



AN EARLY MIOCENE DEEP-WATER DECAPOD CRUSTACEAN FAUNULE FROM THE VIENNA BASIN (WESTERN CARPATHIANS, SLOVAKIA)

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Abstract: A decapod crustacean faunule from the lower Miocene (upper Burdigalian, ‘Karpatian’) of the Slovakian part of the Vienna Basin comprise five new species: *Callianopsis marianae* (Ctenochelidae), *Crosniera schweitzeriae* (Thomassiniidae), *Agononida cerovensis* and *Munidopsis lieskovensis* (both Galatheidae) plus *Mursia harnicari* (Calappidae). The new species of *Callianopsis* is the first undoubted member of the genus to be recorded from Europe; it is based on sexually dimorphic major and minor chelae as well as on portions of carapace and abdomen. *Crosniera schweitzeriae* sp. nov. and *Agononida cerovensis* sp. nov. constitute the first fossil members of these genera. Additional material of an enigmatic crab,

Styrioplax exiguus, and a re-examination of the type material, confirms assignment of that genus to the subfamily Rhizopinae (family Pilumnidae). Palaeoecological data suggest that deposition of the levels (Lakšárska Nová Ves Formation) from which these taxa were collected took place under generally low-energy, deep-water conditions that were conducive to the preservation of delicate structures. Palaeobiogeographical affinities of the described taxa suggest a trans-Atlantic migration during the early Miocene.

Key words: lower Miocene, Vienna Basin, Slovakia, decapod crustaceans, palaeobiogeography, palaeoecology.

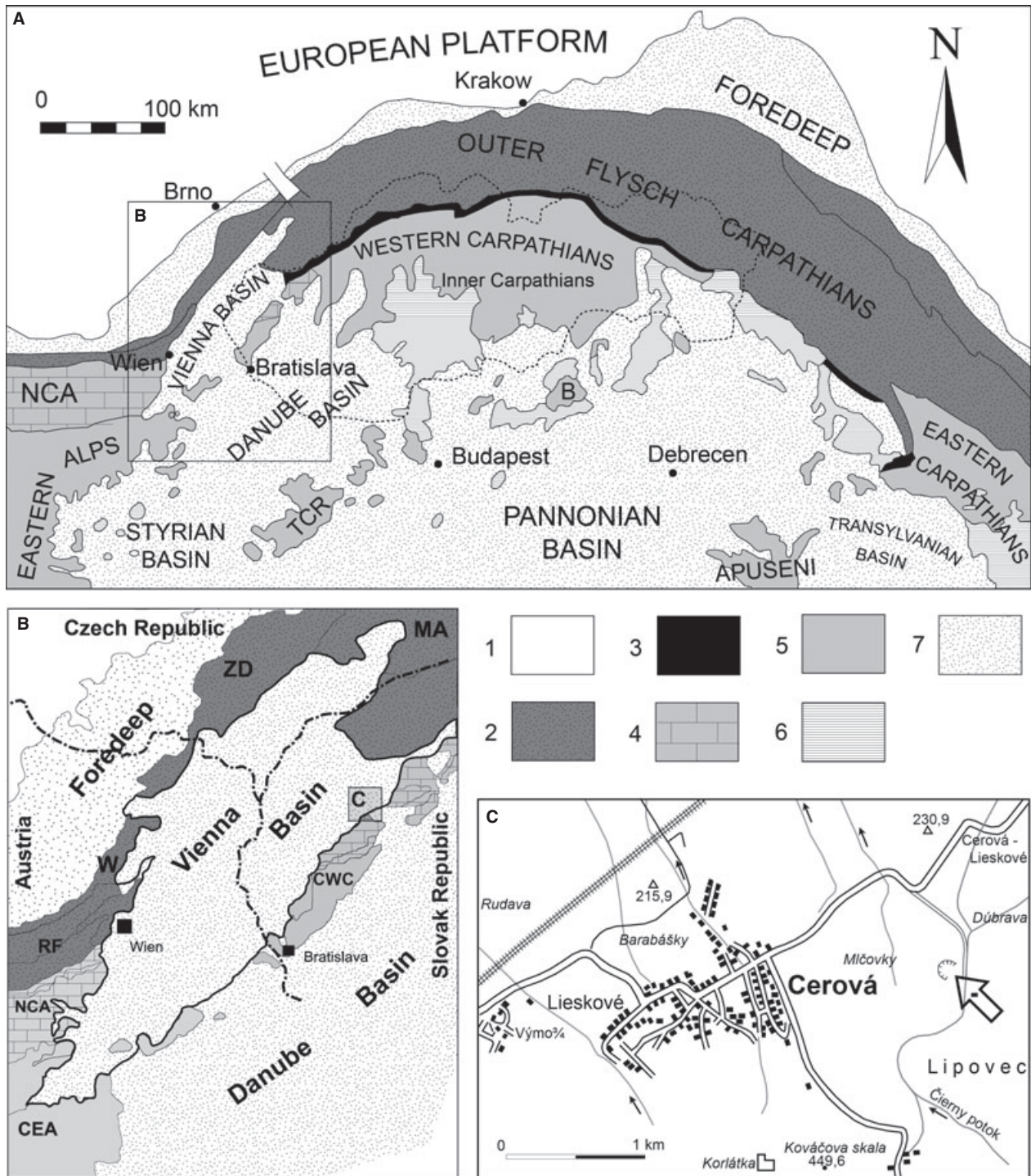
PREVIOUS records of decapod crustaceans from Miocene strata in the Vienna Basin are those by Reuss (1859), Glaessner (1928), Bachmayer (1953a, b, 1954, 1962), Bachmayer and Küpper (1952) and Bachmayer and Tollmann (1953). However, all of these refer to ‘Badenian’ (middle Miocene) levels in the Austrian part of that basin. The present study records a decapod crustacean faunule, collected recently by ourselves, from upper Burdigalian (‘Karpatian’, uppermost lower Miocene) deposits in the Slovakian part of the Vienna Basin for the first time. Several new taxa are described, some of them constituting the first mention of their respective genera from the fossil record. The type material of *Styrioplax exiguus* (Glaessner, 1928) is reassessed; this revision, and the new collection, allows the genus to be placed firmly in the subfamily Rhizopinae (family Pilumnidae). In addition, the palaeoecological and palaeobiogeographical significance of the present faunule is discussed.

STRATIGRAPHICAL AND GEOGRAPHICAL SETTING

The decapod crustacean faunule presented herein comes from Cerová-Lieskové, a locality situated at the foothills

of the Malé Karpaty Mountains, in the north-eastern part of the Vienna Basin (Text-fig. 1). During the Miocene, this basin formed part of the Central Paratethys. At this locality, upper Burdigalian (‘Karpatian’) sediments, assigned to the Lakšárska Nová Ves Formation (Špička and Zapletalová 1964), are well exposed in a former clay-pit. These strata are a grey, calcareous pelitic schlier, representing an offshore facies, massive to very finely laminated, with silty lenses a few centimetres to several decimetres in lateral extent and rare sandstone intercalations (up to 5 cm thick). The total thickness of the section exposed amounts to more than 15 m thick, but the lower 5 m currently are covered by scree. Macrofossil assemblages comprise abundant vertebrates (fishes, bathyal sharks) and a wide spectrum of invertebrates (bivalves, gastropods, cephalopods, scaphopods, regular and irregular echinoids, ophiuroids, siliceous sponges, crustaceans and rare corals). Microfossil suites include both benthic and planktonic foraminifera, radiolarians, sponge spicules, ostracods, crinoid ossicles, fish otoliths and, in places, extremely abundant Bacillariophyta. Macroflora is rare, composed mainly of Lauraceae and grasses.

Age assignment of these deposits relies on the co-occurrence of the foraminifera *Uvigerina graciliformis* Papp and Turnovsky, 1953 and *Globigerinoides bisphericus* Todd



TEXT-FIG. 1. A, The Vienna Basin in the Carpathian-Pannonian system. B, Vienna Basin. C, Location of the Cerová-Lieskové claypit (arrowed). 1. European platform. 2. Carpathian-Alpine externides. 3. Pieniny Klippen Belt. 4. Alpien-Carpathian-Dinaride and Pannonian internids. 5. Neogene volcanics. 6. Neogene basins. B – Bükk, CEA – Central Eastern Alps, CWC – Central Western Carpathians, M – Mecsek, MA – Magura Group, NCA – Northern Calcareous Alps, RF – Rhenodanubian Flysch Zone, TCR – Transdanubian Central Range, W – Waschberg Unit, ZD – Ždánice Unit (simplified from Kováč 2000).

in Todd, Cloud, Low and Schmidt, 1954 and the absence of the genus *Praeorbulina* Olsson, 1964. The first appearance datum (FAD) of *Uvigerina graciliformis* marks the base of the 'Karpatian' stage (e.g. Piller *et al.* 2007), while that of *G. bisphericus* is within Zone M4b of Berggren *et al.* (1995), correlating with the upper 'Karpatian'. The appearance of *Praeorbulina* marks the start of the middle Miocene. The regional Paratethyan 'Karpatian' stage has consistently been considered to be the time-equivalent of the latest Burdigalian (Piller *et al.* 2007).

Decapod crustaceans are distributed rather randomly within the section studied. Although ctenochelids occur throughout, some horizons are particularly rich in articulated remains. Other groups are rare, being often represented by a single or a few specimens only, which means that their distribution within the section does not reflect any palaeoecological or other trends. In addition, there is a certain sampling artefact, because some levels have been sampled more extensively than others. The material is preserved as internal moulds, while impressions of soft parts of the exoskeleton are occasionally seen.

Based on foraminiferal evidence, these sediments were laid down in temperate waters of normal salinity (Joniak *et al.* 2005). A relatively high percentage of planktonic forms indicate deeper-water conditions. Spezzaferri *et al.* (2002) suggested deposition at a depth of *c.* 300 m for a similar foraminiferal association from the 'Steirischer Schlier' of the Styrian Basin, Austria.

Institutional abbreviations. The repositories of specimens illustrated or referred to below are as follows: SNM-Z, Natural History Museum SNM, Bratislava, Slovakia; LMJ, Landesmuseum Joanneum, Graz, Austria; PM, P. Müller Collection, Budapest, Hungary; GW, G. Wanzenböck Collection, Bad Vöslau, Austria.

SYSTEMATIC PALAEOLOGY

Order DECAPODA Latreille, 1802

Infraorder AXIIDEA de Saint Laurent, 1979b

Remarks. On the basis of nuclear and mitochondrial genes, Tsang *et al.* (2008) and Robles *et al.* (2009) have recently noted that the infraorder Thalassinidea was paraphyletic and suggested a twofold subdivision into the infraorders Gebiidea and Axiidea, following de Saint Laurent (1979b). This classification has been adopted by De Grave *et al.* (2009).

Family CTENOCHELIDAE Manning and Felder, 1991

Remarks. This family is considered a sister taxon to the Callianassidae (Robles *et al.* 2009). Fossil ctenochelids are represented mainly by isolated chelae, which can be explained by the delicate nature of most of the cuticular surfaces. Thus, extinct material usually lacks the characters held to be diagnostic in extant taxa, such as structure of the pleopods and maxillipeds, dorsal carapace architecture and form of the abdomen. For this reason, some ctenochelids in the fossil record can easily have been misinterpreted as callianassids, as a few examples illustrate. *Callianassa aquilae* Rathbun, 1935 from the Turonian (Upper Cretaceous) of Texas and Mexico has recently been reassigned to *Gourretia* de Saint Laurent, 1973 (Vega *et al.* 2007), and numerous extinct species of *Callianopsis* de Saint Laurent, 1973 were formerly referred to *Callianassa* Leach, 1814 (see Table 1). In short, in cases where only distal parts of chelipeds (dactylus, propodus, carpus) are available, ctenochelids and callianassids occasionally cannot be distinguished, with the exception of the genus

TABLE 1. Species assigned to *Callianopsis* and their age and geographic range.

Species	Age	Geographic distribution
<i>C. clallamensis</i> (Withers, 1924)	late Eocene	Washington, USA
<i>C.?</i> <i>inornatus</i> Schweitzer and Feldmann, 2001b	late Eocene	Washington, USA
<i>C.?</i> <i>microspineus</i> Beschin <i>et al.</i> , 2005	middle Eocene	North-east Italy
<i>C. muratai</i> (Nagao, 1932)	late Eocene–early Oligocene	Japan
<i>C. elongatodigitata</i> (Nagao, 1941)	late Eocene–early Oligocene	Japan
<i>C. kusiroensis</i> (Nagao, 1941)	late Eocene–early Oligocene	Japan
<i>C. australis</i> Casadío <i>et al.</i> , 2004	middle Oligocene	Argentina
<i>C. marianae</i> new species	early Miocene	Slovakia
<i>C. titaensis</i> (Nagao, 1941)	early–middle Miocene	Japan
<i>C. goniophthalma</i> (Rathbun, 1902)	Holocene	East Pacific
<i>C. anovalis</i> Lin <i>et al.</i> , 2007	Holocene	West Pacific (Taiwan)
<i>C.?</i> <i>caecigena</i> (Alcock and Anderson, 1894)	Holocene	Indo-West Pacific

Kato (1996) recorded two species of *Callianopsis*, both in open nomenclature, from the middle Miocene of Japan. *Callianopsis muratai*, *C. elongatodigitata* and *C. kusiroensis* may be identical; re-examination of the type material is called for (Schweitzer Hopkins and Feldmann 1997).

Ctenocheles Kishinouye, 1926. Numerous authors have therefore used *Callianassa* as a collective name. The first article in which a more realistic picture of the relationship between fossil and extant taxa is illustrated is by Manning and Felder (1991), who recognized several morphological characters of the first pereopods, which helped elucidate the taxonomic position within callianassids *sensu lato*. These authors erected the family Ctenochelidae to accommodate a number of genera (*Ctenocheles*, *Gourettia*, *Paracalliax* de Saint Laurent, 1979a, *Dawsonius* Manning and Felder, 1991, *Anacalliax* de Saint Laurent, 1973 and *Callianopsis*), which had previously been considered to be callianassids (see De Grave *et al.* 2009 for their current taxonomic status). The study by Manning and Felder (1991), which dealt solely with American taxa, stimulated reassessment of several fossil taxa from other regions as well (e.g. Schweitzer Hopkins and Feldmann 1997; Schweitzer and Feldmann 2002; Todd and Collins 2005; Schweitzer *et al.* 2006).

Subfamily CALLIANOPSINAE Manning and Felder, 1991

Remarks. Sakai (1999) erected the subfamily Gourettiinae to contain *Gourettia* and *Dawsonius*, placing *Paracalliax* in the Ctenochelinae. However, Sakai (2004) later elevated it to family rank and added *Callianopsis*, *Laurentgourettia* Sakai, 2004 and *Paragourettia* Sakai, 2004, transferring *Paracalliax* to the Callianassidae. De Grave *et al.* (2009) classified *Anacalliax* and *Paracalliax* within the Callianassidae. They divided the Ctenochelidae into four subfamilies: Callianopsinae (*Callianopsis*), Ctenochelinae (*Ctenocheles*), Gourettiinae (*Dawsonius*, *Gourettia*, *Laurentgourettia* and *Paragourettia*) and Pseudogourettiinae (*Pseudogourettia* Sakai, 2005). We adopt this classification here.

Genus CALLIANOPSIS de Saint Laurent, 1973

Type species. *Callianassa goniophthalma* Rathbun, 1902, by original designation.

Included species. See Table 1.

Diagnosis. Carapace with or without dorsal oval, cardiac prominence on dorsal carapace, low rostral carina, rostral spine; sixth abdominal somite with acute lateral projections; uropod lacking notch or incision; major cheliped with small proximal meral hook and keel; carpus of major cheliped with flange extending from lower margin. Manus of male rectangular, with large tubercles on outer surface; distal margin with spine at midheight; dactylus usually with large nodes and keel on outer surface. Manus

of female narrow, gracile, with smaller tubercles on outer surface; dactylus with small nodes and less robust keel. Minor chela smaller and more slender than major chela; fixed finger with tooth on the cutting edge (after Manning and Felder 1991; Schweitzer Hopkins and Feldmann 1997; Casadío *et al.* 2004; Lin *et al.* 2007).

Remarks. Schweitzer Hopkins and Feldmann (1997) documented the sexual dimorphism of the extant species, *Callianopsis goniophthalma* and showed that the form of the major cheliped plays a key role in sex discrimination. They also demonstrated ways of identifying sexual dimorphism in the fossil record by re-examining the extinct *Callianassa clallamensis* Withers, 1924 and *Callianassa twinensis* Rathbun, 1926, identifying these as sexual morphs to be named *Callianopsis clallamensis* (Withers, 1924).

The extant *Callianassa caecigena* was transferred to *Callianopsis* by de Saint Laurent and Le Loeuff (1979), and Sakai (2005) accepted this decision. However, Lin *et al.* (2007) pointed out that that species was represented only by the type material which is not well enough for firm generic placement.

Beschin *et al.* (2005) erected *Callianopsis microspineus* for two fragmentary propodi from the middle Eocene of north-east Italy. However, in these specimens, the carpus and merus are not preserved, which means that characters of considerable taxonomic importance for the genus *Callianopsis* cannot be observed. For such cases, Feldmann *et al.* (2005) noted that use of only the manus of the major cheliped for generic assignment was very difficult, and the merus was usually needed for a firm generic placement. A distinct tooth on the fixed finger is the sole character displayed by the Italian material, but this feature is of less importance than the others mentioned above. Casadío *et al.* (2004) recorded a fossil species of *Callianopsis* from the middle Oligocene of Argentina which lacked this character. The same holds true for the new material from the Miocene of Slovakia described below.

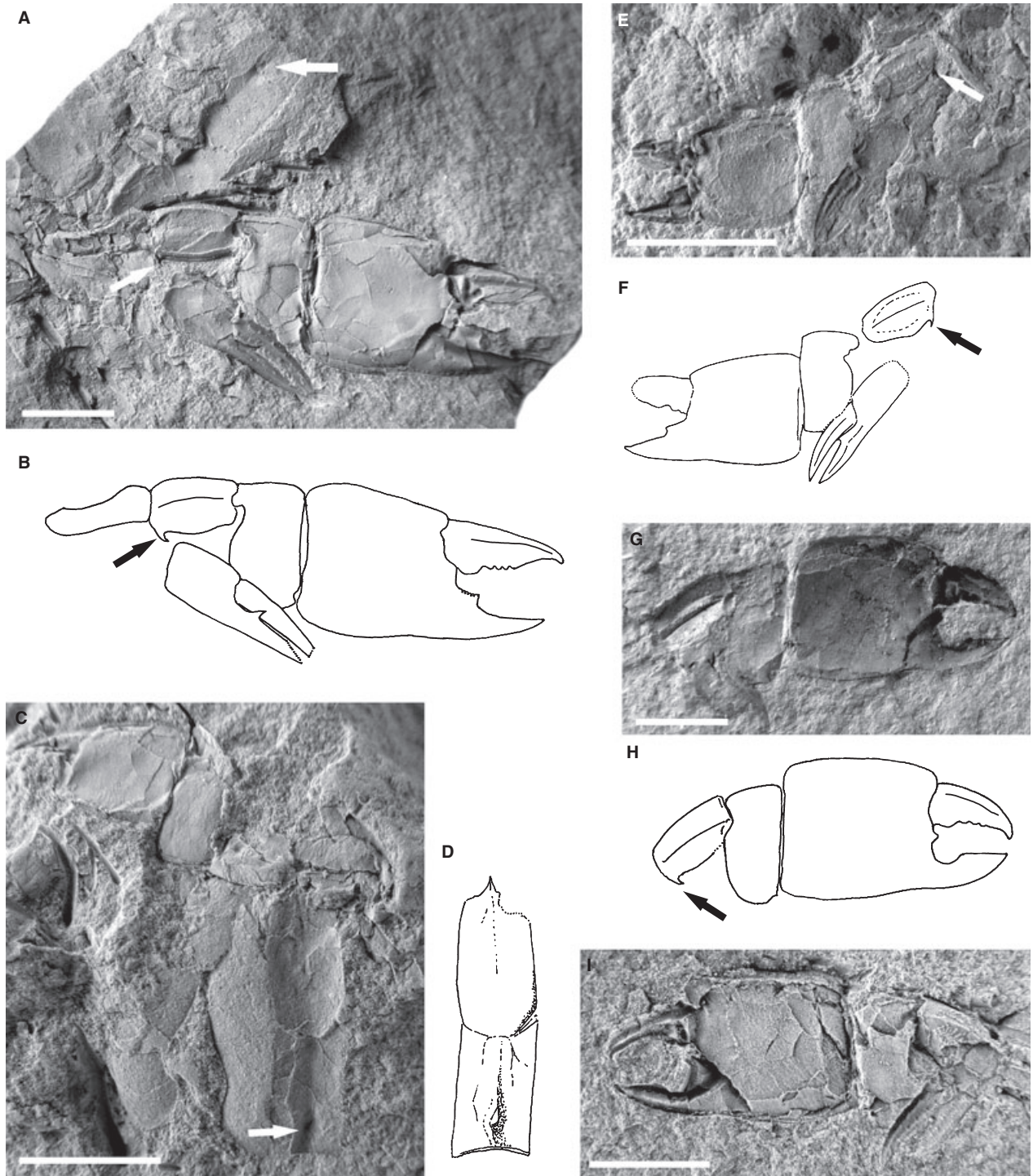
Callianopsis marianae sp. nov.

Text-figures 2A–I, 3

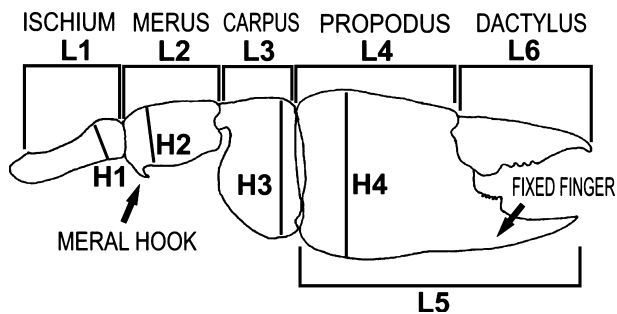
Derivation of name. Named after Mariana Hyžná, the senior author's wife.

Holotype. SNM-Z-24.810, a female specimen with both major and minor chelae preserved, as well as a portion of the dorsal carapace (Text-fig. 2A, B).

Paratypes. SNM-Z-24.811–SNM-Z-24.812 (both females) and SNM-Z-24.813–SNM-Z-24.814 (both males) (Text-fig. 2C–H).



TEXT-FIG. 2. *Callianopsis marianae* sp. nov. A, B, part of holotype (SNM-Z-24.810), female specimen; line drawing illustrating both chelipeds, with a portion of dorsal carapace. Note proximal meral hook and cardiac prominence in posterior part of dorsal carapace (upper white arrow in Text-fig. 2A). C, paratype (SNM-Z-24.811), female specimen, preserving complete dorsal carapace and left major cheliped (left upper corner). Note cardiac prominence on dorsal carapace (white arrow). D, line drawing of dorsal carapace of specimen in Text-figure 2C. E, F, part of paratype (SNM-Z-24.812), female specimen; line drawing illustrating both chelipeds. Note the presence of proximal meral hook (arrows). G, H, counterpart of paratype (SNM-Z-24.813), male specimen; line drawing. Note proximal meral hook (black arrow). I, male specimen (SNM-Z-24.835). All specimens from the type locality, Cerová-Lieskové. Scale bar represents 5 mm.



TEXT-FIG. 3. Measured parameters of major cheliped of *Callianopsis marianae* sp. nov. used in Table 2.

Type locality. Cerová-Lieskové (Vienna Basin, Slovakia); Lakšárska Nová Ves Formation (middle–upper ‘Karpatic’, uppermost Burdigalian, lower Miocene).

Additional material. SNM-Z-7.157, SNM-Z-24.815–SNM-Z-24.850, SNM-Z-24.852–SNM-Z-24.861, SNM-Z-35.095, SNM-Z-35.097 and SNM-Z-35.102, a total of 58 specimens.

Specimens are preserved mainly as isolated chelipeds. In five cases, both chelae are preserved (SNM-Z-24.810, SNM-Z-24.812–SNM-Z-24.814 and SNM-Z-24.832), while SNM-Z-24.810, SNM-Z-24.811, SNM-Z-24.813, SNM-Z-24.815, SNM-Z-24.817, SNM-Z-24.822, SNM-Z-24.832, SNM-Z-24.833, SNM-Z-24.835, SNM-Z-24.839, SNM-Z-24.842 and SNM-Z-24.845 retain portions of carapace. In five other specimens (SNM-Z-24.810, SNM-Z-24.811, SNM-Z-24.832, SNM-Z-24.842 and SNM-Z-24.845), the position of the carapace is such that these may represent moults (Glaessner 1929*b*). In several other examples, remains of original cuticle are preserved (e.g. SNM-Z-24.826, SNM-Z-24.833 and SNM-Z-24.841). Two specimens (SNM-Z-24.814 and SNM-Z-24.822) have well-preserved thoracic sternites; the former retains the 1st, 2nd or 3rd sternite, while in the latter the 4th is preserved. The abdomen, preserved in one specimen (SNM-Z-24.839), is laterally compressed, thus precluding observation of the 6th somite, characters of which are important. In one matrix sample (SNM-Z-35.096), two propodi of opposite sex are preserved.

Diagnosis. Markedly heterochelous ctenochelid without dorsal oval, distinct cardiac prominence and rostral carina; first pereopods exhibiting strong sexual dimorphism; merus of major cheliped subelliptical with distinct proximal spine on lower margin; manus of major cheliped with tubercles distally on lateral surface; manus of male major cheliped with blunt spine on distal margin above position of fixed finger; fixed finger curving upwards with prominent rounded notch; manus of female major cheliped with large triangular tooth at base of fixed finger; fixed finger triangular; manus of minor chela of both sexes with distinct, sharp tooth on cutting edge of fixed finger, directed forwards.

Description. Length of dorsal carapace four times width; rostral spine triangular with low rostral carina; carapace without dorsal

oval; cervical groove clearly delineated; distinct ridge beginning at centre of posterior half of carapace and extending posteriorly, ridge terminating in distinct cardiac prominence with a median pit; posterior margin prominently concave (Text-fig. 2C, D).

First pereopods (chelipeds) unequal and highly dissimilar, showing striking sexual dimorphism in the shape of the manus; major cheliped massive and stout compared to the minor one.

Length of ischium about 2.5 times height, widest at articulation with merus, thinning proximally, upper margin distinctly sinuous.

Merus 1.5–2.4 times longer than high, subelliptical; lateral surface convex; with prominent longitudinal keel, more pronounced near distal end, keel dividing merus longitudinally into two portions, lower portion slightly larger; lower margin bearing proximal spine (Text-fig. 2B, F, H), spine directed downwards and obliquely forwards, remainder of lower margin convex and smooth; upper margin slightly convex and smooth.

Carpus broad, 1.7–2.5 times higher than long, shorter than merus; upper and lower margins keeled, terminating distally in blunt corners; lateral surface smooth and convex; proximal margin sinuous, merging with lower margin; proximal margin with long projection at articulation with merus; together with lower margin forming a paddle-like flange extending downwards; distal margin weakly concave, rimmed at articulation with manus.

Manus of male major cheliped (Text-fig. 2G–I) nearly squarish, 1–1.4 times longer than high, lateral surface convex, distally covered with 5–7 tubercles, with setal pits on the inner surface of lower margin extending onto fixed finger; proximal margin straight; upper margin slightly convex; lower margin slightly convex proximally, becoming occasionally slightly concave just proximal to fixed finger; distal margin extending slightly obliquely from upper to lower margin, bearing a single distinct tooth at the centre pointing forwards (proximally). Fixed finger equalling 35–60 per cent of the length of manus, curving slightly upwards, with blunt tooth and sharp tip; with deep rounded notch situated at base of fixed finger. Dactylus stout, narrowing distally, weakly arched, with three molar-like, blunt teeth situated proximally and one tooth distally forming curved tip; outer margin with ridge, tuberculate.

Manus of female major cheliped (Text-fig. 2A, B, E, F) usually square, occasionally slightly longer than high, lateral surface convex, distally covered with up to nine tubercles, some of them may extend onto fixed finger, with setal pits on inner surface of lower margin extending onto fixed finger; proximal margin slightly sinuous, rounded articulations with carpus on upper and lower corners of margin; upper margin convex; lower margin straight or slightly convex; distal margin straight, with large, near-triangular tooth at base of fixed finger, upper margin of tooth parallel to upper margin of manus and cutting edge of fixed finger, with up to 10 tiny denticles; lateral edge of tooth almost perpendicular to cutting edge of fixed finger forming a blunt projection pointing proximally. Fixed finger 40–65 per cent of the length of manus, thin, triangular in shape. Dactylus with up to six molar-like, blunt teeth on cutting edge, being smaller proximally, with a sharp slightly curved tip; outer margin with ridge, tuberculate.

Minor chela of both sexes slender, much smaller than major chela; manus longer than high; fixed finger about as long as

TABLE 2. Measurements of major chelipeds of the best-preserved specimens of *Callianopsis marianae* sp. nov.

Specimen	Sex	Handedness	Ischium		Merus		Carpus		Propodus		Dactylus	
			L1	H1	L2	H2	L3	H3	L4	H4	L5	L6
SNM-Z-24.810	F	L	6.1	2.1	5.2	3.2	4.5	7.5	8.2	9.2	13.6	7.2
SNM-Z-24.811	F	L	–	–	2.8	2.1	2.5	3.7	4.5	4.1	6.8	–
SNM-Z-24.812	F	R	–	–	3.0	1.7	2.2	3.5	3.6	3.6	5.8	2.2
SNM-Z-24.813	M	L	–	–	5.7	3.0	3.1	6.6	8.3	7.6	12.2	5.2
SNM-Z-24.814	M	R	6.0	2.3	4.3	3.2	2.7	6.6	7.0	6.5	11.3	5.2
SNM-Z-24.815	F	R	–	–	6.6	4.0	5.4	8.6	9.6	9.6	15.3	7.2
SNM-Z-24.818	F	L	–	–	6.0	3.7	4.0	7.7	9.0	9.0	14.0	8.6
SNM-Z-24.832	M	L	–	–	5.0	3.5	3.5	5.8	7.7	7.0	11.8	5.3
SNM-Z-24.833	M	L	7.4	2.6	7.2	3.5	–	–	10.8	8.0	17.2	–
SNM-Z-24.835	M	L	6.0	2.6	5.0	3.5	4.1	–	8.1	8.2	12.3	4.8
SNM-Z-24.841	M	L	–	–	–	–	6.1	10.0	13.0	13.5	20.3	9.4
SNM-Z-24.842	M	R	6.0	2.5	–	–	–	–	8.1	5.6	12.6	–
SNM-Z-35.095	F	L	7.0	2.0	7.0	4.0	4.9	7.1	10.8	9.2	16.1	–

Measurements in mm. For explanation of measured parameters, see Text-figure 3.

manus, narrow, with distinct, sharp tooth situated in proximal third, directed obliquely forwards; dactylus slightly longer than fixed finger, narrow, incurved, cutting edge smooth.

Measurements. About 50 specimens were measured. Measurements of major chelipeds of the best-preserved specimens are summarized in Table 2. For explanation of measured parameters and their abbreviations, see Text-figure 3.

Discussion. Schweitzer Hopkins and Feldmann (1997) opined that the combination of a small, distal meral spine and a central meral keel, a carpus with a paddle-shaped flange, major chelae with a tooth on the distal margin and on the fixed finger (in males only), and unequal major chelipeds was unique for the genus *Callianopsis*. Although the present material lacks a distinct tooth on the fixed finger (as in *C. australis* from the middle Oligocene of Argentina; see Casadío *et al.* 2004), it does demonstrate all of the above-mentioned features, as well as characters of the dorsal carapace, namely a distinct cardiac prominence and rostral carina. The combination of all these characters confirms assignment of the present material to *Callianopsis*. The character of dorsal oval, which has been considered of taxonomic significance (Manning and Felder 1991), is held to be less useful, in view of the recent discovery that extant *C. anovalis* lacks dorsal oval (Lin *et al.* 2007). This character is also difficult to demonstrate in several members of the Callianassidae (P. C. Dworschak, pers. comm. to MH 2008).

Callianopsis marianae sp. nov. lacks the spine on the fixed finger in males which is present in other species of *Callianopsis* except *C. australis*. The latter can be differentiated from the new species by a stouter merus.

The present material extends the fossil record of the genus *Callianopsis* to Europe. A previous mention from the

middle Eocene of northern Italy (Beschin *et al.* 2005) cannot be substantiated unequivocally (see remarks above).

The only feature on which to distinguish sex amongst specimens of *C. marianae* sp. nov. is the nature of the major chelae. The two sexes are similar as far as ischium, carpus and merus are concerned, but can be distinguished by the manus. An identical pattern was recorded for the extant *C. goniophthalma* and fossil *C. clallamensis* (Schweitzer Hopkins and Feldmann 1997). The minor chela of *C. marianae* sp. nov. is similar to that of the extant species, *C. goniophthalma*, *C. caecigena* and *C. anovalis*.

Within the material of *C. marianae* sp. nov., it is also possible to note intraspecific variations in the major cheliped, specifically in the length/height ratios of manus, carpus and merus. In females, variations in size and shape of the triangular tooth at the base of the pollex can be observed. In all specimens measured, there is a near-equal ratio of males and females (about 50 per cent). A similar pattern is also seen in the handedness, without any correlation with sex.

Family THOMASSINIIDAE de Saint Laurent, 1979a

Remarks. Originally, de Saint Laurent (1979a) considered this to be a subfamily of the Callianassidae, with *Thomassinia* de Saint Laurent, 1979a as type genus. Kensley and Heard (1991) transferred *Thomassinia* to the Callianideidae, which comprises several other genera, including *Crosniera* Kensley and Heard, 1991. Sakai (1992) subdivided the family Callianideidae into four subfamilies, one of them being the Thomassiniinae with the genera *Thomassinia*, *Crosniera* and *Mictaxius* Kensley and Heard, 1991. This taxon was ranked as a family by Manning and Felder

(1991) and Poore (1994). A review of this family, and the families Callianideidae and Micheleidae, was carried out by Poore (1997). The Thomassiniidae is based mainly on features that usually are not preserved in the fossil record, such as carapace, mouth parts and pleopods (Poore 1997). However, it is possible to distinguish members of the families Callianideidae, Micheleidae and Thomassiniidae broadly on cheliped features. Micheleids are homochealous, whereas Callianideidae and Thomassiniidae are heterochealous. Callianideids differ from thomassiniids in having complexly toothed cheliped dactyls. Recently, in a molecular study, Robles *et al.* (2009) have opined that the family Thomassiniidae should be merged with the Callianideidae. However, De Grave *et al.* (2009) retained the family rank of Thomassiniidae, and we here follow their opinion.

Remarks. Until now, there were no records of fossil representatives of the Thomassiniidae. In view of their generally diminutive size and weak calcification of cuticular surfaces, it is not surprising that thomassiniids have a poor fossil record.

Genus CROSNIERA Kensley and Heard, 1991

Type species. *Callianassa minima* Rathbun, 1901, by original designation.

Diagnosis. Rostrum spike-like; *linea thalassinica* incomplete; first maxilliped exopod flagellate; third maxilliped

exopod as long as merus, ischium and merus without brush of stiff setae. Chelipeds dissimilar. First abdominal somite usually with row of setae; sixth somite typically with three rows of setae. Uropodal endopod without transverse row of short spiniform setae; exopod simply ovate. First male pleopod present (after Poore 1997).

Remarks. This genus is assigned to the Thomassiniidae mainly on the basis of having a *linea thalassinica* which commences anteriorly near the eyestalks and by wide, asymmetrical chelipeds (Poore 1997). The present specimens are assigned to this family on the evidence of shape of the merus, propodus and dactylus. Placement in the genus *Crosniera* is based exclusively on the nature of the manus, and it should thus be considered preliminary.

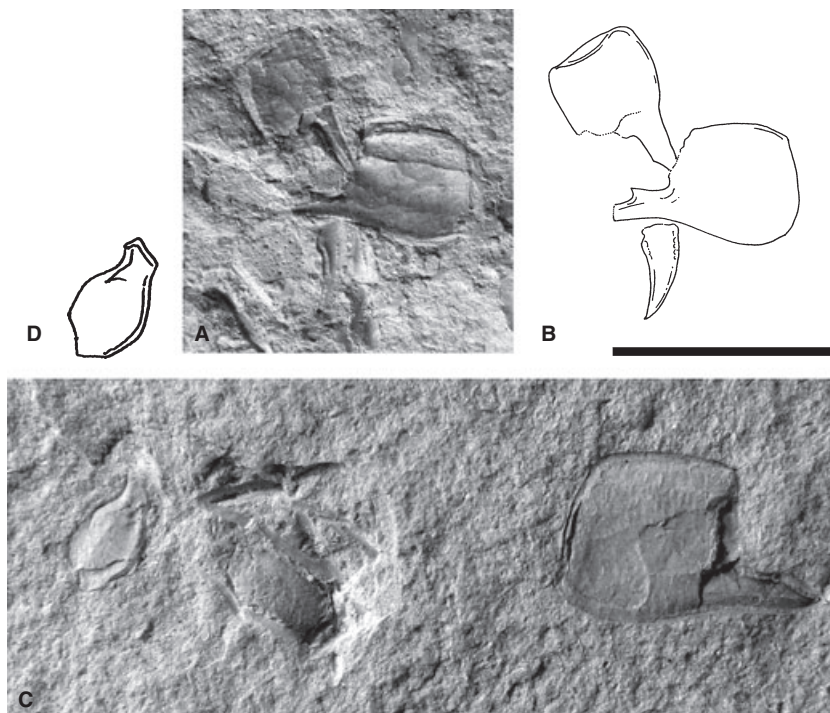
Crosniera schweitzerae sp. nov.

Text-figures 4A–D, 5

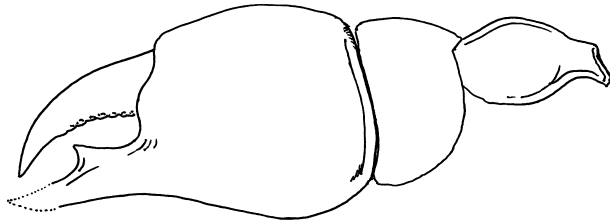
Derivation of name. Named after Dr Carrie E. Schweitzer, Department of Geology, Kent State University, Kent, Ohio.

Holotype. SNM-Z-24.862, comprising two propodi (major and minor) and one dactylus of the same specimen (Text-fig. 4A, B).

Paratype. SNM-Z-24.863, a minor chela with merus, carpus and propodus preserved (Text-fig. 4C, D).



TEXT-FIG. 4. *Crosniera schweitzerae* sp. nov. A, B, holotype (SNM-Z-24.862) showing propodi of both chelipeds and one dactylus. C, paratype (SNM-Z-24.863) showing disarticulated merus, carpus and propodus of left minor cheliped. D, line drawing of merus of specimen in Text-figure 4C. All specimens from the type locality, Cerová-Lieskové. All figures at the same scale; scale bar represents 5 mm.



TEXT-FIG. 5. Reconstruction of the major cheliped of *Crosniera schweitzeriae* sp. nov., based on the type material.

Type locality. Cerová-Lieskové (Vienna Basin); Lakšárska Nová Ves Formation; middle to upper Karpatian (uppermost Burdigalian, lower Miocene).

Other material. SNM-Z-35.099, a single propodus.

Diagnosis. Chelipeds subequal, similar, unarmed except for fixed finger; merus with convex lower and upper margins. Dactylus with curved tip, cutting edge with tiny denticles.

Description. Chelipeds subequal, similar, right slightly stouter than left.

Merus with convex lower and upper margins, highest distally; with longitudinal keel over the centre, dividing the merus into two portions.

Carpus higher than long, highest distally at the point of articulation with propodus, not well preserved.

Manus near-rectangular, length and height of minor propodus equal, major somewhat longer than high; proximal and upper margin convex; lower margin convex, becoming slightly concave just proximal to fixed finger. Fixed finger shorter than palm in both chelipeds, fixed finger of major propodus bearing anteriorly directed tooth near presumed mid-length (Text-fig. 5), tip of fixed finger not preserved; fixed finger of minor cheliped with sharp tip, concave distally, forming a tiny protuberance about centre of fixed finger.

Dactylus with curved tip, cutting edge with tiny denticles in proximal portion.

Measurements. See Table 3.

Discussion. Morphologically, the closest extant species is *Crosniera dayrati* Ngoc-Ho, 2005 from French Polynesia, from which the new species differs in having a somewhat

shorter merus and manus. The fixed fingers of both chelae in *C. schweitzeriae* sp. nov. are also narrower. The fixed finger of the minor chela is shorter in *C. schweitzeriae* sp. nov. than in *C. dayrati* and has a concave, sharp tip. All other living species differ from *C. schweitzeriae* sp. nov. in the general shape of the manus and the nature of the fixed finger.

Infraorder ANOMURA MacLeay, 1838

Superfamily GALATHEOIDEA Samouelle, 1819

Family GALATHEIDAE Samouelle, 1819

Remarks. Because numerous systematically important characters of biological classification are usually not preserved in the fossil record, Schweitzer and Feldmann (2000b) made an attempt to evaluate the characters of the dorsal carapace in fossil galatheoid genera. They produced a key to the fossil Galatheaidea and argued that arrangement of genera within the Galatheaidea, based solely on dorsal carapace features, generally agrees with subfamilial taxa defined on biological criteria. The importance of general carapace shape and the form of rostrum was later emphasized by Poore (2004). A review of extant records of Galatheaidea was published by Baba *et al.* (2008).

Remarks. For an overview of fossil galatheids, reference is made to De Angeli and Garassino (2002). The fossil record of the Galatheaidea is not very extensive compared to its modern status (690 species in 34 genera; census September 2009; see De Grave *et al.* 2009), and it is considered one of the most diverse of all decapod groups. However, quite speciose galatheid faunules have been recorded from the Upper Cretaceous of Spain (Vía Boada 1982) and Morocco (Garassino *et al.* 2008), the Paleocene of Denmark (Jakobsen and Collins 1997) and the Eocene and Oligocene of northern Italy (De Angeli and Garassino 2002).

Subfamily GALATHEINAE Samouelle, 1819

Remarks. The Galatheinae is the most diverse subfamily, which includes seven exclusively fossil genera (for details,

TABLE 3. Measurements (in mm) of *Crosniera schweitzeriae* sp. nov.

Specimen	Minor/major chela	Merus		Carpus		Propodus		Dactylus
		L	H	L	H	L	H	L
SNM-Z-24.862	Major	–	–	–	–	2.6	2.4	2.4
SNM-Z-24.862	Minor	–	–	–	–	2.0	1.9	–
SNM-Z-24.863	Minor	2.8	1.7	>1.3	>3.1	3.4	3.6	–
SNM-Z-35.099	Minor	–	–	–	–	3.0	3.3	–

see Schweitzer and Feldmann 2000b), three genera with both extinct and extant representatives (*Galathea* Fabricius, 1793; *Munida* Leach, 1820 and *Agononida* Baba and de Saint Laurent, 1996) and 24 exclusively extant genera (Baba *et al.* 2008).

Genus AGONONIDA Baba and de Saint Laurent, 1996

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

Diagnosis. Carapace with distinct transverse ridges, rendering a granulated appearance. Rostral spine rather far removed from supraocular spines. A pair of epigastric spines, situated directly behind supraocular spines, sometimes followed by 1–2 additional pairs, in longitudinal rows; pair of postcervical spines consistently present, each sometimes followed by one or more spines in a row. Cardiac region having elevated transverse ridge often armed with one or more median spines. Posterior ridge of carapace unarmed, with one, or more, median spines. Second to fourth abdominal tergites with two elevated, transverse ridges. Telsonal subdivision incomplete. Merus of third maxilliped with prominent submedian spine on flexor margin. Chelipeds slender, elongated, frequently with

squamate ornament. No gonopods on first abdominal segment of male (Baba and de Saint Laurent 1996).

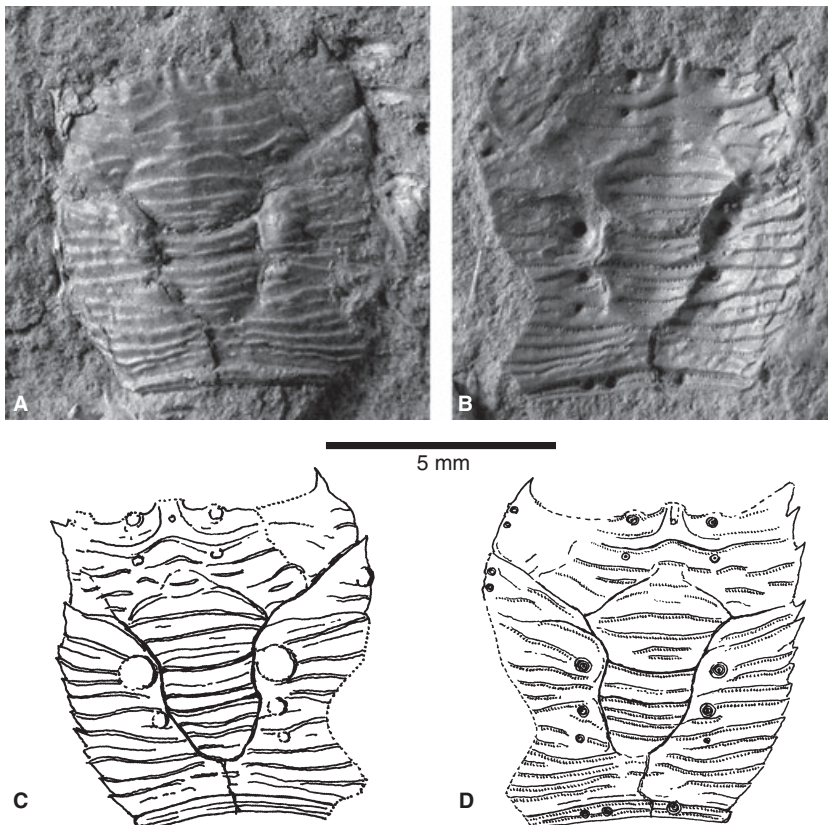
Remarks. The genus was distinguished from *Munida* by Baba and de Saint Laurent (1996) on the presence of gonopods on the second abdominal segment only, a carapace with a pair of epigastric spines and a postcervical spine on each side, second to fourth abdominal tergites each with four spines on the anterior ridge, and the merus of the third maxilliped bearing only a single, well-developed spine on the flexor margin. The genera *Munida* and *Agononida* can be differentiated by the presence of fewer carapace spines, dominated by pairs of epigastric and postcervical spines in the latter (Poore 2004). The present material is the first record of fossil members of this genus.

Agononida cerovensis sp. nov.

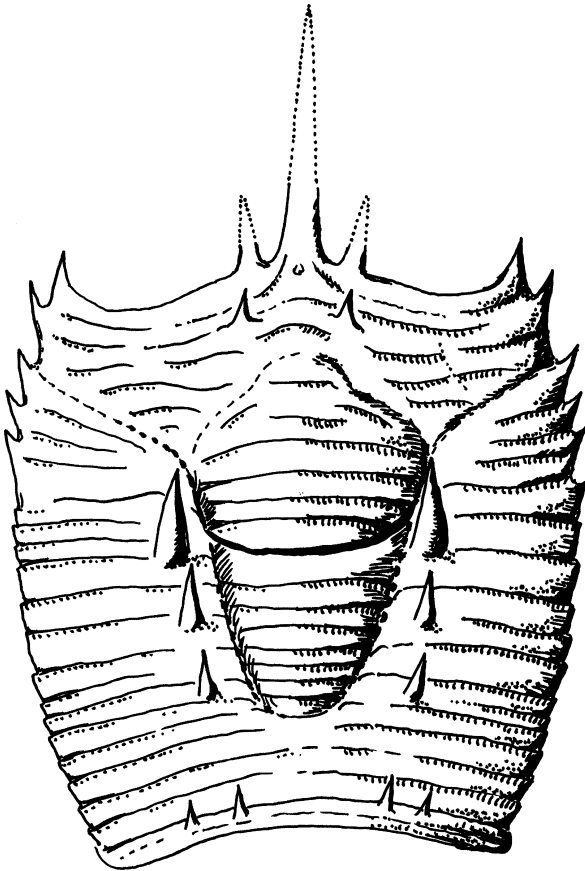
Text-figures 6A–D, 7

Derivation of name. In reference to the type locality, Cerová-Lieskové.

Holotype. SNM-Z-24.864, a dorsal carapace without rostrum (Text-fig. 6).



TEXT-FIG. 6. *Agononida cerovensis* sp. nov. A, B, part and counterpart of holotype (SNM-Z-24.864). C, D, line drawings of the same specimen, from the type locality, Cerová-Lieskové.



TEXT-FIG. 7. Reconstruction of the dorsal carapace of *Agononida cerovenssis* sp. nov.

Type locality. Cerová-Lieskové (Vienna Basin); Lakšárska Nová Ves Formation; middle to upper 'Karpatian' (uppermost Burdigalian, lower Miocene).

Diagnosis. Carapace cordate, nearly as long (without rostrum) as wide, with convexly rounded lateral margins; transverse carapace ridges distinct, ridge edges ornamented with granules, ridges mostly parallel, becoming more complex anteriorly and posteriorly; partially preserved rostrum with two smaller supraorbital spines; anterolateral margin with three spines; cervical and branchiocardiac grooves deeply incised; epigastric spines, postcervical spines and spines on the posterior rim form two distinct rows oriented longitudinally.

Description. The carapace is small for the family, about as long (without rostrum) as wide, widest at the point of cervical groove lateral termination about 33 per cent of the distance anteriorly on carapace; oblong in shape; lateral margins distinctly convex; the whole surface is covered with distinct transverse ridges which are lined with small granules.

Rostrum missing; however, at the base, it seems that it has a pair of supraorbital spines and larger central rostral spine; the

supraorbital spines have at their bases a distinct tubercle forming most likely a spine (epigastric) when complete (Text-fig. 7).

Frontal margin gently arcuate, entire. Anterolateral margin with three spines directed anterolaterally, at least four spines on branchial lateral margin, which is crenulate owing to intersection of transverse ridges with margin. Posterior margin concave, rimmed, with three preserved spines, two of them on right portion of rim.

Carapace regions and grooves well developed. Cervical and branchiocardiac grooves deep and broad. Epigastric region with two pairs of distinct spines, each of them oriented longitudinally just at base of rostrum. Hepatic region small. Mesogastric region weakly but clearly delineated, posterior margin distinctly convex. Metagastric region narrow longitudinally. Cardiac region well delineated, narrowing distally, posterior margin strongly convex forming a U-shaped apex. Epibranchial region triangular, bounded by cervical and branchiocardiac grooves. Mesobranchial and metabranchial regions weakly delineated, ornamented with three postcervical spines forming a line directed longitudinally parallel to branchiocardiac groove; the largest spines oriented anteriorly, broken at their bases, therefore preserved as a pair of large tubercles at the concavity of the branchiocardiac groove. Epigastric spines, postcervical spines and spines on the posterior rim form two distinct rows oriented longitudinally parallel to lateral margins. Sternum, abdomen and appendages unknown.

Measurements. Length of carapace (without rostrum) 6.8 mm; maximum width 7 mm.

Discussion. The sole specimen known is well preserved, but it lacks the rostrum. Despite that, it possesses a small number of anterolateral spines; a deeply incised, arcuate cervical groove and well-developed transverse ridges. Most importantly, the nature and arrangement of epigastric and postcervical spines allow assignment of this material to the genus *Agononida*, at least until better-preserved specimens become available.

The new species differs from extant congeners mainly in the general shape of carapace and number and position of spines. The morphologically similar *Agononida eminens* (Baba, 1988), *A. imitata* Macpherson, 2006, *A. normani* (Henderson, 1885) and *A. procera* Ahyong and Poore, 2004 all have two or more spines in the cardiac region, whereas *A. cerovenssis* sp. nov. has none. *Agononida aequalis* Macpherson, 2006 differs from *A. cerovenssis* sp. nov. in the possession of parahepatic spines. The main distinction of *Agononida cerovenssis* sp. nov. from all other species is the number, position and size of postcervical spines.

Subfamily MUNIDOPSINAE Ortmann, 1898

Remarks. The subfamily comprises five exclusively fossil genera (see Schweitzer and Feldmann 2000b), one genus

TABLE 4. Fossil species assigned to *Munidopsis* and their age and geographic distribution.

Species	Age	Geographic distribution
<i>M. foersteri</i> Feldmann <i>et al.</i> , 1993	Campanian	Antarctica
<i>M. scabrosa</i> Feldmann and Wilson, 1988	late Eocene	Antarctica
<i>M. lieskovensis</i> new species	early Miocene	Slovakia

Takeda *et al.* (1986) recorded another occurrence of *Munidopsis* spp. from the Miocene of Japan.

with both fossil and extant members (*Munidopsis*) and one exclusively extant genus, *Galacantha* (re-established by Ahyong 2007, previously treated as a synonym of *Munidopsis*).

Genus MUNIDOPSIS Whiteaves, 1874

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

Included fossil species. See Table 4.

Diagnosis. Carapace longer than wide, roughly rectangular or pentagonal in outline, integument strongly calcified; dorsal surface of carapace with well-defined cardiac and gastric regions; anterolateral margins usually spinose or dentate, occasionally entire. Eyestalks free or fused with orbits, eyes without facets or pigment. Rostrum well developed, triangular or spatulate (after Ambler 1980; Ingle and Christiansen 2004).

Remarks. General carapace shape is the most useful means of species distinction within *Munidopsis*, particularly rostrum shape and arrangement of spines on the carapace and also on abdominal somites (Ambler 1980; Poore 2004). There are also some other important characters, such as the nature of chelipeds (Ambler 1980); these are, however, quite rarely preserved in fossil Galatheidae.

More than 220 extant species of *Munidopsis* are currently known (Baba *et al.* 2008).

Munidopsis lieskovensis sp. nov. Text-figures 8A–D, 9

Derivation of name. In reference to the type locality, Cerová-Lieskové.

Holotype. SNM-Z-24.865, a near-complete dorsal carapace, preserving the rostrum (Text-fig. 8).

Paratypes. SNM-Z-24.866 and SNM-Z-24.867, both near-complete dorsal carapaces.

Type locality. Cerová-Lieskové (Vienna Basin); Lakšárska Nová Ves Formation; middle to upper 'Karpatian' (uppermost Burdigalian, lower Miocene).

Diagnosis. *Munidopsis* with elongate triangular rostrum, external orbital swellings and well-defined regions; antero-lateral margin with one spine; surface of carapace covered with short, semicircular striae; cervical groove axially V-shaped.

Description. The carapace is small for family, slightly longer than wide, vaulted transversely, widest at the point of branchiocardiac groove lateral termination; outline quadrate, lateral margins slightly convex; surface striate.

Frontal margin sinuous. Rostrum elongate triangular, about one-third total length of remainder of carapace, margin with narrow, smooth rim; distinctly keeled axially, remainder of surface slightly pustulose. Anterolateral margin with one distinct spine.

Carapace regions and grooves well defined; domed regions covered with short, semicircular, raised striae; grooves smooth, moderately deep. Hepatic regions nearly quadrate. Mesogastric region slightly wider than half the carapace, epigastric regions well defined as distinct spherical elevations, protogastric regions very poorly defined. Cervical groove deep and broad, axially V-shaped. Cardiac region moderately defined, narrowest axially and widest near adaxial terminations. Intestinal region large, triangular, as wide as long. Branchiocardiac groove less deep than cervical, quite shallow. Epibranchial regions almost triangular.

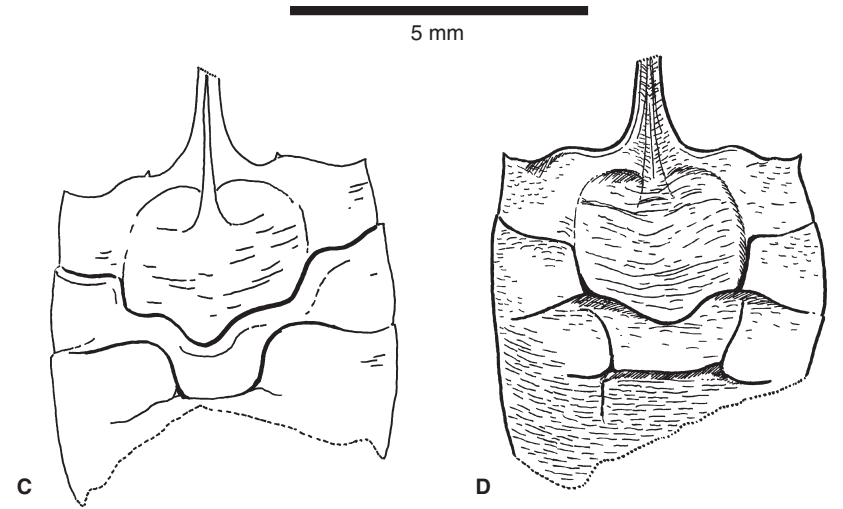
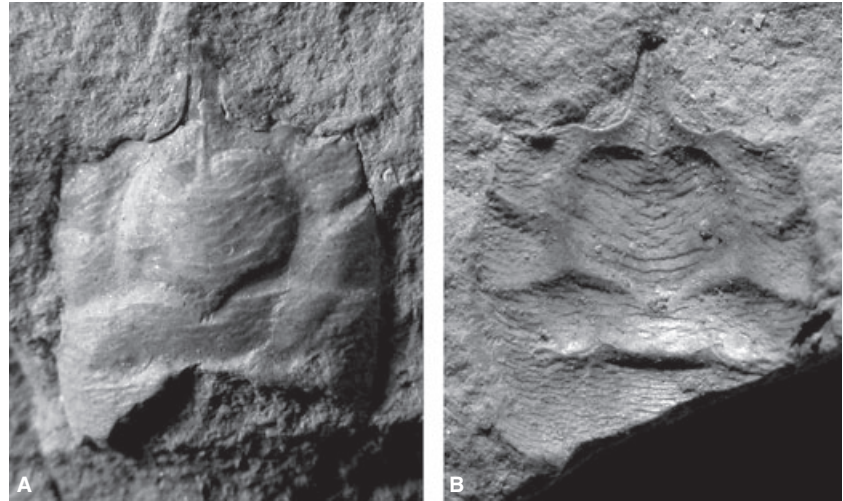
Sternum, abdomen and appendages unknown.

Measurements. SNM-Z-24.865: carapace length (without rostrum) >5.5 mm, carapace width 5.7 mm. SNM-Z-24.866: length >5.5 mm; width 5 mm. SNM-Z-24.867: length >6 mm; width 5.1 mm.

Discussion. The new species differs from *Munidopsis scabrosa* (upper Eocene, Antarctica; see Feldmann and Wilson 1988) in having a differently shaped frontal margin and cervical groove. *Munidopsis foersteri* from the Upper Cretaceous of Antarctica (Feldmann *et al.* 1993) differs mainly in having a rather pear-shaped carapace and very long and slender rostrum. *Munidopsis* spp. reported by Takeda *et al.* (1986) from the Miocene of Japan differs in having a pear-shaped carapace and more spines on the lateral margins.

There are 13 extant species of *Munidopsis* in the Mediterranean area (Baba *et al.* 2008). Most closely similar to *M. lieskovensis* sp. nov. are *M. polymorpha* Koelbel, 1892 and *M. centrina* Alcock and Anderson, 1894. However, the former possesses a distinctly shorter rostrum and external orbital spines, while the latter has a longer rostrum and differently shaped branchiocardiac groove.

TEXT-FIG. 8. *Munidopsis lieskovensis* sp. nov. A, B, part and counterpart of holotype (SNM-Z-24.865). C, D, line drawings of the same specimen, from the type locality, Cerová-Lieskové.



Infraorder BRACHYURA Linnaeus, 1758
 Superfamily CALAPPOIDEA de Haan, 1833
 Family CALAPPIDAE de Haan, 1833

Remarks. There is an extensive fossil record of calappids, which comprises eight of twelve known genera (see De Grave *et al.* 2009). Seven of them are exclusively fossil (*Calappella* Rathbun, 1919; *Calappilia* A. Milne Edwards, 1873; *Mursilata* Hu and Tao, 1996; *Mursilia* Rathbun, 1918; *Mursiopsis* Ristori, 1889; *Stenodromia* A. Milne Edwards, 1873 and *Tutus* Collins, Portell and Donovan, 2009). A systematic reassessment of fossil Calappidae was published by Schweitzer and Feldmann (2000a), who produced a key to the family based on a detailed analysis of dorsal carapace characters of fossil and extant genera.

Genus MURSIA Desmarest, 1823

Type species. *Mursia cristiata* H. Milne Edwards, 1837, by subsequent designation (monotypy).

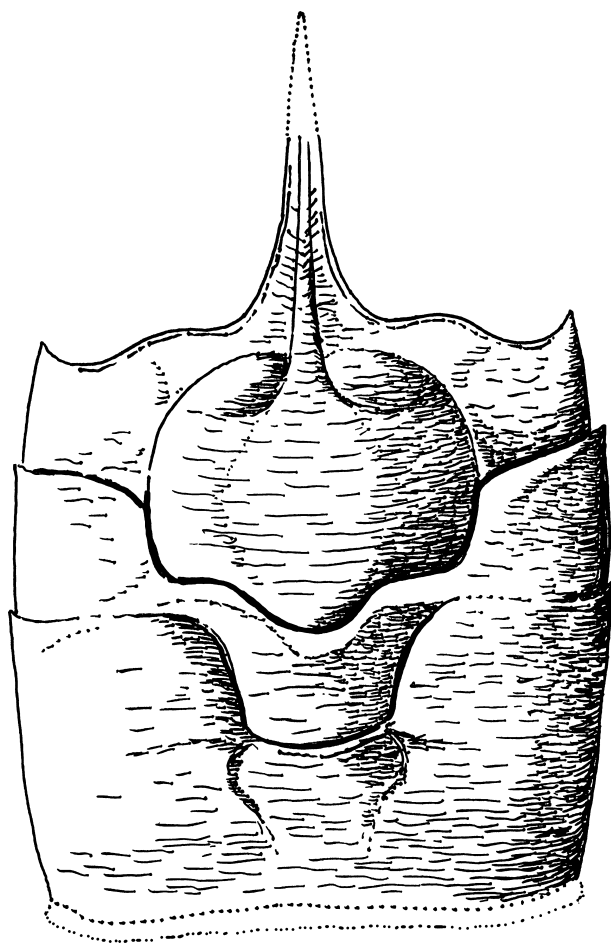
Included fossil species. See Table 5.

Diagnosis. Carapace subcircular to transversely oval, convex, granulate; outline rounded anteriorly, but constricted and blunt posteriorly, with or without long lateral spines. Front wider than orbit, trilobate, median lobe projecting. Orbits large and rimmed, with two orbital fissures. Dorsal surface with undefined regions and with five or seven longitudinal ridges of tubercles (after Galil 1993; Collins and Donovan 2002).

Remarks. The fossil record of the genus is quite extensive; see Table 5 for details. There are 28 extant species (Ng *et al.* 2008).

Mursia harnicari sp. nov.
 Text-figures 10A, B, 11

Derivation of name. Named in honour of Adrián Harničár, a Slovak freelance geologist.



TEXT-FIG. 9. Reconstruction of the dorsal carapace of *Munidopsis lieskovensis* sp. nov., based on the type material.

Holotype. SNM-Z-35.100, a near-complete dorsal carapace, slightly deformed transversely and compressed dorso-ventrally (Text-fig. 10A).

Type locality. Cerová-Lieskové (Vienna Basin); Lakšárska Nová Ves Formation; middle to upper 'Karpatian' (uppermost Burdigalian, lower Miocene).

Diagnosis. Carapace weakly ovate in outline, ornamented with five rows of tubercles forming distinct ridges; anterolateral margin with small, blunt teeth; well-developed, long lateral spine, length nearly equal to half the carapace width, spine directed slightly forwards; regions moderately well defined.

Description. Carapace (without spines) circular to weakly ovate, slightly longer than wide, widest at position of lateral spine, situated at position of mid-length of the carapace. Front prominent, trilobate. Orbits circular, deep, directed forwards, the margin with two fissures. Anterolateral margin convex, arcuate, the left side crenulated with eight (as preserved) distinct blunt teeth, the right side deformed, lacking teeth. The row of anterolateral teeth terminating posteriorly by a pronounced long lateral spine. Spine acute, pointing slightly forwards, as long as half the carapace width without spines. Posterolateral and posterior margin not preserved.

Axial regions not well differentiated from one another, distinctly inflated. Protogastric region moderately inflated, ornamented with several tubercles, lateral margins convex. Axial regions beginning with mesogastric with three large tubercles forming subparallel transverse row. Hepatic region weakly inflated, ornamented with one distinct tubercle and a few smaller ones. Branchial regions with two inflated rows of distinct tubercles slightly diverging posteriorly. The middle row of tubercles is the most pronounced, other two rows on each side somewhat less distinct and less inflated.

Cuticular surface granular over the entire carapace. Venter and appendages unknown.

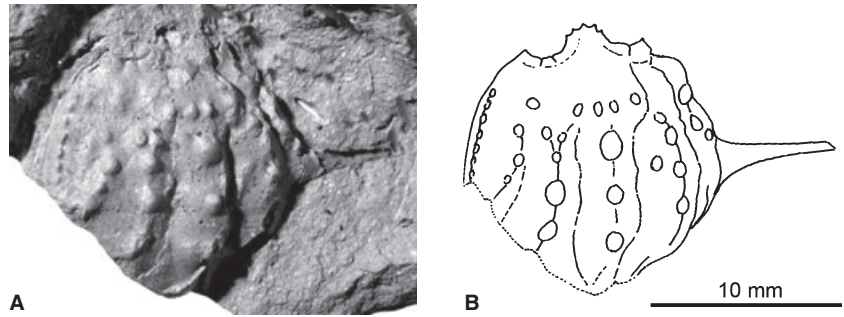
Discussion. The new species is close to *Mursia lienharti* (Bachmayer, 1962), from the lower Miocene of Belgium (Müller 1984a) and the middle Miocene of Hungary,

TABLE 5. Fossil species assigned to *Mursia* and their age and geographic range.

Species	Age	Geographic distribution
<i>M. aspina</i> Schweitzer and Feldmann, 2000a	late Eocene	Washington, USA
<i>M. granulosa</i> Collins and Donovan, 2002	late Oligocene	Antigua
<i>M. macdonaldi</i> Rathbun, 1919	late Oligocene–early Miocene	Panama
<i>M. obscura</i> Rathbun, 1919	middle Oligocene	Panama
<i>M. marcusana</i> Rathbun, 1926	Oligocene–early Miocene	Washington, USA
<i>M. yaquinensis</i> Rathbun, 1926	Oligocene–middle Miocene	Oregon, USA
<i>M. harnicari</i> new species	early Miocene	Slovakia
<i>M. lienharti</i> (Bachmayer, 1962)	early–middle Miocene	Belgium, Hungary, Austria, Germany
<i>M. bekeniensis</i> Collins in Collins <i>et al.</i> , 2003	early Miocene	Sarawak (Borneo)
<i>M. takahashii</i> Imaizumi, 1952	middle Miocene	Japan
<i>M. circularis</i> (Karasawa, 1989)	middle Miocene	Japan
<i>M. creutzbergi</i> Collins and Donovan, 2004	Miocene/Pliocene	Aruba
<i>M. minuta</i> Karasawa, 1993	Pliocene	Japan

There are records of *Mursia* spp. from the Miocene and Pliocene of Japan (Karasawa 1993) and the Pleistocene/Holocene of Guam (Schweitzer and Feldmann 2000a); and a single, questionable occurrence of *Mursia?* sp. in the Miocene of Mexico (Vega *et al.* 1999).

TEXT-FIG. 10. *Mursia harnicari* sp. nov. A, B, Holotype (SNM-Z-35.100) showing deformed, near-complete dorsal carapace and interpretative line drawing. Specimen from the type locality, Cerová-Lieskové.



Austria and Germany (Müller 1984b; Moths 2005). The tubercle arrangement on the dorsal carapace is roughly the same, but *M. harnicari* sp. nov. differs in possessing much longer lateral spines that point slightly forwards; in *M. lienharti* they are much smaller and point slightly backwards. A similar pattern can be observed in several extant species, where the length of the anterolateral spine is particularly significant (Galil 1993). The occurrence of *M. harnicari* sp. nov. in the Paratethys predates known occurrences of *M. lienharti* in the same palaeobiogeographic region. However, the latter is known from roughly coeval strata in the Boreal realm (Müller 1984a) suggesting, in addition to their similar appearance, a close relationship between the two forms. It seems that one of them is predecessor of the other one, or they represent sister taxa.

Superfamily PILUMNOIDEA Samouelle, 1819

Family PILUMNIDAE Samouelle, 1819

Remarks. According to De Grave *et al.* (2009), this family can be subdivided into five subfamilies: Calmaniinae, Eumedoninae, Pilumninae, Rhizopinae and Xenophthalmodinae. However, as Ng *et al.* (2008) admitted, the classification of Pilumnidae is not ideal as its members are

too diverse in form and relationships between them are not clear.

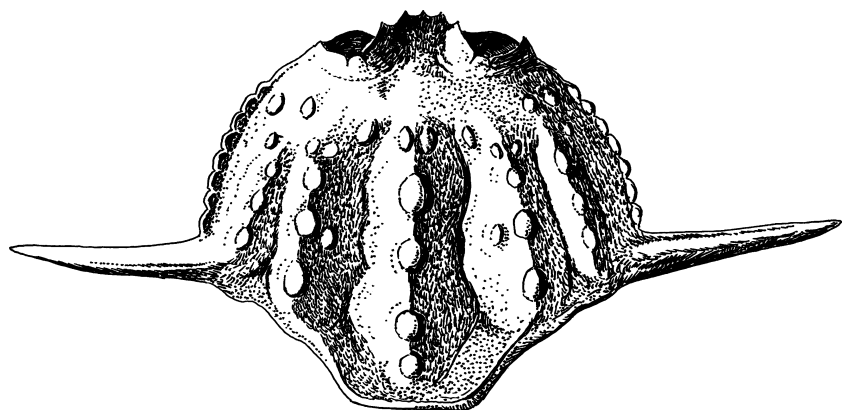
A diagnosis of the family based on characters that are most likely to be preserved in the fossil record was published by Schweitzer (2000) and Karasawa and Schweitzer (2006).

Remarks. Members of this family have been recorded frequently in the fossil record. Karasawa and Schweitzer (2006) listed 22 pilumnid genera known from the fossil record up to that date; 13 of them being exclusively fossil. Recently, Karasawa *et al.* (2008) identified an additional genus, *Cryptolutea* Ward, 1936, in the fossil record.

Subfamily RHIZOPINAE Stimpson, 1858

Remarks. This subfamily was previously referred to the Goneplacidae (Serène 1964; Sakai 1976). Guinot (1969a–c, 1971, 1978), however, argued that the Rhizopinae had so-called pilumien tendencies. Within the Pilumnidae, Serène (1984) recognized five subfamilies: Pilumninae, Heteropanopeinae, Halimedinae, Planopilumninae and Heteropilumninae. The last-named was considered to be a junior synonym of Rhizopinae (Ng 1987; Davie 2002). Ng (1985, 1987) in part revised and formally transferred

TEXT-FIG. 11. Reconstruction of the dorsal carapace of *Mursia harnicari* sp. nov. Posterolateral and posterior margins are reconstructed using material of *Mursia lienharti* (Bachmayer, 1962).



the Rhizopinae into the Pilumnidae. A diagnosis for the subfamily was provided by Davie (2002) and Feldmann *et al.* (2005), to whom reference is made.

Genus STYRIOPLAX Glaessner, 1969

Type species. *Microplax exiguus* Glaessner, 1928, by monotypy.

Emended diagnosis. As for species.

Remarks. Glaessner (1969) introduced *Styrioplax* as a replacement name for *Microplax* Glaessner, 1928, *non* Fieber, 1861 (*nec* Lilljeborg, 1865). The genus contains solely the type species.

Glaessner (1928) noted that the shape of the carapace of *Microplax* resembled that of some members (e.g. *Typhlocarcinus* Stimpson, 1858 and *Ceratoplax* Stimpson, 1858) of the Rhizopinae, at that time considered a subfamily of the Goneplacidae, but that it also showed morphological affinities to the family Pinnotheridae. Later (Glaessner 1969), he placed it within the Goneplacidae, subfamily uncertain. The revision of Goneplacidae by Karasawa and Kato (2003) noted that the familial and subfamilial placements of *Styrioplax* were obscure because detailed characters of the male abdomen of *S. exiguus* were poorly known. They suggested possible assignment to the chasmocarcinid subfamilies Chasmocarcininae or Troglolacinae, or the pilumnid Rhizopinae *sensu lato*. Examination of newly collected material and a re-examination of the type material suggest that *Styrioplax* is a rhizopine pilumnid. Morphological characters of this subfamily with a potential to be preserved in the fossil record include a near-smooth subrectangular carapace, which is wider than long; with broad and square or narrow, bilobed and deflexed front; convex, usually entire anterolateral margins; and shallow orbits. All male abdominal somites are free and usually do not cover the entire space between the coxae of the fifth pereopods (Ng 1987; Davie 2002). All of the above-mentioned characters are present in the material of *Styrioplax*. Possible affinities of *Styrioplax* to Rhizopinae were already discussed (Glaessner 1928; Karasawa and Kato 2003), and the present study substantiates previous conclusions.

The dorsal carapace of *Styrioplax* resembles that of the varunid *Asthenognathus* Stimpson, 1858 in several respects. However, both genera differ in the shape of the pereopods, which are longer and more slender in *Styrioplax* (compare Schweitzer and Feldmann 2001a, text-fig. 5.9; *Asthenognathus urretae* Schweitzer and Feldmann, 2001). In *Asthenognathus*, as in the entire subfamily Asthenognathinae Stimpson, 1858, the male abdominal somites 4–6 are typically fused and the branchial regions have ridges (Schweitzer and Feldmann 2001a), whereas in *Styrioplax*

the abdominal somites are free and there are no branchial ridges. Taxa in the Asthenognathinae have well-developed posterolateral reentrants, which are quite specific. However, in part, this character occurs also in the extant monotypical genus, *Rhizopa* Stimpson, 1858 (for details see Ng 1987). Species of *Rhizopa* exhibit slightly concave posterolateral margins (see Ng 1987, fig. 1A). The same can be said for *Styrioplax*; however, this character, which is present in the type material, was apparently overlooked by Glaessner (1928). Thus it seems that the closest living relative of *Styrioplax* is *Rhizopa*, at least morphologically.

Styrioplax exiguus (Glaessner, 1928)

Text-figures 12A–D, 13A–G, 14, 15A, B

- v*1928 *Microplax exiguus* Glaessner, 1928, p. 195, pl. 3, fig. 14, 14a; text-fig. 8.
- 1929a *Microplax exiguus* Glaessner; Glaessner, p. 258.
- 1969 *Styrioplax exiguus* (Glaessner); Glaessner, p. R527, fig. 335/2 (= copy of Glaessner, 1928, text-fig. 8).
- 2003 *Styrioplax exiguus* (Glaessner); Karasawa and Kato, p. 145.

Holotype. LMJ 5.453 (Text-fig. 12A).

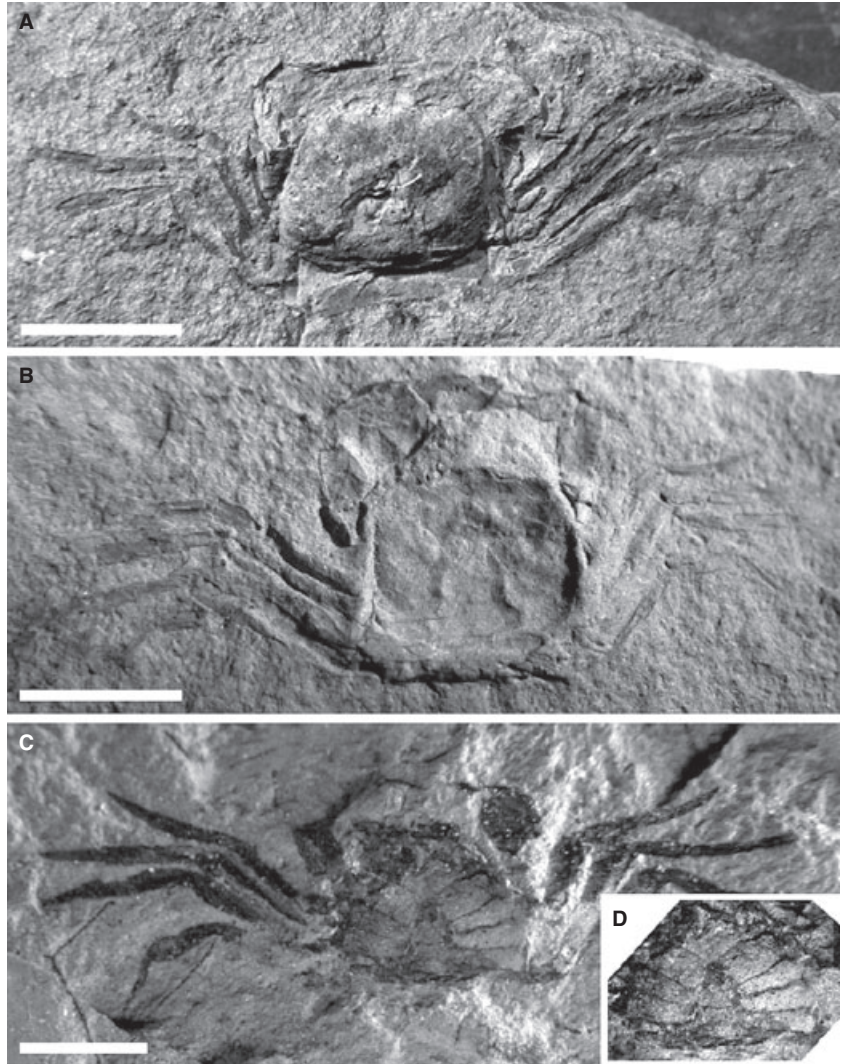
Other material. LMJ 5.753 and 77.875, SNM-Z-24.868–SNM-Z-24.871, SNM-Z-35.098 and SNM-Z-35.507, PM-MSZU 1, PM-MASZ 2, GW-RET92-001. All specimens exhibit a similar mode of preservation, being compressed dorso-ventrally.

Emended diagnosis. Carapace small, transversely rectangular, weakly vaulted, slightly narrowing anteriorly. Rostrum protruding, downturned, bilobed, rimmed. Orbits relatively small. Anterolateral angles rounded. Only cardiac region well defined. Surface of carapace granulated. Sternite sutures slightly curved. Female abdomen broadening posteriorly in ventral view, all somites free, 6th being the longest. Male abdomen narrow, all somites free, 3rd being the widest. Telson triangular. Second to fifth pereopods long and slender. Third pereopods longest, longer than 1st pereopod. Dactyls straight, large and pointed. Chelipeds similar, unequal (modified from Glaessner 1928, 1969).

Description. Carapace small, transversely rectangular, moderately vaulted longitudinally, wider than long in juveniles, widest at posterolateral margins, approximately as long as wide in adults; carapace regions poorly defined; the whole surface of the carapace finely granulated, tiny tubercles especially distinct on the lateral sides of the branchial regions being largest on posterolateral margin.

Front 24–30 per cent maximum carapace width. Rostrum protruded, downturned, slightly broader posteriorly, divided into two slightly distended lobes by shallow notch and a furrow. In

TEXT-FIG. 12. *Styrioplax exiguus* (Glaessner, 1928). A, holotype (LMJ 5.453) from St. Egydi, Slovenia. B, counterpart of specimen LMJ 5.753 from St. Leonhard, Slovenia. C, male specimen (GW-RET92-001) showing venter, from Retznei, Austria. D, venter of the same specimen, under different light showing free abdominal somites. For line drawing of the venter see Text-figure 15B. Scale bar represents 5 mm.



juveniles, lobes are more rounded. They project clearly in front of frontal margin and are bordered by a rim.

Fronto-orbital width about 55–60 per cent maximum carapace width; orbits narrower than rostrum, shallower in adults, directed forwards.

Lateral margins diverging slightly posteriorly, entire; anterolateral margin arcuate, convex, entire; posterolateral margin almost straight, slightly concave posteriorly.

Posterior margin straight, rimmed.

Cardiac region well defined, one-third carapace width. Gastric region separated from the branchial region only posteriorly. The outlines of the regions form H-shaped central depressions (Text-figs 13A, B, 14), which are distinct but shallow.

Subhepatic and pterygostomial regions sparsely granulated.

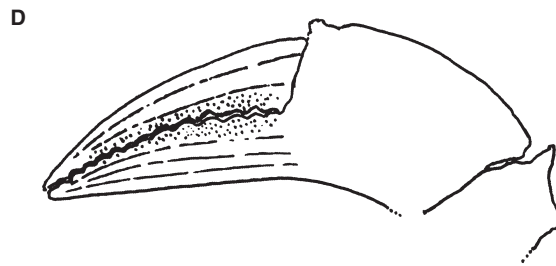
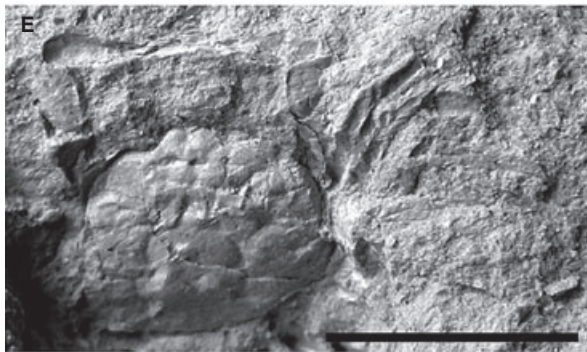
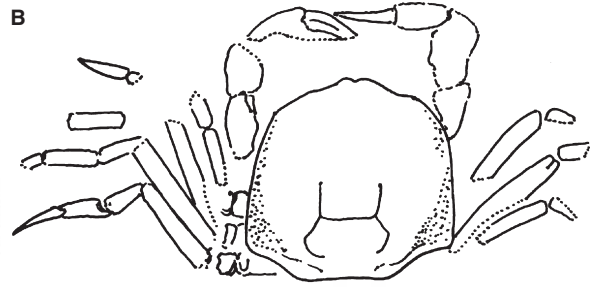
Chelipeds unequal. Right cheliped larger. Carpus quadrate with dorsal spine distally (Text-fig. 13D); propodus slender, lower margin concave, bent at the base of fixed finger, upper margin slightly convex, articulation with dactylus rimmed; fixed finger and dactylus tuberculate, tubercles forming several rows; cutting edge of fixed finger and dactylus denticulate; tips pointed.

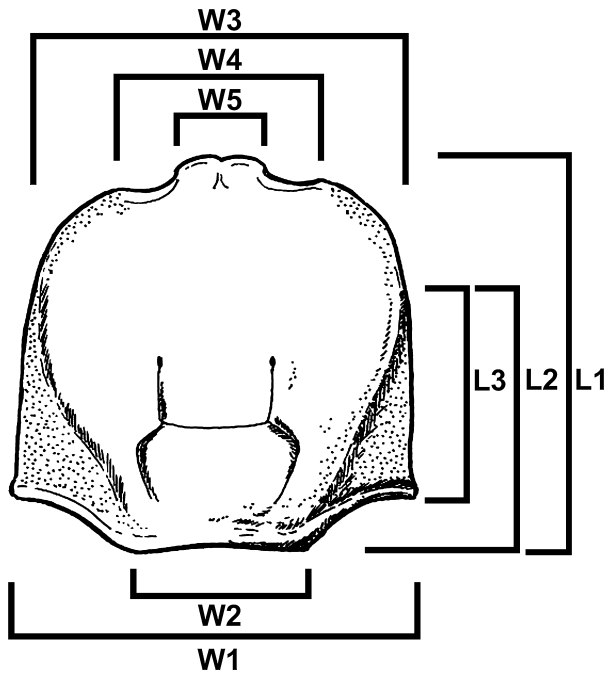
Pereiopods 2–5 long, slender, surfaces smooth, margins rectangular, unarmed; dactyls styliform, third leg longest. Merus is longest segment.

Sternum shows concave sutures of the separated sternites anteriorly, grooves dividing the anterior sternites converge in one point in the middle. Sternum broadening posteriorly, widest at seventh sternite; sutures between sternites 1–4 fused, sutures between sternites 4–8 long and distinct. Sternite 8 visible in females ventrally.

Female abdomen not fused, all somites free, narrowing anteriorly in ventral view, laterally convex; telson about as long as wide, triangular in shape (Text-fig. 15A). Male abdomen not fused, all somites free, third being the widest, slightly convex laterally, almost straight sided, somites 4–6 almost equally wide; telson about as long as wide, triangular (Text-fig. 15B).

Distribution and stratigraphical range. The material of *Microplax exiguus* described by Glaessner (1928) came from two localities. The holotype (LMJ 5.453) and one additional specimen (LMJ 77.875) originated from 'St. Egydi' and another specimen (LMJ





TEXT-FIG. 14. Reconstruction of the dorsal carapace of *Styrioplax exiguus* (Glaessner, 1928) with measurements used in Table 6.

5.753) from 'St. Leonhard'. Both localities are situated in Slovenian Gorce (occasionally referred to as Slovene vineyards), Slovenia. At the time of description, this area belonged to Austria. Karasawa and Kato (2003) still recorded *Styrioplax* from the Miocene of Austria, rather than Slovenia.

The male specimen preserving the venter (GW-RET92-001; see Text-fig. 12C, D) comes from the lower 'Badenian' (lower middle Miocene) Weissenegg Formation at Retznei, south-east Austria (Styrian Basin) (Friebe 1990; Gross *et al.* 2007). Another male specimen (PM-MASZ 2) stems from borehole Alsószuha-1 in the Borsod Basin, northern Hungary (Báldi and Radócz 1971), at a depth of 128 m in the *Hinia-Turritella* Zone of the Salgótarján Formation, the age being 'Karpatian' (early Miocene).

Five other specimens described herein, including the female with venter preserved (SNM-Z-24.868; Text-fig. 13C), were collected from the Lakšárska Nová Ves Formation at Cerová-Lieskové (Vienna Basin).

The monotypical genus *Styrioplax* appears to be confined to lower-middle Miocene strata.

Measurements. For measurements, see Table 6; for abbreviations of the measured parameters, see explanatory sketch in Text-figure 14.

Discussion. During re-examination of the type material at the Landesmuseum Joanneum, the counterpart exhibiting the male venter of one of the specimens mentioned and described by Glaessner (1928) could not be found. The re-examination also revealed that Glaessner (1928) did not describe the posterolateral margin in sufficient detail. Moreover, the figure (Glaessner 1928, fig. 8) does not correspond in detail with the type material. The figure shows the posterolateral margin as convexly rounded; re-examination of type material (holotype, plus two more specimens) reveals that the posterolateral margin is almost straight and concave posteriorly. That concavity was not mentioned in the original description (Glaessner 1928).

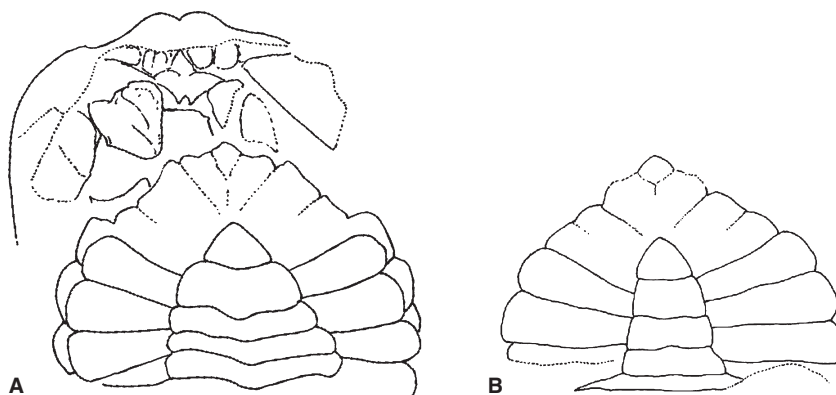
All specimens of *Styrioplax exiguus* known to date, irrespective of locality, exhibit a closely similar mode of preservation, occurring in fine-grained sandstones or siltstones and more or less compressed dorso-ventrally. It is difficult to determine whether specimens collected at Cerová-Lieskové locality are corpses or moults. They are preserved in the relaxed normal position *sensu* Bishop (1986), which is typical of both cases. The female specimen (SNM-Z-24.868; Text-fig. 13C) exhibiting a venter may suggest that it, in fact, was a corpse; however, Bishop (1986) noted that in lobsters the carapace often falls back from the open moult position to a relaxed normal position, which could be the case also for the crabs. Another specimen (SNM-Z-24.871; Text-fig. 13G) is preserved with rusty stains around the posterior parts of the carapace and the last pairs of pereopods, which may represent body fluids squeezed from the corpse embedded within the sediment.

DISCUSSION

Palaeobiogeography

The dispersal pattern of decapod crustaceans is roughly similar to that of gastropods and bivalves, as decapod larvae also are generally planktonic and, therefore, are passively drifted by ocean currents. In addition, some decapods are active swimmers (e.g. *Portunidae*), so the dispersal and migration of decapods can be very quick (Por 1986). Results of previous palaeobiogeographic studies of decapods (Schweitzer 2001; Feldmann and Schweitzer 2006) document closely similar migratory pathways as those observed in molluscs.

TEXT-FIG. 13. *Styrioplax exiguus* (Glaessner, 1928). A–B, counterpart of near-complete female specimen (SNM-Z-24.868) and line drawing. C, part of specimen in Text-figure 13A, B showing the venter. For its line drawing, see Text-figure 15A. D, detail of the right chela from specimen in Text-figure 13C. E–F, specimen (SNM-Z-24.870) showing broken dorsal carapace and line drawing. G, near-complete specimen (SNM-Z-24.871) of indeterminate sex. All specimens from the locality Cerová-Lieskové. Scale bar represents 5 mm.



TEXT-FIG. 15. *Styrioplax exiguus* (Glaessner, 1928). A, line drawing of female venter (SNM-Z-24.868). B, line drawing of male venter (GW-RET92-001).

TABLE 6. Measurements (in mm) of *Styrioplax exiguus*.

Specimen	L1	L2	L3	W1	W2	W3	W4	W5
LMJ 5.453	5.6	3.9	2.7	6.1	4.2	5.6	3.3	1.5
LMJ 5.753	5.5	4.6	3.5	6.9	4.0	6.0	3.2	1.3
LMJ 77.875	4.5	3.6	–	5.6	–	5.0	2.6	1.2
SNM-Z-24.868	8.3	6.5	5.0	8.5	3.8	6.6	4.5	1.4
SNM-Z-24.869	3.1	2.5	–	4.0	–	3.2	2.3	0.7
SNM-Z-24.870	4.0	3.0	1.8	5.0	–	4.2	2.1	1.0
SNM-Z-24.871	5.2	3.5	–	6.4	–	5.7	3.0	1.2
SNM-Z-35.507	6.5	5.4	3.6	8.0	–	6.0	4.5	1.5
PM-MASZ-2	4.3	3.5	–	4.3	–	3.4	2.4	1.2
PM-MSZU-1	9.4	6.8	6.1	9.5	5.0	8.4	5.2	2.2
GW-RET92-001	5.5	–	–	>6	–	–	3.2	1.3

For explanation of measured parameters, see Text-figure 15.

The most important palaeobiogeographic conclusions of all genera studied herein are based on *Callianopsis* and *Mursia*, which both have more extensive fossil records than all other taxa considered herein.

As to *Callianopsis*, Schweitzer (2001) and Casadío *et al.* (2004) favoured a North Pacific Ocean origin during the Eocene and subsequent dispersal to high southern latitudes. They noted that this migration probably was controlled by temperature and depth preferences. The genus is known from the Miocene of Europe (present study) and Japan (Karasawa 1993).

A very similar pattern typifies the genus *Mursia*, which appears to have originated in the North Pacific during the Eocene, with subsequent dispersal westwards to Japan and eastwards to the Atlantic Ocean, most probably through the Central American Seaway (Schweitzer 2001). During the early Miocene, it is already known from Europe (Müller 1984a; Moths 2005; present study). Today the genus inhabits the Indian Ocean as well as the North and South Pacific, being distributed from the east coast of Africa to the Hawaiian Islands.

The distribution of *Callianopsis* in today's oceans is rather patchy, with records from a limited number of

localities in the north-east Pacific and Indo-West Pacific. On account of the cryptic mode of life and its preference of deep water, the collection bias is not surprising. To date, *Mursia* exhibits a similar distribution in the North and South Pacific and Indian Ocean, however, with as many as 25 described species to date. The known occurrences comprise 10s of localities including the east coast of Africa. Assumed to have originated in the North Pacific Ocean (Schweitzer 2001) and dispersing eastwards and westwards, it is difficult to decide by which way the genus entered Tethyan waters. The fossil record of the genus documents its presence in the West Atlantic Ocean between the Oligocene and Pliocene (Rathbun 1918; Collins and Donovan 2002, 2004; Collins *et al.* 2003). Thus, it was quite well established in that area through most of the Neogene and vanished only during the last several millions of years. The hypothesis of transatlantic migration of decapod faunas during the early Miocene is supported by data from coeval gastropod faunas (Harzhauser *et al.* 2002).

On the other hand, the lack of a sufficient fossil record of *Mursia* suggesting possible migratory way from the North Pacific Ocean in a westward direction could be influenced by collecting and preservation biases. Harzhauser *et al.* (2007) documented the migration of several marine groups (bivalves, gastropods, echinoderms) of Tethyan origin from the Eocene onwards to Indo-Pacific waters, but not the opposite way. Following their results, the migration of at least part of studied decapod fauna from the Pacific to Europe via Atlantic Ocean seems more likely than the opposite direction through the Indo-Pacific Ocean.

Other taxa studied present little in the way of palaeobiogeographic distribution. *Munidopsis* probably originated during the Late Cretaceous in high southern latitudes (Feldmann and Schweitzer 2006); however, its subsequent dispersal pathways are very difficult to reconstruct because of its sparse fossil record. Today, it is a cosmopolitan genus.

Styrioplax occurs exclusively in Miocene deposits of the Central Paratethys (Glaessner 1928; present study), and so far it is considered to be an endemic genus. However, the family Pilumnidae has a rich fossil record with the oldest occurrence from the Maastrichtian (uppermost Cretaceous) of Belgium (Karasawa and Schweitzer 2006). During the Eocene, the family was well established throughout Europe.

The two new species of *Crosniera* and *Agononida* are the sole fossil records known to date, so it is impossible to reconstruct the area of their origin and subsequent dispersal. However, extant species of *Crosniera* are known from the Pacific (Indonesia, French Polynesia) and Western Atlantic (off North Carolina, Gulf of Mexico, Caribbean). Concerning *Agononida*, there are 31 known living species of the genus (Baba *et al.* 2008); only two of them from the Atlantic Ocean and the same number from the Indian Ocean. Most species inhabit the Pacific Ocean.

Palaeoecology

The whole crustacean assemblage described here represents predominantly deep-water genera such as *Callianopsis*, *Agononida*, *Munidopsis* and *Mursia*. A deep-water environment for the sediments from the Cerová-Lieskové locality was proposed by Spezzaferri *et al.* (2002) on the basis of foraminiferal associations. Ecological preferences of decapod species described and reported herein are briefly discussed below.

Although we have very limited information on the ecological requirements and life habits of the genus *Callianopsis*, we are able to consider it to be a deep-water genus. The extant East Pacific species *C. goniophthalma* generally is referred to as an inhabitant of deep waters (between 351 and 595 m; Sakai 2005), where it probably lives in burrows (Hart 1982). Alcock and Anderson (1894) mentioned a depth range for the Indo-West Pacific *C. caecigena* of 365–690 m. The most recently discovered species in the West Pacific, *C. anovalis*, was collected from a depth of around 300 m (Lin *et al.* 2007).

It also seems that all fossil species had similar preferences as extant taxa and thus inhabited deep and quite cold waters (Casadío *et al.* 2004). Takeda *et al.* (1986) recorded several deep-water genera (*Munida*, *Munidopsis*, *Paralomis* and *Dicranodromia*) to co-occur with *Callianopsis titaensis*. Karasawa (1991) concluded that the *C. titaensis* assemblage from the early to early middle Miocene of south-west Japan indicated the upper bathyal zone. That author (Karasawa 1991, 1993) inferred the substrate from the fossil record of *C. titaensis* to be a muddy bottom. Burrowing habits of *Callianopsis* were confirmed by

Kato (1996), who described frequent specimens of *C. spp.* in association with fossil burrows.

The depth distribution of *Crosniera* seems to be considerably wide. The deepest record of 2570 m for the genus is that of Poore (1997), which far exceeds that of any other thomassiniid. However, the specimen coming from that depth lacks pereopods, and its generic placement should be regarded as tentative (Poore 1997). Another record of a tentatively assigned specimen comes from a depth of only 4 m (Poore 1997). All other reported specimens, undoubtedly identified as members of the genus, stem from depths of 35–448 m (Poore 1997; Ngoc-Ho 2005). The new fossil species described herein, *Crosniera schweitzeriae* sp. nov., matches the preference for deep-water habitats.

Extant representatives of the family Galatheididae are found throughout nearly the entire spectrum of temperatures and depths. The genus *Agononida* is a typical deep-water inhabitant (Poore 2004); however, there are also some records from depths <100 m. According to Baba *et al.* (2008), the genus inhabits most typically environments shallower than 300 m.

Species of *Munidopsis* today inhabit intertidal to abyssal waters, but in general the genus is considered to be a deep-water inhabitant (Ambler 1980). Baba *et al.* (2008) also pointed out that it was found mainly on the continental slopes and abyssal plains. Osawa *et al.* (2008) characterized *Munidopsis* as a typical animal of the deep sea usually ranging between 700–3000 m. Contrary to that, two fossil species from Antarctica, the Late Cretaceous *Munidopsis foersteri* (Feldmann *et al.* 1993) and late Eocene *M. scabrosa* (Feldmann and Wilson 1988), were found in shallow-water deposits representing nearshore or continental shelf habitats and so their environmental preference were significantly different from those living today.

The known bathymetric range of extant species of *Mursia* is from littoral to 700 m (Galil 1993); however, most occurrences are known from depths >100 m, so the genus is considered as occurring predominantly in deep-water environments.

The co-occurrence of the genera *Callianopsis* and *Mursia* has also been described from the upper Oligocene to lower Miocene Pysht Formation of the Washington state (USA), for which deep-water sedimentation is typical (Feldmann *et al.* 1991).

Taphonomy

The sedimentary conditions at the locality studied apparently favoured the preservation of delicate structures, such as those seen in *Callianopsis marianae* sp. nov. and *Crosniera schweitzeriae* sp. nov. Several specimens of the former retain abdomen, dorsal carapace and thoracic

sternites, which are not usually present in the fossil record suggesting rather rapid burial without subsequent physical or biological disturbance. At the locality studied, also several specimens of cirrolanid isopods have been noted. Some of them represented recently shed moults, showing the typical pattern of biphasic moulting (George 1972), the anterior part being relatively upturned to the position of the posterior part. Both parts are preserved close to one another suggesting no subsequent transport, but rapid burial.

CONCLUSIONS

Five new species are described from 'Karpatian' (uppermost Burdigalian) strata of the Slovakian part of the Vienna Basin, providing new information on their systematics, palaeoecological preferences and palaeobiogeographic distribution.

Two genera (*Crosniera* and *Agononida*) are described for the first time from the fossil record, tracing their origin at least into early Miocene time. *Callianopsis marianae* sp. nov. extends the fossil record of the genus to the Miocene of Europe. Its material allows the recognition of the sexual dimorphism of the species. The new material of the monotypic brachyuran genus *Styrioplax* permits classification within the family Pilmunidae, subfamily Rhizopinae. The assignment is based mainly on characters of abdomen of both sexes and additional morphological features present on dorsal carapace (subrectangular outline, poorly defined regions; bilobed front, entire anterolateral margins, shallow orbits).

The decapod association described herein possess all features of a deep-water assemblage. All species, except one (*Styrioplax exiguus*), have extant congeners that are rather deep-water inhabitants. The association of similar generic composition were previously reported from the fossil record and interpreted as deep-water assemblages (Feldmann *et al.* 1991; Karasawa 1991).

Two reported genera (*Callianopsis* and *Mursia*) exhibit similar migratory traits, originating in the North Pacific Ocean and subsequent dispersal to Japan and through the Atlantic Ocean to European shores. A similar transatlantic migration during the early Miocene has also been documented for gastropods (Harzhauser *et al.* 2002).

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