On the occurrence of *Ctenocheles* (Decapoda, Axiidea, Ctenochelidae) in the Bohemian Cretaceous Basin

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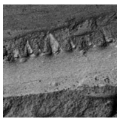

Because of close morphological affinities, fossil cheliped fragments of the ghost shrimp *Ctenocheles* (Decapoda, Axiidea, Ctenochelidae) can be easily misidentified as remains of different decapod crustacean taxa. Re-examination of the Cretaceous decapods deposited in the National Museum in Prague revealed that all supposed specimens of the lobster genus *Oncopareia* found in the Middle Coniacian calcareous claystones of the Březno Formation, including one of the Fritsch's original specimens of *Stenocheles parvulus*, actually belong to *Ctenocheles*. This material together with newly collected specimens from the same locality, allowed for erection of a new species, *Ctenocheles fritschi.* Its major chela possesses a serrated ischium and ovoid, unarmed merus; therefore, it is considered a close relative of the extant *C. collini* and *C. maorianus*. *Ctenocheles fritschi* sp. nov. represents the first report on the occurrence of the genus from the Bohemian Cretaceous Basin. It is one of the oldest records of *Ctenocheles* and simultaneously one of the best preserved fossils of the genus reported to date. Confusing taxonomy of *S. parvulus* is reviewed and shortly discussed. • Key words: Bohemian Cretaceous Basin, Březno Formation, Coniacian, decapod crustaceans, *Oncopareia*, *Stenocheles*, *Ctenocheles.*

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Ctenocheles Kishinouye, 1926 (Decapoda, Axiidea, Ctenochelidae) is a heterochelous ghost shrimp exhibiting a typically pectinate (comb-like) major claw. Isolated chelipeds are the most common fossil remains of decapod crustaceans and the same is also true for *Ctenocheles* (Schweitzer & Feldmann 2001). In fact, several fossil species of the genus were described on the basis of isolated cheliped fragments only, such as *Ctenocheles cultellus* (Rathbun, 1935), *C. dentatus* (Rathbun, 1935), and *C. sujakui* Imaizumi, 1957. Distinctive pectinate claws, *i.e.* claws with long fingers and acicular teeth, evolved several times in different lineages of decapods and, thus, they are a result of convergent evolution (Tshudy & Sorhannus 2000). Because of close morphological similarities, cheliped fragments of *Ctenocheles* can be misinterpreted as remains of different taxa. Tshudy & Sorhannus (2000) reviewed shrimps and lobsters with pectinate claws and provided a synoptic table with differences between respective taxa (see also Tshudy & Saward 2012). They also noted for fossils, the pectinate claws are mostly identified as *Ctenocheles* or an astacidean genus *Oncopareia* Bosquet, 1854. Whereas *Oncopareia* has been considered a relatively well represented genus in the Bohemian Cretaceous Basin (BCB) (Mertin 1941), *Ctenocheles* has not been identified in the studied area until now. Interestingly, part of the material attributed to *Ctenocheles* as presented herein has been known since the 19th century, but because of confusing taxonomy of isolated pectinate claws (see Feldmann *et al.* 1990, Tshudy & Sorhannus 2000) its identity has not been recognised. Recent re-examination of the Cretaceous decapods deposited in the National Museum in Prague revealed that all supposed *Oncopareia* specimens originating from the Middle Coniacian calcareous claystones of the Březno locality (including one of the Fritsch's original specimen of *Stenocheles parvulus* Fritsch *in* Fritsch & Kafka, 1887) actually belong to *Ctenocheles*. Recently, one of the authors (PD) found several additional specimens of *Ctenocheles* in the upper part of the Gastropod Bed (the Březno Formation) at Březno

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locality. These decapods are associated with the ammonite *Peroniceras tridorsatum* (Schlüter, 1867), clearly documenting a Middle Coniacian age (see below). The aims of the present study are the re-examination of Fritsch's material and description of newly recovered specimens from the Březno locality resulting in the description of a new species of *Ctenocheles*.

Taxonomic status of *Stenocheles* Fritsch *in* Fritsch & Kafka (1887)

Decapod crustaceans of the BCB were extensively reported by Reuss (1845–1846), Fritsch & Kafka (1887), Fritsch (1893) and Mertin (1941). Since then the systematics and taxonomy changed significantly and much of the material is in a need of a revision (Veselská 2009, 2010, 2011). Moreover, numerous new decapod specimens have been recovered in the last decade; virtually all *Ctenocheles* specimens reported herein represent new findings.

Fritsch *in* Fritsch & Kafka (1887) erected the genus *Stenocheles* to accommodate two new species, *Stenocheles esocinus* Fritsch *in* Fritsch & Kafka, 1887 and *S. parvulus*. Glaessner (1929) considered the genus a junior subjective synonym of *Ischnodactylus* Pelseneer, 1886. Mertin (1941) questionably synonymised *Stenocheles* with *Oncopareia*, which was followed by Glaessner (1969). Because Fritsch *in* Fritsch & Kafka (1887) did not state the type species of *Stenocheles*; Glaessner (1969) chose *S. esocinus* as the type species. *Stenocheles esocinus* is based on a single fragmentary specimen consisting of a major chela and an abdomen (no carapace is preserved) from the Lower Coniacian of the Rohatce Member of the Teplice Formation. Their morphology is very close to *Oncopareia bredai* Bosquet, 1854, the type species of *Oncopareia*; thus, we agree with the synonymisation of *Stenocheles* with *Oncopareia* (as already suggested by Tshudy 1993, Tshudy & Sorhannus 2000, Schweitzer *et al.* 2010).

Stenocheles parvulus is based on two, rather poorly preserved specimens originating from two different localities. A re-examination of the material revealed that these specimens represent two entirely different decapod infraorders, none of them being closely allied with *S. esocinus*. Whereas one specimen is an isochelous astacidean (as already noted by Fritsch & Kafka 1887; see also Fritsch & Kafka 1887, pl. 3, fig. 3; Figs 1B, C), the other one (Fritsch & Kafka 1887, pl. 3, fig. 4; Fig. 1A) represents a member of *Ctenocheles* (infraorder Axiidea). It is worth noting that Glaessner (1929) recognised that these specimens are not taxonomically identical, as he listed one of Fritsch's figures (Fritsch & Kafka 1887, pl. 3, fig. 4; refigured here as Fig. 2A) as belonging to *Ischnodactylus parvulus* with a question mark. Also Secrétan (1964, p. 152), in discussing affinities of *Ctenocheles madagascariensis* Secrétan, 1964, noted that: "the small propodus (of *C. madagascariensis*) is also close enough to the chelipeds described by Fritsch as *Stenocheles parvulus* and figured as *S. gracilis*." Thus, the identity of one of Fritsch's specimens was recognised but not explicitly stated. Fritsch *in* Fritsch & Kafka (1887) did not state which specimen of the two specimens of *S. parvulus* is the holotype of *S. parvulus*; thus, they both are syntypes. Because the isochelous specimen is mentioned first in the original description, we select it herein as a lectotype for *S. parvulus*. A new species of *Ctenocheles* is erected on the basis of the second specimen (see below).

Stenocheles parvulus has been considered a member of *Oncopareia* by several authors (Mertin 1941, Schweitzer *et al.* 2010); it (isochelous specimen), however, does not seem to have affinities to *Oncopareia bredai*. Most importantly, *O. bredai* possesses noticeably heterochelous chelipeds (Mertin 1941, Tshudy & Sorhannus 2000), which can be characterised as morphological analogues of the crusher and cutter claw of homarine lobsters; nothing like that applies to *S. parvulus*. *Oncopareia* has a fixed finger at no angle to the long axis of palm (Tshudy & Sorhannus 2000, figs 4.1, 4.3), whereas the fixed finger of at least one chela of *S. parvulus* is angled at about 20° to the long axis of palm (Fig. 1B, C). The specimen is very poorly preserved without any visible grooves on the carapace (Fig. 1B, C). For the reasons discussed above, we consider the generic or familial placement of *S. parvulus* as recognised herein unresolved at least until a more detailed study on this taxon appears. For now we refer to it as ?*Oncopareia parvulus*.

Finally, a short remark on the inconsistency in Fritsch's usage of name *S. parvulus* should be made. In the publication describing *S. parvulus* (see Fritsch & Kafka 1887), the figures are labelled as *S. gracilis*. The same name is also used in several subsequent works (Fritsch 1893, 1894). *Stenocheles gracilis* is considered a *nomen nudum* herein.

Geological and stratigraphical settings

The Březno locality is situated on the NNE slope of Březno Hill, on the right bank of the Ohře River in the vicinity of Louny (Czech Republic; Fig. 3); GPS co-ordinates: 50° 21´ 23.864˝ N, 13° 44´ 16.919˝ E. Calcareous claystones and siltsones of the Teplice and Březno formations are exposed in the outcrop (Čech *et al.* 1980). The outcrop represents the type locality of the Priesener Schichten *sensu* Fritsch (1893) and Krejčí (1869) and the lower boundary stratotype of the Březno Formation *sensu* Čech *et al.* (1980). Čech *in* Čech & Švábenická (1992) placed the Turonian-Coniacian stage boundary in the upper part of the Teplice Formation, which was encountered in the Pd-1 Březno borehole about 15 m below the Ohře river level. Currently, the outcrop is partly covered by debris.

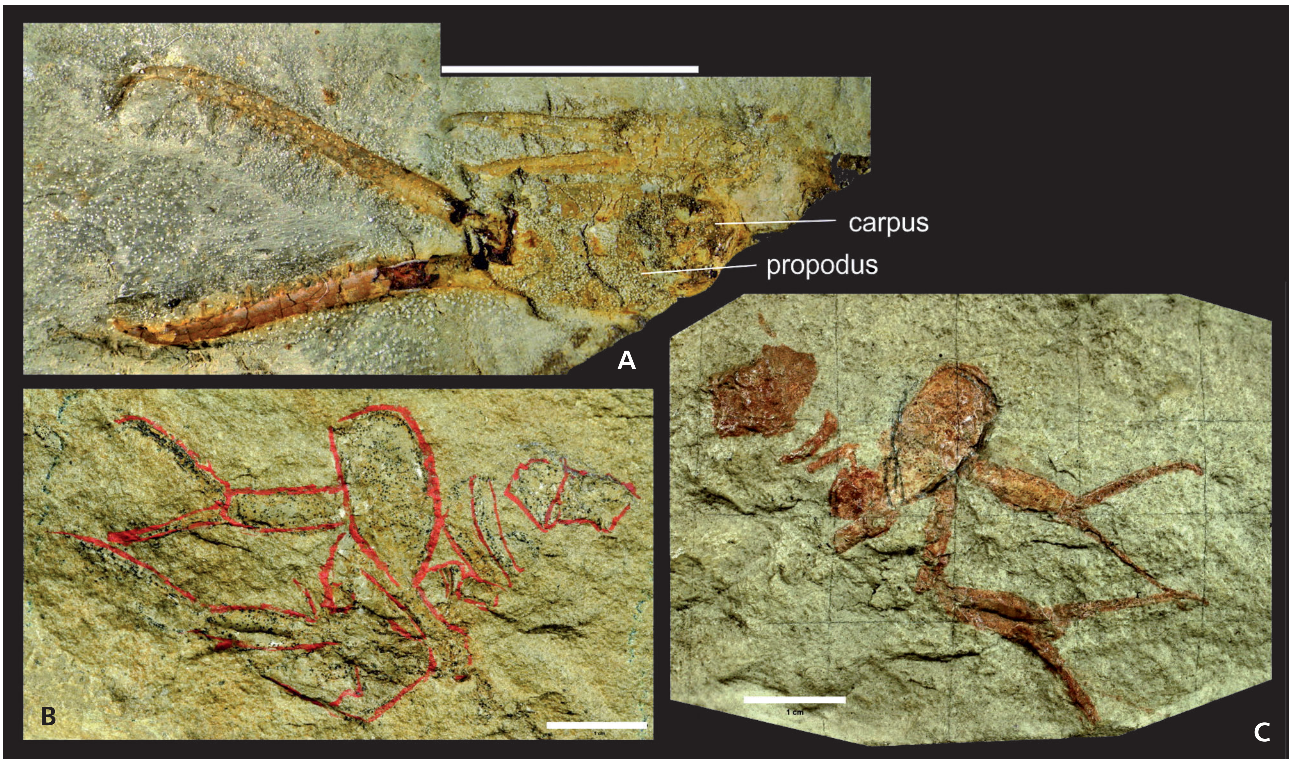


Figure 1. A – the holotype of *Ctenocheles fritschi* sp. nov. (NM O3456) originally described as one of the specimens of *Stenocheles parvulus* Fritsch *in* Fritsch & Kafka, 1887 (figured in Fritsch & Kafka 1887, pl. 3, fig. 4). • B, C – lectotype of *S. parvulus* (NM O3455, NM O6862), part and counterpart (figured in Fritsch & Kafka 1887, pl. 3, fig. 3). Scale bar equals 10 mm.

Figure 2. Digital images of *Stenocheles parvulus* Fritsch *in* Fritsch & Kafka, 1887 published in Fritsch & Kafka (1887) as pl. 3, fig. 3 (A) and fig. 4 (B); • A – holotype of *Ctenocheles fritschi* sp. nov. (NM O3456). • B – lectotype of *S. parvulus* (NM O6862).

The first description of the outcrop was provided by Fritsch (1893), who distinguished altogether six lithological members (called "beds") from the stratigraphic bottom to the top: Nucula Bed, Geodia Bed, Radiolaria Bed, Gastropod Bed, Sphaerosiderite Bed and Crab Bed (Fig. 4).

The Nucula Bed is represented by dark calcareous claystones with thin intercalations of calcareous siltstones of the Teplice Formation. These sediments are accessible only when the water level is low. Stratigraphically, the Nucula Bed belongs to the lowermost Coniacian (*Cremnoceramus erectus* Zone; Čech & Švábenická 1992, Čech *et al.* 1996, Košťák *et al.* 2004, Lees 2008). An Early Coniacian age is also supported by a single record of the index belemnite *Goniocamax lundgreni* (Stolley, 1897) (Košťák 1996, Košťák *et al.* 2004).

The Geodia and Radiolaria beds are composed of the glauconitic calcareous clayey siltstones of the Rohatce Member (Teplice Formation). The beds contain abundant

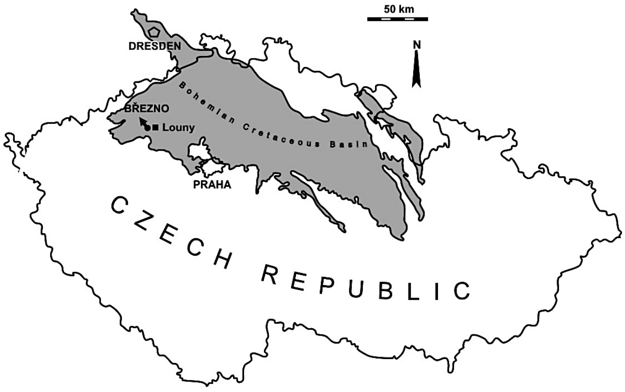


Figure 3. Location of the Březno locality within the Bohemian Cretaceous Basin.

shells of the ammonite *Cremnoceramus crassus* (Petrascheck, 1903) and *C. inconstans s.l.* (Čech & Švábenická 1992, Lees 2008). Stratigraphically, the beds correspond to the Lower Coniacian (*Cremnoceramus crassus* Zone).

The Gastropod, Sphaerosiderite and Crab beds are characterised by calcareous claystones of the Březno Formation. These beds are very rich in fossils. Ammonites are very abundant (for details see Fritsch 1893); stratigraphically significant taxa are represented by *Foresteria* (*Harleites*) *petrocoriensis* (Coquand, 1859) and *Peroniceras tridorsatum* (Schlüter, 1867). Calcareous nannofossils and foraminifers are more abundant in these beds than in the underlying beds (Fritsch 1893, Čech & Švábenická 1992, Čech *et al.* 1996, Lees 2008). An almost complete absence of glauconite is typical for the Sphaerosiderite Bed, whereas sphaerosiderite concretions, exhibiting a gray core enveloped by red or yellow (oxidised) surface and up to 60 cm in diameter, are common. The yellowish-gray and orange coloured sediments of the Crab Bed contain higher carbonate content (about 25%) than stratigraphically lower beds (Pokorný *et al.* 1983). The Gastropod, Sphaerosiderite and Crab beds can be assigned to the Lower–Middle Coniacian (upper part of the *Cremnoceramus crassus* and *Volviceramus koeneni* zones). The first occurrence of the calcareous nannoplankton taxon *Micula staurophora* (Gardet, 1955) is known from the Gastropod Bed (*V. koeneni* Inoceramid Zone; for details see Čech & Švábenická 1992, Lees 2008).

Invertebrate fauna of the Březno locality

The sediments from the Březno locality are rich in micro- and macrofossils. Macrofaunal remains can be found especially in the lower part of the Březno Formation, mainly in the Gastropod Bed. Pyritised fossils are fairly common in the Geodia and Radiolaria beds. Except for the stratigraphically highest part of the section, numerous foraminifers, ostracods and other microfossils are also abundant (Pokorný *et al.* 1983). The fauna of the outcrop was studied in detail by Reuss (1845–1846), Fritsch (1867, 1893) and Fritsch & Kafka (1887). Later works focused on foraminifers (Čepková 1969; Štemproková *in* Pokorný *et al.* 1983), ostracods (Pokorný *et al.* 1983), bivalves (Macák 1966, Čech 1989, Čech & Švábenická 1992) and calcareous nannofossils (Švábenická 1983, 1991; Čech & Švábenická 1992; Lees 2008).

Fossil decapods from the locality were described by Reuss (1845–1846), Fritsch (1867, 1893), Fritsch & Kafka (1887), and more recently by Veselská (2009, 2010). Fritsch (1893) reported a single specimen of *Enoploclytia leachi* (Mantell, 1822) from a sphaerosiderite concretion in the Sphaerosiderite Bed. From the Crab Bed, he reported a single specimen of *Callianassa brevis* Fritsch, 1867 together with brachyurous crabs *Microcorystes parvulus* Fritsch, 1893, *Polycnemidium pustulosum* (Reuss, 1845) and ?*Palaeocorystes* sp. [currently classified as *Cretacoranina fritschi* (Glaessner, 1929)]; from the Gastropod Bed, he reported a single specimen of both *P. pustulosum* and *Stenocheles parvulus* = *Ctenocheles fritschi* sp. nov. A list of 20 decapod taxa known from the Březno Formation was recently provided by Klompmaker (2013, appendix B).

Material and methods

Both specimens described as *Stenocheles parvulus* by Fritsch *in* Fritsch & Kafka (1887) were examined. The isochelous specimen (NM O3455 with its plaster cast NM O6862; Figs 1B, C, 2B) originates from the Lower–Middle Turonian strata of the Bílá Hora locality in Prague, and represents the type specimen (lectotype selected herein) of ?*Oncopareia parvulus*. The heterochelous specimen from the Gastropod Bed of Březno (NM O3456; Figs 1A, 2A) is considered the holotype of *Ctenocheles fritschi* sp. nov.

In addition to Fritsch's original material numerous new specimens of *Ctenocheles fritschi* sp. nov. (Figs 5, 6) have been collected by one of the authors from the same locality (PD). Furthermore, one specimen of *C. fritschi* sp. nov. (NM O7121 collected from the Crab Bed; Fig. 6) was recently discovered in NM (originally belonging to Václav Houša); this material was collected in the 1970s and was thought to be lost.

The standard procedure of using ammonium chloride sublimate was initially used to achieve a higher contrast when photographing the specimens. The results were, however, not satisfactory. Therefore, different photo-documenting methods were used. Photos of Fritsch's original material was photographed under angled light using Canon EOS 550D digital camera; a photo of *C. fritschi* sp. nov. (O3456) was taken using the microphotography setting

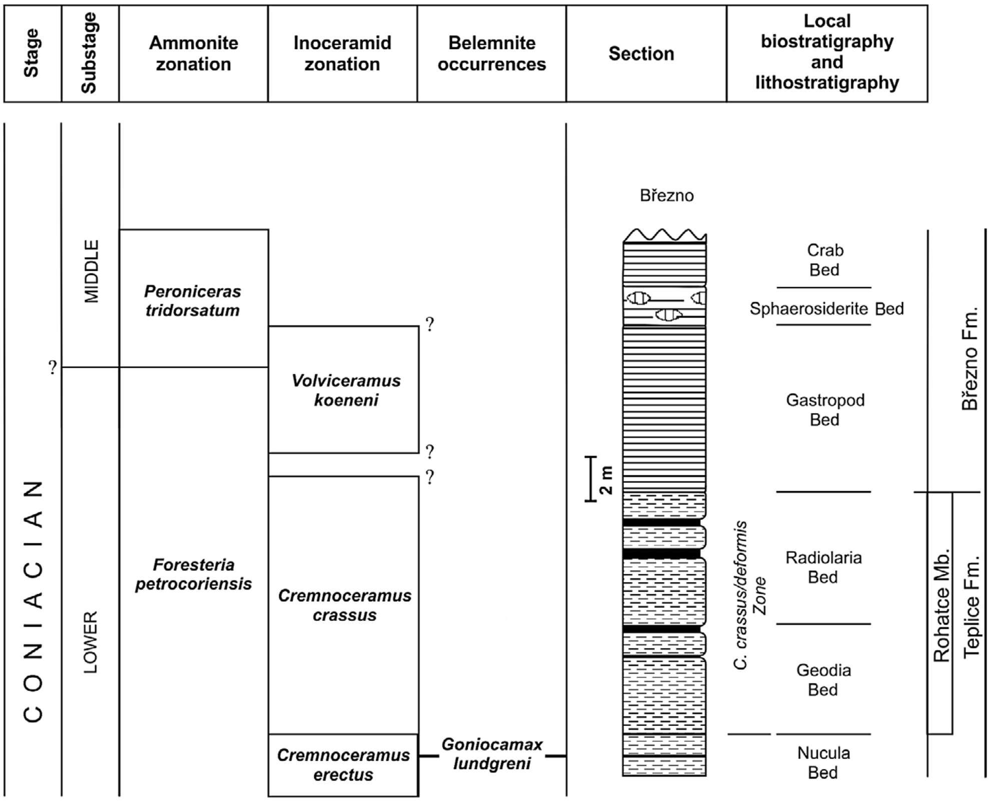


Figure 4. Bio- and lithostratigraphical correlation of the section at Březno. *Ctenocheles fritschi* sp. nov. is found in the Gastropod and Crab beds of the Březno Formation. Modified from Košťák *et al.* (2004).

Olympus DP70. Photographs of additional material deposited in NM (O7116–O7120) were taken using scanning electron microscope (SEM) Hitachi S-3700N in low vacuum. New material collected by PD (RMM GPa 1030–1031) was photographed using SEM in low vacuum (JEOL JSM-6380LV) at the Institute of Geology and Palaeontology (Charles University, Prague). The specimens were not coated with any metal and therefore low vacuum was used instead. Series of photographs taken with SEM were assembled into final images using the computer freeware Microsoft Image Composite Editor 1.4.4. Plates were made using Corel Graphic Suite X5.

Repositories. – Regional Museum in Most, Czech Republic (RMM) and the National Museum in Prague, Czech Republic (NM).

Systematic palaeontology

Order Decapoda Latreille, 1802
Infraorder Axiidea de Saint Laurent, 1979
Family Ctenochelidae Manning & Felder, 1991

Genus *Ctenocheles* Kishinouye, 1926

Type species. – *Ctenocheles balssi* Kishinouye, 1926, by monotypy.

Species included. – See Hyžný & Dulai (in press, table 2) and *Ctenocheles fritschi* sp. nov.

Diagnosis. – Rostral carina and rostral spine present; dorsal surface of eye flattened; third maxilliped with or without exopod, distal margin of merus usually with spine; chelipeds unequal, and dissimilar; carpus of major cheliped small, cup shaped; merus of major cheliped with or without hook; palm of major cheliped bulbous, longer than high, narrowing distally; fingers elongate and pectinate; fixed finger straight or arcuate; occlusal surface of fixed finger with long, needle-like teeth, teeth of variable size, tips curving proximally. Palm of minor cheliped rectangular; fixed finger long, narrow, straight; uropodal exopod with lateral incision (emended from Manning & Felder 1991, p. 784).

Discussion. – *Ctenocheles* is a poorly known genus. Even from extant environments only a handful of specimens are known and complete animals have rarely been found: Kishinouye (1926) reported one specimen of *Ctenocheles balssi* Kishinouye, 1926; Ward (1945) reported three complete specimens and two fragments of *C. collini* Ward, 1945; Powell (1949) reported two specimens of *C. maorianus* Powell, 1949; Holthuis (1967) summarised older collections and reported two isolated chelipeds of *Ctenocheles* as "species A" and "species B"; Rodrigues (1978) reported one specimen of *C. holthuisi* Rodrigues, 1978; Rabalais (1979) reported five specimens of *C. leviceps* Rabalais, 1979; Sakai (1999a)

Table 1. Measurements (in mm) of studied specimens of *Ctenocheles fritschi* sp. nov. Note that some specimens have collective repository numbers. Explanations: M = major chela; m = minor chela; L = length; H = height.

		merus		carpus		manus		fixed finger	dactylus
specimen	M/m	L	H	L	H	L	H	L	L
NM O3456 (Fig. 1A, D)	M	–		1.7	3.9	7.3	5.0	15.2	15.7
NM O3456 (Fig. 1A, D)	m	–	–	1.7	2.2	4.1	2.5	6.3	7.0
NM O7116 (Fig. 5D)	M	–	–	–	–	6.0	5.0	13.5	–
NM O7118a (Fig. 5E)	M	–	–	–	–	–	–	–	14.0
NM O7118a (Fig. 6)	M	9.0	4.5	2.0	3.3	9.5	9.0	–	–
RMM G-Pa 1030 (Fig. 5A, B)	M	–	–	–	–	5.0	3.7	9.0	–
RMM G-Pa 1030 (Fig. 5A, B)	m	–	–	–	–	3.3	1.5	–	–
RMM G-Pa 1031 (Fig. 5C)	M	–	–	–	–	2.4	2.5	–	–
RMM G-Pa 1031 (Fig. 5C)	m	–	–	–	–	1.7	1.0	–	–
RMM G-Pa 1031 (Fig. 5F)	M	–	–	–	–	5.7	5.3	10.7	–
RMM G-Pa 1031 (Fig. 5G)	M	–	–	–	–	7.4	6.0	16.0	–

redescribed *C. balssi* based on one additional specimen; the largest sample of *Ctenocheles* was examined by Matsuzawa & Hayashi (1997); they reported three specimens and 40 detached chelipeds of *C. balssi*.

The fossil record of the genus consists almost exclusively of chelae (Schweitzer & Feldmann 2001). The genus has been widely reported from the Cenozoic from all over the world (Schweitzer & Feldmann 2001, 2002; Feldmann *et al*. 2010; Hyžný & Dulai in press and references therein). With the herein newly described taxon the number of *Ctenocheles* species known from the Upper Cretaceous increased to three: *C. madagascariensis* from Madagascar; *C. inaequidens* (Pelseneer, 1886) from the Netherlands, and *C. fritschi* sp. nov. from the Czech Republic. Today, there are six named and a few unnamed species. Its generic distribution covers the marine part of the world except for eastern Pacific (Sakai 1999a, 1999b, 2005, 2011).

The diagnosis presented herein is taken from Manning & Felder (1991) and emended with details on chelipeds, which are often preserved as fossils.

Ctenocheles fritschi sp. nov.
Figures 1A, 2A, 5, 6

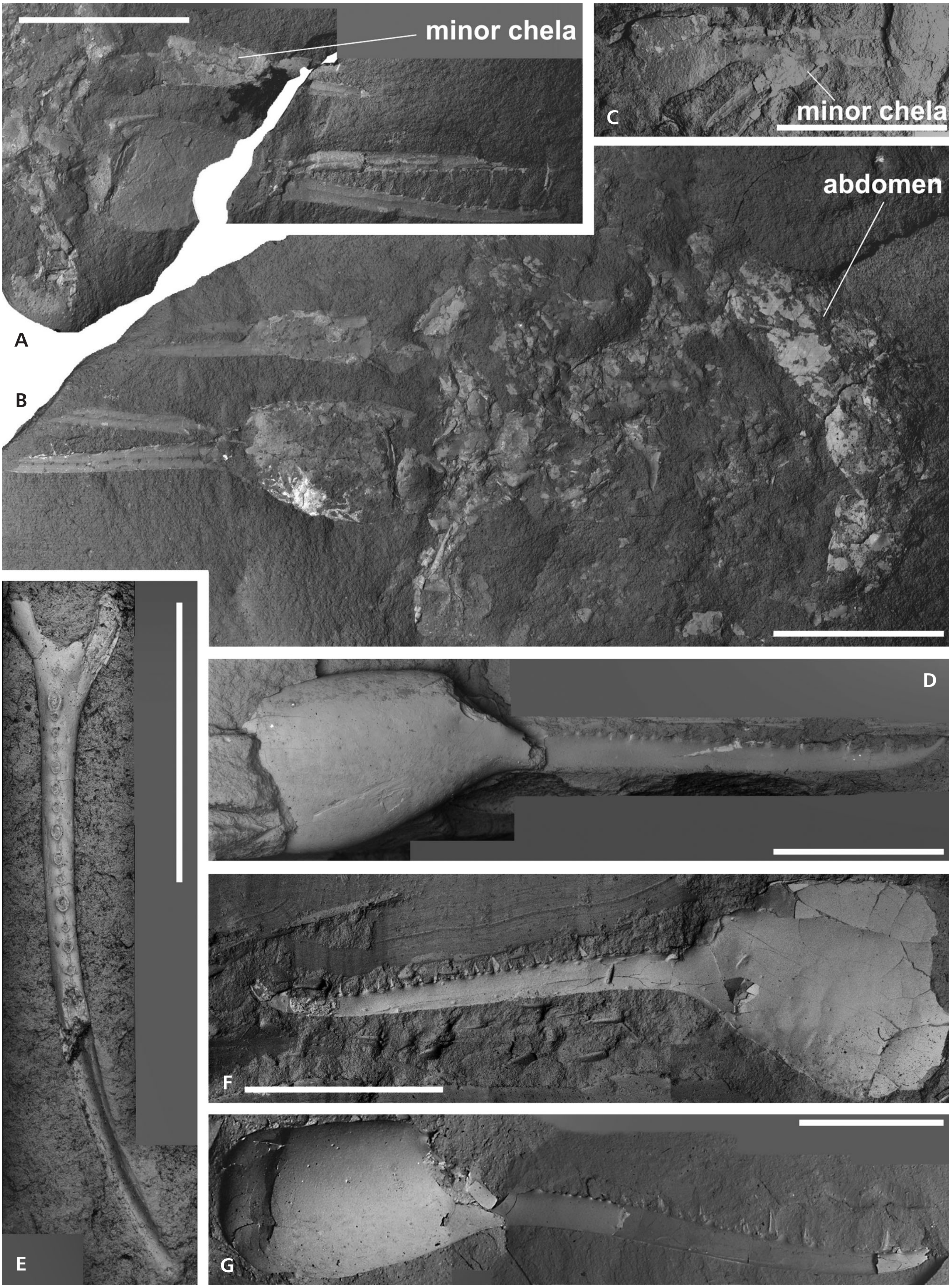
partim 1887 *Stenocheles parvulus*; Fritsch & Kafka, p. 40.
partim 1887 *Stenocheles gracilis* (nomen nudum) – Fritsch & Kafka, pl. 3, fig. 4 (non fig. 3).
?1893 *Stenocheles gracilis* (nomen nudum). – Fritsch, p. 106.
?1894 *Stenocheles gracilis* (nomen nudum). – Fritsch, p. 103.
partim 1929 *Ischnodactylus parvulus* (Fritsch). – Glaessner, p. 226.
partim 1941 *Stenocheles parvulus* Fritsch. – Mertin, p. 188 (non), text-fig. 10g.
1964 *Stenocheles parvulus* Fritsch *in* Fritsch & Kafka. – Secrétan, p. 152.
partim 2009 *Oncopareia parvulus* (Fritsch *in* Fritsch & Kafka). – Veselská, p. 21, pl. 2, fig. 2 (non figs 3, 4).
partim 2010 *Oncopareia parvulus* (Fritsch & Kafka). – Schweitzer *et al*., p. 32.
partim 2013 *Oncopareia parvulus* (Fritsch & Kafka). – Klompmaker, Appendix A, B, D.

Type. – Holotype NM O3456 selected herein from two syntypes of *S. parvulus*. The specimen consists of a major and minor chela.

Type horizon and locality. – Gastropod Bed (Lower–Middle Coniacian) of the Březno Formation at the Březno locality, Czech Republic.

Material. – NM O7118–7120: three cheliped fragments consisting mostly of isolated major propodi and dactyli originating from the Gastropod Bed; NM O7121: a near complete specimen found in the Crab Bed; RMM G-Pa 1030, RMM G-Pa 1031 (collective number): several samples showing isolated major propodi, but also a near complete specimen with preserved abdomen and both chelae (RMM G-Pa 1030) – all these specimens origi-

Figure 5. *Ctenocheles fritschi* sp. nov. • A, B – nearly complete specimen RMM G-Pa 1030 showing both chelae and remains of abdomen. • C – specimen RMM G-Pa 1031 with major and minor chela. • D – isolated major propodus NM O7116. • E – isolated major dactylus NM O7118a. • F, G – major isolated propodi RMM G-Pa 1031. All specimens are from the Gastropod Bed of Březno. Scale bar equals 5 mm.


minor chela
C
minor chela
A
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G

nate from the Gastropod Bed. For measurements see Table 1.

Etymology. – The epithet honours Anton Fritsch (originally as Antonín Frič; 1832–1913), famous Czech palaeontologist, biologist and geologist, who described numerous taxa from the Bohemian Cretaceous Basin.

Diagnosis. – Ischium of major cheliped long and slender, lower margin serrated proximally; merus ovoid, about twice as long as high, upper margin straight.

Description. – Dorsal carapace not preserved. Chelipeds (first pereiopods) distinctly unequal in size and dissimilar in shape. Ischium of major cheliped elongated, with faint serration on lower margin proximally; merus ovoid, about twice as long as high, unarmed, upper margin straight; carpus very short, distinctly higher than long, cup-shaped; palm bulbous, rounded or slightly elongate, longer than high, narrowing distally, upper margin forms rounded curve proximally; fingers slender and elongate, about 1.5–2 times as long as palm; fixed finger is at angle of about 20–40° to long axis of palm; occlusal surface of both fingers armed with long, needle-like teeth of two sizes, two to three smaller teeth between two large teeth; tips of fingers proximally curved forming large teeth crossing each other and exceeding length of large teeth on occlusal surface. Minor cheliped slender and less massive than major cheliped; carpus about as high as long, with rounded proximo-lower margin; palm rectangular, about 2.5–3 times longer than high, only slightly tapering distally; fixed finger long, narrow and straight, approximately as long as palm; occlusal margin of both fingers armed with a row of denticles of two sizes, occlusal margin of fixed finger has proximal concavity.

Second to fifth pereiopods insufficiently preserved. Abdomen elongated and smooth, preserved in lateral aspect. Pleura little developed, rounded. Second segment longest. Sixth segment, telson and uropods poorly preserved. No pleopods preserved.

Discussion. – The typical shape of the major propodus and dactylus, i.e. a bulbous palm with long pectinate fingers, usually permits immediate determination to the genus level. Several specimens have the minor chela preserved (Figs 1A, 5A–C), and in a few cases also an abdomen and other appendages are preserved (Figs 5B, 6). The shape of the major and minor chelae clearly point to ascription of the material to *Ctenocheles*.

The material shows intraspecific variability in the length of major cheliped fingers (Fig. 5). All specimens exhibit fingers that are approximately up to twice as long as the palm, but usually they are shorter. Hyžný & Dulai (in press) discussed this issue with regard to species identification and concluded that *Ctenocheles* species cannot be distinguished from each other based on the length of fingers alone. Similarly, the angle of the major cheliped fixed finger to the long axis of palm is uninformative for species identification (Hyžný & Dulai in press). Differentiation between fossil species of *Ctenocheles* was discussed at various lengths by several authors (Schweitzer & Feldmann 2002, Collins & Jakobsen 2003, Feldmann *et al.* 2010, Hyžný & Dulai in press). Although, the shape of the propodus, the ratio between the length of the palm and fingers, dentition of the fingers, and the angle of the fixed finger seem to be intraspecifically variable characters, their combination can define the species (*e.g.* Schweitzer & Feldmann 2002).

Matsuzawa & Hayashi (1997) considered (among other characters) the morphology of the ischum and merus of the major cheliped as taxonomically important on the species level (for details see the key in Matsuzawa & Hayashi 1997, p. 44). As summarised by Hyžný & Dulai (in press), three major cheliped morphotypes present can be distinguished in extant *Ctenocheles*; they may represent three different lineages, which can eventually lead to definition of three separate genera. *Ctenocheles fritschi* sp. nov. with its serrated ischium and ovoid, unarmed merus corresponds to the morphotype to which extant taxa *C. collini* Ward, 1945 and *C. maorianus* Powell, 1949 belong. From the other fossil *Ctenocheles* species, only a few preserve the morphology of the merus of the major cheliped. *Ctenocheles madagascariensis* from the Upper Cretaceous of Madagascar as figured by Charbonnier *et al.* (2012, fig. 18B) shows also the merus (apparently not recognised previously). Its ovoid outline can be compared to the above mentioned taxa as well. The morphotype exhibiting an elongate, slender and completely unarmed ischium and merus is represented by the type species *C. balssi* (extant). The oldest fossil record of this supposed lineage may be represented by *C. rupeliensis* (Beurlen, 1939) from the Oligocene of Hungary, recently redescribed by Hyžný & Dulai (in press). The third morphotype, typified by a spinulous lower margin of the ischium and merus, is represented by the extant *C. holthuisi* Rodrigues, 1978; no fossil representative with a similar ischium and merus morphology is known so far.

Ctenocheles fritschi sp. nov. differs from other fossil and extant congeners in several aspects. Its major cheliped fingers are longer than *C. secretanae* Schweitzer & Feldmann, 2002 from the Eocene of California and *C. ornatus* Beschin, De Angeli, Checchi & Zarantonello, 2005 from the Eocene of Italy. In *C. anderseni* Collins & Jakobsen, 2003 from the Eocene of Denmark, the manus of both chela is longer and more rectangular than manus in *Ctenocheles fritschi* sp. nov.; the same applies for taxa described from propodal fragments, *e.g. C. bakeri* (Glaessner, 1947) from the Paleocene of Australia and *C. burlesonensis* (Stenzel, 1935) from the Eocene of Texas. When considering mor-

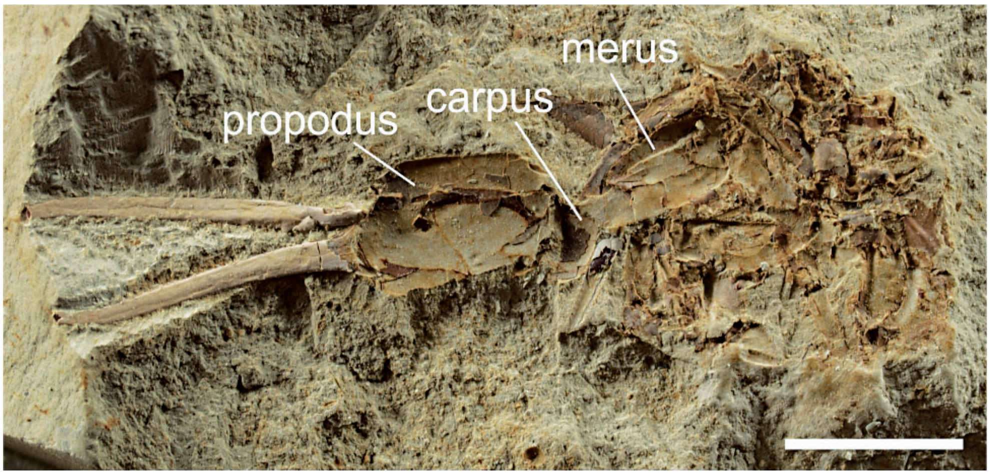

Figure 6. *Ctenocheles fritschi* sp. nov., nearly complete specimen NM O7121 from the Crab Bed of Březno. Scale bar equals 10 mm.

phology of merus and ischium of major cheliped, *C. fritschi* sp. nov. is close to *C. madagascariensis*. In the latter, however, the proximal portion of the merus is more rounded (Charbonnier *et al.* 2012, fig. 18B). Extant *C. collini* and *C. maorianus*, today living in the Indo-West Pacific, are morphologically close to *C. fritschi* sp. nov. Both *Ctenocheles collini* and *C. maorianus* possess a merus with a strongly arcuate upper margin in its proximal third (see Ward 1945, pl. 13 and Powell 1949, pl. 68, figs 4, 5, respectively); however, this convexity is not present in *C. fritschi* sp. nov.

Occurrence. – The occurrence of *Ctenocheles fritschi* sp. nov. is so far limited to the Gastropod and Crab beds (Lower–Middle Coniacian) of the Březno Formation at the Březno locality, Czech Republic. Fritsch (1894) reported the presence of possible conspecific *Stenocheles gracilis* (sic!) from the Rohatce Member of the Teplice Formation at the villages Hostín and Řepín near Mělník and at Bílá Cesta in Teplice (Czech Republic). He, however, supplied neither description nor figures. The specimens are lost; hence, their true identity (either *Ctenocheles fritschi* sp. nov. or an isochelous astacidean) is unknown.

Discussion

Revision of Fritsch's taxa. – In the time of major systematic revisions and re-evaluations of numerous Mesozoic decapod groups (*e.g.* Karasawa *et al.* 2011, 2013; Klompmaker *et al.* 2011; Robins *et al.* 2013; Schweitzer *et al.* 2012; Van Bakel *et al.* 2012) there is a need for a thorough revision of Fritsch's original material. It should be stressed that the figures and animal restorations (drawings) presented in works by Fritsch (notably in Fritsch & Kafka 1887) often do not fully correspond with the original specimens (pers. obs. MH, MKV) as in many cases his reconstructions are idealised. Thus, caution must be taken when dealing with Fritsch's taxa on the basis of published figures only. Physical re-examination of the material and new photodocumentation is planned for future revisions. In revising Fritsch's taxa, new (topotypic) material is usually needed to resolve taxonomic identification of the original material. For example, Fritsch sometimes painted or varnished the specimens to enhance contrast of the fossil, and, as a result, many details are obscured by painting and proper re-examination is hindered. This is especially true for ?*O. parvulus* (*sensu* this paper).

Taphonomy of ghost shrimps. – The material is partially flattened in very fine-grained calcareous claystones typical for the Gastropod and Crab beds, allowing preservation even of poorly calcified exoskeleton parts (Fig. 6). Interestingly, isolated cheliped elements are usually preserved three-dimensionally (Fig. 5D–G), whereas specimens with preserved abdomen and other exoskeleton parts (including appendages) are strongly laterally compressed (Figs 5B, 6).

At Březno *Ctenocheles* remains are known from the Gastropod and Crab beds. From these horizons also burrows attributable to the ichnogenus *Thalassinoides* Ehrenberg, 1944 are known (MKV, unp. data). Although no corpses or moults have been found inside a burrow structure, we questionably ascribe the burrows to *Ctenocheles*. The diameter of approximately 5 mm (MKV pers. obs.) would roughly correspond to the height of major propodus (Table 1) of *C. fritschi* sp. nov. Ghost shrimp body fossils preserved within the burrows or associated with them have been considered rare (*e.g.* Bishop & Williams 2005, Hyžný 2011, Hyžný & Hudáčková 2012), and, therefore, the report of any such preservation is of note.

Convergence. – Interestingly, several unrelated decapod taxa with pectinate claws have been reported from the Březno Formation, namely *Enoploclytia leachi* (Erymidae), *Oncopareia esocinus* (Nephropidae), ?*Oncopareia parvulus* (Nephropidae), and *Ctenocheles fritschi* sp. nov.

(Ctenochelidae). The claw function is usually directly linked to environmental pressures (*e.g.* diet or burrow construction). Tshudy & Sorhannus (2000, p. 481), however, stated that: "direct observations of decapods bearing pectinate claws have been few. Consequently, the adaptive significance of this claw form can be addressed only by speculation". They further noted that some or all of the pectinate-clawed shrimps and lobsters are burrowers. Interestingly, whereas *E. leachi* is isochelous and *Oncopareia* is moderately heterochelous (cutter and crusher claw), *Ctenocheles* is a strongly heterochelous animal. Among permanent burrow-dwellers (*i.e.* ghost shrimps), *Ctenocheles* is the only genus with pectinate claws. Tshudy & Sorhannus (2000) discussed various food-gathering functions of pectinate claws; this will not be repeated here. Nevertheless, pectinate claws in the four above mentioned genera do not seem to represent adaptation to the same activity. Whereas relatively large sized *E. leachi* with strongly calcified exoskeleton (*e.g.* Reuss 1853, Fritsch & Kafka 1887) was probably an epibenthic lobster (similar to homarine lobsters from recent environments), *C. fritschi* sp. nov. was a tiny burrower.

Conclusions

1. *Stenocheles parvulus* as originally described by Fritsch *in* Fritsch & Kafka (1887) was based on two specimens – their re-examination revealed that they represent two different taxa from two different infraorders. The isochelous specimen is selected herein a lectotype of *S. parvulus* (= ?*Oncopareia parvulus* sensu this paper) whereas the heterochelous one is selected a holotype of *Ctenocheles fritschi* sp. nov. Because of the poor preservation of the type (and only) material taxonomic affinities of ?*O. parvulus* remain unresolved.

2. Description of *Ctenocheles fritschi* sp. nov. is largely based on new well-preserved material from the topotypic locality. The major chela of the species possesses a serrated ischium and an ovoid, unarmed merus, in this respect it is morphologically close to extant *C. collini* and *C. maorianus*.

3. *Ctenocheles fritschi* sp. nov. represents the first report on the occurrence of the genus from the Bohemian Cretaceous Basin. It is one of the oldest records of *Ctenocheles* and simultaneously one of the best preserved fossil material of the genus reported to date.

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References

Beschin, C., de Angeli, A., Checchi, A. & Zarantonello, G. 2005. Crostacei eocenici di Grola presso Spagnago (Vicenza, Italia settentrionale). *Studi e Ricerche, Associazione Amici del Museo, Museo Civico "G. Zannato", Montecchio Maggiore (Vicenza) 12*, 5–35.

Beurlen, K. 1939. Neue Dekapoden-Krebse aus dem ungarischen Tertiär. *Paläontologische Zeitschrift 21*, 135–161. DOI 10.1007/BF03043252

Bishop, G.A. & Williams, A.B. 2005. Taphonomy and preservation of burrowing thalassinidean shrimps. *Proceedings of the Biological Society of Washington 118*, 218–236. DOI 10.2988/0006-324X(2005)118[218:TAPOBT]2.0.CO;2

Bosquet, J. 1854. Les Crustacés fossiles du Terrain Crétacé du Limbourg. *Verhandelingen van den Commissie van de Geologische Kaart van Nederland 2*, 12–128.

Čech, S. 1989. Upper Cretaceous Didymotis Events from Bohemia, 657–676. *In* Wiedmann, J. (ed.) *Cretaceous of the Western Tethys: proceedings of the 3rd International Cretaceous Symposium, Tübingen 1987.* E. Sweizerbart, Stuttgart.

Čech, S., Hradecká, L., Laurin, J., Štaffen, Z., Švábenická, L. & Uličný, D. 1996. Locality 3: Úpohlavy quarry, 32–42. *In* Čech, S., Uličný, D. & Voigt, T. (eds) *Fifth International Cretaceous Symposium and Second Workshop on Inoceramids, Field Excursion B1, Stratigraphy and Facies of the Bohemian-Saxonian Cretaceous Basin*. Freiberg University of Mining and Technology, Freiberg/Saxony.

Čech, S., Klein, V., Kříž, J. & Valečka, J. 1980. Revision of the Upper Cretaceous stratigraphy of the Bohemian Cretaceous Basin. *Věstník Ústředního ústavu geologického 55*, 227–296.

Čech, S. & Švábenická, L. 1992. Macrofossils and nannofossils of the type locality of the Březno Formation (Turonian-Coniacian, Bohemia). *Věstník Českého geologického ústavu 67*, 311–326.

Čepková, J. 1969. *Rod Lenticulina Lamarck, 1804 v české křídě.* 72 pp. Master thesis, Charles University, Prague, Czech Republic.

Charbonnier, S., Garassino, A. & Pasini, G. 2012. Revision of Mesozoic decapod crustaceans from Madagascar. *Geodiversitas 34*, 313–357. DOI 10.5252/g2012n2a5

COLLINS, J.S.H. & JAKOBSEN, S.L. 2003. New crabs (Crustacea, Decapoda) from the Eocene (Ypresian/Lutetian) Lillebælt Clay Formation of Jutland, Denmark. *Bulletin of the Mizunami Fossil Museum 30*, 63–96.

EHRENBERG, K. 1944. Ergänzende Bemerkungen zu den seinerzeit aus dem Miozän von Burgschleinitz beschriebenen Gangkernen un Bauten dekapoder Krebse. *Paläontologische Zeitschrift 23*, 354–359. DOI 10.1007/BF03160443

FELDMANN, R.M., JAGT, J.W.M. & TSHUDY, D.M. 1990. Late Maastrichtian isopod and decapod Crustacea from Haccourt (Liège), northeastern Belgium. *Mededelingen Rijks Geologische Dienst 44*, 23–35.

FELDMANN, R.M., SCHWEITZER, C.E. & ENCINAS, A. 2010. Neogene decapod Crustacea from southern Chile. *Annals of Carnegie Museum 78*, 337–366. DOI 10.2992/007.078.0404

FRITSCH, A. 1867. Über die Callianassen der böhmischen Kreideformation. *Abhandlungen der königlischen Böhmischen Gesellschaft der Wissenschaften 5, 15*, 1–12.

FRITSCH [as FRIČ], A. 1893. Studien im Gebiete der Böhmischen Kreideformation. V. Priesener Schichten. *Archiv der Naturwissenschaftlichen Landesdurchforschung von Böhmen 9*, 1–135.

FRITSCH [as FRIČ], A. 1894. Studie v oboru křídového útvaru v Čechách. V. Březenské vrstvy. *Archiv pro přírodovědné prozkoumání Čech 9*, 1–129.

FRITSCH, A. & KAFKA, J. 1887. *Die Crustaceen der böhmischen Kreideformation*. 53 pp. Selbstverlag in Commission von F. Řivnáč, Prag.

GLAESSNER, M.F. 1929. Crustacea decapoda. *In* POMPECKJ, J.F. (ed.) *Fossilium Catalogus I: Animalia (41)*. 464 pp. W. Junk, Berlin.

GLAESSNER, M.F. 1947. Decapod Crustacea (Callianassidae) from the Eocene of Victoria. *Proceedings of the Royal Society of Victoria 59*, 1–7.

GLAESSNER, M.F. 1969. Decapoda, R400–R533, R626–R628. *In* MOORE, R.C. (ed.) *Treatise on Invertebrate Paleontology. Part R, Arthropoda 4(2)*, University of Kansas Press, Lawrence.

HOLTHUIS, L.B. 1967. Biological investigations of the deep sea. 30. A survey of the genus *Ctenocheles* (Crustacea: Decapoda, Callianassidae), with a discussion of its zoogeography and its occurrence in the Atlantic Ocean. *Bulletin of Marine Science 17*, 376–385.

HYŽNÝ, M. 2011. *In situ* mud shrimps (Decapoda: Axiidea: Callianassidae) preserved within their burrows from the middle Miocene of the Central Paratethys. *Bulletin of the Mizunami Fossil Museum 37*, 37–46.

HYŽNÝ, M. & DULAI, A. in press. Deep-water fossorial shrimps from the Oligocene Kiscell Clay of Hungary: Taxonomy and palaeoecology. *Acta Palaeontologica Polonica*.

HYŽNÝ, M. & HUDÁČKOVÁ, N. 2012. Redescription of two ghost shrimps (Decapoda: Axiidea: Callianassidae) from the Middle Miocene of the Central Paratethys: systematics, intraspecific variation, and *in situ* preservation. *Zootaxa 3210*, 1–25.

IMAIZUMI, R. 1957. An interesting crustacean remain, *Ctenocheles sujakui* n. sp. from the Paleogene of Kyushu, Japan. *Transactions and Proceedings of the Palaeontological Society of Japan (new series) 32*, 299–304.

KARASAWA, H., SCHWEITZER, C.E. & FELDMANN, R.M. 2011. Phylogenetic analysis and revised classification of podotrematous Brachyura (Decapoda) including extinct and extant families. *Journal of Crustacean Biology 31*, 523–565. DOI 10.1651/10-3423.1

KARASAWA, H., SCHWEITZER, C.E. & FELDMANN, R.M. 2013. Phylogeny and systematics of extant and extinct lobsters. *Journal of Crustacean Biology 33*, 78–123. DOI 10.1163/1937240X-00002111

KISHINOUYE, K. 1926. Two rare and remarkable forms of macrurous Crustacea from Japan. *Annotationes Zoologicae Japonenses 11*, 63–70.

KLOMPMAKER, A.A. 2013. Extreme diversity of decapod crustaceans from the mid-Cretaceous (late Albian) of Spain: Implications for Cretaceous decapod paleoecology. *Cretaceous Research 41*, 150–185. DOI 10.1016/j.cretres.2012.12.003

KLOMPMAKER, A.A., ARTAL, P., FRAAIJE, R.H.B. & JAGT, J.W.M. 2011. Revision of the family Gastrodoridae (Crustacea, Decapoda), with description of the first species from the Cretaceous. *Journal of Paleontology 85*, 226–233. DOI 10.1666/10-028.1

KOŠŤÁK, M. 1996. Late Turonian-Coniacian belemnites (genera *Actinocamax* Miller and *Gonioteuthis* Bayle) from the Bohemian Cretaceous Basin. *Věstník Českého geologického ústavu 71*, 97–105.

KOŠŤÁK, M., ČECH, S., EKRT, B., MAZUCH, M., WIESE, F., VOIGT, S. & WOOD, C.J. 2004. Belemnites of the Bohemian Cretaceous Basin in a global context. *Acta Geologica Polonica 54*, 511–533.

KREJČÍ, J. 1869. Studien im Gebiete der böhmischen Kreide-Formation. I. Allgemeine und orographische Verhältnisse, sowie Gliederung der böhmischen Kreide-Formation. *Arbeiten der geologischen Section in den Jahren 1864–1868. Das Archiv für die naturwissenschaftliche Landesdurchforschung von Böhmen 1(2)*, 39–179. Commissions-Verlag Fr. Řivnáč, Prague.

LATREILLE, P.A. 1802–1803. *Histoire naturelle, générale et particulière des Crustacés et des Insectes*. 468 pp. F. Dufart, Paris.

LEES, J.A. 2008. The calcareous nannofossil record across the Late Cretaceous Turonian/Coniacian boundary, including new data from Germany, Poland, the Czech Republic and England. *Cretaceous Research 29*, 40–64. DOI 10.1016/j.cretres.2007.08.002

MACÁK, F. 1966. *Křídový útvar v sz. Čechách (svrchní turon až santon)*. 82 pp. Candidate thesis, Charles University, Prague, Czech Republic.

MANNING, R.B. & FELDER, D.L. 1991. Revision of the American Callianassidae (Crustacea: Decapoda: Thalassinidea). *Proceedings of the Biological Society of Washington 104*, 764–792.

MATSUZAWA, K. & HAYASHI, K.-I. 1997. Male of *Ctenocheles balssi* (Crustacea, Decapoda, Callianassidae) from off Muroto Peninsula, Shikoku, Japan. *Journal of the National Fisheries University 46*, 39–46.

MERTIN, H. 1941. Decapode Krebse aus dem Subherzynen und Braunschweiger Emscher und Untersenon sowie Bemerkungen über einige verwandte Formen in der Oberkreide. *Nova Acta Leopoldina, Neue Folge 10(68)*, 149–264.

PELSENEER, P. 1886. Notice sur les Crustacés décapodes du

Maastrichtien du Limbourg. *Bulletin du Musée royal d'histoire naturelle de Belgique 4(3)*, 161–175.

Powell, A.W.B. 1949. New species of Crustacea from New Zealand of the genera *Scyllarus* and *Ctenocheles* with notes on *Lyreidus tridentatus. Records of the Auckland Institute and Museum 3*, 368–371.

Pokorný, V., Štemproková, D. & Švábenická, L. 1983. Loc. 31 – Březno near Louny – Coniacian, Rohatce Member and Březno Formation, 198–202. *In* Samuel, O. & Gašparíková, V. (eds) *18th European Colloquy on Micropaleontology, Excursion-guide*. Geologický ústav Dionýza Štúra, Bratislava.

Rabalais, N.N. 1979. A new species of *Ctenocheles* (Crustacea: Decapoda: Thalassinidea) from the northwestern Gulf of Mexico. *Proceedings of the Biological Society of Washington 92*, 294–306.

Rathbun, M.J. 1935. Fossil Crustacea of the Atlantic and Gulf Coastal Plain. *Geological Society of America Special Papers 2*, viii + 160 pp.

Reuss, A.E. 1845–1846. *Die Versteinerungen der böhmischen Kreideformation*. 58 + 148 pp. I.E. Schweizerbart, Stuttgart.

Reuss, A.E. 1853. Über Clytia leachi Rss. einen langschwänzigen dekapoden der Kreideformation. *Denkschriften der mathematisch-naturwissenschaftlichen Klasse der kaiserlichen Akademie der Wissenschaften 6*, 1–10.

Robins, C.M., Feldmann, R.M. & Schweitzer, C.E. 2013. Nine new genera and 24 new species of the Munidopsidae (Decapoda: Anomura: Galatheoidea) from the Jurassic Ernstbrunn Limestone of Austria, and notes on fossil munidopsid classification. *Annalen des Naturhistorischen Museums in Wien, Serie A 115*, 167–251.

Rodrigues, S. de A. 1978. *Ctenocheles holthuisi* (Decapoda, Thalassinidea), a new remarkable mud shrimp from the Atlantic Ocean. *Crustaceana 34(2)*, 113–120. DOI 10.1163/156854078X00691

Saint Laurent, M. de 1979. Sur la classification et la phylogénie des Thalassinides: définitions de la superfamille des Axioidea, de la sous-famille des Thomassiniinae et de deux genres nouveaux (Crustacea Decapoda). *Comptes Rendus hebdomadaires de Séances de l'Académie des Sciences, Paris 288*, 1395–1397.

Sakai, K. 1999a. Redescription of *Ctenocheles balssi* Kishinouye, 1926, with comments on its systematic position and establishment of a new subfamily Gourretiinae (Decapoda, Callianassidae). *Crustaceana 72*, 85–97. DOI 10.1163/156854099502899

Sakai, K. 1999b. Synopsis of the family Callianassidae, with keys to subfamilies, genera and species, and the description of new taxa (Crustacea: Decapoda: Thalassinidea). *Zoologische Verhandelingen, Leiden 326*, 1–152.

Sakai, K. 2005. Callianassoidea of the world (Decapoda: Thalassinidea). *Crustaceana Monographs 4*, 1–285.

Sakai, K. 2011. Axioidea of the world and a reconsideration of the Callianassoidea (Decapoda, Thalassinidea, Callianassida). *Crustaceana Monographs 13*, 1–520.

Schweitzer, C.E. & Feldmann, R.M. 2001. New Cretaceous and Tertiary decapod crustaceans from western North America. *Bulletin of the Mizunami Fossil Museum 28*, 173–210.

Schweitzer, C.E. & Feldmann, R.M. 2002. New Eocene decapods (Thalassinidea and Brachyura) from Southern California. *Journal of Crustacean Biology 22*, 938–967.

Schweitzer, C.E., Feldmann, R.M., Franțescu, O. & Klompmaker, A. 2012. Revision of Etyidae Guinot and Tavares, 2001 (Crustacea: Brachyura). *Journal of Paleontology 86*, 129–155. DOI 10.1666/11-060.1

Schweitzer, C.E., Feldmann, R.M., Garassino, A., Karasawa, H. & Schweigert, G. 2010. Systematic list of fossil decapod crustacean species. *Crustaceana Monographs 10*, 1–222.

Secrétan, S. 1964. Les crustacés décapodes du Jurassique Supérieur et du Crétacé de Madagascar. *Mémoires du Muséum national d'histoire naturelle, Nouvelle série A, Zoologie 19*, 1–223.

Stenzel, H.B. 1935. Middle Eocene and Oligocene decapod crustaceans from Texas, Louisiana, and Mississippi. *The American Midland Naturalist 16*, 379–400. DOI 10.2307/2420033

Švábenická, L. 1983. Calcareous nannoplancton of the Turonian and Coniacian stage from the Ohře-river region in the Bohemian Cretaceous Basin. *Miscellanea Micropaleontologica 4*, 267–282.

Švábenická, L. 1991. Locality Březno near Louny, 21–28. *In* Hamršmíd, B. (ed.) *4th INA Conference. Excursion guide. Knihovnička zemního plynu a nafty 13*.

Tshudy, D. 1993. *Taxonomy and evolution of the clawed lobster families Chilenophoberidae and Nephropidae*. 472 pp. Unpublished dissertation. Kent State University, Ohio, USA.

Tshudy, D. & Saward, J. 2012. *Dinochelus steeplensis*, a new species of clawed lobster (Nephropidae) from the London Clay (Eocene) of England. *Journal of Crustacean Biology 32*, 67–79. DOI 10.1163/193724011X615343

Tshudy, D. & Sorhannus, U. 2000. Pectinate claws in decapod crustaceans: convergence in four lineages. *Journal of Paleontology 74*, 474–486. DOI 10.1666/0022-3360(2000)074<0474:PCIDCC>2.0.CO;2

Van Bakel, B.W.M., Guinot, D., Artal, P., Fraaije, R.H.B. & Jagt, J.W.M. 2012. A revision of the Palaeocorystoidea and the phylogeny of raninoidian crabs (Crustacea, Decapoda, Brachyura, Podotremata). *Zootaxa 3215*, 1–216.

Veselská, M. 2009. *Vybrané skupiny řádu Decapoda Latreille, 1802 z české křídové pánve*. 99 pp. Master thesis, Charles University, Prague, Czech Republic.

Veselská, M. 2010. Revision of selected groups of decapods (infraorder Astacidea Latreille, 1802 and Glypheidea Winckler, 1882) from the Bohemian Cretaceous Basin. *Zprávy o geologických výzkumech v roce 2009*, 172–174. [in Czech with English abstract]

Veselská, M. 2011. Preliminary revision of the Cenomanian and Turonian decapods – genera *Necrocarcinus* Bell, 1863 and *Graptocarcinus* Roemer, 1887 (order Decapoda Latreille, 1802, infraorder Brachyura Latreille, 1802) from the Bohemian Cretaceous Basin. *Zprávy o geologických výzkumech v roce 2010, Paleontologie*, 128–131.

Ward, M. 1945. A new crustacean. *Memoirs of the Queensland Museum 12*, 134–135.