

# Miocene squat lobsters (Decapoda, Anomura, Galatheoidea) of the Central Paratethys – a review, with description of a new species of *Munidopsis*

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Key words – Neogene, Austria, Slovakia, revision, new species.

All squat lobsters of the families Galatheidae, Munididae and Munidopsidae from the Miocene of the Central Paratethys are reviewed taxonomically. Based on additional observations emended diagnoses are provided for *Agononida cerovensis* and *Galathea weinfurteri*, from the Lower and Middle Miocene, respectively. *Munidopsis* is represented by two species in the study area; additional data for *M. lieskovenensis* from the Lower Miocene of Slovakia are presented and a new species, *M. palmuelleri*, from the Middle Miocene of Slovenia is erected. Implications for palaeoenvironmental reconstructions are briefly discussed for each taxon.

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## Introduction

The superfamily Galatheoidea currently comprises five families; Galatheidae Samouelle, 1819, Munididae Ah Yong, Baba, Macpherson & Poore, 2010, Munidopsidae Whiteaves, 1874, Porcellanidae Haworth, 1825 and Retrorsichelidae Feldmann, Tshudy & Thomson, 1993. The last-named is known exclusively from the fossil record. Except for the Retrorsichelidae, all galatheid families have previously been recorded from the Miocene of the Central Paratethys (see e.g., Bachmayer, 1950; Müller, 1984a; Hyžný & Schlögl, 2011; see Table 1). The present contribution is a review of galatheid, munidid and munidopsid squat lobsters from the Miocene of the Central Paratethys; the porcelain crabs (Porcellanidae) will be revised in a forthcoming paper.

Table 1. Galatheoid taxa recorded from the Miocene of the Central Paratethys (CP).

Family	Taxon	Stratigraphic range in CP
Galatheidae	<i>Galathea weinfurteri</i> Bachmayer, 1950	'Badenian'
Munididae	<i>Agononida cerovensensis</i> Hyžný & Schlögl, 2011	'Karpatian'
Munidopsidae	<i>Munidopsis lieskovensis</i> Hyžný & Schlögl, 2011	'Karpatian'
Munidopsidae	<i>Munidopsis palmuelleri</i> n. sp.	'Badenian'
Porcellanidae	<i>Petrolisthes haydni</i> Müller, 1984a	'Badenian'
Porcellanidae	<i>Petrolisthes magnus</i> Müller, 1984a	'Badenian'
Porcellanidae	<i>Pisidia kokayi</i> (Müller, 1974a)	'Badenian'
Porcellanidae	<i>Pisidia</i> aff. <i>viai</i> Müller, 1984b	'Badenian'

The Paratethys was an extensive network of inland seas intermittently connected to the Mediterranean and Indo-West Pacific (Rögl & Steininger, 1983; Rögl, 1998, 1999; Popov *et al.*, 2004; Harzhauser & Piller, 2007; Harzhauser *et al.*, 2007). Changing seaways and landbridges led to internal differentiation of the northern domain into a Western, Central and Eastern Paratethys. The Central Paratethys covered the area from present-day Austria to Poland, Ukraine and Romania; this includes the eastern Alpine-Carpathian Foreland basins (from Lower Austria to Moldavia) and the Pannonian Basin System (see Harzhauser *et al.*, 2003, fig. 10). Summaries of the palaeogeography and stratigraphy of the Central Paratethys include those by Rögl (1998, 1999), Popov *et al.* (2004), Harzhauser & Piller (2007) and Piller *et al.* (2007), to which reference is made.

Extinct galatheoids have recently been discussed and/or listed by Schweitzer & Feldmann (2000), De Angeli & Garassino (2002), Schweitzer *et al.* (2010) and Ahyong *et al.* (2011). Recently, numerous Jurassic taxa have been reassessed, and a range of new taxa have been erected (Robins *et al.*, 2012a, 2013).

### Material and methods

The material studied often is preserved in different ways, being dependent of the sedimentary facies. In carbonates usually isolated carapaces, of which often the rostra are broken, are found; (semi-)articulated specimens have yet to be discovered from such facies. This is the case for a widely distributed species, *Galathea weinfurteri* (see below). In fine siliciclastic sediments, specimens may retain articulated appendages, but usually only dorsal carapaces are preserved. In addition, the rostrum may be broken (*e.g.*, *Agononida cerovensensis*), but in many cases it is retained, as in both species of *Munidopsis* described below. Our terminology follows Klomp maker *et al.* (2012) and Robins *et al.* (2013).

The material studied was obtained either from institutional repositories (*e.g.*, *G. weinfurteri*) or recent collections made by three of us (MH, RG and JS). Specimens were prepared with needles and, where deemed necessary, by using a vibrating pneumatic needle. Where only imprints were preserved, a cast was produced (Stomaflex® Putty). Specimens were photographed dry, either uncoated or coated with ammonium chloride.

*Measurements* – The following parameters were measured: LR – total length of carapace, including rostrum; L – length of carapace, excluding rostrum; GH – length of

gastric region; TW – total width of anterior margin; MW – maximum carapace width. All measurements are in millimetres.

*Repositories* – Specimens studied are housed in the following institutions: IPUW, Institut für Paläontologie, Universität Wien, Vienna (Austria); KGP-MH, Department of Geology and Palaeontology, Comenius University, Bratislava (Slovakia); NHMW, Naturhistorisches Museum Wien, Vienna (Austria); RGA/SMNH, Slovenian Museum of Natural History, Ljubljana (Slovenia); SNM, Natural History Museum of the Slovak National Museum, Bratislava.

### Systematic palaeontology

**Order Decapoda Latreille, 1802**  
**Infraorder Anomura MacLeay, 1838**  
**Superfamily Galatheoidea Samouelle, 1819**  
**Family Galatheidae Samouelle, 1819**  
**Genus *Galathea* Fabricius, 1793**

*Type species* – *Cancer strigosus* Linnaeus, 1761, by subsequent designation of Latreille (1810).

*Diagnosis* – See Baba (2005, p. 74).

*Remarks* – In the fossil record, the present genus is represented by twelve species (see Garassino *et al.*, 2008; Schweitzer *et al.*, 2010), the oldest being *G. sahariana* Garassino, De Angeli & Pasini, 2008 from the Upper Cretaceous of Morocco. However, it should be noted that the chelae of *G. sahariana* possess proportionally long palms with rather short fingers (Garassino *et al.*, 2008, figs. 11, 12), while typical *Galathea* chelae have relatively short and spinose palms (Baba, 2005).

***Galathea weinfurteri* Bachmayer, 1950**  
 Figs. 1, 7A; Pls. 1, 2.

- 1928 *Galathea* sp.; Glaessner, pp. 164, 206, pl. 3, fig. 1.
- 1950 *Galathea weinfurteri* Bachmayer, p. 135, pl. 1, figs. 2-4.
- 1952 *Galathea weinfurteri*; Papp, p. 124.
- 1953 *Galathea weinfurteri*; Bachmayer, pp. 242, 243, pl. 5, figs. 3, 4, 6.
- 1953 *Galathea* spec. ind.; Bachmayer & Tollmann, p. 312.
- 1974b *Galathea weinfurteri*; Müller, p. 276, pl. 1, fig. 4.
- 1976 *Galathea weinfurteri*; Müller, p. 516.
- 1979 *Galathea weinfurteri*; Müller, p. 274.
- 1984a *Galathea weinfurteri*; Müller, p. 60, pl. 21, figs. 4, 5, pl. 22, figs. 1-5.
- 1996 *Galathea weinfurteri*; Müller, p. 8.
- 1998 *Galathea weinfurteri*; Müller, p. 14.
- 2002 *Galathea weinfurteri*; De Angeli & Garassino: p. 26.
- 2002 *Galathea weinfurteri*; Górká, p. 528.
- 2006 *Galathea weinfurteri*; Radwański *et al.*, pp. 96, 97, pl. 2, fig. 1.
- 2010 *Galathea weinfurteri*; Gatt & De Angeli, p. 1326, pl. 2, fig. 4.

2010 *Galathea* sp.; Gatt & De Angeli, p. 1326, text-fig. 3, pl. 2, fig. 3.

2010 *Galathea weinfurteri*; Schweitzer et al., p. 49.

2011 *Galathea weinfurteri*; Ossó & Stalennuy, figs. 3.7, 3.13.

*Emended diagnosis* – Carapace subrectangular (L/MW 1-1.1); slightly vaulted transversely. Rostrum subtriangular with three pairs of lateral spines, one pair of supraorbital spines; no median carina. Rostrum ornamented with small, irregularly spaced tubercles. Cervical groove deep; anterior and posterior branch equally incisive. Carapace ornamented with transverse striae; lateral margins with seven spines; carapace surface ornamented with transverse striae; two postfrontal striae, curved in median part and interrupted by short groove.

*Type material* – The type lot originated from the locality of Furth in Lower Austria (Bachmayer, 1950). That author mentioned that the type material was held in the ‘Weinfurter Sammlung’ at IPUW. However, even after repeated searches by one of us (MH), this material could not be traced. We here consider the holotype (carapace without rostrum) and two paratypes (fragmentary carapace with left part of the rostrum, and left propodus) lost. For comparison, we here reproduce (Pl. 1) the original illustrations of the types.

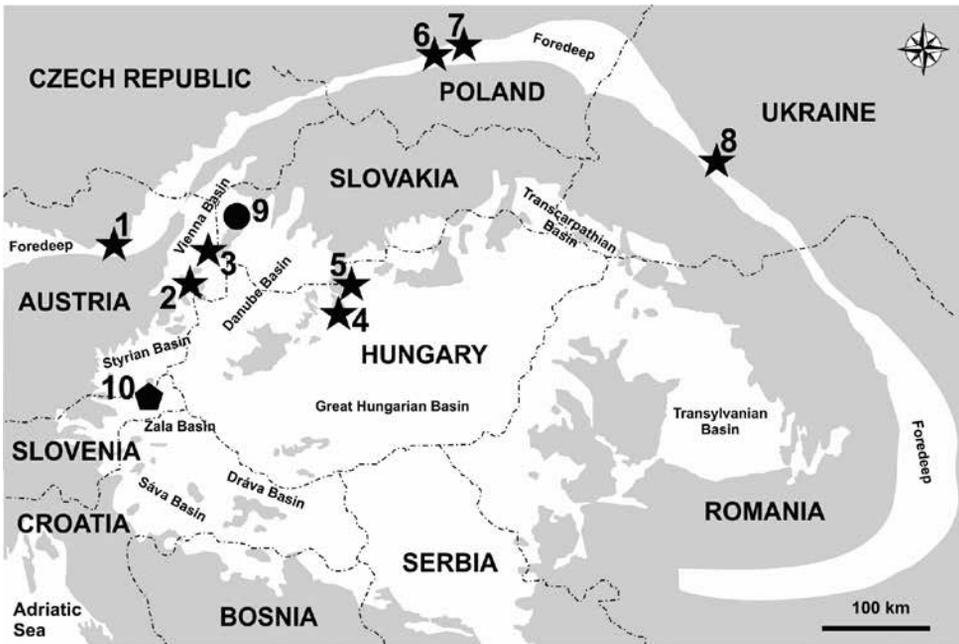


Fig. 1. Distribution of squat lobsters in the Central Paratethys during the Miocene, projected onto the Recent Carpathian-Pannonian Basin complex (after Harzhauser et al., 2003). White areas represent respective Neogene basins. Legend: ‘star’ = *Galathea weinfurteri* Bachmayer, 1950; ‘circle’ = *Agononida cerovensensis* Hyžný & Schlögl, 2011 and *Munidopsis lieskovensis* Hyžný & Schlögl, 2011; ‘pentagon’ = *Munidopsis palmuelleri* n. sp.; 1 - Furth; 2 - Fenk quarry at Gross Höflein; 3 - Bad Deutsch-Altenburg; 4 - Budapest area; 5 - Visegrád and Nagymaros; 6 - Grobie; 7 - Węgleinek; 8 - Maksymivka; 9 - Cerová-Lieskové; 10 - Košaki.

*Other material* – From the Austrian part of the Vienna Basin: six specimens (NHMW 2011/0167/0132-0137), Fenk quarry (Gross Höflein, Lower Austria; for details see Bachmayer & Tollmann, 1953; Riegl & Piller, 2000; Wiedl *et al.*, 2013); 20 specimens (NHMW 2013/0580/0001-0020), quarry in the Hundsheim Hills (Deutsch-Altenburg, Lower Austria). From the Budapest area, Hungary (for details see Müller, 1984a): numerous specimens from the Tétényi Plateau (M.86.21, M.86.191, M.86.507, M.86.831), Diósd (M.89.64), Kerepesi út (M.86.417), keresztúri út (M.86.231), Örs vezér tere (M.86.73) and Rákos (M.86.493). From the Hungarian part of the Danube Basin (for details see Müller, 1984a): several specimens from Visegrád (M.86.342) and Nagymaros-Törökmező (M.86.103).

*Measurements* – Measurements (only of sufficiently well-preserved specimens) are as follows:

NHMW 2011/0167/0134: L=11.8; GH=6.4; TW=9.0; MW=11.8; L/MW=1.0

NHMW 2013/0580/0005: L=11.0; GH=5.5; TW=8.0; MW=10.5; L/MW=1.05

NHMW 2013/0580/0014: LR=4.9; L=3.6; GH=2.0; TW=2.9; MW=3.6; L/MW=1.0

NHMW 2013/0580/0012: LR=5.3; L=4.0; GH=2.2; TW=3.0; MW=3.6; L/MW=1.1

NHMW 2013/0580/0016: L=5.3 (estimated value); GH=3.0; TW=4.4; MW=5.4; L/MW=0.99

*Description* – Carapace subrectangular, slightly longer than wide, excluding rostrum, lateral margins convex, widest in posterior-median part. Rostrum projects slightly downwards, concave at midline, subtriangular, with three pairs of lateral spines, with one pair of supraorbital spines. Rostral surface ornamented with small, irregularly spaced tubercles, no median carina. Orbits with concave margins and one small, anteriorly directed outer-orbital spine. Lateral margins slightly convex, with seven spines. Posterior margin slightly concave, rimmed. Cervical groove deep; postcervical groove weakly indicated. Carapace surface ornamented with transverse, sinuous and parallel striae. Striae occasionally interrupted. On rostral base two postfrontal raised striae, curved in the median part and interrupted by a short groove. Postfrontal striae ornamented with several spines pointing forwards. Epigastric regions ornamented with up to four pairs of small spines. Gastric regions with three continuous transverse striae and several interspersed and interrupted striae. Posterior area of the carapace undivided by grooves, ornamented with three or four continuous transverse striae and several interrupted ones. Cardiac region weakly marked by interruptions in groove pattern.

Sternum slightly longer than broad, maximum width at sternites 6 and 7; sternite 3 narrowest; sternites 4 and 5 narrowing anteriorly; sternites 6 and 7 approximately 2.5 times wider than sternite 3; sternum surface depressed in midline. Abdominal tergites smooth, unarmed.

*Remarks* – Bachmayer (1950, p. 136) provided a rather vague diagnosis, which is here emended. In view of the fact that the type material is here considered lost, our emendation is based both on the illustrations of the original material (see Pl. 1) and on additional material from Deutsch-Altenburg which Bachmayer himself considered to be conspecific (see Bachmayer, 1953). However, there do appear to be some differences between Bachmayer's original description and the material examined herein. Bachmayer (1950) noted that in the type material the carapace was widest anteriorly. Interestingly, in all other specimens known, the carapace is widest posteriorly. This discrepancy

may be explained by diverging styles of preservation; the type material came from marls, while all other material is from carbonates. In the original sketch (Bachmayer, 1950, pl. 1, fig. 2a) the cardiac region is relatively well marked, which is not true for other material. In fact, an indistinct cardiac region is typical of *Galathea* (see Baba, 2005). However, this feature is less well visible in the photograph (Bachmayer, 1950, pl. 1, fig. 1). In the interest of taxonomic stability we attribute these differences (if they do exist) to intraspecific variation, until the issue can be studied in more detail on the basis of topotypical material, or in case the type lot is traced. Müller (1984a, p. 60) noted that there had already been some doubts on the unity of this particular taxon. It should be noted, however, that carapace ornament remains reasonably constant in all specimens studied. Bachmayer (1953) provided a drawing of the sternum, but failed to add a photograph of the same. Re-examination of this specimen (NHMW 2013/0580/0010) has now shown that Bachmayer's illustration is slightly inaccurate, in that sternites 5-7 were shown to be more or less parallel (Bachmayer, 1953, pl. 5, fig. 6), while in actual fact they are convergent (Pl. 2, fig. 5).

The present species is fairly similar to the extant *G. squamifera* Leach, 1814 and *G. strigosa*. However, the former has less prominent postfrontal striae, while these are always well developed in *G. weinfurteri*. *Galathea strigosa* has more discontinuous transverse striae than *G. weinfurteri*.

Gatt & De Angeli (2010) recorded *Galathea* sp. from the Upper Miocene of Malta, together with *G. weinfurteri*. Of the former only a single fragmentary specimen is known; this differs *G. weinfurteri* in showing a larger number of sinuous secondary striae interspersed with primary ones and in having some spines on the hepatic and epibranchial regions (Gatt & De Angeli, 2010, p. 1326). It should be noted that this particular specimen is significantly larger than co-occurring *G. weinfurteri*, which suggests that these differences may be ontogenetic. Similarly, at Deutsch-Altenburg larger-sized specimens of *G. weinfurteri* exhibit more secondary striae than smaller ones (Pl. 2). Another point is that secondary striae are often better visible when lit from different angles. Gatt & De Angeli (2010) also noted the presence of small spines on the hepatic and epibranchial regions in what they named *Galathea* sp. Although spine position is considered taxonomically significant (Poore, 2004), this may vary to a certain degree (e.g., Baba, 2005). In fact, Bachmayer (1950) described *G. weinfurteri* with more than seven spines in the area of 'the upper margin of the mesogastric region'. These may correspond to the spines recorded in *Galathea* sp. by Gatt & De Angeli (2010). Similarly, Müller (1984a, p. 60) pointed out that, 'behind the rostrum there is a spiny ridge but the spines are very small or even rudimentary on some specimens'.

Bachmayer (1950) and Müller (1984a) also described isolated propodi which they attributed to *G. weinfurteri*. These are stout and striated as is typical of members of the genus. However, it should be noted that they have never been found directly associated with carapaces, although they occur at localities where *G. weinfurteri* is the sole species of squat lobster on record. Specimens with 'bopyriform' swellings have also been recorded; Müller (1984, pl. 22, fig. 5) mentioned a specimen with a swelling on the left branchial area, whereas the one illustrated herein (Pl. 2, fig. 3) has a swelling on the right-hand side.

*Occurrence* – This species is known from the Middle Miocene ('Badenian'; Langhian) of Austria (Bachmayer, 1950, 1953), Hungary (Müller, 1984a), Poland (Müller,

1996; Górká, 2002), Ukraine (Radwański *et al.*, 2006; Ossó & Stalennuy, 2011) and the Upper Miocene of Malta (Gatt & De Angeli, 2010).

**Family Munididae Ahyong, Baba, Macpherson & Poore, 2010**  
**Genus *Agononida* Baba & de Saint Laurent, 1996**

*Type species* – *Munida incerta* Henderson, 1888, by original designation.

*Diagnosis* – See Baba & de Saint Laurent (1996, p. 441).

*Remarks* – To date, there is only a single fossil record of this genus (Hyžný & Schlögl, 2011). *Agononida* is closely similar to *Munida* Leach, 1820, but differs in the constant possession of pairs of epigastric and postcervical spines (Baba & de Saint Laurent, 1996; Poore, 2004). It should be noted that spines are very delicate structures and in the sole fossil member known, *Agononida cerovensis* Hyžný & Schlögl, 2011, they were identified only on the basis of the counterpart of the fossil, whereas the latter shows only large swellings or tubercles (Hyžný & Schlögl, 2011, text-fig. 6A). Fossil crustaceans often occur in fragments, which holds true in particular for material preserved in carbonates; this might, in part, explain the paucity of the genus in the fossil record. In contrast, extinct members of a close relative, *Munida*, are well known from different parts of the world (Schweitzer & Feldmann, 2000; Robins *et al.*, 2012b).

***Agononida cerovensis* Hyžný & Schlögl, 2011**  
 Figs. 2, 7B; Pl. 3.

2011 *Agononida cerovensis* Hyžný & Schlögl, p. 332, text-figs. 6, 7.

2011 *Agononida cerovensis*; Ahyong *et al.*, p. 96.

*Emended diagnosis* – Carapace cordate, nearly as long as wide, with convexly rounded lateral margins; transverse carapace ridges (striae) distinct, anterior of ridges ornamented with granules, ridges subparallel, becoming less so in anteriormost and posteriormost portions of carapace; anterolateral margin with three spines; cervical and postcervical grooves deeply incised; 4 epigastric spines, 6 postcervical spines and spines on the posterior rim form two distinct rows oriented longitudinally.

*Holotype* – Carapace without rostrum (SNM Z-24.864); L = 6.8; GH = 3.6; TW = 6.0; MW = 7.0; L/MW = 0.97.

*Remarks* – Hyžný & Schlögl (2011) interpreted the four tubercles in the anterior portion of the carapace to be bases of two supraorbital and two epigastric spines. A re-examination of the holotype has now shown that all of them are in fact bases of epigastric spines. In the illustration (see Fig. 6B), the rostrum and supraorbital spines are conjectural, being based on comparisons with extant members of the genus. This species is based upon a single individual; in spite of numerous visits to the type locality during the last two years, no additional material has so far come to light.

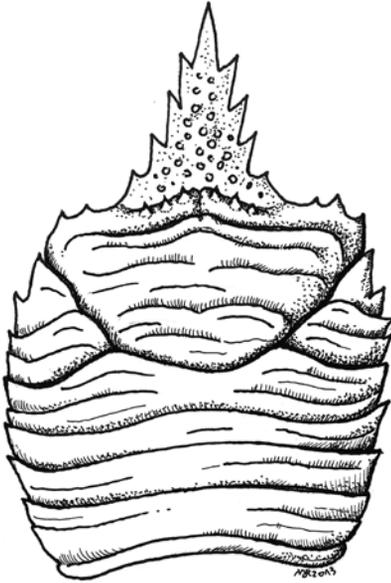


Fig. 2. *Galathea weinfurteri* Bachmayer, 1950. Schematic reconstruction of dorsal carapace based on material from the Fenk quarry (Gross Höflein, Lower Austria) and Bad Deutsch-Altenburg (Austria).

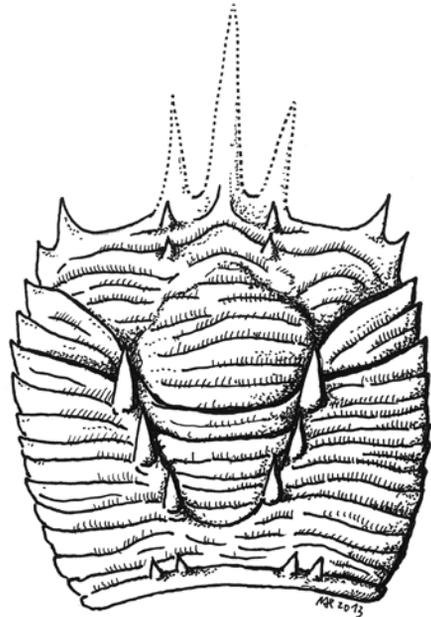


Fig. 3. *Agononida cerovensis* Hyžný & Schlögl, 2011. Schematic reconstruction of dorsal carapace based on the holotype. The shape of the rostrum is conjectural.

*Occurrence* – The present species is known exclusively from the Lower Miocene ('Karpatian') of Slovakia (Hyžný & Schlögl, 2011).

**Family Munidopsidae Ortmann, 1898**  
**Genus *Munidopsis* Whiteaves, 1874**

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

*Diagnosis* – See Ambler (1980, p. 15) and Ingle & Christiansen (2004, p. 142).

*Remarks* – *Munidopsis* is one of the most speciose decapod genera, embracing more than 220 species (Baba *et al.*, 2008). Its diagnosis is rather broad, accommodating an array of morphologies that, at times, have been treated as several distinct genera (for details see Robins *et al.*, 2013). For a discussion on the differentiation of the genus from other, exclusively fossil, genera reference is made to Robins *et al.* (2013). Despite its speciose nature, the genus has a poor fossil record; merely a handful of taxa have been described to date (Hyžný & Schlögl, 2011, table 4).

*Munidopsis lieskovensis* Hyžný & Schlögl, 2011

Figs. 3, 7C; Pl. 4.

2011 *Munidopsis lieskovensis* Hyžný & Schlögl, p. 334, text-figs. 8, 9.2011 *Munidopsis lieskovensis*; Ahyong et al., p. 96.2013 *Munidopsis lieskovensis*; Robins et al., table 9.

*Diagnosis* – Carapace subsquare; moderately convex transversely. Rostrum styliform, keeled, unidentate. Anterolateral margin with one spine at anterior of hepatic region. Circumgastric groove strong; V-shaped in posteriormost part. Regions slightly inflated. Epigastric regions circular in outline. Urogastric region extending across width of carapace; twice as wide as cardiac region. Cardiac region triangular, apex directed posteriorly. Carapace uniformly ornamented with short, transverse, squamous ridges.

*Type material* – The holotype is a near-complete dorsal carapace with the rostrum (SNM Z-24.865); both paratypes are near-complete dorsal carapaces, lacking the rostrum (SNM Z-24.866 and SNM Z-24.867).

*Other material* – Six near-complete dorsal carapaces (KGP-MH CL-002-007) and a single sternum (KGP-MH CL-008).

*Measurements* – Measurements were taken only from sufficiently well-preserved specimens:

SNM Z-24.865 (holotype): GH=2.6; TW=5.1; MW=5.7

SNM Z-24.866 (paratype): GH=2.3; TW=4.8; MW=5.0

SNM Z-24.867 (paratype): GH=2.6; TW=4.7; MW=5.1

KGP-MH CL-002: LR=6.1; L=4.3; GH=2.0; TW=3.8; MW=4.3; L/MW=1

KGP-MH CL-003: LR=5.1; L=3.7; GH=1.8; TW=3.6 (reconstructed); MW=3.6; L/MW=1

KGP-MH CL-004: GH=1.9; TW=3.8; MW=4.1

KGP-MH CL-005: GH=1.6; TW=2.9; MW=3.4

KGP-MH CL-006: L=3.4; GH=1.7; TW=2.8 (estimated); MW=3.4; L/MW=1

KGP-MH CL-007: LR=6.6 (estimated); L=4.4; GH=2.1; TW=3.4; MW=4 (estimated); L/MW=1.1

*Emended description* – Carapace subsquare (L/MW 1-1.1); moderately convex transversely. Rostrum styliform, keeled, unidentate, bearing pustular ornamentation. Anterior margin sinuous. Lateral margins slightly convex, with two spines. Circumgastric groove strong; V-shaped in posteriormost part. Branchiocardiac groove strongest approaching lateral margins. Epigastric, hepatic, epibranchial, urogastric and cardiac regions well defined. Regions slightly inflated. Hepatic region quadrate with one spine at its anterior; epigastric regions circular and inflated. Urogastric region extending across width of carapace; twice as wide as cardiac region. Cardiac region triangular, apex directed posteriorly. Carapace uniformly ornamented with short, transverse, squamous ridges. Posterior margin inflected concave posterior, strongly rimmed. Ornamentation does not continue onto rim. Sternum: sternites 4 and 5 narrowing anteriorly; sternite 5 approximately 1.5 times wider than sternite 4; sternum surface depressed in midline.

*Remarks* – The type lot comprises three incomplete specimens. Recently, new material has been recovered from the type locality, Cerová-Lieskové, including numerous complete specimens (Pl. 4) that allows the original description to be emended in terms of rostral length and details of posterior margin and sternum.

*Occurrence* – The species is known exclusively from the Lower Miocene ('Karpatian') of Slovakia (Hyžný & Schlögl, 2011).

*Munidopsis palmuelleri* n. sp.

Figs. 5, 7D; Pl. 5.

*Diagnosis* – Carapace with well-defined regions; rostrum styliform, unkeeled, unidentate, flat in cross section; carapace surface covered with short, parallel striae, striae forming longer ridges in mesogastric region and posterior part of carapace.

*Etymology* – The specific name honours Pál Müller, who greatly improved our knowledge of Miocene decapod crustaceans of the Central Paratethys.

*Holotype* – The holotype (RGA/SMNH 0351) is an imprint of a complete carapace; measurements: LR=8.9; L=6.6; GH=3.5; TW=5.3; MW=5.6; L/MW=1.18.

*Description* – Carapace subrectangular, slightly longer than wide, L/W 1.18; moderately convex transversely. Rostrum styliform, unkeeled, unidentate, flat in cross section. Anterolateral margin with small, anteriorly directed spine. Lateral margins subparallel. Circumgastric groove strong; V-shaped in posteriormost part. Branchiocardiac groove strongest approaching lateral margins. Hepatic, epibranchial, urogastric and cardiac regions well defined. Epigastric regions poorly defined. Urogastric region extending across middle half of carapace; wider than cardiac region. Cardiac region strongly defined anteriorly, less defined posteriorly; triangular in shape with apex directed posteriorly. Carapace ornamented with narrow, short, sinuous transverse ridges anteriorly; ridges broaden posteriorly. Posterior margin inflected concave posterior, weakly rimmed. Ornamentation not continuing onto rim. Ventral surface and appendages not preserved.

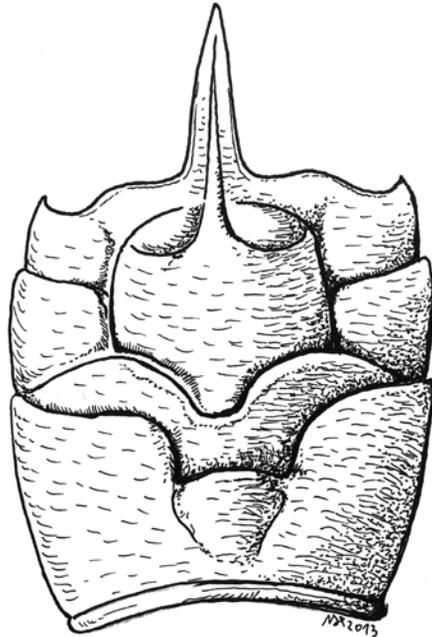


Fig. 4. *Munidopsis lieskovensis* Hyžný & Schlögl, 2011. Schematic reconstruction of dorsal carapace based on newly collected material (presented herein).

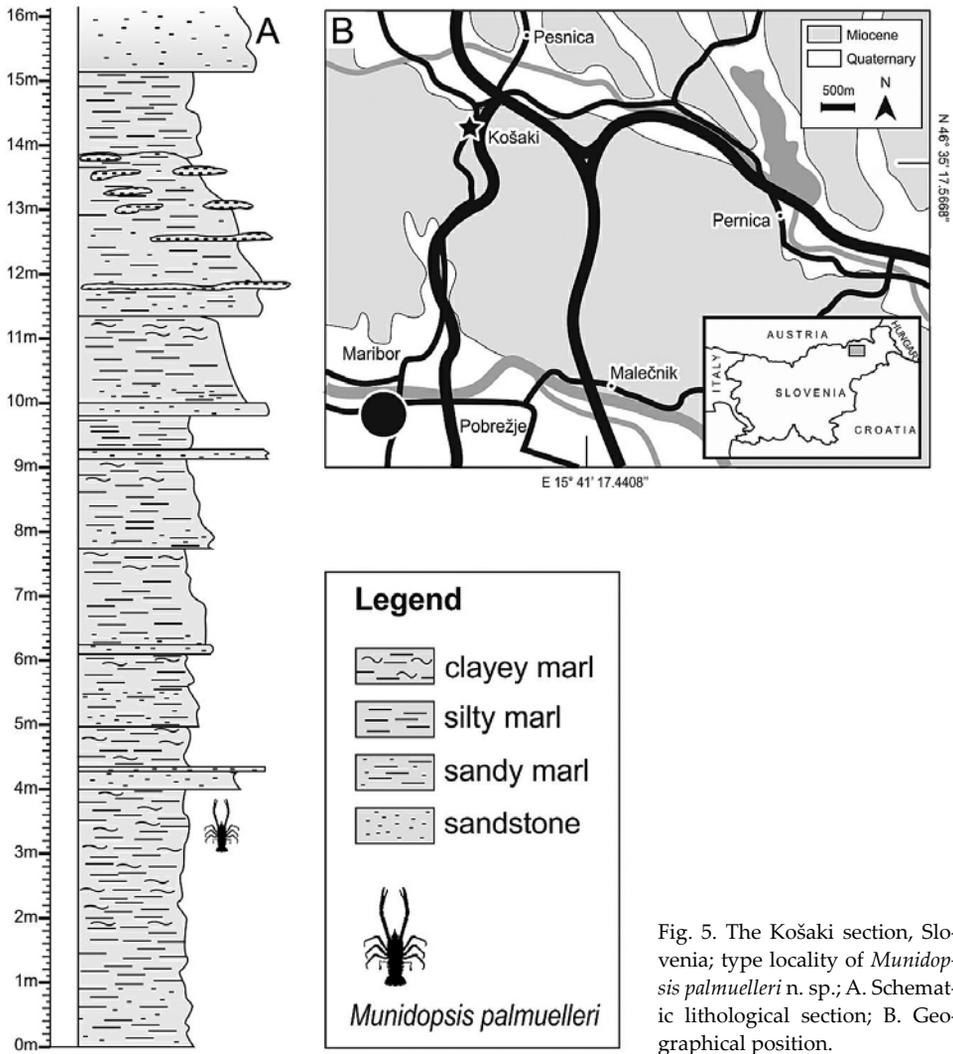


Fig. 5. The Košaki section, Slovenia; type locality of *Munidopsis palmuelleri* n. sp.; A. Schematic lithological section; B. Geographical position.

*Remarks* – Although the species is based on a single specimen, it differs significantly from all other extinct congeners. It can be differentiated from *M. scabrosa* Feldmann & Wilson, 1988 and *M. foersteri* Feldmann, Tshudy & Thompson, 1993 by the shape of the circumgastric groove. The base of the circumgastric groove of *M. palmuelleri* n. sp. is V-shaped, while it is rounded in the other two. Moreover, *M. foersteri* has a pyriform carapace and the rostrum is nearly as long as the carapace (Feldmann *et al.*, 1993), quite unlike *M. palmuelleri* n. sp. *Munidopsis scabrosa* has a subsquare carapace with forwardly directed scabrose ornamentation and a keeled rostrum (Feldmann & Wilson, 1988). The closest morphological match with *M. palmuelleri* n. sp. is *M. lieskovensis* (see above), but the former can be differentiated on ornamentation; that of *M. palmuelleri* n. sp. is much more ridge like than the squamous sculpture in *M. lieskovensis*. The rostrum in

the latter also has a different shape, while the lateral carapace margins are near parallel at the base, whereas in *M. palmuelleri* n. sp. they are strongly convergent, yielding a more triangular carapace shape. Moreover, unlike *M. lieskovensis*, the new species has a rostrum without a keel and the epigastric regions are poorly defined.

*Occurrence* – The holotype and sole specimen known to date (RGA/SMNH 0351) was recovered from monotonous grey marls at a construction site in the now abandoned Košaki brickyard. The locality is situated approximately 2 km northeast of the city of Maribor in north-eastern Slovenia (GPS co-ordinates: 46°35'27.62"N, 15°39'56.25"E; see Fig. 5). The Košaki section consists of a rather uniform succession of poorly fossiliferous (macrofossil) grey clayey marl beds of the Slovenske Gorice Formation which is the lithological equivalent of the Kreuzkrumpel Formation (Steirischer Schlier) exposed in the Austrian part of the Styrian Basin (Gross *et al.*, 2007). Near the top of the 15-m-thick section the carbonate content of the marl increases, the marl becoming much harder and lamellate. The sequence is here interrupted by several thin (up to 10 cm) sandstone interbeds.

The carbonate fraction of 'lower Badenian' marls of the Slovenske Gorice Formation consists mainly of nannofossils, whereas clastic components are predominantly clay and silt (Bartol, 2009). The marls usually contain only rare macrofossils, but are rich in calcareous nannoplankton. Apart of the present specimen, we are not aware of any additional decapod remains from this locality. An enrichment of thin-shelled pectinid bivalves (*Amusium cristatum*) was observed in the same layer, along with rare schizasterid echinoids (RG, pers. obs.).

Bartol (2009) recorded a nannoplankton assemblage from a several sampling sites near the Košaki section within the same lithological unit; this defines the interval zone MuN5a *sensu* Martini (1971). This interval was correlated with the lower part of NN5 *sensu* Martini (1971) and probably corresponds to the transition between the lower and middle 'Badenian' (Rögl *et al.*, 2002). Thus, *Munidopsis palmuelleri* n. sp. is of Middle Miocene age.

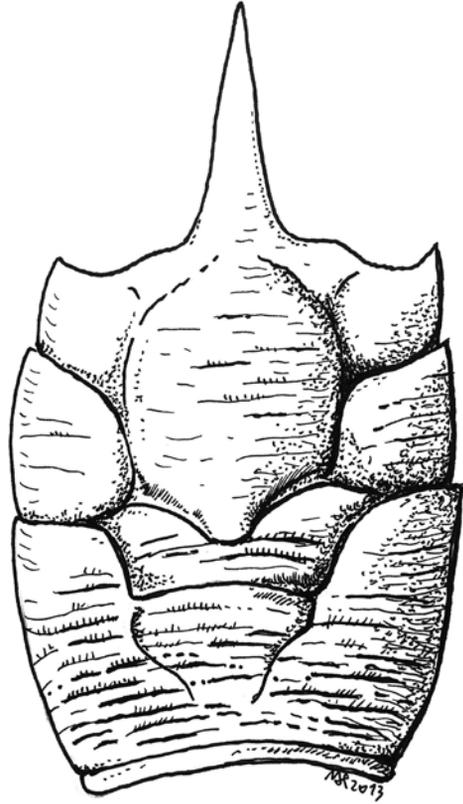


Fig. 6. *Munidopsis palmuelleri* n. sp. Schematic reconstruction of dorsal carapace based on the holotype.

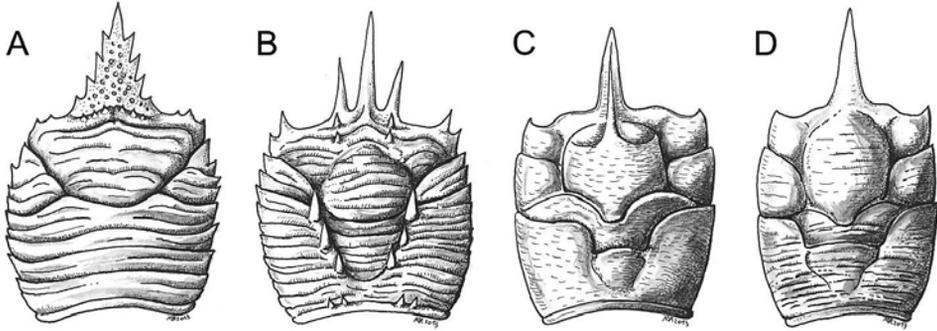


Fig. 7. Miocene squat lobsters of the Central Paratethys; reconstructions (not to scale) of dorsal carapaces of *Galathea weinfurteri* (A), *Agononida cerovensis* (B), *Munidopsis lieskovensis* (C) and *M. palmuelleri* n. sp. (D). The shape of the rostrum in *A. cerovensis* is based on extant congeners.

### Galatheoidea genus and species indeterminate

Pl. 6.

*Material* – A single specimen (NHMW 2013/0607/0001), consisting of four articulated pereopods, without dorsal carapace, sternum or pleon.

*Description* – Pereiopod 1 (cheliped), with propodus twice as long as dactylus, carpus short, merus approximately 2.5 times length of carpus; all elements ornamented with rows of prominent spines (Pl. 6, fig. 2); occlusal surface of fingers armed with tiny teeth (Pl. 6, fig. 3). Pereiopods 2 and 3(?) long and slender, no details discernible.

*Remarks* – Unfortunately, a family-level identification of this material is impossible in the absence of a dorsal carapace. The preservation of appendages of galatheoids in the fossil record is rare, which also means that comparative material is scant. Modern galatheoids are quite variable in appendage size and structure, even within genera. Munidids tend to have long chelae (Ahyong *et al.*, 2010), which would suggest that the present specimen is not a member of this family; however, this is inconclusive.

*Occurrence* – Kummer quarry at Sankt Margarethen, Burgenland, Austria (Eisenstadt-Sopron Basin). A detailed sedimentological description and facies analysis of the strata exposed here was provided by Schmid *et al.* (2001). The age is based on calcareous nannoplankton, which indicates zone NN5b *sensu* Martini (1971), *i.e.*, Middle Miocene, around the Langhian/Serravallian boundary (late ‘Badenian’).

### Notes on palaeoenvironment

Squat lobsters inhabit a wide range of habitats, ranging from the intertidal zone to hydrothermal vents, and are typically members of benthic communities (Baba, 2005; Baba *et al.*, 2008; Lowrich & Thiel, 2011). Occasionally, they occur in dense aggregations, which is especially true for taxa that live on the continental shelf and often are

Table 2. Palaeoenvironment of Miocene squat lobsters from the Central Paratethys.

Taxon	Substrate	Palaeoenvironment
<i>Galathea weinfurteri</i>	carbonate, siliciclastic	reefal, non-reefal (shallow-water)
<i>Agononida cerovenssis</i>	Siliciclastic	muddy bottom (deep-water)
<i>Munidopsis lieskovensis</i>	Siliciclastic	muddy bottom (deep-water)
<i>Munidopsis palmuelleri</i> n. sp.	Siliciclastic	muddy bottom (deep-water)

associated with other species of animal (for a review see Lowrich & Thiel, 2011; references therein). Squat lobsters commonly inhabit coral reefs, rocky or muddy bottoms (Baba *et al.*, 2008; Lowrich & Thiel, 2011); our fossil material from the Central Paratethys is no exception in that respect (Table 2).

*Galathea weinfurteri* – This is the most widely distributed squat lobster in the Miocene of the Central Paratethys known to date. Extant species of *Galathea* usually inhabit shallow waters (Baba *et al.*, 2008); indeed, most material of *G. weinfurteri* comes from shallow-marine reefal facies (*e.g.*, Bachmayer & Tollmann, 1953; Müller, 1984a, 1996; Radwański *et al.*, 2006) and specimens from Deutsch-Altenburg are confined to bryozoan marls and calcarenites with typical reefal decapods (Bachmayer, 1953). Interestingly, the type collection came from a different facies (marls; see above), and differs slightly from other occurrences of this species. Some squat lobster species may exhibit rather broad ecological preferences, and assuming that all reported occurrences of *G. weinfurteri* belong to the same species, this indicates that *G. weinfurteri* followed such a pattern. An alternative interpretation would be that the type specimens of *G. weinfurteri* are not conspecific with other specimens assigned to that species, as discussed above. Studies by Nicol (1932) and Pike (1947) demonstrated that the mouth parts of *Galathea* are ill-adapted for life on muddy substrates. For instance, *G. squamifera* and *G. strigosa*, extant relatives of *G. weinfurteri*, are restricted to rocky areas (De Grave & Turner, 1997).

*Agononida cerovenssis* – The species is known from a single locality, the sedimentary setting of which has been interpreted to represent bathyal settings of depths between 240 and 330 m (Schlögl *et al.*, 2011). Today, the genus *Agononida* is considered to be a typical deep-water inhabitant (Poore, 2004). Baba *et al.* (2008) stated that it inhabited most typically environments shallower than 300 m. Because *A. cerovenssis* is the sole fossil member of the genus known, its ecological preferences cannot be compared with any extinct relative.

*Munidopsis lieskovensis* – The species has been recorded only from its type locality (Cerová Liesková), but, unlike *A. cerovenssis* from the same setting, it is known from numerous specimens. *Munidopsis* is generally considered a deep-water taxon, commonly inhabiting the continental slope, often below 500 m (Ambler, 1980; Baba *et al.*, 2008; Osawa *et al.*, 2008; Macpherson, 2011). The palaeobathymetry at Cerová-Liesková has been estimated to have been 240–330 m, thus confirming the bathymetric preference of the genus also in Miocene times (see also Takeda *et al.*, 1986). Late Cretaceous (Feldmann *et al.*, 1993) and Eocene (Feldmann & Wilson, 1988) occurrences of *Munidopsis*, however, are known from shallow-marine settings, implying different

environmental preferences. A scant fossil record does not allow further speculations on this issue.

*Munidopsis palmuelleri* n. sp. – The type locality of this new species is in the Mari-bor subbasin of the Mura Depression. The time of deposition of the Slovenske Gorice marls was characterised by the ‘early Badenian’ transgression from the Mediterranean through the Slovenian corridor (Pavšič & Horvat, 2009). The extensional tectonics at that time were intense and subsidence very rapid, which resulted in basins exceeding 500 m in depth (Mioč & Žnidarčič, 1989). The highly diverse nannoplankton assemblage in the marls with *M. palmuelleri* n. sp. is consistent with an offshore depositional environment (Bartol, 2009); foraminifera from the same strata (Rijavec, 1976) and planktonic molluscs such as *Clio pedemontana* (Mayer, 1868) from similar layers of the nearby locality of Polički Vrh (Mikuž *et al.*, 2012) corroborate the bathymetrical setting inferred.

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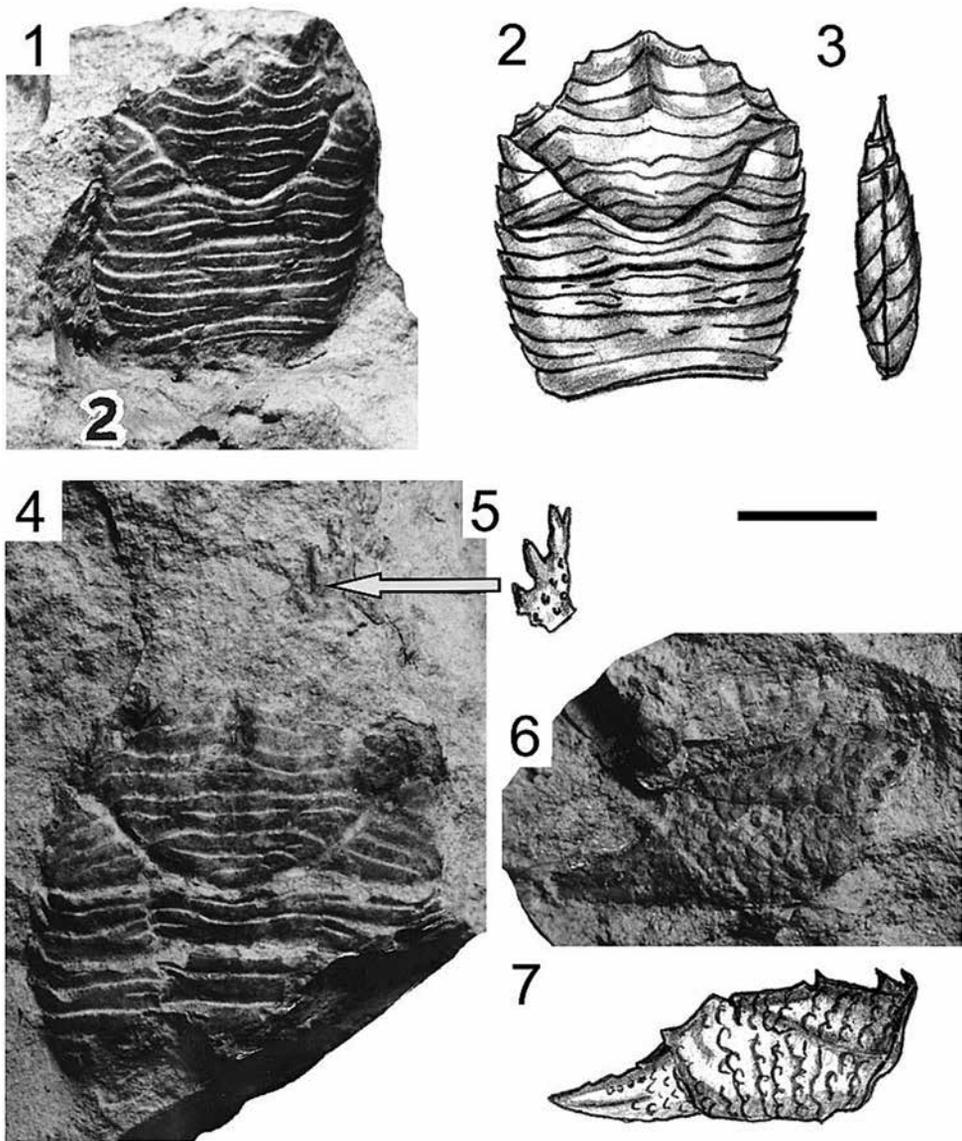
**Plate 1**

*Galathea weinfurteri* Bachmayer, 1950; type collection (considered lost), reillustrated from Bachmayer (1950, pl. 1, figs. 2-4). All figures are to scale; scale bar equals 5 mm.

Figs. 1-3. Carapace without rostrum (holotype), in dorsal (1, 2) and lateral (3) views.

Figs. 4, 5. Carapace with fragmentary rostrum (detail).

Figs. 6, 7. Left propodus.



**Plate 2**

*Galathea weinfurteri* Bachmayer, 1950

Fig. 1. Carapace without rostrum (NHMW 2011/0167/0134).

Fig. 2. Carapace without rostrum (NHMW 2013/0580/0005).

Fig. 3. Carapace with 'bopyriform' swelling (NHMW 2011/0167/0137).

Fig. 4. Sternum (NHMW 2013/0580/0010).

Fig. 5. Abdominal somite (NHMW 2011/0167/0133).

Fig. 6. Carapace with rostrum (NHMW 2013/0580/0014).

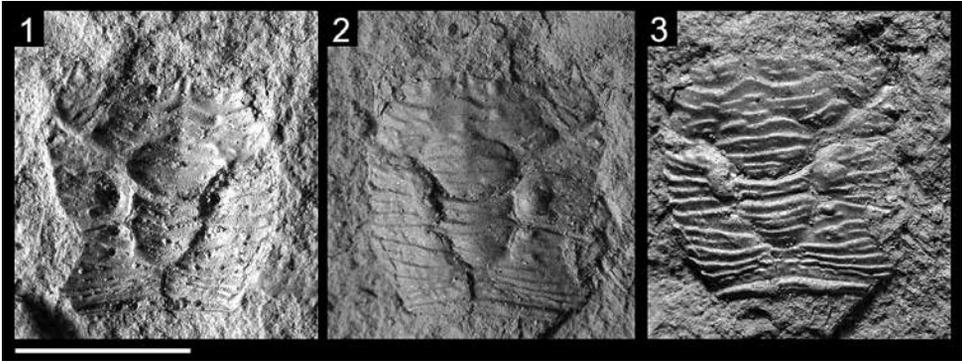
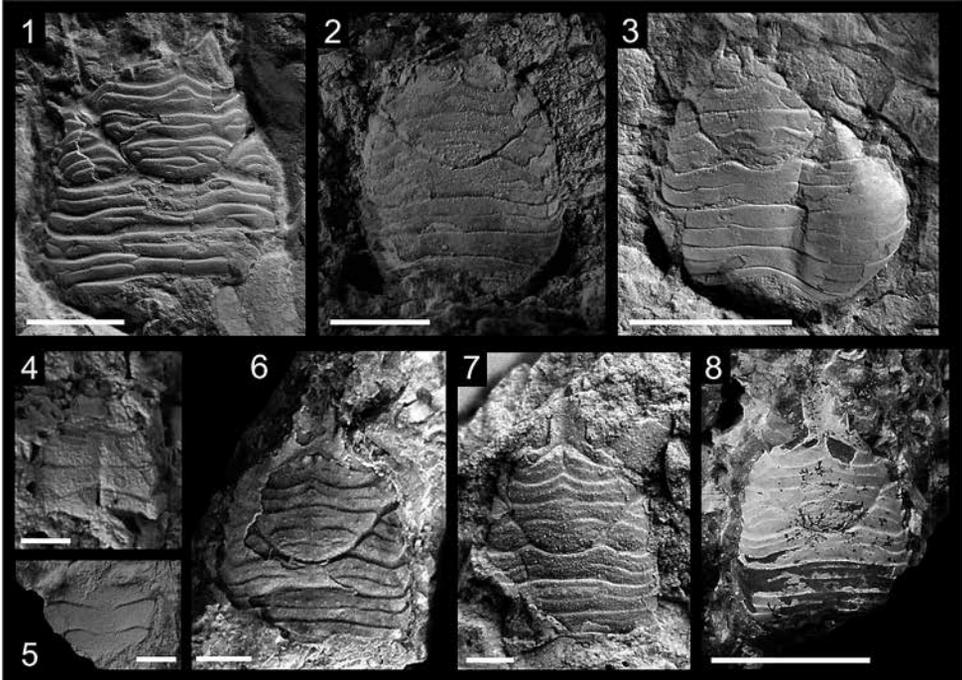
Fig. 7. Carapace with rostrum (NHMW 2013/0580/0012).

Fig. 8. Carapace with rostrum (NHMW 2013/0580/0016).

Specimens of Figs. 1, 3 and 4 are from the Fenk quarry (Austria), those of Figs. 2 and 5-8 are from Bad Deutsch-Altenburg (Austria). All specimens, except that of Fig. 8, were covered with ammonium chloride prior to photography. Scale bars equal 1 mm (Figs. 4-7) and 5 mm (Figs. 1-3, 8).

**Plate 3**

Figs. 1-3. *Agononida cerovenssis* Hyžný & Schlägl, 2011, holotype (SNM Z-24.864); part (Figs. 2, 3) and counterpart (Fig. 1), photographed under different light conditions. All photos are to scale; scale bar equals 5 mm.



**Plate 4**

*Munidopsis lieskovensis* Hyžný & Schlögl, 2011

Figs. 1, 2. Carapace, and counterpart of the same specimen (KGP-MH CL-002).

Fig. 3. Imprint of carapace (KGP-MH CL-003).

Fig. 4. Sternum (KGP-MH CL-008).

Fig. 5. Carapace (KGP-MH CL-004).

Fig. 6. Carapace (KGP-MH CL-005)

Fig. 7. Carapace (KGP-MH CL-006).

Fig. 8. Carapace (KGP-MH CL-007).

Scale bar equals 1 mm.

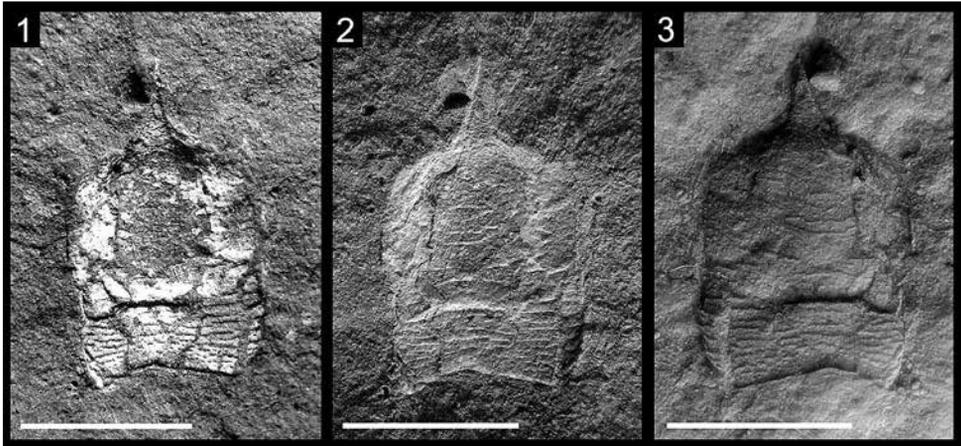
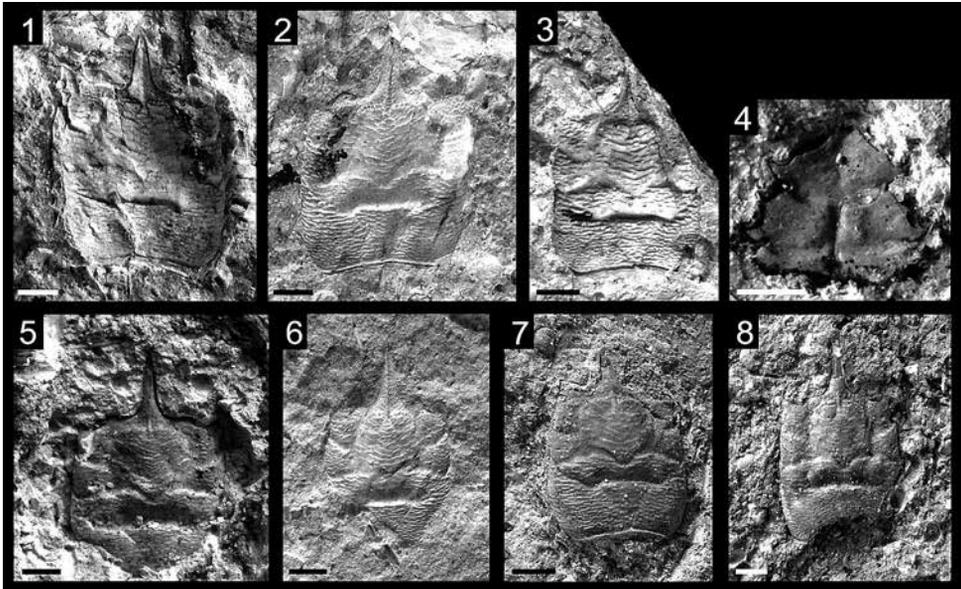
**Plate 5**

*Munidopsis palmuelleri* n. sp.

Figs. 1, 2. Imprint of holotype (RGA/SMNH 0351) photographed uncoated and coated with ammonium chloride, respectively.

Fig. 3. Stomaflex® Putty cast of same specimen, coated with ammonium chloride prior to photography.

Scale bars equal 5 mm.



**Plate 6**

Figs. 1-3. Galattheoidea, genus and species indeterminate. Associated pereopods without carapace or venter. Note spines arranged in rows on P1 merus (arrows in Fig. 2) and tiny teeth on the occlusal surface of P1 fingers (arrows in Fig. 3).

Scale bar equals 5 mm.

