

# Euryhaline preferences of the decapod crab *Mioplax socialis* enabled it to survive during the Badenian/Sarmatian extinction (Miocene) in the Central Paratethys

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**Abstract:** Although decapod crustaceans of the Central Paratethys were diverse during the Badenian (Langhian–Early Serravallian), a dramatic drop in their diversity occurred at the boundary with the Sarmatian. A crab *Mioplax socialis* is one of the few decapods reported from the Lower Sarmatian (*Mohrensternia* Zone) of the Paratethys. Until now, this species has been known from only a handful of specimens from Austria, Croatia and Bulgaria (Central Paratethys), and its systematics and ecology remain poorly known. Here, on the basis of new specimens from the Sarmatian tuffitic clays of the Stretava Formation (Skároš, Eastern Slovakia) we confirm that this species belongs to the subfamily Chasmocarcininae. The diagnostic characters of the male sternum that allow this classification are reported for the first time. The molluscan assemblage co-occurring with *M. socialis* demonstrate that this species tolerated conditions with variable salinity. Its tolerance of a broad range of salinity regimes may thus explain its survival across the Badenian–Sarmatian extinction event. Preservation of near-complete and fully articulated individuals of *M. socialis* suggests calm conditions and short residence times on the sediment–water interface.

**Key words:** Sarmatian, Crustacea, Mollusca, stratigraphy, euryhaline assemblage.

## Introduction

Decapod crustaceans are important components of marine benthic associations of the continental shelf and slope (Boudreau & Worm 2012; Lee 2015). Their evolutionary success is connected with several major diversification events; one of them occurred during the Miocene (Schweitzer 2001; Feldmann & Schweitzer 2006). This Miocene diversification was enhanced by the biogeographical differentiation of the Western Tethys into two different palaeogeographical areas, including the circum-Mediterranean and the Paratethys (Rögl 1998, 1999; Popov et al. 2004; Harzhauser & Piller 2007). Numerous decapod species have been recorded especially in the Central Paratethys, many of them being Paratethyan endemites.

One of the latest marine decapod associations of the Central Paratethys occurs in the lowermost Sarmatian strata (upper Serravallian) at Devínska Kobyla in the Slovak part of the Vienna Basin (Hyžný 2012; Hyžný & Hudáčková 2012; Hyžný et al. 2012). The stenohaline communities seem to disappear at the Badenian/Sarmatian boundary (Harzhauser & Piller 2007; Studencka & Jasionowski 2011) or during the earliest Sarmatian (Hyžný et al. 2012), depending on the regional differences in environmental conditions. They were replaced by homogeneous euryhaline biota, most of which were endemic to the region (Rögl 1998, 1999; Popov et al. 2004). However, occurrences of a single crab species, *Mioplax socialis* Bittner, 1884, were reported from the Lower

Sarmatian of Waldhof, Austria (Glaessner 1928), Kochava, Bulgaria (Müller 1979) and Skároš, Slovakia (Hyžný & Ledvák 2014); all these occurrences postdate the Badenian decapod associations from Devínska Kobyla (Hyžný et al. 2012). *Mioplax socialis*, until now known only from the Paratethys, seems to be such a Lower Sarmatian endemic species adapted to euryhaline conditions. This species probably represents the last marine crab of the Central Paratethys.

The type collection of *M. socialis* has not been studied since its description in the 19<sup>th</sup> century and only a few specimens of this species were known. As a consequence, all taxonomic treatments have been largely based on figures and original description of Bittner (1884); later reports by Glaessner (1928) and Müller (1979) did not add much to the knowledge of this crab. Recently, new *Mioplax* specimens were found in the Eastern Slovakia (Hyžný & Ledvák 2014). In this study, we analyse the co-occurring molluscan-bryozoan assemblage, revisit and re-figure the type material, and document the environmental preferences of this last marine crab of the Central Paratethys.

## Geological setting

The macrobenthic assemblage documented here is derived from a locality situated on the western slope of the Slanské Mts., approximately 1 km SE from the Skároš village (GPS N 48°34'49.58", E 21°24'19.43"), Eastern Slovakia

(Fig. 1b). In the right bank of the creek, a sequence of calcareous tuffitic clays of the Stretava Formation (Vass & Čverčko 1985) is exposed, locally with thin layers of pumice. The studied section is approximately 2.5 m-thick. At the base and on the top of the section, tuffs are exposed (Fig. 1c). They are largely composed of well-sorted volcanoclastics and pumice. The tuffs do not contain any fossil macrofauna. Among the tuffs, several layers of calcareous tuffitic clay with a total thickness of approximately 1.5 m are exposed. Calcareous clays (Fig. 1e) contain molluscs, crabs (a monospecific suite of *Mioplax socialis*) and bryozoans. On the basis of the molluscan assemblage, the exposed strata at the locality are estimated to be of Lower Sarmatian of age (*Mohrensternia* Zone).

### Material and methods

The specimens of *Mioplax socialis* described by Bittner (1884) and Glaessner (1928) and newly collected material from several localities in Eastern Slovakia, namely Skároš, Trstené pri Hornáde and Nižná Myšľa. More extensive sampling at one of these localities, Skároš (see above; Fig. 1), also provided a molluscan assemblage that allows us

to evaluate the palaeoenvironmental conditions (see Discussion).

Both, molluscs and decapods, were preserved largely as internal moulds. The material (1733 g) comprised presorted sediment samples with remains of macrofauna, including 83 specimens of molluscs (bivalves and gastropods) and 10 specimens of brachyurous crabs.

The aragonitic mollusc shells were completely leached; therefore, casts have been produced using two component vinyl polysiloxane (VPS), allowing an insight into original morphology. The specimens of decapods were photographed dry and uncoated or coated with ammonium chloride; for details see figure captions.

The repositories of specimens illustrated or referred to below are as follows:

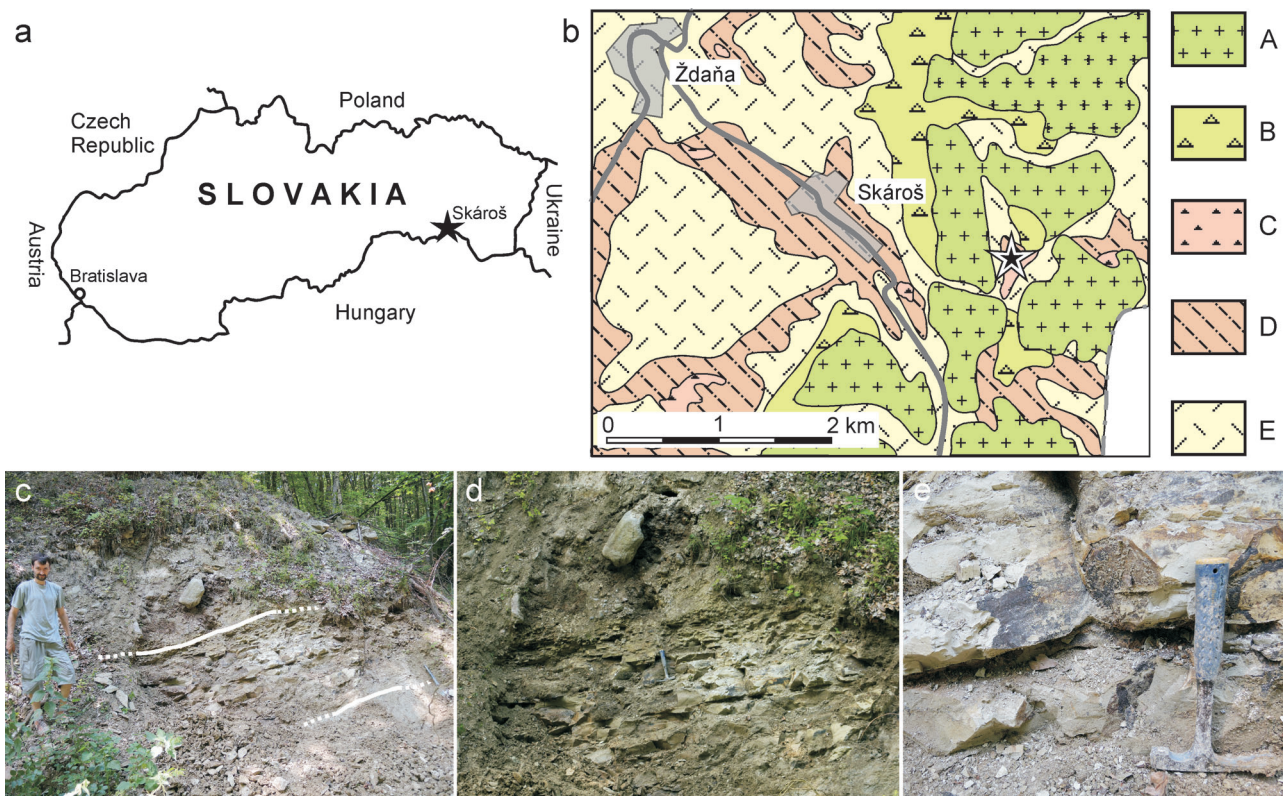
**GBA** — Geological Survey, Vienna (Austria)

**KGP-MH** — “Matúš Hyžný collection” at Department of Geology and Palaeontology, Faculty of Natural Sciences, Comenius University, Bratislava (Slovakia)

**NHMW** — Geological-palaeontological Department, Natural History Museum, Vienna

**UMJGPA** — Geological-palaeontological Department, Universalmuseum Joanneum, Graz (Austria)

**VSM** — The East Slovak Museum, Košice (Slovakia)



**Fig. 1.** Geographical position (a) and geological setting (b) of the surroundings of the locality Skároš. Legend: **A** — andesites and dacites (Sarmatian–?Pannonian); **B** — andesitic pyroclastics and epiclastics (Sarmatian–?Pannonian); **C** — rhyolitic tuffs and tuffites (Lower Sarmatian); **D** — clays and tuffites of the Stretava Formation (Lower and Middle Sarmatian); **E** — Quaternary deposits. **c** — Outcrop in the Stretava Formation. Fossiliferous tuffitic clays (demarcated by white lines) are exposed between volcanoclastics above and below them. **d–e** — Detailed view on the clays with Lower Sarmatian macrofauna. Map (b) modified after Kaličiak et al. (1996). Photographs in c and e by MH, d by PL.

### Systematic Paleontology

Identifications of molluscs are based on Kolesnikov (1935), Papp (1954, 1974), Boda (1959), Kojumdieva (1969), Švagrovský (1971), Neveškaya et al. (1993), Schultz (2001, 2003, 2005), Harzhauser & Kowalke (2002), Kowalke & Harzhauser (2004), and Lukeneder et al. (2011). Mollusc synonymy lists include only the first descriptions and the most recent or important references. Works of Ng et al. (2008), De Grave et al. (2009) and Schweitzer et al. (2010) are followed for higher classification of *Mioplax socialis* crabs. Synonymy of *M. socialis* is extensive.

Phylum Mollusca Linnaeus, 1758  
 Class Bivalvia Linnaeus, 1758  
 Subclass Pteriomorpha Beurlen, 1944  
 Superfamily Mytiloidea Rafinesque, 1815  
 Family Mytilidae Rafinesque, 1815

Genus *Musculus* Röding, 1798

**Type species:** *Mytilus discors* Linnaeus, 1767; subsequent designation by Iredale (1915); Recent, European Seas.

#### *Musculus sarmaticus* (Gatujev, 1916)

Fig. 2b

\*1916 *Modiolus* (*Brachydontes*) *sarmaticus* m. - Gatujev, p. 148-149, pl. 12, fig. 1.

2001 *Musculus* (*Musculus*) *sarmaticus* (Gatujev, 1916) - Schultz, p. 109-114, pl. 8, fig. 16.

**Material examined:** Five small sized (maximum length: 11.4 mm), disarticulated specimens preserved as interior and exterior valve imprints.

**Remarks:** They are of subtriangular outline, flattened, with weak radial riblets on central and dorsal shell exterior, interior margin shows minute crenulations.

**Occurrence:** Sarmatian of the Central Paratethys; Konkian to Bessarabian of the Eastern Paratethys (Schultz 2001).

Subclass Heterodonta Neumayr, 1884  
 Superfamily Cardioidea Lamarck, 1809  
 Family Cardidae Lamarck, 1809  
 Subfamily Lymnocardiinae Stoliczka, 1870  
 Genus *Obsoletiforma* Kolesnikov, 1948

**Type species:** *Cardium vindobonense* Laskarev, 1903, original designation. Miocene, Europe.

#### *Obsoletiforma cf. vindobonensis* (Laskarev, 1903)

Figs. 2c-e

\* 1903 *Cardium vindobonense* Partsch - Laskarev, p. 79, 141, pl. 3, figs. 14-19.

2003 *Obsoletiforma* (*Obsoletiforma*) *vindobonensis vindobonensis* (Laskarev, 1903) - Schultz, p. 585-595, pl. 87, figs. 1-2.

**Material:** 16 disarticulated and 7 articulated specimens are available, with a maximum length of 11.2 mm.

**Remarks:** Outline is anteriorly rounded, posteriorly truncated, transversal keel is moderately prominent. Ribs (~16

on the anterior to central and 8 on posterior shell portion) are flattened and smooth except for delicate scales present on anterior rib tops.

Shells are identical in size and in sculpture with specimens from the *Mohrensternia* Zone of Aspersdorf/Hollabrunn in Lower Austria (Papp 1954, 1974; Mandic et al. 2008). Both, however, lack the dense transversal scale ornamentation on rib tops typical for *Obsoletiforma vindobonensis* (Laskarev, 1903), but absent in *O. lithopodolica* (du Bois 1831), which seems to have in contrast a different outline (Kojumdieva 1969; Neveškaya et al. 1993). Both latter species were originally described from the Carpathian Foredeep, demanding a thorough revision of their true relationship to the Pannonian Basin *Obsoletiforma*. Yet, the preservation of the studied material does not allow more precise species-level identification at the moment.

**Occurrence:** Badenian to Sarmatian of the Central Paratethys, Konkian to Lower Bessarabian of the Eastern Paratethys (Schultz 2003).

Superfamily Tellinoidea Blainville, 1814

Family Semelidae Stoliczka, 1870

Genus *Abra* Lamarck, 1818

**Type species:** *Maetra tenuis* Montagu, 1803; by subsequent designation (Herrmannsen 1846); Recent, NE Atlantic and Mediterranean Sea.

#### *Abra reflexa* (Eichwald, 1830)

Fig. 2a

\*1830 *Donax reflexa*, m. - Eichwald, p. 208.

2005 *Abra* (*Syndosmya*) *reflexa* (Eichwald, 1830) - Schultz, p. 746-748, pl. 102, figs. 1-2.

**Material:** 3 articulated and 17 disarticulated specimens.

**Remarks:** Flattened, smooth shell, subtriangular in outline rounded anteriorly, and pointed posteriorly. With maximum shell length of 18.4 mm this is the largest mollusk species present in the samples.

**Occurrence:** Badenian to Lower Sarmatian of the Central Paratethys, Konkian to Bessarabian of the Eastern Paratethys (Kojumdieva 1969; Papp et al. 1974; Studencka et al. 1998; Schultz 2003).

Class Gastropoda Cuvier, 1795

Subclass Vetigastropoda Salvini-Plawen, 1980

Superfamily Trochoidea Rafinesque, 1815

Family Trochidae Rafinesque, 1815

Genus *Gibbula* Risso, 1826

**Type species:** *Trochus magus* Linnaeus, 1758, by subsequent designation (Herrmannsen 1847). Recent, Mediterranean Sea.

#### *Gibbula cf. guttenbergi* (Hilber, 1897)

Fig. 2h

\*1897 *Trochus Guttenbergi* Hilber, species nova - Hilber, p. 194-195, figs. 7-8.

1974 *Calliostoma* (*F[eneoniana]*.) *guttenbergi* (Hilber) - Papp, p. 325, pl. 1, figs. 1-3.



**Material:** With 17 specimens it is relatively abundant in the studied material.

**Remarks:** With only 6.5 mm maximum shell height this is a very small trochoid species. The trochiform shell comprises about 6 slightly convex whorls continuously increasing in size, ornamented by numerous delicate spiral ribs. Although highly similar to specimens from the *Mohrensternia*-beds of Waldhof in the Styrian Basin (e.g. Papp 1954), representing its type locality, complete specimens are missing and therefore the identification remains uncertain. As shown by Harzhauser & Kowalke (2002), the Sarmatian species formerly treated as *Calliostoma* Swainson, 1840 have to be placed in *Gibbula* Risso, 1826 based on protoconch morphology.

**Occurrence:** Lower Sarmatian of the Central Paratethys (Papp et al. 1974).

***Gibbula cf. blainvillei* (d'Orbigny, 1844)**

Fig. 2f

\*1844 *Trochus blainvillei* d'Orb., 1844- d'Orbigny, p.446-447, pl. 2, figs. 3-5.

1969 *Gibbula* (*Gibbula*) *blainvillei* (d'Orbigny, 1844) - Kojumdgieva, p. 68, pl. 24, fig. 20, pl. 25, fig. 1.

**Material:** A single depressed conical shell of 16.8 mm diameter.

**Remarks:** A shell with wide, moderately convex last whorl, flaring keel and smooth shell surface except for a single spiral cord is available. It seems to represent this generally rare species. *Gibbula papilla* (Eichwald, 1853), which has a comparable shape, is smaller. Both species are known so far only from Bessarabian deposits. This species group, however, has its roots in the Early Sarmatian *Gibbula sopronensis* (Papp, 1954), which is higher and has flat whorls. Due to this stratigraphic gap and the poor preservation we prefer to identify the specimen in open nomenclature.

**Occurrence:** Bessarabian of the Carpathian Foredeep and the Black Sea Basin (Kojumdgieva 1969); this is its first record from the Sarmatian of the Pannonian Basin System, namely the Central Paratethys.

Subclass Caenogastropoda Cox, 1960  
Superfamily Cerithioidea Fleming, 1822  
Family Batillariidae Thiele, 1929

Genus *Granulolabium* Cossmann, 1889

**Type species:** *Cerithium plicatum* Bruguière, 1792, by original designation. Early Miocene, France.

***Granulolabium bicinctum* (Brocchi, 1814)**

Fig. 2g

\*1814 *Murex bicinctus* nob.- Brocchi, p. 446, pl. 9, fig. 13.

2013 *Granulolabium bicinctum* (Brocchi, 1814) - Landau et al., p. 45, pl. 4, figs. 3-4. [cum. syn.]

**Material:** Only four specimens are present with maximum height of 18.0 mm.

**Remarks:** Shell comprises about 9 whorls, ultimate whorl attains 42 % of shell height. Sculpture, fully developed in last three whorls only, comprising three spiral keels and about

10 axial folds producing nodes at intersection with the ribs. Shell base bears two strong spiral keels. The species originated in the Early Miocene of the Eastern Atlantic, Mediterranean and Paratethys domain (Landau et al. 2013), and represents a survivor of the Badenian/Sarmatian extinction event. *G. pictum* (Defrance in Basterot, 1825), a name previously widely used for the Sarmatian records, is its junior synonym (Landau et al. 2013).

**Occurrence:** Early Miocene of NE Atlantic Ocean, Early to Middle Miocene of Paratethys, and Early Miocene to Pliocene of (Proto-)Mediterranean Sea (Landau et al. 2013).

Superfamily Rissooidea Gray, 1847

Family Rissoidae Gray, 1847

Subfamily Mohrensterniinae Korobkov, 1955

Genus *Mohrensternia* Stoliczka, 1868

**Type species:** *Rissoa angulata* Eichwald, 1853, subsequent designation (Nevill, 1885). Badenian and Early Sarmatian of Central and Eastern Europe.

**Remarks:** *Mohrensternia* is quite frequent in the samples (13 specimens) but a species level identification is difficult due to the poor preservation. Beside *Mohrensternia pseudoinflata* Hilber, 1897 the samples also seem to contain *Mohrensternia inflata* (Hörnnes, 1856).

***Mohrensternia cf. pseudoinflata* Hilber, 1897**

Fig. 2i-j

\*1897 [*Mohrensternia*] *pseudoinflata* Hilb. - Hilber, p. 201.

1971 *Mohrensternia pseudoinflata* Hilber, 1897 - Švagrovský, p. 285-287, pl. 44, figs. 6-9.

**Material:** At least one specimen.

**Remarks:** Shell minute, with maximum height of 8 mm, ovate conic, with 6 moderately inflated, slightly angular whorls; last whorl attaining 68% of shell height. Sculpture consists of prominent axial ribs with delicate spiral threads in the interspaces (Fig. 2i). This species differs from *M. inflata* in the presence of spiral threads and in the more conical outline and the distinctly less inflated and angulated last whorl. *Mohrensternia pseudosarmatica* Friedberg, 1923 (*sensu* Švagrovský 1971) is similar in sculpture but has deeper sutures and strongly convex whorls.

**Occurrence:** Lower Sarmatian of the Central and Eastern Paratethys (Švagrovský 1971; Papp et al. 1974). Kowalke & Harzhauser (2004) reported it from the Konkian, which is the Eastern Paratethys equivalent of Late Badenian.

Phylum Arthropoda von Siebold, 1848

Class Malacostraca Latreille, 1802

Order Decapoda Latreille, 1802

Infraorder Brachyura Latreille, 1802

Section Eubrachyura de Saint Laurent, 1980

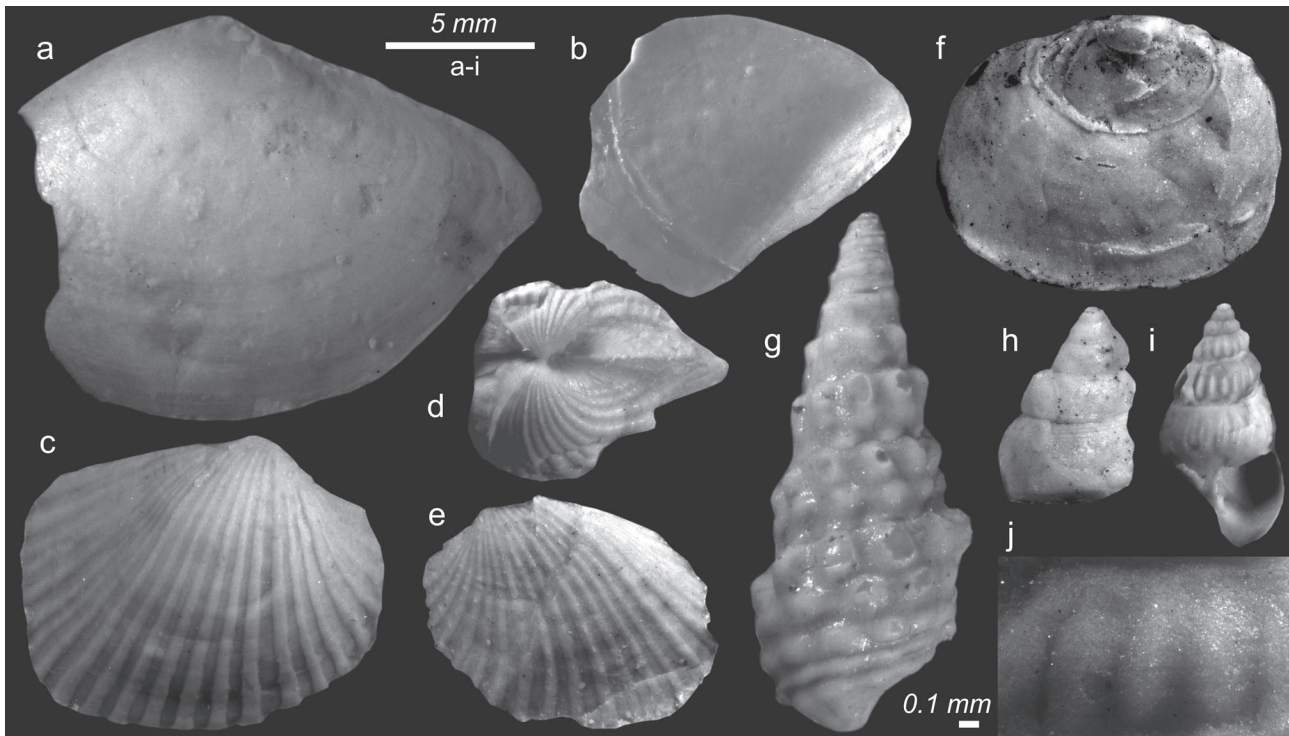
Subsection Heterotremata Guinot, 1977

Superfamily Goneplacoidea MacLeay, 1838

Family Chasmocarcinidae Serène, 1964a

Subfamily Chasmocarcininae Serène, 1964a

Genus *Mioplax* Bittner, 1884



**Fig. 2.** Molluscs identified in the studied samples from the Stretava Formation exposed at Skároš, Slovakia. **a** — *Abra reflexa* (Eichwald, 1830), left valve exterior (NHMW 2015/0400/0001); **b** — *Musculus sarmaticus* (Gatujev, 1916), right valve exterior (NHMW 2015/0400/0002); **c–e** — *Obsoletiforma* cf. *vindobonensis* (Laskarev, 1903), (**c**) right valve exterior (NHMW 2015/0400/0003), **d** — articulated shell dorsal view (NHMW 2015/0400/0004), **e** — left valve exterior (NHMW 2015/0400/0005); **f** — *Gibbula* cf. *blainvillei* (d'Orbigny, 1844) (NHMW 2015/0400/0006); **g** — *Granulolabium bicinctum* (Brocchi, 1814) (NHMW 2015/0400/0007); **h** — *Gibbula* cf. *guttenbergi* (Hilber, 1897) (NHMW 2015/0400/0008); **i–j** — *Mohrensternia* cf. *pseudoinflata* Hilber, 1897 (NHMW 2015/0400/0009). All photographs by OM.

**Type species:** *Mioplax socialis* Bittner, 1884, by monotypy.

**Diagnosis:** As for the type species.

**Remarks:** The genus was erected to accommodate a single species, *Mioplax socialis*, from the Badenian strata of present day Croatia (Bittner 1884). Later, it has also been reported from the Sarmatian of Austria (Glaessner 1928) and the genus was placed within the subfamily Goneplacinae MacLeay, 1838, the family Goneplacidae MacLeay, 1838 (Glaessner 1969). Karasawa & Kato (2003) argued that the presence of a small orbit and long, slender deflexed fingers of chelipeds strongly suggest assignment to the Chasmocarcininae Serène, 1964a. The subfamily was elevated to family level by Karasawa & Schweitzer (2006), and this was also followed by subsequent workers (see classifications by Ng et al. 2008; De Grave et al. 2009; Schweitzer et al. 2010). Presence of the supplementary coxosternal plate on male sternite 8 (Guinot et al. 2013), documented herein for the first time (Fig. 4f), and possession of male pleonal somites 3–5 fused (Feldmann et al. 2010) further strengthen inclusion of the genus into the Chasmocarcinidae. *Mioplax* is similar to other chasmocarcinids, however, it possesses a well-developed anterolateral spine, which is not present in any other genus of the family. The genus is rather close to *Collinsius* Karasawa, 1993, *Falconoplax* Van Straelen, 1933, *Orthakrolophos* Schweitzer & Feldmann, 2001, and *Styrioplax* Glaessner,

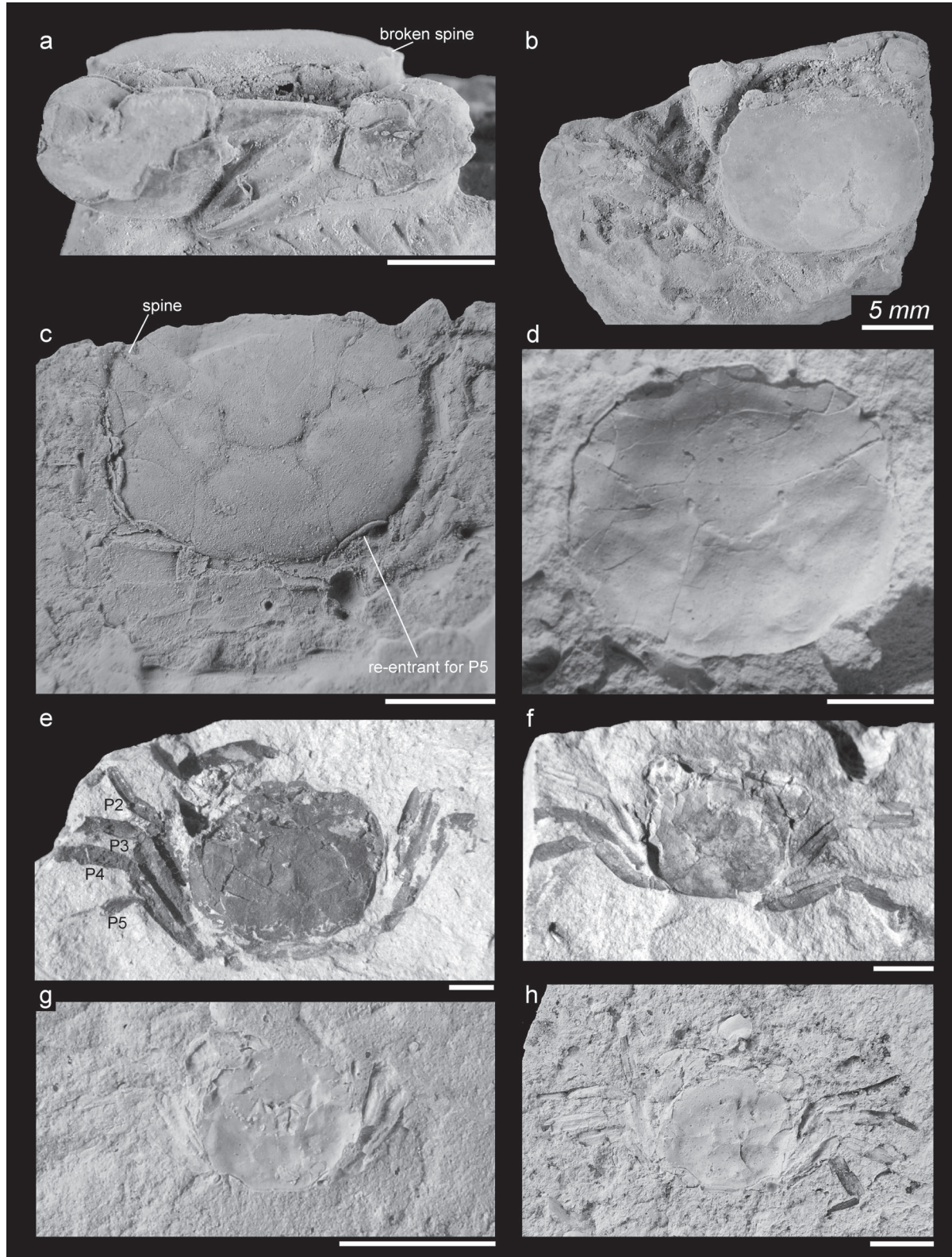
1969 (all four genera are known exclusively as fossils), but can be immediately distinguished from them based on the presence of the aforementioned anterolateral spine. Another exclusively fossil genus, *Gillcarcinus* Collins & Morris, 1978, is characterized by mesobranchial ridges, quite untypical for any other chasmocarcinid. Similarly, representatives of extant genera, *Camatopsis* Alcock & Anderson, 1899, *Chasmocarcinus* Rathbun, 1898, *Chasmocarcinops* Alcock, 1900, and *Hepthopelta* Alcock 1899, do not have distinct anterolateral spine (e.g., Rathbun 1898; Serène 1964b).

#### *Mioplax socialis* Bittner, 1884

Figs. 3–4

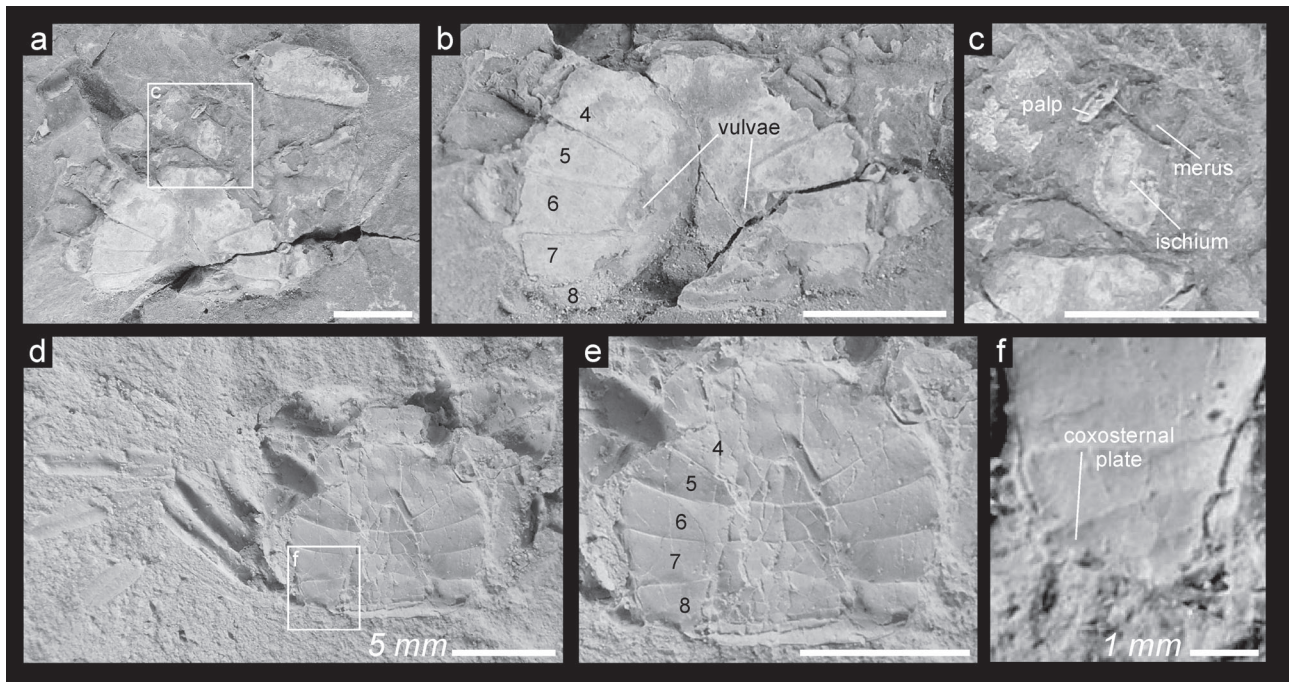
- 1884 *Mioplax socialis* Bittner, p. 23, pl. 2, figs. 3a–f.  
 1897 “*Krabbe*, Fam. *Catometopa*”. – Hilber, p. 109.  
 1928 *Mioplax socialis* Bittner. – Glaessner, p. 194.  
 1929 *Mioplax socialis* Bittner. – Glaessner, p. 258.  
 1929 *Mioplax socialis* Bittner. – Lörenthey & Beurlen, p. 258, pl. 16, fig. 10.  
 ?1940 *Potamon hungaricum* Körössy, fig. 9.  
 ?1955 *Pseudopotamon hungaricum* (Körössy) – Bott, p. 310.  
 ?1969 *Pseudopotamon hungaricum* (Körössy) – Bott, p. 272.  
 1969 *Mioplax socialis* Bittner. – Glaessner, p. R524, fig. 333.1.  
 1979 *Mioplax* cf. *socialis* Bittner. – Müller, p. 6, pl. 3, fig. 3.  
 2003 *Mioplax socialis* Bittner. – Karasawa & Kato, table 8.  
 2010 *Mioplax socialis* Bittner. – Schweitzer et al., p. 133.  
 ?2010 *Potamon?* *hungaricum* Körössy. – Klaus & Gross, p. 49, fig. 5D.  
 2014 *Mioplax socialis* Bittner. – Hyžný & Ledvák, p. 28, figs. 1–2.





**Fig. 3.** *Mioplax socialis* Bittner, 1884. **a–b** — Lectotype from Radoboj, Croatia (GBA 2009/0014/0029/01). **c** — Carapace in dorsal view with remains of sternum and pleonal segments from Waldhof, Austria (UMJGPA 4695). **d** — Carapace in dorsal view from Skároš, Slovakia (VSM/P-1131). **e** — Near-complete individual with venter preserved under superimposed carapace from Trstené pri Hornáde, Slovakia (VSM/P-1132). **f** — Complete individual with both chelipeds from Nižná Myšľa, Slovakia (VSM/P-1133). **g–h** — Near-complete individuals from Skároš (NHMW 2015/0401/0001-0002). The specimens in a–c were coated with ammonium chloride prior to photography. The scale bar equals 5 mm. Photographs in a–c, g–h by MH, d–f by Róbert Zajac.





**Fig. 4.** *Mioplax socialis* Bittner, 1884. **a-c** — Paralectotype from Radoboj, Croatia (GBA 2009/0014/0029/02). Female sternum (a-b) with preserved third maxilliped (c). **d-f** — Male individual in ventral aspect with complete sternum and pleon (d) from Skároš, Slovakia (NHMW 2015/0401/0003). Note the presence of coxosternal plate (f). Numbers in b and e denote sternites. The specimens in a-c were coated with ammonium chloride prior to photography. The scale bar equals 5 mm (all except f) and 1 mm (f). All photographs by MH.

**Emended diagnosis:** Carapace flat, square, only cardiac region marked; front wide, straight, single well-developed anterolateral spine directed forward.

**Type material (chosen herein from the syntype collection):** Radoboj, Croatia: lectotype GBA 2009/0014/0029/01 (a near-complete specimen with preserved carapace, both chelipeds and partly-preserved walking legs), paralectotype GBA/0014/0029/02 (a female specimen in ventral aspect with partially preserved chelipeds and left third maxilliped), paralectotype GBA/0014/0029/03 (a specimen in dorsal aspect with preserved carapace and left cheliped), and paralectotype GBA/0014/0029/04 (a male specimen in ventral aspect with partially preserved pereiopods).

**Additional material:** Waldhof, Austria: UMJGPA 4695 (carapace with partially preserved venter); Skároš, Slovakia: NHMW 2015/0401/0001-0002 (two near-complete individuals in dorsal aspect), NHMW 2015/0401/0003 (male individual in ventral aspect), NHMW 2015/0404/0004-0005, KGP-MH SK-001-008 and VSM/P-1131; Trstené pri Hornáde, Slovakia: VSM/P-1132; Nižná Myšľa, Slovakia: VSM/P-1133.

**Description:** Carapace sub-rectangular, slightly wider than long, widest at midlength; carapace transversely and longitudinally convex, with steep lateral margins. Front straight, with faint median notch; orbits shallow, orbital margins entire; anterolateral margin with one prominent spine directed forward and separated with a notch towards the orbit; posterolateral margin with concave re-entrants for pereiopods 5; posterior margin straight, rimmed. Carapace surface mostly smooth, tiny tubercles present at carapace

margins; most regions poorly defined; gastric region well-defined, posterior border delimited by cervical groove; cardiac region well-defined, sub-trapezoid in outline, slightly raised centrally, posterior border poorly defined.

Buccal frame narrowing anteriorly; third maxillipeds not closing buccal cavity; merus of third maxilliped endopod suboval, about half the length of ischium, palp (carpus-propodus-dactylus) distal; third maxilliped exopod not preserved. Sternum wide, all sutures interrupted; sterno-pleonal cavity reaching anterior of sternite 4; sternite 8 visible in ventral view; overlying posterior part of sternite 7. Sternite 8 in males with a groove in the middle covered by intercalated supplementary coxosternal plate, coxosternal plate as long as sternite 8. Male abdomen not entirely filling space between coxae of pereiopods 5; male pleonal somites 3-5 fused, narrowing slightly posteriorly, telson triangular.

Chelipeds (pereiopods 1) unequal, right chela stout and larger than left chela; carpus quadrate, propodus sub-quadrate with smooth surface, fingers long and slender. Pereiopods 2-5 achelate, long and slender.

**Remarks:** The material from Skároš fully conforms to the type material from Radoboj, Croatia (Bittner 1884). The difference is only in the type of preservation. Whereas the type series is represented by three-dimensional preservation of crabs within the concretions (Fig. 3a-b), specimens from the tuffitic clays of the Stretava Formation are flattened (Fig. 3d-h) and in many aspects they resemble another Miocene chasmocarcinid from the Paratethys, *Styrioplax exiguus* (Glaessner, 1928) reported from the Karpatian of Cerová-Lieskové, Slovakia (Hyžný & Schlögl 2011,

text-fig. 13). Similarly, specimens of *Mioplax socialis* reported by Glaessner (1928) from Waldhof (Austria) exhibit a flattened carapace (Fig. 3c).

All the specimens possess one anterolateral spine. Its presence is recognizable due to the indent (or notch) towards the front. The spine itself is not always preserved in its entirety, frequently it is broken (e.g. Fig. 3a, b, d). However, its base is invariably present in all specimens. The well-preserved spine is clearly visible in the Waldhof specimen (Fig. 3c). The specimen from Kochava (Bulgaria) is crushed and shows a poorly preserved anterolateral margin (Müller 1979, pl. 3, fig. 3), therefore, the diagnostic spine is not preserved. The morphology of the carapace, however, clearly indicates that this specimen belongs to the subfamily Chasmocarcininae and given its Sarmatian age there is little doubt about its assignment to *Mioplax socialis*.

The male pleon is described and figured here for the first time for *M. socialis* (Fig. 4d–e). Bittner (1884) reported on only one poorly preserved male specimen, all others were females. The male pleon of *M. socialis* is distinctly broader than that in *Styrioplax exiguus* (Glaessner, 1928) (see Gašparič & Hyžný 2015, figs. 10D–E, 11B), another chasmocarcinid crab from the Paratethys. This species, however, occurs in the Karpatian and Lower Badenian strata (Hyžný & Schlögl 2011; Gašparič & Hyžný 2015).

Apart from the material from Waldhof, Glaessner (1928) also reported two dactyli from the Sarmatian of Hernals (Vienna Basin) which he questionably attributed to *M. socialis*.

Based on two specimens from the Lower Sarmatian deposits of the Stretava Formation exposed at Ždaňa (Slovakia) Körössy (1940) described two crab specimens as *Potamon hungaricum*. Klaus & Gross (2010) in their synopsis of European fossil freshwater crabs provided a brief overview of this taxon and re-printed an original (rather poor) photograph of the holotype. They considered the species unlikely to represent a potamid crab. Not only the long and narrow legs argue against the assignment to the genus *Potamon* Savigny, 1816, but the material comes from marine to brackish pelites of the Stretava Formation which are unlikely to contain articulated remains of freshwater crabs. The type material of *P. hungaricum* is lost (Müller, pers. comm. in Klaus & Gross 2010) and the comparison with *Mioplax socialis* is thus not possible. However, according to Körössy (1940), the front of *P. hungaricum* is straight and typical also of *Mioplax*. The relatively small carapaces of *P. hungaricum* (max. carapace width 14 mm) also fit within the size-range of *M. socialis*. Both sedimentological settings (pelites of the Stretava Formation) and stratigraphy (Early Sarmatian), are shared by the occurrences of *P. hungaricum* from Ždaňa and *M. socialis* of Skároš. Moreover, both localities are only few kilometres apart. Finally, Zlinská & Fordinál (1995) mentioned the presence of crab claws that may belong to *M. socialis* from the same formation at Slanská Huta.

**Occurrence:** *Mioplax socialis* has been reported from the Badenian of Radoboj in Croatia (Bittner 1884), and Lower Sarmatian of Waldhof (*Mohrensternia* beds) in Austria (Glaessner 1928), Kochava in Bulgaria (Müller 1979), and Skároš, in eastern Slovakia (Hyžný & Ledvák 2014; herein). Müller (1979, p. 6) also mentioned occurrences in Hungary

(boreholes in the vicinity of Nagybózsza and Mány), however, he did not supply any figure. Occurrences of *Potamon hungaricum* from the Lower Sarmatian of Ždaňa and Slanská Huta in eastern Slovakia seem to belong to *M. socialis*.

## Discussion

**Stratigraphy:** A poorly diverse, euryhaline-type molluscan-assemblage from Skároš, dominated by cardiids, semmelids, rissoids, and gibbulids, implies its Sarmatian (Middle Miocene) age (Papp et al. 1974). In addition, the presence of *Mohrensternia*, allows a clear correlation with the Lower Sarmatian *Mohrensternia* Zone (Papp 1954; Kowalke & Harzhauser 2004). This zone represents the lowermost interval of the Sarmatian ecostratigraphic zonation in the Central Paratethys and correlates with the time interval of 12.7 to 12.4 Ma (Harzhauser & Piller 2004).

At the genus level, all identified molluscan taxa represent survivors of the Badenian-Sarmatian extinction event (Harzhauser & Piller 2007; Studencka & Jasionowski 2011). At the species level and in the Central Paratethys domain, *Obsoletiforma vindobonensis* is restricted to the Sarmatian, *Gibbula guttenbergi* and *Mohrensternia pseudoinflata* to the Early Sarmatian, whereas the other three species (*Musculus sarmaticus*, *Abra reflexa*, and *Granulolabium bicinctum*) existed already during the Badenian (Papp 1974; Studencka et al. 1998; Landau et al. 2013). Similarly, the crab component of the association, *Mioplax socialis*, is known not only from the Early Sarmatian (Glaessner 1928; Müller 1979), but also from the Badenian strata as documented by occurrence of marine fauna with *Anadara diluvii* (Lamarck), *Nucula* cf. *mayeri* (Hörnes), *Perna aquitanica* (Mayer), *Psammotreta* aff. *papyracea* (Chemnitz), and *Ptychidia* cf. *vindobonensis* (Handmann) at the type locality Radoboj, NW Croatia (Bittner 1884). Moreover, Bittner (1884) expressively stated that the crab-bearing strata probably underlie the Leitha limestone (Badenian in age). Glaessner (1928, p. 194) expressed some doubts about the age of the specimens from Radoboj. The euryhaline preferences of *Mioplax socialis* would explain why the crab has been found both in the Badenian and Sarmatian strata without questioning the statement of Bittner (1884).

**Environment and ecology:** Taxonomic abundances at Skároš are rather evenly distributed, with a mixture of suspension-feeders and deposit-feeders, and show that the community was heavily dominated by a single species (Fig. 5). Such evenness may imply stable environmental conditions, without strong fluctuation of chemical or physical parameters such as salinity, oxygen, or water energy, although multiple other ecologic and taphonomic factors, other than environmental stability affect the community structure (Kidwell & Bosence 1991). The abundant rissoids point to calm littoral conditions (Kowalke & Harzhauser 2004). The thin-shelled generalistic species *Abra reflexa* occurs in estuarine settings during the Sarmatian (Mandić et al. 2008), but monospecific occurrences are reported only from calm, oxygen poor, and deeper water settings (Studencka & Jasionowski 2011). In contrast, *Granulolabium bicinctum* is typically dominant on algal mats in lower intertidal settings



(Harzhauser & Kowalke 2002; Lukeneder et al. 2011; Landau et al. 2013). We suggest the assemblage from Skároš is most likely derived from the subtidal zone, close to the shore, but at least beneath the fair-weather wave base.

With the exception of complete aragonite leaching and micro-fractures (originating from post-depositional compaction processes), the shells are relatively well-preserved, the fragmented shells are rare. The proportion of articulated bivalve shells is moderate to low (44 % of cardiiids, 18 % of semelids, and no mytilids are articulated). Among the articulated shells, the fully open individuals in butterfly position dominate, whereas closed individuals are rare. In particular, only one such cardiid shell is present in the samples, suggesting that shells are basically never found in their living position. In contrast, four cardiid and one semelid shells show butterfly position. Shells are oriented concordantly with the bedding planes. Such preservation supports a previous interpretation of a calm depositional setting and low degree of benthic mixing due to bioturbation (Kidwell & Bosence 1991). Thus, after their natural death, the shells were gradually covered by pelitic sediment. As suggested by the frequent articulated shells, this preservation occurred without

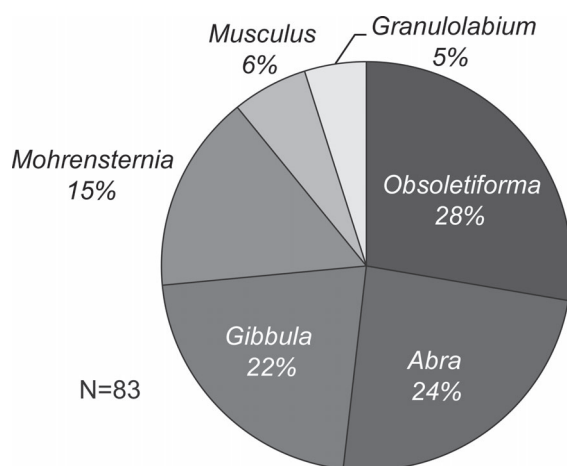
previous dragging from the sea bottom by currents or wave action. *Mioplox socialis* crabs are commonly preserved as fully articulated individuals which corroborates the interpretation of low-energy conditions with a relatively short residence time on the sediment-water interface. Bodies of decapod crustaceans decompose relatively quickly (Schäfer 1951; Plotnick 1986; Plotnick et al. 1988; Stempien 2005; Mutel et al. 2008); a calm depositional setting coupled with burial without subsequent physical disturbance is a prerequisite for preservation of complete or near-complete specimens (Müller et al. 2000, fig. 23).

This interpretation of rather stable conditions some distance from the high-energy environments is in accordance with the monospecific presence of the bryozoans *Schizoporella* cf. *tetragona* (Reuss, 1847), which is common in the investigated samples (see also Filipescu et al. 2014; Fig. 6).

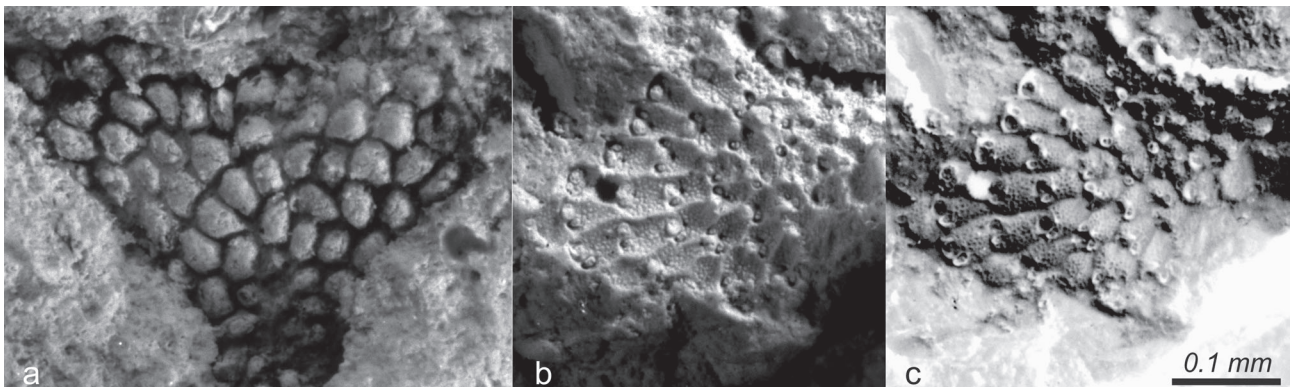
## Conclusions

With the exception of some lowermost Sarmatian decapods occurring in the Vienna Basin, *Mioplox* is the sole decapod crab occurring in the Lower Sarmatian of the Central Paratethys (*Mohrensternia* Zone). The molluscan assemblage from the tuffitic clays of the Stretava Formation exposed in Eastern Slovakia (Central Paratethys) demonstrates that *M. socialis* was a euryhaline species, which was likely the reason why it survived the Badenian/Sarmatian extinction event (Harzhauser & Piller 2007). Preservation of near-complete and articulated individuals at virtually all localities with *M. socialis* suggests that the species inhabited a calm, low-energy setting and most probably environmental conditions without a strong fluctuation in oxygen or water energy.

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**Fig. 5.** Chart showing the overall abundance of molluscs in studied samples from Skároš, Slovakia.



**Fig. 6.** Bryozoan *Schizoporella* cf. *tetragona* (Reuss, 1847) from Skároš, Slovakia (NHMW 2015/0400/0010). a — cast fossil; b — mold fossil; c — as previous, colour inverted. All photographs by OM.

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## References

- Alcock A. 1899: Materials for a carcinological fauna of India. No. 4. The Brachyura Cyclometopa. Part II. A revision of the Cyclometopa with an account of the families Portunidae, Cancridae and Corystidae. *J. As. Soc. of Beng.* 68, 1–104.
- Alcock A. 1900: Materials for a carcinological fauna of India. No. 6. The Brachyura Catometopa, or Grapsoidea. *J. As. Soc. of Beng.* 69, 2, 279–456.
- Alcock A. & Anderson A.R.S. 1899: Natural history notes from H.M. Royal Indian Marine Survey Ship 'Investigator,' Commander T.H. Heming, R.N., commanding.—Series III., No. 2. An account of the deep-sea Crustacea dredged during the surveying-season of 1897–98. *Ann. Mag. Nat. Hist., series 7*, 3, 1–27.
- Basterot M. De 1825: Mémoire Géologiquesur les Environs de Bordeaux, Première partie [Texte imprimé] : comprenant les observations générales sur les mollusque fossiles, et la description particulière de ceuxqu'on rencontre dans ce bassin. Paris, 1–112.
- Beurlen K. 1944: Beiträge zur Stammesgeschichte der Muscheln. *Math.-Naturwiss. Abt. Bayer. Akad. Wiss. München, Sitzber.* 1944/1–2, 133–145.
- Bittner A. 1884: Beiträge zur Kenntniss Tertiärer Brachyuren-Faunen. *Denkschr. kais. Akad. Wiss. math.-naturwiss. Kl.* 48, 15–30.
- Blainville H.-M.D. de 1814: Mémoire sur la classification méthodique des animaux mollusques, et établissement d'une nouvelle considération pour y parvenir. *Bull. Sci. Soc. Philomatique de Paris, Zoologie* 1814, 175–180.
- Boda J. 1959: Das Sarmat in Ungarn und seine Invertebraten-Fauna. *Ann. Inst. Geol. Hung.* 47, 569–862.
- Bodreau S.A. & Worm B. 2012: Ecological role of large benthic decapods in marine ecosystems: a review. *Mar. Ecol. Prog. Ser.* 469, 195–213.
- Bott R. 1955: Die Süßwasserkrabben von Afrika und ihre Stammesgeschichte. *Ann. Mus. Royale Congo Belge* 1, 209–352.
- Bott R. 1969: Präadaption und Besiedlungsgeschichte der Süßwasserkrabben der Erde. *Natur und Museum* 99, 266–275.
- Brocchi G.V. 1814: Fossil shells from the Subapennin and geological observations on the apennin and the surrounding area. [Conchiologia fossile subapennina, con osservazioni geologiche sugli Apennini e sul suolo adiacente.] *Dalla Stamepria Reale*, Milano, 1–712 (in Italian).
- Bruguière J.G. 1789–1792: Encyclopédie méthodique ou par ordre de matières. Histoire naturelle des vers. Paris, 1–2. 1: xviii + 1–344 (1789); 2: 345–757 (1792).
- Collins J.S.H. & Morris S.F. 1978: New Lower Tertiary crabs from Pakistan. *Palaeontology* 19, 957–981.
- Cossmann M. 1889: Catalogue illustré des coquilles fossiles de l'Éocène des environs de Paris (4ème fascicule). *Ann. Soc. Royale Malacol. Belg.* 24, 3–385.
- Cox L.R. 1960: Thoughts on the classification of the Gastropoda. *Proc. of the Zoological Soc. London* 33, 239–261.
- Cuvier G. 1795: Second Mémoire sur l'organisation et les rapports des animaux à sang blanc, dans lequel on traite de la structure des Mollusques et de leur division en ordre, lu à la société d'Histoire Naturelle de Paris, le 11 prairial an troisième [30 May 1795]. *Magazin Encyclopédique, ou Journal des Sciences, des Lettres et des Arts*, 2, 433–449.
- De Grave S., Pentcheff N.D., Ah Yong S.T., Chan T.-Y., Crandall K.A., Dworschak P.C., Felder D.L., Feldmann R.M., Fransen C.H.J.M., Goulding L.Y.D., Lemaitre R., Low M.E.Y., Martin J.W., Ng P.K.L., Schweitzer C.E., Tan S.H., Tshudy D. & Wetzer R. 2009: A classification of living and fossil genera of decapod crustaceans. *Raffles B. Zool.* 21, 1–109.
- du Bois de Montpéroux F. 1831: Conchiologie fossile et aperçu géognostique des formations du plateau Wolhyni-Podolien. Berlin, *Schropp & Comp.*, 1–76.
- Eichwald E. 1830: Naturhistorische Skizze von Lithauen, Volhynien und Podolien in geognostisch-mineralogischer, botanischer und zoologischer Hinsicht. *Voss*, Wilna, 1–256.
- Eichwald E. 1853: Lethaea Rossicaou Paléontologie de la Russie 3, dernière période. *Schweizerbart*, Stuttgart, 1–533.
- Feldmann R.M. & Schweitzer C.E. 2006: Paleobiogeography of Southern Hemisphere decapod Crustacea. *J. Paleontol.* 80, 83–103.
- Feldmann R.M., Schweitzer C.E. & Encinas A. 2010: Neogene decapod Crustacea from southern Chile. *Ann. Carnegie Mus.* 78, 337–366.
- Filipescu S., Miclea A., Gross M., Harzhauser M., Zágoršek K., & Jipa C. 2014: Early Sarmatian paleoenvironments in the easternmost Pannonian Basin (Borod Depression, Romania) revealed by the micropaleontological data. *Geol. Carpath.* 65, 67–81.
- Fleming J. 1822: Philosophy of Zoology; or a general view of the structure, functions, and classifications of animals. 2, *Hurst*, Edinburgh, 1–618.
- Friedberg W. 1911–1928: Mollusca miocaenica Poloniae, pars I (Gastropoda et Scaphopoda). *Musaeum Dzieduszyckianum*, Lwów-Poznań. 1911: 1–112; 1912: 113–240; 1914: 241–360; 1923: 361–440; 1928: 441–561.
- Gašparič R. & Hyžný M. 2015: 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.
- Gatujev S.A. 1916: The Russian Neogene species of the genus *Modiolus*. *Trudy geol. muzeja AN* 2/5, 141–163. (in Russian)
- 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. 1969: Decapoda. In: Moore R.C. (Ed.): *Treatise on Invertebrate Paleontology*, Part R. Arthropoda 4 (2), Geological Society of America, Boulder, and *University of Kansas Press*, Lawrence, R399–R533.
- Gray J.E. 1847: A list of the genera of recent Mollusca, their synonyma and types. *Proc. of the Zoological Soc. London* 15, 129–219.
- Guinot D. 1977: Propositions pour une nouvelle classification des Crustacés Décapodes Brachyours. *Hebd. Acad. Sci., série D* 285, 1049–1052.
- Guinot D., Tavares M. & Castro P. 2013: Significance of the sexual openings and supplementary structures on the phylogeny of brachyuran crabs (Crustacea, Decapoda, Brachyura), with new nomina for higher-ranked podotreme taxa. *Zootaxa* 3665, 1, 1–414.
- Harzhauser M. & Kowalke T. 2002: Sarmatian (Late Middle Miocene) gastropod assemblages of the Central Paratethys. *Facies* 46, 57–82.
- Harzhauser M. & Piller W.E. 2004: Integrated Stratigraphy of the Sarmatian (Upper Middle Miocene) in the western Central Paratethys. *Stratigraphy* 1, 65–86.
- 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.
- Herrmannsen A.N. 1846–1852: Indiciis generum malacozoorum primordia. Nomina subgenerum, generum, familiarum, tribuum, ordinum, classium: adjectis auctoribus, temporibus, locis systematicis atque literariis, etymus, synonymis. Praetermittuntur Cirripedia, Tunicata et Rhizopoda, *T. Fischeri*, Cassel, 1–2, 1–232 (1846), 233–637 (1847) (1); 1–352 (1847), 353–492 (1848), 493–717 (1849), supplement (1852).
- Hilber V. 1897: Die sarmatischen Schichten vom Waldhof bei Wetzelzdorf, Graz SW. *Mitt. naturwiss. Ver. Steiermark* 33/1896, 182–204.
- Hörnes M. 1856: Die fossilen Mollusken des Tertiär-Beckens von Wien. I. Univalven. *Abh. k.-k. geol. Reichsanst.* 3, 1–736.
- Hyžný M. 2011: Synopsis of fossil decapod crustaceans from Slovakia (Western Carpathians). *N. Jahrb. Geol. Paläont. Abh.* 260, 165–171.
- Hyžný M. 2012: *Callixina chalmasii* (Brocchi, 1883) comb. nov. (Decapoda: Axiidea: Callianassidae: Eucalliinae), a ghost shrimp from the Middle Miocene of Europe, with reappraisal of the fossil record of Eucalliinae. *Zootaxa* 3492, 49–64.
- Hyžný M. & Hudáčková 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. & 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. & Schlögl J. 2011: An early Miocene deep-water decapod crustacean faunas from the Vienna Basin (Western Carpathians, Slovakia). *Palaeontology* 54, 323–349.
- Hyžný M., Hudáčková N., Biskupič R., Rybár S., Fuksi T., Halásová E., Zágorský 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 Geologica Slovaca* 4, 2, 5–21.
- Iredale T. 1915: A commentary on Suter's "Manual of the New Zealand Mollusca". *Trans. Proc. New Zealand Inst.* 49, 417–497.
- Kaličiak M., Baňacký V., Janočko J., Karoli S., Petro L., Spišák Z., Vozár J. & Žec B. 1996: Geological map of the Slanské vrchy Mts. and the Košická kotlina Basin, Southern part, *GS SR*, Bratislava.
- Karasawa H. 1993: Cenozoic decapod Crustacea from southwest Japan. *Bull. Mizunami Fossil Mus.* 20, 1–92, 24 pls.
- Karasawa H. & Kato H. 2003: The family Goneplacidae MacLeay, 1838 (Crustacea: Decapoda: Brachyura): systematics, phylogeny, and fossil records. *Paleontol. Res.* 7, 2, 129–151.
- Karasawa H. & Schweitzer C.E. 2006: A new classification of the Xanthoidea *sensu lato* (Crustacea: Decapoda: Brachyura) based on phylogenetic analysis and traditional systematics and evaluation of all fossil Xanthoidea *sensu lato*. *Contributions to Zoology* 75, 1/2, 23–73.
- Kidwell S.M. & Bosence D.W.J. 1991: Taphonomy and Time-Averaging of Marine Shelly Faunas. In: Allison P.A. & Briggs D.E.G. (Eds.): Taphonomy: Releasing the Data Locked in the Fossil Record. *Topics in Geobiology* 9, *Plenum Press*, New York, 115–209.
- Klaus A. & Gross M. 2010: Synopsis of the fossil freshwater crabs of Europe (Brachyura: Potamoidea: Potamidae). *N. Jahrb. Geol. Paläont. Abh.* 256, 39–59.
- Kojumdgieva E. 1969: Sarmatien. *Lés fossiles de Bulgarie* 8, Sofia, 1–223.
- Kolesnikov V.P. 1935: Sarmatian Molluscs. *Paleontologija SSSR* 10/2, *Akad. Nauk*, Leningrad 1–508. (in Russian)
- Kolesnikov V.P. 1948: Syngenetic schemes. *Biul. Mosk. obchestvaustim. prir., otd. geol.* 23, 1, 15–25. (in Russian)
- Korobkov I.A. 1955: Handbook and methodological guide to Tertiary Mollusca (Gastropoda). *Gostoptehizdat*, Leningrad, 1–795. (in Russian)
- Körössy L. 1940: Kurze geologische Beschreibung der Umgebung von Hernádsaadány. *Földt. Közl.* 70, [Species description in Hungarian], 83–109, 143–144.
- Kowalke T. & Harzhauser M. 2004: Early ontogeny and palaeoecology of the Mid-Miocene rissoid gastropods of the Central Paratethys. *Acta Palaeontol. Pol.* 49, 111–134.
- Lamarck J.B.P.A. de M. de. 1809: Philosophie Zoologique, ou Exposition des Considérations Relative à l'Histoire Naturelle des Animaux 2 vols, *chez Dentu et l'Auteur*, Paris, vol. 1, xxv + 1–422, + Table des Matières, 423–428; vol. 2, 1–466 + Table des Matières, 467–475.
- Lamarck M. 1818: Histoire naturelle des animaux sans vertèbres. Volume 5, *Deterville, Verdier*, Paris, 411–612.
- Landau B.M., Harzhauser M., İslamoğlu Y. & Marques da Silva C. 2013: Systematics and palaeobiogeography of the gastropods of the middle Miocene (Serravallian) Karaman Basin of Turkey. *Cainozoic Research* 11–13, 3–576.
- Laskarev V.D. 1903: Die Fauna der Buglowka-Schichten in Volhynien. *Mém. Com. Géol., Nov. série* 5, 28, 1–148.
- Latreille P.A. 1802–1803: Histoire naturelle, générale et particulière, des Crustacés et des Insectes, 3, *F. Dufart*, Paris, 1–468.
- Lee S.Y. 2015: Ecology of Brachyura. In: Castro P., Davie P., Guinot D., Schram F. & Vaupel Klein J. von (eds): Treatise on Zoology – Anatomy, taxonomy, biology. The Crustacea, vol. 9, Part C-I, Chapter 71–9, *Brill*, Leiden/Boston, 469–542.
- Linnaeus C. 1758: Systema naturae per regna trianaturae, secundum Classes, Ordines, genera, species, cum characteribus, differentiis, synonymis, locis. – Editio Decima, Reformata, Tom. I, *Laurentii Salvi*, Holmiae, iii+1–824.
- Linnaeus C. 1767: Systema naturae sive regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. 12<sup>th</sup> ed. vol. 1 (part 2), *Laurentii Salvi*, Holmiae, 533–1327.
- Lőrenthey E. & Beurlen K. 1929: Die fossilen Dekapoden der Länder der Ungarischen Krone. *Geol. Hungar. Ser. Palaeontol.* 3, 1–421.
- Lukeneder S., Zuschin M., Harzhauser M. & Mandic O. 2011: Mollusc-based statistics in an endemic marine system as tool in palaeoecology and stratigraphy. *Acta Palaeontol. Pol.* 56, 767–784.
- MacLeay W.S. 1838: On the brachyurous decapod Crustacea brought from the Cape by Dr. Smith. In: Smith, A. (Ed.): Illustrations of the Annulosa of South Africa; being a portion of the objects of natural history chiefly collected during an expedition into the interior of South Africa, under the direction of Dr. Andrew Smith, in the years 1834, 1835. and 1836; fitted out by "The Cape of Good Hope Association for Exploring Central Africa", *Smith, Elder, and Co*, London, 53–71, +2 plates.
- Mandic O., Harzhauser M., Roetzel R. & Tibuleac P. 2008: Benthic mass-mortality events on a Middle Miocene incised-valley tidal-flat (North Alpine Foredeep Basin). *Facies* 54, 343–359.
- Montagu G. 1803: Testacea Britannica, or natural history of British shells, marine, land, and fresh-water, including the most minute; systematically arranged and embellished with figures. *White*, London, 1–606.
- Müller P. 1979: Crustacés décapodes du Badénien et Sarmatien de Bulgarie. *Palaeontol. Strat. and Lithol.* 10, 3–8, pls. 1–3.
- 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. *Palaios* 23, 615–623.
- Neumayr M. 1884: Zur Morphologie des Bivalvenschlosses. *Sitzber. Akad. Wiss. Wien* 88, 1, 385–418.
- Neveškaya L.A., Goncharova I.A., Paramonova N.P., Popov S.B., Babak E.B., Bagdasarjan K.G. & Voronina A.A. 1993: Identification guide to the Miocene bivalves of the south-western Eurasia. *Nauka*, Moskva, 1–412. (in Russian)
- Nevill G. 1885: Hand list of Mollusca in the Indian Museum, Calcutta. Part 2. Gastropoda. Prosobranchia-Neurobranchia. *Government Printer*, Calcutta, 1–306.
- Ng P.K.L., Guinot D. & Davie P.J.F. 2008: Systema Brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world. *Raffles Bull. Zool.*, Supplement No. 17, 1–286.
- d'Orbigny A. 1844: Paléontologie du voyage de M. Hommaire de Hell. Dans les steppes de la Mer Caspienne, le Caucase, la Crimée et la Russie Méridionale. In: Hommaire De Hell, X. 1844. Les steppes de la Mer Caspienne, le Caucase, la Crimée et la Russie Méridionale. Voyage pittoresque, historique et scientifique. *Levrault*, Paris, 3, 419–450.
- Papp A. 1954: Die Molluskenfauna im Sarmat des Wiener Beckens. *Mitt. Geol. Ges. Wien* 45, 1–112.
- Papp A. 1974: Die Molluskenfauna der Sarmatischen Schichtengruppe. In: Papp A., Marinescu F. & Seneš J. (Eds.): M5 Sarmatien. *Chronostratigraphie und Neostatotypen* 4, 318–427.
- Papp A., Marinescu F. & Seneš J. 1974: M5 Sarmatien (sensu E. SUESS, 1866). Die Sarmatische Schichtengruppe und ihr Stratotypus. *Chronostratigraphie und Neostatotypen* 4, 1–707.
- Plotnick R.E. 1986: Taphonomy of a modern shrimp: Implications for the arthropod fossil record. *Palaios* 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.
- 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.
- Rafinesque C.S. 1815: Analyse de la nature, ou tableau de l'univers et des corps organisés. Le nature est mon guide, et Linnéus mon maître. Palermo, 1–224.
- Rathbun M.J. 1898: The Brachyura of the biological expedition to the Florida Keys and the Bahamas in 1893. *Bull. Lab. Nat. Hist., State Univ. Iowa* 4, 3, 250–294, +Plates I–IX.
- Reuss A.E. 1847: Die fossilen Polyparien des Wiener Tertiaerbeckens. *Naturwiss. Abh. Haidinger* 2, 1–109.
- Risso A. 1826: Histoire naturelle des principales productions de l'Europe méridionale et particulièrement de celles des environs de Nice et des Alpes Maritimes. Tome deuxième, *Levrault*, Paris, 1–492.
- Röding P.F. 1798: Museum Boltenianum sive Catalogus Cime-liorum è Tribus Regnis Naturae Quae olim Collegerat Joa. Typis Johan. Christi. *Trappii* 2, i–viii, 1–199.
- 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.
- Salvini-Plawen L. 1980: A reconsideration of systematics in the Mollusca (phylogeny and higher classification). *Malacologia* 19, 249–278.
- Saint Laurent M. de 1980: Sur la classification et la phylogénie des Crustacés Décapodes Brachyours. I. Podotremata Guinot, 1977 et Eubrachyura sect. nov. *Cr. Hebd. Acad. Sci., série III* 290, 1265–1268.
- Savigny J.C. 1816: Mémoires sur les animaux sans vertèbres, 1, *Dufour*, Paris, 1–118.
- Schäfer W. 1951: Fossilisations-Bedingungen brachyurer Krebse. *Abh. Senckenberg. Naturforsch. Gesell.* 485, 221–238.
- Schultz O. 2001: Bivalvia neogenica (Nuculacea-Unionacea). In: Piller W.E. (Ed.): *Catalogus Fossilium Austriae* 1/1, *Verlag Österr. Akad. Wiss.*, Wien, 1–379.
- Schultz O. 2003: Bivalvia neogenica (Lucinoidea-Mactroidea). In: Piller W.E. (Ed.): *Catalogus Fossilium Austriae* 1/2, *Verlag Österr. Akad. Wiss.*, Wien, 381–690.
- Schultz O. 2005: Bivalvia neogenica (Solenioidea-Clavagelloidea). In: Piller W.E. (Ed.): *Catalogus Fossilium Austriae* 1/3, *Verlag Österr. Akad. Wiss.*, Wien, 691–1212.
- 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. 2001: Differentiation of fossil Hexapodidae Miers (Decapoda: Brachyura) from similar forms. *J. Paleontol.* 75, 330–345.
- Schweitzer C.E., Feldmann R.M., Garassino A., Karasawa H. & Schweigert G. 2010: Systematic list of fossil decapod crustacean species. *Crustaceana Monographs* 10, 1–222.
- Serène R. 1964a: Redescription du genre *Megaesthesius* Rathbun et definition des Chasmocarcininae, nouvelle sous-famille des Goneplacidae (Decapoda, Brachyura). *Crustaceana* 7, 175–187.
- Serène R. 1964b: Goneplacidae et Pinnotheridae. *Papers from Dr. Th. Mortensen's Pacific Expedition 1914–1916* 80, 181–282, Plates 16–24.
- Stempien J.A. 2005: Brachyuran taphonomy in a modern tidal-flat environment: Preservation potential and anatomical bias. *Palaios* 20, 400–410.
- Stoliczka F. 1868: Cretaceous Fauna of Southern India. The Gastropoda. *Mem. Geol. Surv. India* 2, 1–497.
- Stoliczka F. 1870–1871: Cretaceous fauna of southern India. The Pelycopoda, with a review of all known genera of this class, fossil and recent. *Palaeontologia Indica*, being figures and descriptions of the organic remains procured during the progress of the Geological Survey of India. *Mem. Geol. Surv. India* 6, 3, i–xxii, 1–538.
- 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.
- 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.
- Švagrovský J. 1971: Das Sarmat der Tschechoslowakei und seine Molluskenfauna. *Acta geol. geogr. Univ. Comen. Geologica* 20, 1–473.
- Swainson W. 1840: A treatise on malacology; or the natural classification of shells and shellfish. *Lardner's Cabinet Cyclopaedia*, London, 1–419.
- Thiele J. 1929–1935: Handbuch der systematischen Weichtierkunde, 1–2. *Fischer*, Jena, 1, 1: 1–376 (1929); 1, 2: 377–778 (1931); 2, 3: 779–1022 (1934); 2, 4: 1023–1154 (1935).
- Van Straelen V. 1933: Sur des Crustacés Décapodes Cénozoïques de Venezuela. *Bull. Mus. Royal d'Hist. Nat. Belg.* 9, 10, 1–11.
- Vass D. & Čverčko J. 1985: The Neogene lithostratigraphic units from the Eastern Slovakian Basin. *Geol. Práce, Správy* 82, 111–126. (in Slovak with English summary)
- von Siebold C.T. 1848: Lehrbuch der vergleichenden Anatomie der Wirbellosen Thiere. Erster Theil. In: von Siebold C.T. & Stan-nius H. (Eds.): *Lehrbuch der vergleichenden Anatomie. Verlag von Veit & Comp.*, Berlin, 1–679.
- Zlinská A. & Fordinál K. 1995: Lower Sarmatian Fauna from Drill-hole K-3 (Eastern Slovakian Basin). *Geol. Práce, Správy* 100, 71–75. (in Slovak with English summary)