. *Jahrb. Geol. Bundesanst.* 78, 161–219.
- Glaessner M.F. 1929: Crustacea Decapoda. In: Pompeckj, F.J. (ed.) Fossilium catalogus, 1: Animalium, 41. *W. Junk*, Berlin. 1–464.
- Glaessner M.F. 1965: Vorkommen fossiler Dekapoden (Crustacea) in Fish-Schiefern. *Senck. Leth.* 46a, 111–122.
- Glaessner M.F. 1969: Decapoda. In: Moore R.C. (Ed.): Treatise on Invertebrate Paleontology, Part R. Arthropoda 4 (2), R399–R533. *Geological Society of America, Boulder, and University of Kansas Press*, Lawrence.
- Górka M. 2002: The Lower Badenian (Middle Miocene) coral patch reef at Grobie (southern slopes of the Holy Cross Mountains, Central Poland), its origin, development and demise. *Acta Geol. Pol.* 52, 521–534.
- Górka M., Studencka B., Jasionowski M., Hara U., Wysocka A. & Poberezhskyy A. 2012: The Medobory Hills (Ukraine): Middle Miocene reef systems in the Paratethys, their biological diversity and lithofacies. *Biul. Państw. Inst. Geol.* 449, 147–174.
- Grunert P., Soliman A., Ćorić S., Roetzel R., Harzhauser M. & Piller W.E. 2012: Facies development along the tide-influenced shelf of the Burdigalian Seaway: An example from the Ottnangian stratotype (Early Miocene, middle Burdigalian). *Mar. Micropaleontol.* 84–85, 14–36.
- Gurney R. 1942: Larvae of decapod Crustacea. *Ray Society*, London. 1–306.
- Hammer Ø., Harper D.A.T. & Ryan P.D. 2001: PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontol. Electron.* 4, 1, 1–9.
- Haq B.U., Hardenbol J. & Vail P.R. 1988: Mesozoic and Cenozoic chronostratigraphy and cycles of sea level changes. In: Wilgus C.K. (Ed.): Sea-level changes — an integrated approach. *SEMP Special Publications* 42, 71–108.
- Hardenbol J., Thierry J., Farley M.B., Jacquin T., Graciansky P.C. de & Vail P.R. 1998: Mesozoic and Cenozoic sequence chronostratigraphic framework of European Basins. In: Graciansky P.C. de, Hardenbol J., Jacquin T. & Vail P.R. (Eds.): Mesozoic and Cenozoic sequence stratigraphy of European Basins. *SEMP Special Publications* 60, 3–13.
- Harvey A.W., Martin J.W. & Wetzer R. 2002: Phylum Arthropoda: Crustacea. In: Young C.M., Sewell M.A. & Rice M.E. (Eds.): Atlas of Marine Invertebrate Larvae. *Academic Press, A Harcourt Science and Technology Company*, San Diego, 337–369.
- Harvey A., Boyko Ch.B., McLaughlin P. & Martin J.W. 2014: Anomura. In: Martin J.W., Olesen J. & Høeg J. (Eds.): Atlas of Crustacean Larvae. *The Johns Hopkins University Press*,

283–294.

- Harzhauser M. & Piller W.E. 2007: Benchmark data of a changing sea — Palaeogeography, Palaeobiogeography and events in the Central Paratethys during the Miocene. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 253, 8–31.
- Harzhauser M., Piller W.E. & Steininger F.F. 2002: Circum-Mediterranean Oligo/Miocene Biogeographic Evolution — the Gastropods' Point of View. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 183, 103–133.
- Harzhauser M., Mandić O. & Zuschin M. 2003: Changes in Paratethyan marine molluscs at the Early/Middle Miocene transition: diversity, palaeogeography and palaeoclimate. *Acta Geol. Pol.* 53, 323–339.
- Harzhauser M., Daxner-Höck G. & Piller W.E. 2004: An integrated stratigraphy of the Pannonian (Late Miocene) in the Vienna Basin. *Austrian J. Earth Sci.* 95/96, 6–19.
- Harzhauser M., Kroh A., Mandić O., Piller W.E., Göhlich U., Reuter M. & Berning B. 2007: Biogeographic responses to geodynamics: a key study all around the Oligo-Miocene Tethyan Seaway. *Zool. Anz.* 246, 241–256.
- Harzhauser M., Mandić O., Piller W.E., Reuter M. & Kroh A. 2008: Tracing back the origin of the Indo-Pacific mollusc fauna - basal Tridacninae from the Oligocene and Miocene of the Sultanate of Oman. *Palaeontology* 51, 199–213.
- Herm D. 1988: In memoriam Reinhard Förster 1935–1987. *Mitt. Bayer. Staatsslg. Paläont. Hist. Geol.* 28, 3–7.
- Houša V. 1956: *Bechleja inopinata* n. g., n. sp., ein neuer Krebs aus dem böhmischen Tertiär (Decapoda, Palaemonidae). *Sb. ústř. úst. geol.* 23, 365–395, pl. 17–19 (in Czech, with Russian and German summaries).
- Hsü K.J., Montadert L., Bernoulli D., Cita M.B., Erickson A., Garrison R.E., Kidd R.B., Mélières F., Müller C. & Wright R. 1978: History of the Mediterranean Salinity Crisis. *Initial Rep. Deep Sea* 42, 1053–1078.
- Hyžný M. 2011a: Revision of *Jaxea kuemeli* Bachmayer, 1954 (Decapoda: Gebiidea: Laomedidae) from the Miocene of Europe, with remarks on the palaeobiogeography of the genus *Jaxea* Nardo, 1847. *N. Jahrb. Geol. Paläont. Abh.* 260, 173–184.
- Hyžný M. 2011b: *In situ* mud shrimps (Decapoda: Axiidea: Callianassidae) preserved within their burrows from the middle Miocene of the Central Paratethys. *Bull. Mizunami Fossil Museum* 37, 37–46.
- Hyžný M. 2011c: Synopsis of fossil decapod crustaceans from Slovakia (Western Carpathians). *N. Jahrb. Geol. Paläont. Abh.* 260, 165–171.
- Hyžný M. 2012: *Calliuxina chalmasi* (Brocchi, 1883) comb. nov. (Decapoda: Axiidea: Callianassidae: Eucalliicinae), a ghost shrimp from the Middle Miocene of Europe, with reappraisal of the fossil record of Eucalliicinae. *Zootaxa* 3492, 49–64.
- Hyžný M. 2015: Distributional patterns of decapod crustaceans in the circum-Mediterranean area during the Oligo-Miocene. In: EGU General Assembly 2015, *Geophysical Research Abstracts* 17, EGU2015-3609.
- Hyžný M. 2016: *Balsscallichirus* Sakai, 2011 (Decapoda: Axiidea: Callianassidae) in the fossil record: systematics and palaeobiogeography. *Ann. Naturhist. Mus. Wien A* 118, 39–63.
- Hyžný M. & Dulai A. 2014: Deep-water fossorial shrimps from the Oligocene Kiscell Clay of Hungary: Taxonomy and palaeoecology. *Acta Palaeontol. Pol.* 59, 947–965.
- Hyžný M. & Gašparič R. 2014: Ghost shrimp *Calliax* de Saint Laurent, 1973 (Decapoda: Axiidea: Callianassidae) in the fossil record: systematics, palaeoecology and palaeobiogeography. *Zootaxa* 3821, 37–57.
- Hyžný M. & Hudáčeková N. 2012: Redescription of two ghost shrimps (Decapoda: Axiidea: Callianassidae) from the Middle Miocene of the Central Paratethys: systematics, intraspecific variation, and *in situ* preservation. *Zootaxa* 3210, 1–25.
- Hyžný M. & Klompmaker A.A. 2015: Systematics, phylogeny, and taphonomy of ghost shrimps (Decapoda): a perspective from the fossil record. *Arthropod Syst. Phylo.* 73, 401–437.
- Hyžný M. & Ledvák P. 2014: On the occurrence of the fossil crab *Mioplax socialis* in deposits of the Stretava Formation in the East Slovakian Basin. *Natura Carpatica* 55, 27–30 (in Slovak with English summary).
- Hyžný M. & Müller P.M. 2010a: The first fossil record of the genus *Callichirus* (Decapoda, Axiidea, Callianassidae) from the middle Miocene of Hungary, with description of a new species. *Bull. Mizunami Fossil Museum* 36, 37–43.
- Hyžný M. & Müller P.M. 2010b: *Loerenthopluma* Beschin, Busulini, De Angeli & Tessier, 1996 (Decapoda: Brachyura: Retroplumidae) from the Oligocene of Hungary. *Atti Soc. it. Sci. nat. Museo civ. Stor. nat. Milano* 151, 129–140.
- Hyžný M. & Müller P.M. 2012: The fossil record of *Glypturus* Stimpson, 1866 (Crustacea, Decapoda, Axiidea, Callianassidae) revisited, with notes on palaeoecology and palaeobiogeography. *Palaeontology* 55, 967–993.
- Hyžný M. & Schlögl J. 2011: An early Miocene deep-water decapod crustacean faunule from the Vienna Basin (Western Carpathians, Slovakia). *Palaeontology* 54, 323–349.
- Hyžný M., Hudáčeková N., Biskupič R., Rybár S., Fuksi T., Halášová E., Žágoršek K., Jamrich M. & Ledvák P. 2012: Devínska Kobyla — a window into the Middle Miocene shallow-water marine environments of the Central Paratethys (Vienna Basin, Slovakia). *Acta Geol. Slovaca* 4, 2, 5–21.
- Hyžný M., Bahrami A., Klompmaker A.A., Yazdi M., Portell R.W. & Neumann Ch. 2013: The fossil record of *Glypturus* (Decapoda: Axiidea: Callianassidae) revisited with additional observations and description of a new species. *Swiss J. Palaeontol.* 132, 129–139.
- Hyžný M., Van Bakel B.W.M., Fraaije R.H.B., Jagt J.W.M., Krobicki M. & Magyar I. 2014a: A tribute to Pál Müller; his life, career and scientific output. In: Fraaije R.H.B., Hyžný M., Jagt J.W.M., Krobicki M. & Van Bakel B.W.M. (Eds.): Proceedings of the 5<sup>th</sup> Symposium on Mesozoic and Cenozoic Decapod Crustaceans, Krakow, Poland, 2013: A tribute to Pál Mihály Müller. *Scripta Geol.* 147, 9–20.
- Hyžný M., Gašparič R., Robins C.M. & Schlögl J. 2014b: Miocene squat lobsters (Decapoda, Anomura, Galatheoidea) of the Central Paratethys — a review, with description of a new species of *Munidopsis*. In: Fraaije R.H.B., Hyžný M., Jagt J.W.M., Krobicki M. & Van Bakel B.W.M. (Eds.): Proceedings of the 5<sup>th</sup> Symposium on Mesozoic and Cenozoic Decapod Crustaceans, Krakow, Poland, 2013: A tribute to Pál Mihály Müller. *Scripta Geol.* 147, 241–267.
- Hyžný M., Van Bakel B.W.M. & Guinot D. 2014c: *Etisus evamuelerae*, a new xanthid crab (Decapoda, Brachyura) from the Middle Miocene of Austria and Hungary. In: Fraaije R.H.B., Hyžný M., Jagt J.W.M., Krobicki M. & Van Bakel B.W.M. (Eds.): Proceedings of the 5<sup>th</sup> Symposium on Mesozoic and Cenozoic Decapod Crustaceans, Krakow, Poland, 2013: A tribute to Pál Mihály Müller. *Scripta Geol.* 147, 221–231.
- Hyžný M., Van Bakel B.W.M., Dulai M., Fraaije R.H.B., Jagt J.W.M. & Krobicki M. 2015a: In Memoriam Pál Mihály Müller (14 July 1935–13 September 2015). *Crustaceana* 88, 1457–1462.
- Hyžný M., Harzhauser M. & Danninger W. 2015b: Decapod crustaceans of the Otnangian (middle Burdigalian) Central Paratethys: implications for systematics and biogeography. *Geol. Carpath.* 66, 217–233.
- Hyžný M., Hudáčeková N. & Szalma Š. 2015c: Taphonomy and diversity of Middle Miocene decapod crustaceans from the



- Novohrad-Nógrad Basin, Slovakia, with remarks on palaeobiogeography. *Acta Geol. Slovaca* 7, 139–154.
- Hyžný M., Šimo V. & Starek, D. 2015d: Ghost shrimps (Decapoda: Axiidea: Callianassidae) as producers of an Upper Miocene trace fossil association from sublittoral deposits of Lake Pannon (Vienna Basin, Slovakia). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 425, 50–66.
- Hyžný M., Mandić O., Harzhauser M. & Ledvák P. 2016: Euryhaline preferences of the decapod crab *Mioplox socialis* enabled it to survive during the Badenian/Sarmatian extinction (Miocene) in the Central Paratethys. *Geol. Carpath.* 67, 165–176.
- Janakevich A.N. 1969: On the character of crabs from bioherm limestones of north-western Moldavia. *Paleontologičeskij sbornik Lvovskogo geologičeskogo Obscestva* 6, 25–27 (in Russian).
- Janakevich A.N. 1977: Middle Miocene reefs of Moldova. *Shtiintsa Publishers*, Kishinev, 1–116 (in Russian).
- Janssen A.W. & Müller P. 1984: Miocene Decapoda and Mollusca from Ramsel (province of Antwerpen, Belgium), with a new crab genus and a new cephalopod species. *Scripta Geol.* 75, 1–26.
- Jaroš Z. 1939: *Portunus oligocenicus* Pauca im mährischen Palaeogen. *Příroda* 32, 3, 1–3 (in Czech with German summary).
- Jerzmańska A. 1967: Crabs of the genus *Portunus* Weber from the Menilite Series of the Carpathians. *Ann. Soc. Géol. Pologne* 37, 539–545 (in Polish with English summary).
- Karami M.P., de Leeuw A., Krijgsman W., Meijer P.Th. & Wortel M.J.R. 2011: The role of gateways in the evolution of temperature and salinity of semi-enclosed basins: An oceanic box model for the Miocene Mediterranean Sea and Paratethys. *Glob. Planet. Change* 79, 73–88.
- Klaus A. & Gross M. 2010: Synopsis of the fossil freshwater crabs of Europe (Brachyura: Potamoidea: Potamidae). *N. Jahrb. Geol. Paläont. Abh.* 256, 39–59.
- Klompaker A.A., Schweitzer C.E., Feldmann R.M. & Kowalewski M. 2013: The influence of reefs on the rise of Mesozoic marine crustaceans. *Geology* 41, 1179–1182.
- Kocsis L., Dulai A., Bitner M.A., Vennemann T. & Cooper M. 2012: Geochemical compositions of Neogene phosphatic brachiopods: Implications for ancient environmental and marine conditions. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 326–328, 66–77.
- Kollmann H.A. & Zapfe H. 1979: Wirkl. Hofrat Prof. Dr. Friedrich Bachmayer zum 65. Geburtstag. *Ann. Naturhist. Mus. Wien* 82, 1–9.
- Kováč M., Andreyeva-Grigorovich A.S., Brzobohatý R., Fodor L., Harzhauser M., Oszczytko N., Pavelić D., Rögl F., Saftić B., Sliva L. & Stráník Z. 2003: Karpatian Paleogeography, Tectonics and Eustatic Changes. In: Brzobohatý R., Cicha I., Kováč N. & Rögl F. (Eds.): *The Karpatian — A Lower Miocene stage of the Central Paratethys*. *Masaryk University, Brno*, 49–72.
- Kováč M., Barath I., Harzhauser M., Hlavatý I. & Hudáčková N. 2004: Miocene depositional systems and sequence stratigraphy of the Vienna Basin. *Cour. Forsch. Senck.* 246, 187–212.
- Kováč M., Fordinál K., Grigorovich S.A., Halášová E., Hudáčková N., Joniak P., Pipík R., Sabol M., Kováčová M. & Sliva L. 2005: Environments and ecosystem dynamics of the Western Carpathian, in context of the Neogene evolution of the Eurasian continent. *Geol. práce, Spr.* 111, 61–121 (in Slovak).
- Kováč M., Andreyeva-Grigorovich A., Bajraktarević Z., Brzobohatý R., Filipescu S., Fodor L., Harzhauser M., Nagymarosy A., Oszczytko N., Pavelić D., Rögl F., Saftić B., Sliva L. & Studencka B. 2007: Badenian evolution of the Central Paratethys Sea: paleogeography, climate and eustatic sea-level changes. *Geol. Carpath.* 58, 579–606.
- Kováč M., Plašienka D., Soták J., Vojtko R., Oszczytko N., Less G., Čosović V., Fügenschuh B. & Králiková S. 2016: Paleogene palaeogeography and basin evolution of the Western Carpathians, Northern Pannonian domain and adjoining areas. *Glob. Planet. Change* 140, 9–27.
- Krijgsman W., Stoica M., Vasiliev I. & Popov V.V. 2010: Rise and fall of the Paratethys Sea during the Messinian Salinity Crisis. *Earth Planet. Sci. Lett.* 290, 183–191.
- Križnar M. 2009: A new occurrence of *Tasadia carnioolica* from the vicinity of Trbovlje. *Proteus* 2008/2009 71, 427–438 (in Slovenian).
- Kroh A. 2007: Climate changes in the Early to Middle Miocene of the Central Paratethys and the origin of its echinoderm fauna. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 253, 185–223.
- Kroh A. & Harzhauser M. 1999: An Echinoderm Fauna from the Lower Miocene of Austria: Paleocology and Implications for Central Paratethys Paleobiogeography. *Ann. Naturhist. Mus. Wien* 101A, 145–191.
- Küpper H.G. 1991: In memoriam M.F. Glaessner 1906–1989; Lebensweg, Arbeits- und Forschungsbereiche. *Ann. Naturhist. Mus. Wien* 92A, 161–170.
- Lăzărescu V. 1959: On a new species of *Coeloma*, with notes on palaeoecology of Brachyura. *Buletin Stiintific, secția de geologie și geografie* 2, 665–682 (in Romanian).
- Lőrenthey E. 1897: Decapod occurrences from the Hungarian Tertiary. *Math. és Termész. Ért.* 15, 149–169 (in Hungarian).
- Lőrenthey E. 1898a: Beiträge zur Decapodenfauna des ungarischen Tertiärs. *Math. und Naturwiss. Berichte aus Ungarn* 14, 92–115.
- Lőrenthey E. 1898b: New decapod occurrences from the Hungarian Tertiary. *Math. és Termész. Közll.* 27, 103–271 (in Hungarian).
- Lőrenthey E. 1898c: Beiträge zur Decapodenfauna des ungarischen Tertiärs. *Termész. Füzet.* 21, 1–133.
- Lőrenthey E. 1904a: Palaeontological studies on Tertiary decapod crustaceans. *Math. és Termész. Ért.* 22, 160–167 (in Hungarian).
- Lőrenthey E. 1904b: Paläontologische Studien über tertiäre Decapoden. *Math. und Naturwiss. Berichte aus Ungarn* 22, 29–34.
- Lőrenthey E. 1911: New data on Tertiary sediments of the surroundings of Budapest. *Math. és Termész. Ért.* 29, 515–535 (in Hungarian).
- Lőrenthey E. 1913: Neuere Beiträge zur Stratigraphie der Tertiärbildungen in der Umgebung von Budapest. *Math. und Naturwiss. Berichte aus Ungarn* 27, 282–394.
- Lőrenthey E. & Beurlen K. 1929: Die fossilen Dekapoden der Länder der Ungarischen Krone. *Geol. Hungar. Ser. Palaeontol.* 3, 1–421.
- Magyar I., Geary D.H. & Müller P. 1999: Paleogeographic evolution of the Late Miocene Lake Pannon in Central Paratethys. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 147, 151–167.
- Magyar I., Lantos M., Ujszaszi L. & Kordos L. 2007: Magnetostratigraphic, seismic and biostratigraphic correlations of the Upper Miocene sediments in the northwestern Pannonian Basin System. *Geol. Carpath.* 58, 277–290.
- Mandić O. & Steininger F.F. 2003: Computer-based mollusc stratigraphy – a case study from the Eggenburgian (Lower Miocene) type region (NE Austria). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 197, 263–291.
- Mandić O., De Leeuw A., Bulić J., Kuiper K., Krijgsman W. & Jurišić-Polšak Z. 2012: Paleogeographic evolution of the Southern Pannonian Basin: 40Ar/39Ar age constraints on the Miocene continental series of northern Croatia. *Int. J. Earth Sci.* 101, 1033–1046.
- Martin J.W. 2014a: Introduction to the Decapoda. In: Martin J.W., Olesen J. & Høeg J. (Eds.), *Atlas of Crustacean Larvae*. *The Johns Hopkins University Press*. 230–234.

- Martin J.W. 2014b: Brachyura. In: Martin J.W., Olesen J. & Høeg J. (Eds.): Atlas of Crustacean Larvae. *The Johns Hopkins University Press*. 295–310.
- Martini E. 1990: The Rhinegraben system, a connection between northern and southern seas in the European Tertiary. *Veröffentlichungen aus dem Übersee-Museum (A)* 10, 83–98.
- Melinte-Dobrinescu M. & Brustur T. 2008: Oligocene–Lower Miocene events in Romania. *Acta Palaeontol. Romaniae* 6, 203–215.
- Mikuž V. 2003a: The Miocene crabs from vicinity Šentilj in Slovenske Gorice, Slovenia. *Razprave IV. razreda SAZU* 44, 187–199 (in Slovenian, with English summary).
- Mikuž V. 2003b: The first finding of the crab *Ctenocheles* (Decapoda) in Oligocene beds in Slovenia. *Geologija* 46, 89–92 (in Slovenian, with English summary).
- Mikuž V. 2010: Crabs from Middle Miocene beds of quarries above Trbovlje, Slovenia. *Folia Biol. Geol.* 51, 13–20 (in Slovenian, with English summary).
- Mikuž V. & Pavšič J. 2003: The “Carniolian crab” from Middle Miocene — Badenian beds in the Lipovica quarry above Briše, Slovenia. *Geologija* 46, 245–250 (in Slovenian, with English summary).
- Milne Edwards A. 1860: Histoire des Crustacés podophthalmiques fossiles et Monographie des Décapodes Macroures de la famille des Thalassinens. *Ann. Sci. Nat., 4e série* 14, 129–357.
- Moissette P., Dulai A. & Müller P. 2006: Bryozoan faunas in the Middle Miocene of Hungary: biodiversity and biogeography. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 233, 300–314.
- Moore R.C. & McCormick L. 1969: General features of Crustacea. In: Moore R.C. (Ed.): Treatise on Invertebrate Paleontology. Part R (Arthropoda) 4, 1, R57–R120. *Geological Society of America*, Boulder and *University of Kansas Press*, Lawrence.
- Müller P. 1974a: Les faunes de crustacés décapodes des calcaires miocènes de Budapest (1). *Földtani Közlöny* 104, 119–132 (in Hungarian, with French summary).
- Müller P. 1974b: Faune de décapodes (crustacés) du Miocène de Budapest (2). *Földtani Közlöny* 104, 275–287 (in Hungarian, with French summary).
- Müller P. 1975a: Faune de décapodes (crustacés) du Miocène de Budapest (3). *Földtani Közlöny* 105, 506–515 (in Hungarian, with French summary).
- Müller P. 1975b: *Trapezia* (Crustacea. Decapoda) dans l’Eocène et le Miocène de Hongrie. *Földtani Közlöny* 105, 516–523 (in Hungarian, with French summary).
- Müller P. 1976: Faune de décapodes (crustacés) dans le Miocène de Budapest (4). *Földtani Közlöny* 106, 149–160 (in Hungarian, with French summary).
- Müller P. 1978: Faune de décapodes (Crustacea) dans le Miocène de Budapest (5). *Földtani Közlöny* 108, 272–312 (in Hungarian, with French summary).
- Müller P. 1979a: The Indo-West-Pacific character of the Badenian decapod crustaceans of the Paratethys. In: VII International Congress on Mediterranean Neogene. Athens, September 27–October 2. *Ann. Géol. Pays Hell.*, Tome Hors Série 2, 865–869.
- Müller P. 1979b: Crustacés décapodes du Badénien et Sarmatien de Bulgarie. *Palaeontol. Strat. and Lithol.* 10, 3–8, pls. 1–3.
- Müller P. 1984a: Decapod Crustacea of the Badenian. *Geol. Hung. Ser. Palaeontol.* 42, 3–317.
- Müller P. 1984b: Messinian and older decapods from the Mediterranean with description of two new species. *Ann. Geol. Pays Hellen.* 32, 25–34.
- Müller P. 1987: Imre Lörenthey (1867–1917). In: Hála J. (Ed.): Rocks, Fossils and History – Italian–Hungarian Relations in the Field of Geology. XIIIth Symposium of INHIGEO Pisa–Padova, Italy 1987. *Ann. Hist. Hungarian Geol. Special Issue*, 91–93.
- Müller P. 1993: Neogene Decapod Crustaceans from Catalonia. *Scripta Mus. Geol. Semin. Barcinonensis* 225, 1–39.
- Müller P. 1996: Middle Miocene decapod Crustacea from southern Poland. *Prace Muzeum Ziemi* 43, 3–14, pls. 1, 2.
- Müller P. 1998: Decapode Crustacea aus dem Karpat des Korneuburger Beckens (Unter-Miozän, Niederösterreich). *Beitr. Paläont.* 23, 273–281.
- Müller P.M. 2004: History of reef-dwelling decapod crustaceans from the Paleocene to the Miocene with comments about Mesozoic occurrences. *Földtani Közlöny* 134, 237–255.
- Müller P.M. 2006: New decapods from the Miocene of Hungary — with remarks about their environment. *Földtani Közlöny* 136, 37–49.
- Müller P., Krobicki M. & Wehner G. 2000: Jurassic and Cretaceous primitive crabs of the family Prosopidae (Decapoda: Brachyura) — their taxonomy, ecology and biogeography. *Ann. Soc. Geol. Pol.* 70, 49–79.
- Mutel M.H.E., Waugh D.A., Feldmann R.M. & Parsons-Hubbard K.M. 2008: Experimental taphonomy of *Callinectes sapidus* and cuticular controls on preservation. *Palaaios* 23, 615–623.
- Nardo G.D. 1847: Modern Synonymy of the species recorded in the work entitled: Descriptions of crustaceans and fishes inhabiting the lagoons of the Veneto gulf, represented in black-and-white and colour by Abate Stefano Chierighini Ven. Venezia, XI+1–127 (in Italian).
- Ngoc-Ho N. 2003: European and Mediterranean Thalassinidea (Crustacea, Decapoda). *Zoosystema* 25, 439–555.
- Noël P., Monod T. & Laubier L. 2014: Crustacea in the biosphere. In: von Vaupel Klein J.C., Charmanatier-Daures M. & Schram F.R. (Eds.): Treatise on Zoology — Anatomy, Taxonomy, Biology. The Crustacea, Volume 4B. *BRILL*, Leiden, 3–116.
- Ossó A. & Stalennuy O. 2011: Description of the first fossil species of Bathynectes (Brachyura, Polybiidae) in the Badenian (middle Miocene) of the Medobory Hills (Ukraine, Central Paratethys), with remarks on its habitat ecology. *Treb. Mus. Geol. Barcelona* 18, 37–46.
- Paucă M. 1929: Zwei neue fossile Decapoden aus den Oligozänen Clupea crenata Schiefer von Suslăneski-Muscel und über die Bildung der Menilitschiefer. *A. R. Bulletin scientifique* 12, 4–5, 40–44.
- Piller W.E. & Harzhauser M. 2005: The Myth of the Brackish Sarmatian Sea. *Terra Nova* 17, 450–455.
- Piller W.E., Harzhauser M. & Mandic O. 2007: Miocene Central Paratethys stratigraphy – current status and future directions. *Stratigraphy* 4, 71–88.
- Pisera A. 1996: Miocene reefs of the Paratethys: a review. *SEPM Conc. Sediment. Paleont.* 5, 97–104.
- Plotnick R.E. 1986: Taphonomy of a modern shrimp: Implications for the arthropod fossil record. *Palaaios* 1, 286–293.
- Plotnick R., Baumiller T. & Wetmore K.L. 1988: Fossilization potential of the mud crab, *Panopeus* (Brachyura: Xanthidae) and temporal variability in crustacean taphonomy. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 63, 27–43.
- Polkowsky S. 2014: Krebse un Krabben aus nord-deutschen Geschieben. *Books on Demand*, Norderstedt, 1–444.
- Popov S.V., Rögl F., Rozanov A.Y., Steininger F.F., Shcherba I.G. & Kováč M. (Eds.) 2004: Lithological/Paleogeographic maps of Paratethys. *Cour. Forsch. Senck.* 250, 1–46.
- Popov S.V., Shcherba I.G., Ilyina L.B., Nevesskaya L.A., Paramonova N.P., Khondkarian S.O. & Magyar I. 2006: Late Miocene to Pliocene palaeogeography of the Paratethys and its relation to the Mediterranean. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 238, 91–106.
- Por D.D. 1986: Crustacean biogeography of the late Middle Miocene Middle Eastern landbridge. In: Gore R.H. & Heck



- K.L. (Eds.): Crustacean Biogeography. *Balkema*, 69–84.
- Radwański A., Górka M. & Wysocka A. 2006: Middle Miocene corallgal facies at Maksymivka near Ternopil (Ukraine): A preliminary account. *Acta Geol. Pol.* 56, 89–103.
- Renema W., Bellwood D.R., Braga J.C., Bromfield K., Hall R., Johnson K.G., Lunt P., Meyer C.P., McMonagle L.B., Morley R.J., O'Rea A., Todd J.A., Wesselingh F.P., Wilson M.E.J. & Pandolfi J.M. 2008: Hopping hotspots: global shifts in marine biodiversity. *Science* 321, 654–657.
- Reuss A.E. 1859: Zur Kenntnis fossiler Krabben. *Denkschr. kaiserl. Akad. Wiss. Wien* 17, 1–90.
- Reuss A.E. 1867: Die fossile Fauna der Steinsalzablagerungen von Wieliczka in Galizien. *Sitzungsber. Math. Naturwiss. Cl. Akad. Wiss., Wien* 55, 1, 173–176.
- Reuter M., Piller W.E., Harzhauser M., Mandic O., Berning B., Rögl F., Kroh A., Aubry M.P., Wielandt-Schuster U. & Hamedani A. 2009: The Oligo-/Miocene Qom Formation (Iran): evidence for an early Burdigalian restriction of the Tethyan Seaway and closure of ist Iranian gateways. *Int. J. Earth Sci.* 98, 627–650.
- Reuter M. & Piller W.E. 2011: Volcanoclastic events in coral reef and seagrass environments: evidence for disturbance and recovery (Middle Miocene, Styrian Basin, Austria). *Coral Reefs* 30, 889–899.
- Reuter M., Piller W.E. & Erhart C. 2012: A Middle Miocene carbonate platform under silici-volcanoclastic sedimentation stress (Leitha Limestone, Styrian Basin, Austria) – Depositional environments, sedimentary evolution and palaeoecology. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 350–352, 198–211.
- Riegl B. & Piller W.E. 2000: Biostromal coral facies — A Miocene example from the Leitha Limestone (Austria) and its actualistic interpretation. *Palaios* 15, 399–413.
- Rögl F. 1998: Palaeogeographic considerations for Mediterranean and Paratethys seaways (Oligocene to Miocene). *Ann. Naturhist. Mus. Wien, Ser. A*, 99, 279–310.
- Rögl F. 1999: Mediterranean and Paratethys. Facts and hypotheses of an Oligocene to Miocene paleogeography (short overview). *Geol. Carpath.* 50, 339–349.
- Rögl F. & Steininger F. 1983: Vom Zerfall der Tethys zu Mediterran und Paratethys. Die Neogene Paläogeographie und Palinspastik des zirkum-mediterranen Raumes. *Ann. Naturhist. Mus. Wien, Ser. A*, 85, 135–163.
- Roveri M., Flecker R., Krijgsman W., Lofi J., Lugli S., Manzi V., Sierro F.J., Bertini A., Camerlenghi A., De Lange G., Govers R., Hilgen F.J., Hübscher Ch., Meijer P.Th. & Stoica M. 2014: The Messinian Salinity Crisis: Past and future of a great challenge for marine sciences. *Mar. Geol.* 352, 25–58.
- Sakai K. 1988: A new genus and five new species of Callianassidae (Crustacea: Decapoda: Thalassinidea) from Northern Australia. *The Beagle, Records of the Northern Territory Museum of Arts and Sciences* 5, 51–69.
- Schäfer W. 1951: Fossilisations-Bedingungen brachyurer Krabbe. *Abh. Senckenberg. Naturforsch. Gesell.* 485, 221–238.
- Schoupe A. 1949: Zwei Decapoden aus dem Torton von Retznei. *Mitt. Naturwiss. Verein Steiermark* 77/78, 139–141.
- Schulz H.-M., Bechtel A. & Sachsenhofer R.F. 2005: The birth of the Paratethys during the Early Oligocene: From Tethys to an ancient Black Sea analogue? *Global Planet. Change* 49, 163–176.
- Schweitzer C.E. 2001: Paleobiogeography of Cretaceous and Tertiary decapod crustaceans of the North Pacific Ocean. *J. Paleontol.* 75, 808–826.
- Schweitzer C.E., Feldmann R.M. & Lazăr I. 2009: Fossil Crustacea (excluding Cirripedia and Ostracoda) in the University of Bucharest Collections, Romania, including two new species. *Bull. Mizunami Fossil Museum* 35, 1–14.
- Steininger F. 1973: Die Molluscenfauna des Ottnangien. In: Papp A., Rögl F. & Seneš J. (Eds.): M2 Ottnangien. Die invertebraten, Salgótarján, Bántapusztaer Schichtgruppe und die Rzehakia Formation. *Chronostratigraphie und Neostratotypen, Miozän der zentralen Paratethys* 3, 380–615.
- Stempion J.A. 2005: Brachyuran taphonomy in a modern tidal-flat environment: Preservation potential and anatomical bias. *Palaios* 20, 400–410.
- Stimpson W. 1866: Descriptions of new genera and species of Macrurous Crustacea from the coasts of North America. *Proceedings of the Chicago Academy of Sciences* 1, 46–48.
- Studencka B. & Jasionowski M. 2011: Bivalves from the Middle Miocene reefs of Poland and Ukraine: A new approach to Badenian/Sarmatian boundary in the Paratethys. *Acta Geol. Pol.* 61, 79–113.
- Studencka B., Gontsharova I.A. & Popov S.V. 1998: The bivalve faunas as a basis for reconstruction of the Middle Miocene history of the Paratethys. *Acta Geol. Pol.* 48, 285–342.
- Studer T. 1892: Über zwei fossile dekapode Krabbe aus den Molasseablagerungen des Belpberges. *Abh. Schweiz. Pal. Ges.* 19, 1–11.
- Studer T. 1898: Zwei neue Brachyuren aus der miocänen Molasse. *Abh. Schweiz. Pal. Ges.* 25, 1–11.
- Sztano O. 1994: The tide-influenced Petrvasara sandstone, Early Miocene, Northern Hungary: sedimentology, palaeogeography and basin development. *Geol. Ultraiectina* 120, 1–155.
- Špinar Z., Čepek P., Bouček B., Eliášová-Frajová H., Havlíček V., Horný R., Houša V., Kalabis V., Kukulová J., Marek L., Nekvasilová O., Pokorný V., Prokop R., Příbyl A., Ružička B., Šnajdr M., Štemproková D. & Zikmundová J. 1965: Systematic palaeontology of invertebrates. *Academia*, Praha, 704–746 (in Czech).
- Toula F. 1904: Über eine neue Krabbe (*Cancer Bittneri* n. sp.) aus dem miocänen Sandsteine von Kalksburg bei Wien. *Jahrb. kaiserl.-königl. Geol. Reichsanst.* 54, 161–168.
- Von Reuss R. 1871: *Phymatocarcinus speciosus*, eine neue fossile Krabbe aus dem Leithakalke des Wiener Beckens. *Sitzungsber. österr. Akad. Wiss., math.-naturwiss. Kl.* I 63–64, 325–330.
- Wear R.G. & Yaldwyn J.C. 1966: Studies on Thalassinid Crustacea (Decapoda, Macrura Reptantia) with a Description of a New *Jaxea* from New Zealand and an Account of its Larval Development. *Zool. Publ. Victoria Uni. Wellington* 41, 1–27.
- Whiteaves J.F. 1874: On recent deep-sea dredging operations in the Gulf of St. Lawrence. *Am. J. Sci., ser.* 37, 210–219.
- Wolff C. 2014: Amphipoda. In: Martin J.W., Olesen J. & Høeg J. (Eds.): Atlas of Crustacean Larvae. *The Johns Hopkins University Press*, 206–209.
- Zázvorka V. 1956: *Micropsalis papyracea* Meyer, 1859 (Decapoda — Macrura natantia, Familie Palaemonidae) aus den oligozänen Süßwasserablagerungen Nordböhmens. *Sb. Nár. musea v Praze (Acta Mus. Nat. Pragae)* 12B, 1, 45–57, pl. 2–3.