Silurian carcinosomatid eurypterids from the Prague Basin (Czech Republic)

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The eurypterid record from the Prague Basin includes occasional Ludlow faunas, but in the uppermost Silurian (Přídolí) eurypterids suddenly become common in relatively deep water facies. Pterygotids clearly dominate these late Silurian faunas, whereas carcinosomatids are represented by the single species *Eusarcana acrocephala*, known from only a few specimens. This species is revised and its validity is discussed herein. A new eurypterid fauna found in deep water shale facies is described from the lower and middle part of the Motol Formation, Wenlock, Sheinwoodian–Homerian, *Cyrtograptus murchisoni* to *C. lundgreni* graptolite biozones, at Praha-Lochkov. It consists of common fragments of the carcinosomatid eurypterid described here as *Eusarcana*? sp. A and rare possible pterygotid fragments. This is the earliest evidence of carcinosomatids outside Laurentia and one of the earliest records of the group worldwide. This early occurrence outside a hypothetical Laurentian evolutionary centre is discussed with respect to the palaeobiogeography of other faunas colonising peri-Gondwanan basins after the decline of widespread early Silurian anoxia. A previous suggestion that carcinosomatids (presumed basal members of the Carcinosomatoidea) had similar distribution patterns to pterygotoids is discussed. Eurypterids migrated into the peri-Gondwanan realm from the tropical zone, but the dispersion potential of carcinosomatids into the temperate and cool water realm was probably lower than that of pterygotids. In the Prague Basin, the carcinosomatid-dominated fauna of the Wenlock age was replaced in the late Silurian by a pterygotid-dominated fauna. • Key words: Eurypterida, Carcinosomatidae, Prague Basin, Wenlock, Přídolí.

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Eurypterids form a prominent component of Silurian faunas in the peri-Gondwanan Prague Basin and, together with cephalopods, are the largest known animals of the Silurian (Lamsdell & Braddy 2010). The oldest eurypterids previously described from the Prague Basin originate from the Ludlow cephalopod limestones, and the acme of the group starts in the lowermost Přídolí but they remain common until the upper Lochkovian. Published data (*e.g.* Prantl & Přibyl 1948) clearly demonstrate that pterygotids are dominant in the Prague Basin whereas carcinosomatids are very rare. Pterygotids have also been recorded from other peri-Gondwanan basins such as Catalonia, Iberia (Chlupáč *et al.* 1997) and Sardinia (Gnoli 1992, Corradini *et al.* 2009). Increasing abundance of eurypterids throughout the Silurian is a feature shared between the peri-Gondwanan and perhaps even the global marine faunas (Lamsdell & Braddy 2010).

The Czech representatives of the Family Carcinosomatidae Størmer, 1934 are poorly known compared to the well-documented Pterygotoidea Clarke & Ruedemann, 1912, which were thoroughly revised by Chlupáč (1994). Following the pioneering work of Barrande (1872) on pterygotids, the first descriptions of carcinosomatids from the Barrandian area were published by Semper (1898) and Seemann (1906). Some of these carcinosomatid specimens were also figured and prepared for formal description by O.P. Novák (MS), who unfortunately died (1892) before his post-Barrande volume of the *Système silurien du centre de la Bohême* was finished. The most recent description of carcinosomatid remains from the Barrandian area was published more than sixty years ago by Prantl & Přibyl (1948).

The new discovery of carcinosomatids in the Sheinwoodian and lower Homerian (Wenlock) of the Prague Basin, described in this paper, are important for our understanding of the evolution and dispersal of the group during the Silurian. It is apparent that the Silurian faunal associations of Perunica were influenced by the occasional influx of taxa with Laurentian affinities, especially during important faunal exchange events (see also Budil *et al.* 2010).

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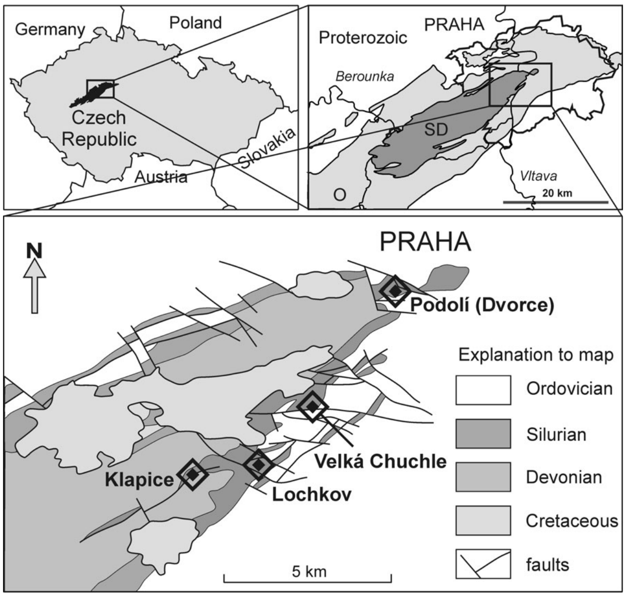


Figure 1. Maps showing the location of the Prague Basin in the Czech Republic, the distribution of Palaeozoic rocks in Central Bohemia, and detail of the NE part of the Prague Basin with localities yielding carcinosomatids. O – Ordovician, SD – Silurian and Devonian.

Systematic palaeontology

The specimens studied are deposited in the Czech Geological Survey, collection of Petr Budil (CGS PB), the National Museum, Prague (NM L), and the Department of Geodynamics and Sedimentology, Universität Wien (UW).

Order Eurypterida Burmeister, 1843
Suborder Eurypterina Burmeister, 1843
Superfamily Carcinosomatoidea Størmer, 1934

Remarks. – During the review process, the handling editor kindly drew our attention to the fact that, in accordance with the Principle of Coordination (ICZN 1999, Article 36.1) Carcinosomatoidea has priority over Mixopteroidea Caster & Kjellesvig-Waering *in* Størmer, 1955 as the name of the superfamily, though the latter name was used by some recent authors.

Family Carcinosomatidae Størmer, 1934

Genus *Eusarcana* Strand, 1942

1875 *Eusarcus*; Grote & Pitt, p. 1 [preoccupied by *Eusarcus* Perty, 1833 (Opiliones)].
1942 *Eusarcana*; Strand, p. 387 [replacement name].
1964 *Paracarcinosoma*; Caster & Kjellesvig-Waering, p. 312 [*fide* Dunlop & Lamsdell 2012].
2012 *Eusarcana* Strand, 1942. – Dunlop & Lamsdell, pp. 19–22.

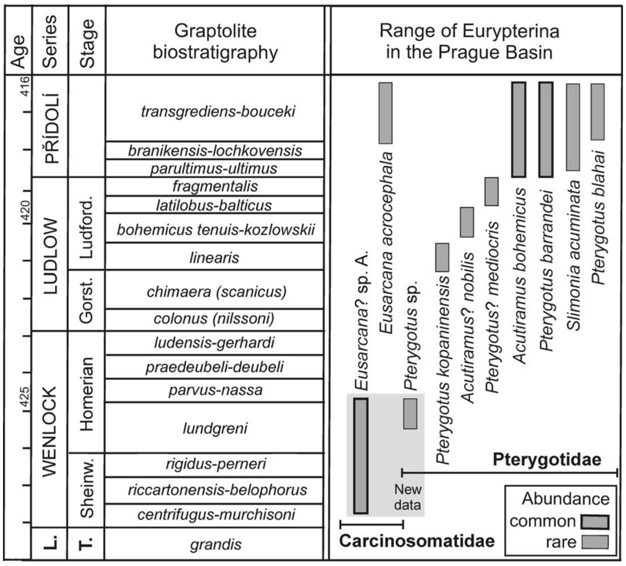


Figure 2. Stratigraphical distribution of eurypterids in the Silurian of the Prague Basin. Ranges of late Silurian eurypterids after Chlupáč *in* Kříž *et al.* (1986) and Chlupáč (1994). Graptolites zones after Štorch (1994, 1995), Manda & Kříž (2006) and Manda *et al.* (2012).

Type species. – *Eusarcus scorpionis* Grote & Pitt, 1875, Přídolí, Williamsville Formation of New York State, USA, and Ontario, Canada.

Other included species. – *E. acrocephala* (Semper, 1898), Přídolí of the Prague Basin, Bohemia, Czech Republic; *E. obesa* (Woodward, 1868), Wenlock–Ludlow of Lesmahagow, South Lanarkshire, Scotland, United Kingdom; *E.*? sp. A, Wenlock of the Prague Basin, Bohemia, Czech Republic.

Diagnosis. – Carcinosomatidae with relatively weakly developed spinosity on appendages II–V and a curved telson (emended from Tetlie 2004).

Eusarcana acrocephala (Semper, 1898)

Figures 3, 4

1898 *Eurypterus acrocephalus* sp. nov.; Semper, pp. 85–87, pl. 13 (2).
1906 *Eurypterus punctatus* Woodward et *acrocephalus* Semper. – Seemann, p. 55, pl. 4, fig. 7.
1948 *Carcinosoma scorpionis* (Grote & Pitt, 1875). – Prantl & Přibyl, pp. 99–102, pl. 7, figs 5, 6; pl. 8, figs 1, 2.
2012 *Eusarcana acrocephala* (Semper, 1898). – Dunlop & Lamsdell, p. 21.

Diagnosis. – *Eusarcana* with strongly recurved lateral carapace sides; metastoma apparently oval; mesosoma very

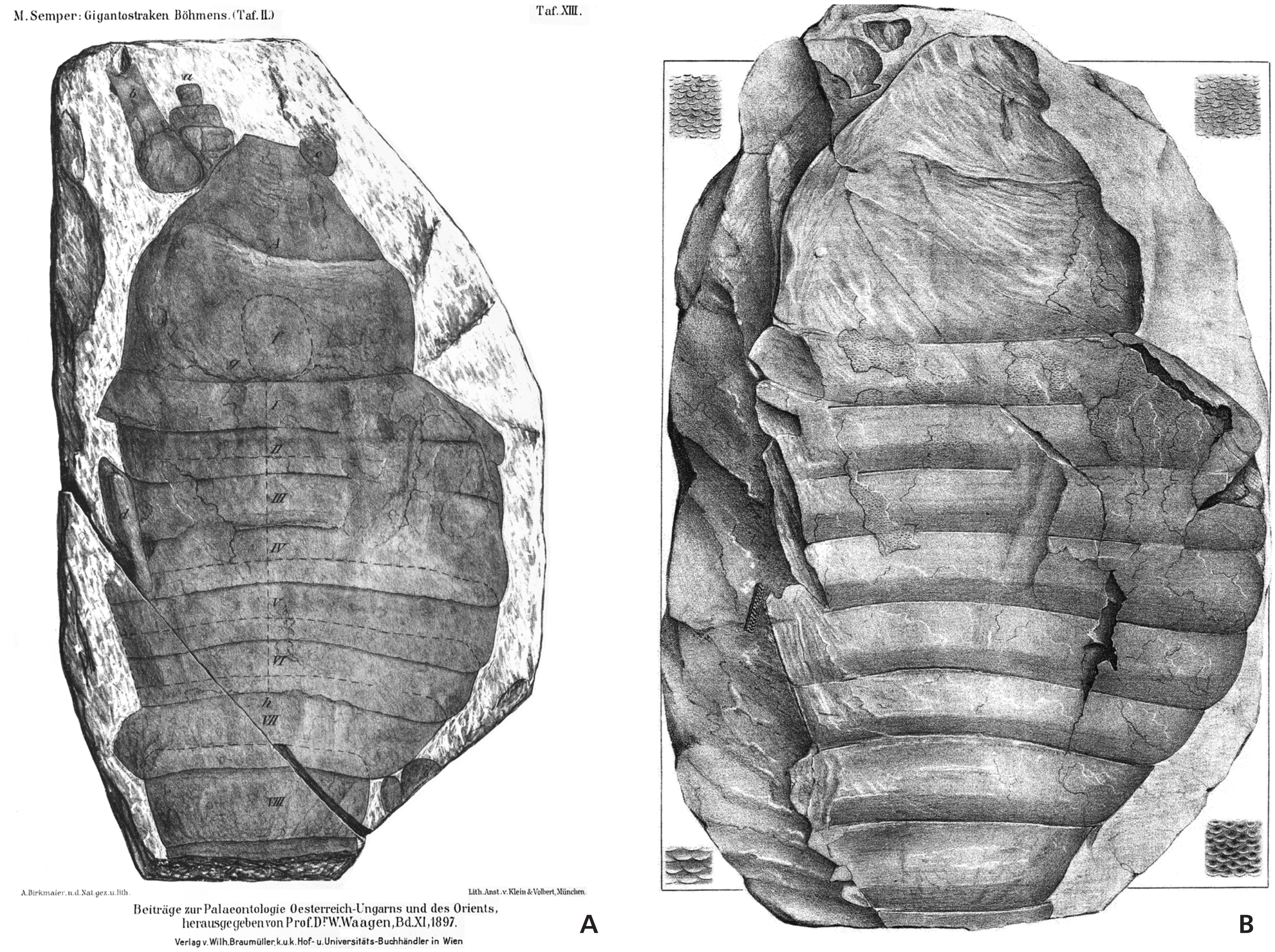


Figure 3. *Eusarcana acrocephala* (Semper, 1898). • A – illustration of the holotype UW 1906/V/2 by Semper [1898, pl. 8 (2)]. • B – illustration of the holotype counterpart NM L 96 by Novák (MS); note the left-right inversion of the illustration.

wide; first segment of metasoma wide and short for the genus; first order opisthosomal differentiation almost absent.

Holotype. – UW 1906/V/2, figured by Semper [1898, pl. 13 (2)], Figs 3A and 4E herein; Přídolí, Požáry Formation, Praha-Dvorce (= Podolí). Compared to the 1898 figure, the left posterior portion of the part with the abdomen is now broken off and missing – it may have been lost during bombing of the University collections towards the end of the Second World War. The counterpart of the specimen, figured by Novák (MS) and Prantl & Přibyl (1948, pl. 8, fig. 1; as *Carcinosoma scorpionis*) and in Figs 3B and 4F herein, is stored in the National Museum Prague, as NM L 96.

Other material. – NM L 30372, incomplete carapace with remains of prosomal appendages and mesosoma, Požáry Formation, Kosoř; NM L 26, 55, isolated prosomal appendages, Požáry Formation, Praha-Dvorce (= Podolí), quarry of former cement works. Prantl & Přibyl (1948, pl. 6, figs 5, 6, p. 49) figured and discussed also remains of walking legs and telson from the Požáry Formation, Praha-Velká Chuchle. They also discussed (p. 49) the occurrence of the species in the Lower Devonian Lochkov Formation at Kosoř, but this material has not been found in the collections of the National Museum, Prague.

Description. – See Prantl & Přibyl (1948, pp. 99–102).

Discussion. – Prantl & Přibyl (1948) pointed out the "relatively well preserved imprint of the dorsal side of the body" – the prosoma (including incomplete appendages), nearly complete mesosoma and three segments of the metasoma – in NM L 96, which they assigned to *Carcinosoma scorpionis* (Grote & Pitt, 1875). Prantl & Přibyl also recognized that this specimen is the counterpart to the original of Semper (1898). Both part and counterpart thus represent the holotype by monotypy, although stored in two different institutions. Semper's original specimen was considered lost, but was discovered in the collections of the Department of Geodynamics and Sedimentology, Universität

Wien, in late 2012 by F. Popp. Together with its unique shape, a label attached directly to the specimen enables its unequivocal identification as the holotype. J.J. Jahn, not Semper, donated the specimen to the collections in 1906, but the species epithet *acrocephalus* is not mentioned in the acquisition list, although other type specimens of the same acquisition (*e.g*. *Pterygotus blahai* Semper, 1898) are correctly listed. The holotype was found in the former "Dvorce" quarry in about 1880 (on a label attached to the counterpart, NM L 96, the year 1882 is mentioned, together with the name Shück or Shüek, probably the person who donated the specimen, see Fig. 4F). The paper of Semper (1898) was discussed shortly afterwards by Perner (1898) who mentioned "comparatively better material stored in the Czech Museum, deposited in the Barrande and Novák collections". However, the first person to illustrate the holotype counterpart was Novák (MS) (see Fig. 3B; illustration kindly provided to us in 2009 by V. Turek). Prantl & Přibyl (1948, pl. 8, fig. 1) also illustrated the counterpart, correctly pointing out that it comes from the Novák collection and stating that Semper's original specimen was unavailable to them. Both part and counterpart of the holotype are re-figured together here for the first time (Fig. 4C, E, F).

Although Prantl & Přibyl (1948) considered the five specimens of *Eurypterus acrocephalus* from diverse localities in the Prague Basin to be conspecific with *Eusarcana scorpionis*, Caster & Kjellesvig-Waering (1964) considered the former to be a valid species. Tetlie (2007) and Dunlop & Lamsdell (2012) supported this conclusion, with which we also agree. The differences between the species, in the shape of carapace, shape of metastoma, shape of mesosoma, shape of the first metasomal segment and first order opisthosomal differentiation, justify the validity of *Eusarcana acrocephala*. The two species are probably closely related, although in some respects *E. acrocephala* is more similar to, for instance, *Carcinosoma newlini* Claypole, 1890 than it is to *E. scorpionis*. The typical crescent-like exoskeletal sculpture of *E. acrocephala* is also unlike that of *E. scorpionis* (for further discussion, see Semper 1898, p. 16 and the reconstruction of Novák, MS, in Fig. 3B herein). The considerable palaeogeographic distance between the respective type areas also suggests the existence of separate geographic species.

Prantl & Přibyl (1948) based their detailed description and discussion of the Bohemian specimens mainly on the holotype counterpart, NM L 96, and this description is for the most part still valid.

Occurrence. – Požáry Formation, Přídolí, *M. bouceki-M. transgrediens* graptolite biozone. Prague Basin (Bohemia, Czech Republic).

***Eusarcana*? sp. A**

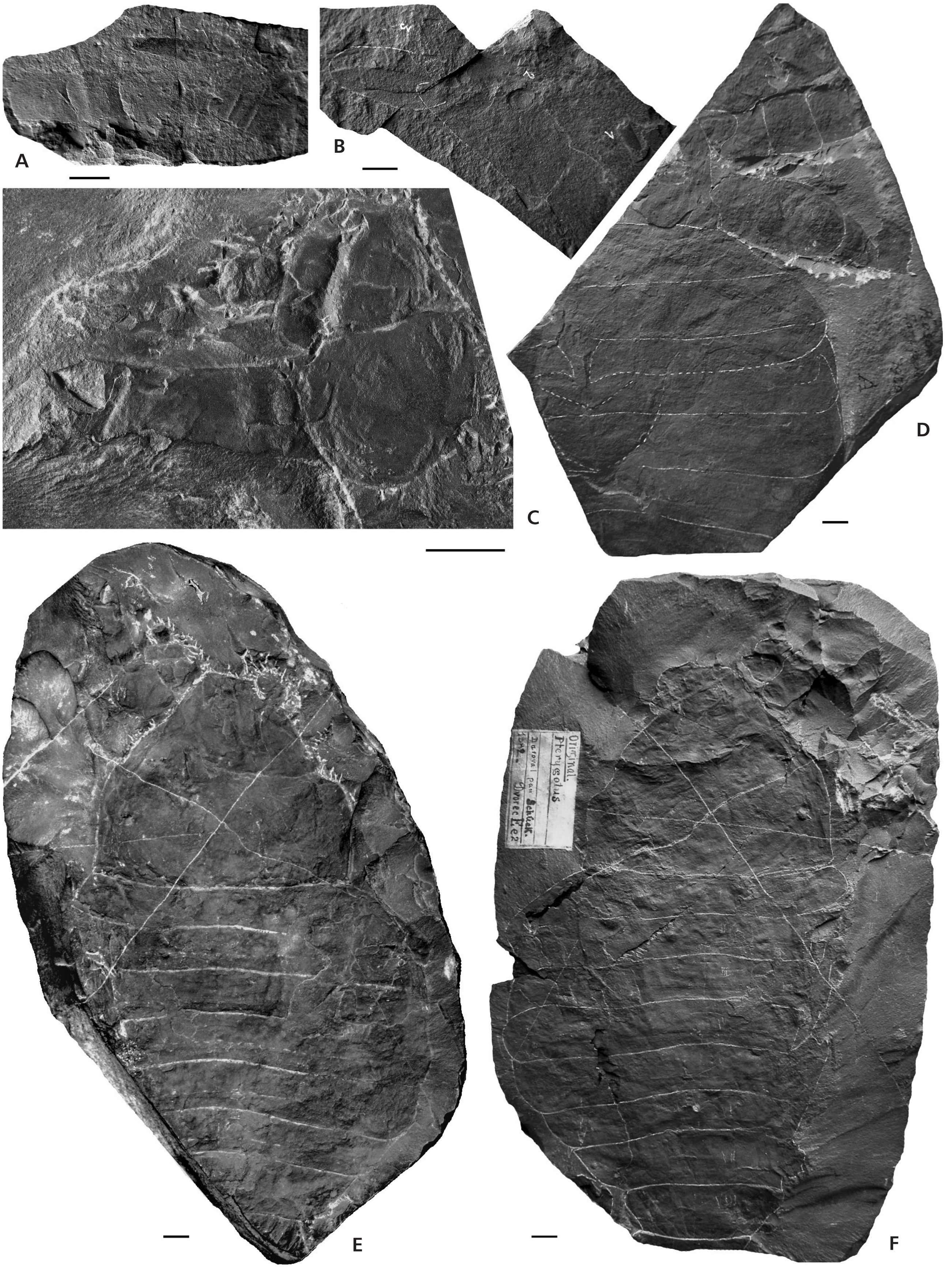
Figures 5, 6A?, D?–L?, M–Q

Material. – The best preserved specimen, CGS PB 1043 (Figs 5, 6M–Q), is an articulated, incomplete, probably third or fourth prosomal appendage, from the Motol Formation (deeper-water facies development, graptolite shale facies), Wenlock, Sheinwoodian, *Cyrtograptus murchisoni* graptolite biozone, in tunnel excavations for a highway at Praha-Lochkov. Thirteen other exoskeletal fragments are known, CGS PB 1034–1037, 1039–1042 and 1044–1048, from the Wenlock, Sheinwoodian–early Homerian, *Cyrtograptus perneri-C. lundgreni* graptolite biozones, at the same locality, but their identification is speculative.

Description. – Prosomal appendage (probably third or fourth) of carcinosomatid type (see Tollerton 1989), with long hook-like distal spine. Podomere 8 of elongate rectangular outline, protruding into a long spine. Podomere 7 short, of rectangular outline, protruding into two long but narrow spines. Podomeres 6–3 of subrectangular outline. Podomere 2 incompletely preserved.

Together with the appendage, fragmentary remains of other body parts are known, mostly coming from younger horizons (Sheinwoodian and Homerian, *Cyrtograptus perneri-C. lundgreni* graptolite biozones) at the same locality. Specimen CGS PB 1040 (Fig. 6L) probably represents four articulated but poorly preserved segments of the mesosoma. The identification of the other specimens is very speculative but they clearly represent eurypterids and/or the remains of other weakly mineralised, medium-sized arthropods (the eurypterid interpretation is the most parsimonious). Specimen CGS PB 1042 (Fig. 6A) may be

Figure 4. *Eusarcana acrocephala* (Semper, 1898). • A – prosomal appendage (endognath), NM L 55, figured by Seemann (1906, pl. 4, fig. 7) as *Eurypterus punctatus* Woodward et *acrocephalus* Semper. Praha-Dvorce, quarry of former cement works. Požáry Formation (originally designated as E$_1$ß). • B – distal portion of swimming appendage, NM L 26, figured by Prantl & Přibyl (1948, pl. 6, fig. 2) as *Carcinosoma scorpionis* (Grote & Pitt). Praha-Dvorce, quarry of former cement works (Prantl & Přibyl 1948 gave the locality incorrectly as Kosoř). Požáry Formation (originally designated as Eß$_2$). • C, E – holotype UW 1906/V/2, incomplete specimen, figured by Semper (1898, pl. 8, fig. 2). Praha-Dvorce, quarry of former cement works. Přídolí, Požáry Formation (originally designated as Ober-Silur e$_1$). A – detail of remnants of the prosomal appendages; B – dorsal side of exoskeleton. • D – ventral side of incomplete prosoma and mesosoma showing part of prosomal appendages, NM L 30372, figured by Prantl & Přibyl (1948, pl. 8, fig. 2) as *Carcinosoma scorpionis* (Grote & Pitt). Kosoř. Požáry Formation. • F – counterpart of the holotype NM L 96, figured by Prantl & Přibyl (1948, pl. 8, fig. 1) as *Carcinosoma scorpionis* (Grote & Pitt); coll. O.P. Novák. Praha-Dvorce, quarry of former cement works. Přídolí, Požáry Formation, *Monograptus bouceki* graptolite zone (originally designated as Eß$_2$). Scale bars represent 10 mm.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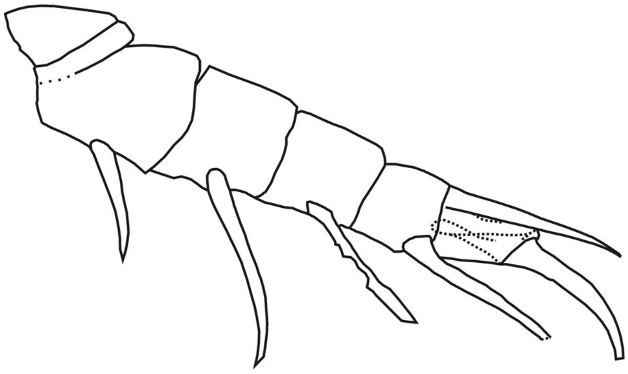


Figure 5. *Eusarcana*? sp. Interpretive drawing of specimen CGS PB 1043, a probable third or fourth prosomal appendage.

the remains of a carapace. CGS PB 1039 and 1045 (Fig. 6D, J respectively) may represent the distal segment of the swimming appendage. CGS PB 1041, 1047 and 1044 (Fig. 6G–I) may be fragments of mesosomal segments. CGS PB 1034 (Fig. 6F) may represent the remains of a telson. A large exoskeletal fragment CGS PB 1037 (Fig. 6E, K) may represent the remains of a large metasomal segment.

Discussion. – Only one well-preserved, articulated third or fourth prosomal appendage with seven distalmost podomeres is known, together with several poorly determinable remains, which makes the generic identification of the new material impossible. The appendage is clearly of carcinosomatid type, with long, slender spines much like those in *Eusarcana scorpionis* and *Carcinosoma newlini*, and unlike the broad, flattened spines in *Carcinosoma*? *punctatum* (Woodward, 1868) (see also Kjellesvig-Waering 1961). According to Caster & Kjellesvig-Waering (1964), this gracile morphology is more consistent with *Eusarcana* than *Carcinosoma*; in the latter genus the prosomal appendages are generally more robust with better-developed spinosity (Kjellesvig-Waering 1958). Since the occurrence of *Eusarcana* is confirmed in the Prague Basin in the Přídolí (based on *E. acrocephala*), it is most parsimonious to suggest that this new material may belong to the same genus. Compared to the much younger type species *E. scorpionis* from the Přídolí, the present material differs especially in the longer and more slender spines on the appendage. *E. obesa* (Woodward, 1868), which is possibly contemporaneous with *E.*? sp. A, differs from it in the shorter and weaker spinosity of the prosomal appendages. Comparison with the poorly preserved prosomal appendages of the late Silurian (Přídolí) *E. acrocephala* is difficult but they also seem to be more robust (*cf.* Fig. 6A, D–Q and Prantl & Přibyl 1948, pl. 7, fig. 5 – this specimen cannot be found in the collections of the National Museum, Prague).

Occurrence. – We have studied only material from Wenlock rocks exposed in the Lochkov Tunnel digging. During excavation of the tunnel several other fragments of eurypterids were found but were not collected due to their poor preservation. Consequently, current knowledge of eurypterid distribution in the Silurian of Bohemia is most probably affected by sampling bias and preservation. The single well-preserved specimen of *Eusarcana*? sp. A was found at the boundary between shales and a limestone bed with common *Phragmoceras* (Manda 2007) – extremely rare in the shale-dominant facies of the Motol Formation. Similarly, the younger Přídolí specimens of *Eusarcana* are usually preserved in platy limestone with intercalations of calcareous shales.

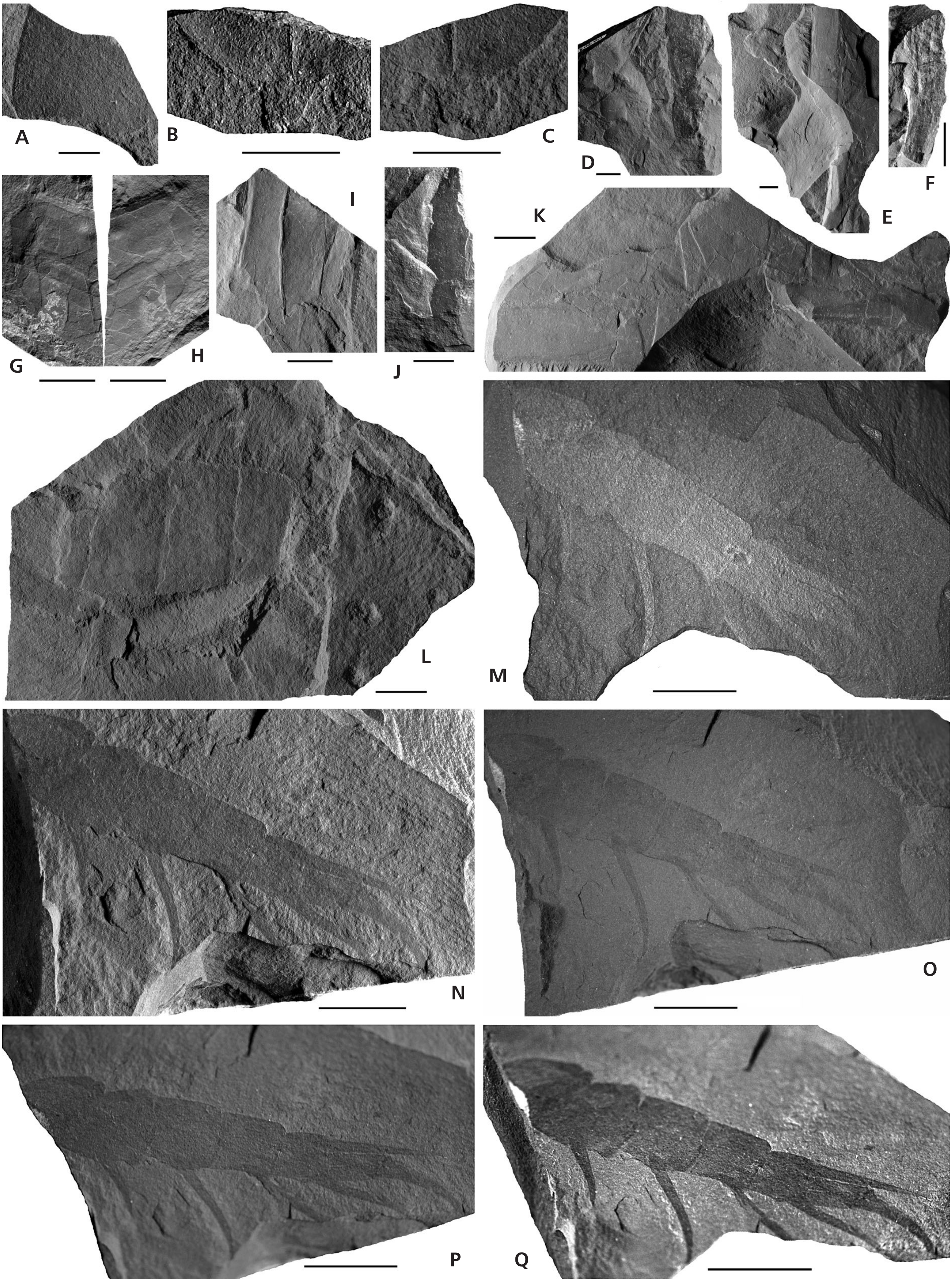
Discussion and conclusions

Carcinosomatoids from Silurian strata of the Prague Basin are of significance in relation to: 1) the composition and dynamics of Silurian faunas; and 2) palaeobiogeographical patterns and the reconstruction of ancient migration routes.

Distribution pattern of eurypterids in the Silurian rocks of the Prague Basin

Eurypterids have previously been known only from the upper Silurian and Lower Devonian of the Prague Basin, with rare remains from the Ludlow cephalopod limestones (Chlupáč 1994) and abundant specimens from shales and

Figure 6. A, D–Q – *Eusarcana*? sp. A, Silurian, Motol Formation, Praha-Lochkov, highway tunnel excavation. All except M–Q from Homerian, *C. lundgreni* graptolite biozone. • A – indeterminable fragment of exoskeleton, possibly part of prosoma, CGS PB 1042. • D – indeterminable fragment of exoskeleton (?segment of walking appendage), CGS PB 1039. • E – indeterminable large fragment of exoskeleton, CGS PB 1037b. • F – indeterminable fragment of exoskeleton (?telson), CGS PB 1034. • G, H – indeterminable fragments of exoskeleton. G – CGS PB 1041; H – CGS PB 1047. • I – indeterminable fragment of exoskeleton, possibly two articulated mesosomal segments, CGS PB 1044. • J – indeterminable fragment of exoskeleton (?swimming appendage), CGS PB 1045. • K – indeterminable larger fragment of exoskeleton (?part of mesosoma), CGS PB 1037b. • L – possible articulated metasoma with indeterminable fragment of exoskeleton, CGS PB 1040a. • M–Q – possibly 3rd or 4th prosomal appendage, CGS PB 1043, Sheinwoodian, *Cyrtograptus murchisoni* graptolite biozone; M – dorsal view; N – dorsal view in right-side lateral illumination; O – dorsal view in right-side illumination; P – dorsolateral view; Q – dorsolateral view in different illumination. • B, C – *Pterygotus* sp., Silurian, Motol Formation, Praha-Lochkov, highway tunnel excavation, *C. lundgreni* graptolite biozone, fragment of questionable telson, CGS PB 1038; B – negative counterpart; C – positive part. Scale bars represent 10 mm.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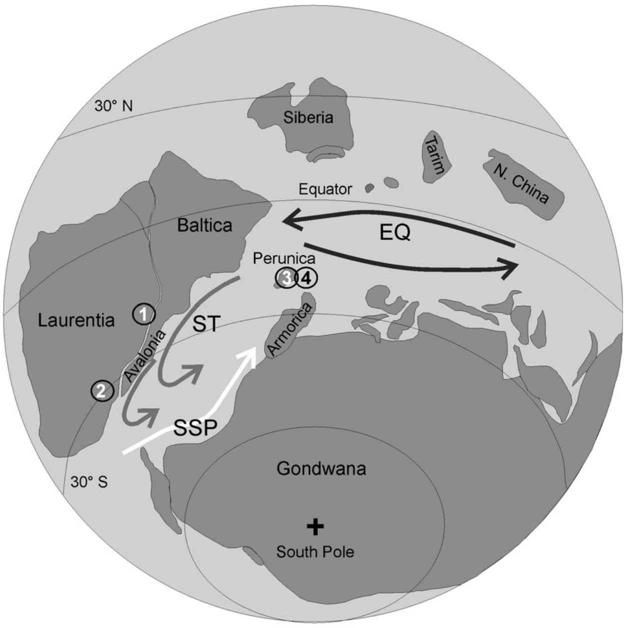

Figure 7. Global palaeogeographic reconstruction for the Wenlock and Ludlow (modified from Cocks & Torsvik 2002, 2006, supplemented by data of Scotese & McKerrow 1990, Wilde *et al.* 1991, Krs *et al.* 2001, Stampfli *et al.* 2002, Kříž *et al.* 2003; position of Perunica slightly modified after Fatka & Mergl 2009). Circles numbered 1–4 show occurrences of *Eusarcana* as follows: 1 – Lesmahagow, South Lanarkshire, Scotland, UK [*E. obesa*, Wenlock to Ludlow; according to Lamsdell & Selden 2013, this species is probably based on a juvenile of *Carcinosoma scorpioides* (Woodward, 1868)]; 2 – Buffalo Waterlime, New York State, USA (*E. scorpionis*, Ludlow); 3 – Motol Formation, Prague Basin. (*E.*? sp. A, Wenlock); 4 – Požáry Formation, Prague Basin (*Eusarcana acrocephala*, Přídolí). Abbreviations: EQ – Equatorial Current; ST – South Tropical Current; SSP – South Subpolar Current. See discussion in the text.

platy limestones of Přídolí age in which they represent, together with phyllocarids and cephalopods, the most common nectobenthic animals. Pterygotids are most common whereas carcinosomatids are extremely rare (Prantl & Přibyl 1948, Chlupáč *in* Kříž *et al.* 1986). The newly collected, common specimens of carcinosomatids from off-shore shale facies of the Motol Formation at the Lochkov tunnel excavation expand our knowledge of Silurian communities of the Prague Basin. The Wenlock carcinosomatids inhabited a very similar environment to the Přídolí pterygotids, but our understanding of eurypterid distribution in the Prague Basin may be affected by sampling bias due to the poor preservation.

Our study supports the suggestion of Tetlie (2007) that the carcinosomatids (basal members of the Carcinosomatoidea) had a similar distribution to that of the pterygotoids. In the Prague Basin carcinosomatids and pterygotids both occur in deep water facies of the Wenlock but carcinosomatids are more abundant. Only one very poorly preserved specimen, CGS PB 1038, a possible telson with characteristic keel-like medial elevation, from the Lochkov highway tunnel excavations (Motol Formation, Sheinwoodian, *Cyrtograptus murchisoni* graptolite Biozone) can be attributed with some confidence to a pterygotid (Fig. 6B, C). By contrast, in late Silurian strata pterygotids are dominant whereas carcinosomatids are very rare.

Palaeobiogeographical significance of carcinosomatoids and their migration pattern

Tetlie (2007) suggested that carcinosomatoids probably originated in Laurentia. The more primitive forms were able swimmers and some forms were able to spread throughout most of the world. Some of the genera (*e.g.* the stem forms of the carcinosomatoid clade) have been interpreted as fully marine (Kjellesvig-Waering 1961), as opposed to more advanced forms with near-shore brackish or hypersaline occurrences. The majority of carcinosomatoid taxa are known from Laurentia, Baltica and Avalonia. Lamsdell *et al.* (2013), on the other hand, tentatively suggested a Gondwanan origination for eurypterids.

The first known representative of *Eusarcana* is *E. obesa* from the Wenlock of Lesmahagow, Scotland, although according to Lamsdell & Selden (2013) the specimen on which this species was based is most likely a juvenile *Carcinosoma scorpioides* (Woodward, 1868). The new discoveries of possible *Eusarcana* in the Prague Basin are thus among the earliest known occurrences of the genus worldwide. Isolated records from the upper Silurian(?) of Vietnam (Braddy *et al.* 2002) and Bohemia (*e.g.* Prantl & Přibyl 1948) also show that the terranes of Annamia and Perunica were within the migration range of these eurypterids at this time (Tetlie 2007). It is apparent, however, that Perunica was accessible for these animals at the latest in the Wenlock. Annamia is considered to have been drifting north of the equator (east of Laurussia and north of Gondwana) at that time, while Perunica was south and west of Laurussia (Tetlie 2007; Torsvik & Cocks 2004; Cocks & Torsvik 2002, 2006). In any case, carcinosomatid immigrants into the Prague Basin would have had to cross a significant portion of the Rheic Ocean, probably including its deeper parts (Fig. 7).

Carcinosomatids appeared in the Prague Basin in the early Wenlock, as early Silurian anoxic conditions declined due to the activation of sea currents. Other immigrants of Laurentian and/or Baltic-Avalonian origin also appeared in the Prague Basin in the Silurian, including brachiopods (Havlíček & Štorch 1990), nautiloids (Manda 2007, 2008), bivalves (Kříž 2008) and bryozoans (Ernst *et al.* 2011). The early to late Wenlock carcinosomatids newly documented herein (the youngest specimens from the *Cyrtograptus lundgreni* Biozone) formed part of a pioneer community (Havlíček & Štorch 1990) that inhabited deeper water conditions in which graptolites were dominant.

Although the Prague Basin was colonised mainly with immigrants from Baltica and Avalonia, there are also some immigrants of Laurentian origin. Laurentian faunas were rather similar to those of Baltica and Avalonia but also included some endemic groups that originated before the collision of all these continents in the latest Silurian. The migration of carcinosomatids into the Prague Basin was very soon followed by the Laurentian phyllocarid crustacean *Ceratiocaris papilio* Salter, 1859 (*in* Murchison 1859) in the lower Ludfordian (see Budil *et al*. 2010). Tetlie (2007) suggested that the carcinosomatids had a similar distribution to the pterygotids (see above), but carcinosomatids appeared earlier in the Prague Basin (middle Wenlock) than pterygotids (late Wenlock–Ludlow).

Although eurypterids of Bohemian affinity were present in other peri-Gondwanan terranes in the late Silurian and early Devonian (*e.g*. Sardinia and northern Spain, see Gnoli 1992, Chlupáč *et al*. 1997, Corradini *et al*. 2009), the only known occurrence of carcinosomatids in European peri-Gondwana is in the Prague Basin. This occurrence is consistent with the dispersion pattern of many other invertebrate groups; *e.g*. nautiloid cephalopods (Gnoli 2003; Manda 2008; Manda & Frýda 2010; Turek & Manda 2011, 2012; Histon 2012a, b), shallow-water bivalve communities (Kříž 2008, Cope & Kříž 2013) and inarticulate brachiopods (Mergl 2006, 2010). We suggest that carcinosomatids had a more nektic lifestyle whereas pterygotids were more demersal, possibly explaining the replacement of a carcinosomatid fauna in the Wenlock by a pterygotid fauna in the Ludlow and Přídolí. If carcinosomatids were predominantly nektic, their migration potential would have been higher than for the pterygotids, and they may have been the earliest immigrants. Their later replacement by pterygotids reflected their lower tolerance to changing environments. A similar pattern has been documented in cephalopods (Manda 2008): earlier immigrants were actively swimming forms that were less tolerant of environmental change, and these were later replaced by demersal cephalopods that were tolerant of change.

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